Understorey Plant Regeneration after Wildfire
in the Boreal Forest of Northwestern Ontario

By

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Abstract

The ecological patterns and processes of the boreal forest of northwestern Ontario are dominated by large-scale disturbances such as wildfire. These disturbances have the potential to control or affect the composition of the regenerating understorey vascular plant communities. This thesis examines vegetation regeneration in *Picea mariana* (black spruce) dominant forests following a wildfire in the boreal forest of northwestern Ontario. The influence of burn intensity and pre-fire spruce composition on understorey species regeneration was examined, and modeled environmental gradients were created using a Geographic Information System (GIS) and remotely sensed imagery. Understorey species composition was sampled using randomly distributed total composition plot clusters within different spruce/burn intensity classes. The influence of burn intensity and pre-fire spruce composition on the regenerating vascular plant community was examined using a two-way analysis of variance (two-way ANOVA), blocked multiple response permutation procedure (MRPP), discriminant function analysis (DFA), and indicator species analysis. The species composition of these regenerating plots was also examined using twenty-four common indices that were modeled with a GIS and Landsat TM satellite imagery. Canonical Correspondence Analysis (CCA) was used to determine the importance of each environmental gradient. Both burn intensity and pre-fire spruce composition classes showed significant differences in post-fire species composition. The combined classes of burn intensity and pre-fire spruce composition better explained the variance in understorey composition. The results also indicate that modeled environmental gradients derived from remote sensing and GIS have the potential to become effective tools to predict regenerating species composition after a major fire disturbance.

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General Introduction

Vegetation distributions and community structures have been studied at a variety of spatial scales (Kuchler, 1947; Drapeau *et al.*, 2000; Cihlar *et al.*, 2003). A global pattern of vegetation distribution was first theorized by Alexander von Humboldt early in the 19th century (Humboldt, 1845). He recognized that elevation and latitude exert great control over the global distribution of different vegetation types. This led to many other types of studies related to vegetation distributions and community structure. The following paragraphs provide a summary of how these theories have evolved to our present outlook on vegetation communities, regeneration strategies, and the ecological roles of large-scale disturbances such as fire.

The analysis of plant distributions evolved over the last century through a series of progressive theories. These theories can be discreetly categorized into three historical paradigms: Clementsian, Gleasonian and the modern synthesis of the two. In the early years of plant succession research, an assumption of consistency in the environment and resource supply rates for a given site was commonly made. Clements (1904) utilized an organism metaphor by relating communities to a "super-organism" to demonstrate that communities changed over time in very discrete ways, much like the development of an organism, which eventually culminates in an endpoint or 'climax'. In this paradigm of plant succession, the developmental climax is to a state of great stability. There are two prevalent concepts under the Clementsian paradigm, namely that there are very tight linkages among species, and there is cooperation among species for the benefit of the community. In Clements' (1916, 1934, 1936) view, communities were distinct spatial

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entities and developed into a major complex of species that gave way to another complex of species in either space or time. This elegant and straightforward theory of community ecology was dominant well into the 1960's (e.g. Odum, 1969).

In a series of papers, Gleason (1917, 1926, and 1939) contested that communities resulted from interactions between individual species and the environment in combination with chance historical events. Gleason (1939) wrote: "... it may be said that environment varies constantly in time and continuously in space; environment selects from all available immigrants those species which constitute the present vegetation, and as a result vegetation varies constantly in time and continuously in space." This paradigm is fundamentally different from the Clementsian view, as it suggests that each species has its own environmental tolerance and that individuals respond to their own local environment. This Gleasonian view of vegetation communities became known as the individualistic concept. The implication of such a paradigm is that species are distributed along environmental gradients with their boundaries determined by their tolerances (Hill et al., 1975; Cole & Smith, 1984; Dufrene & Legendre, 1997).

Curtis (1959) illustrated that floristic composition changed gradually in response to environmental gradients, and species were not limited to discrete environmental conditions as Clements had proposed. Curtis showed no evidence of discrete associations, but rather that richness changed along these gradients in a gradual way (Whittaker, 1956).

The modern view of succession ecology tends to be a synthesis of both the Clementsian and Gleasonian paradigms. Modern theory has adopted the Gleasonian concept that species are distributed based on their tolerances and that community composition generally changes with environmental gradients (Barbour et al., 1998;

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Chipman & Johnson, 2002). However, the Clementsian theories of abrupt changes in community composition still exist, but they are associated with similarly abrupt changes or disturbances in the environment.

All ecosystems are influenced in some way by disturbances, either natural or anthropogenic. White and Pickett (1985) define disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment". This definition of disturbance includes environmental fluctuations and destructive events, whether or not these are perceived as "normal" for a particular system.

Disturbances such as drought, blowdown, and intensive harvesting uniquely alter their respective ecosystem. All terrestrial ecosystems may be affected by drought, but the severity can increase in forested areas where available moisture is usually adequate and severe drought is infrequent. Within an ecosystem, natural selection for species that avoid, tolerate, or resist drought tends to be site specific rather than regionally related. In naturally dry ecosystems, the limited water supply results in selection at a regional and site level for species which are adapted to restricted water availability and are resistant to drought (Mooney *et al.*, 1981). Disturbance from wind also occurs in most terrestrial ecosystems. In a similar manner as fire, wind is a major force in "patch dynamics". Wind creates gaps of varying sizes by toppling trees that are large, old, afflicted by root disease, and exposed on the edges of existing gaps. Areas of disturbance are larger along or near coasts when tropical storms with high-velocity winds make landfall. Damage by large-scale storms is strongly related to elevation, aspect, and vegetation structure (Foster & Boose, 1992). Susceptibility to blowdown in forested ecosystems is related to the amount

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of crown sway and mutual crown support (Baker et al. 2002). Wind also can cause chronic damage that can result in progressive disturbance over time.

Disturbances caused by diseases and insects occur in all terrestrial ecosystems. Studies suggest that most pathogens and insects are ecosystem/species specific, although some can occur in several different ecosystems on related or entirely different species. Some pathogens and insects cause disturbance by attacking healthy host species. Others affect only hosts that have been weakened by a predisposing stress caused by another disturbance agent, while still others act in both capacities. Pathogens and insects, alone or together, are important causes of small gaps, particularly in deciduous forests (Castello et al. 1995). These agents also can disturb large areas resulting in major structural or species changes within an ecosystem. Examples are disturbances in western lodgepole pine forests caused by the mountain pine beetle and in the former chestnut/oak forests of the East due to chestnut blight.

Succession is the term used to describe the changes in physical and biological conditions that follow disturbances. The two major types of succession are primary and secondary. Primary succession occurs when a surface previously devoid of life is colonized by plants and animals. This can be instigated by catastrophic disturbances such as volcanic activities. However, it is virtually impossible for a wildfire to be so severe that primary succession occurs. Secondary succession occurs when the disturbance is not catastrophic and remnants and seeds from the previous ecosystem can regenerate (MacDonald & Thompson, 2003). In the case of the boreal forest, cyclical disturbances promote secondary succession which is vital to maintaining natural stability in the landscape (Perera *et al.*, 2000). For example, Awada *et al.* (2004) indicate that small

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spatial gaps in the forest canopy formed by fallen trees have proven to be very important to *Picea glauca* (white spruce) regeneration in mature forest stands.

Many factors including the type and severity of disturbance affect vascular plant regeneration. For example, Bazzaz (1979) studied the physiological adaptations of early successional plants to environmental variability. Bazzaz noted that the variability of the physical environment is commonly related to the amount of energy reaching the surface of the soil. He also hints at the importance of light as an environmental gradient when he acknowledges that light is a major factor in species replacement and especially in forest succession. He concludes by indicating that both early and late successional plants often have contrasting physiological attributes and it is these physiological differences which facilitate succession.

Although Bazzaz (1979) might have indicated that physiological differences facilitate succession, it is often driven by disturbances. The recurrence of disturbance and recovery within ecosystems is an important mechanism for energy flow and nutrient cycling, and for maintaining age, species, genetic, and structural diversity, all attributes of ecosystem health. Disturbance occurs as a continuum from frequent intervals of low intensity to infrequent occurrences of high intensity (White & Pickett, 1985). Other factors that influence regeneration include environmental gradients such as temperature, soil, water, minerals, and elevation (Barbour *et al.*, 1998). Grime (1979) studied plant distribution and considered that individual plants occurred where the interaction of disturbance, stress and competition reflected their life history strategies.

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Fire as a Disturbance

Fire has influenced the evolution of several terrestrial ecosystems. Barbour *et al.* (1998) identified several ecosystems that are defined by fire, including the tallgrass prairies of central Canada, the pine savannas and forests of the southern United States, the fynbos of Africa, the scrublands of Australia, and the boreal forest of the northern hemisphere. Early studies focused on examining the impacts of fire (Dansereau, 1951; Curtis & McIntosh, 1951). Since then, much of the focus has changed to examining the ecological processes associated with fire (Wright & Heinselman, 1973; Cayford & McRae, 1983; Wein, 1993; Whelan, 1995; Boyce & Haney, 1997; Perera *et al.*, 2000). These were considered stabilizing factors that helps maintain certain types of ecosystems (Scotter, 1972; Heinselman, 1973; Rowe & Scotter, 1973; Wright & Heinselman, 1973; Viereck, 1983; Wein, 1993) although exactly how fire affects the stability in plant community composition remains unresolved for many ecosystems. This is due to both the high variability of the spatial scales and the length of time required assessing the stability of most plant communities. Veblen (1992) describes two methods of assessing ecosystem stability. The first is a quantitative approach which suggests that a stable equilibrium is defined as the state under which a population will remain or to which a population will return. The second method emphasizes the presence or absence of species and does not require that the system remain at or return to a quantitatively defined equilibrium. A stable ecosystem may fluctuate in the abundance of species, but major changes in relative abundance and local extinctions are avoided. The degree of consistency in the relative abundance and dominance of different species will vary according to how narrowly the idea of compositional equilibrium is applied. In a study by Anderson and Brown (1986),

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a suitable definition of ecosystem stability is "an ecosystem that maintains species composition and abundance, and community structure over time".

Nilsson & Grelsson (1995) suggest that change and dynamics are integral parts of ecosystem stability. In this respect, stability is seen as a reference against which the ecosystem response to change is measured. Many properties of ecosystem stability have been defined (Nilsson & Grelsson, 1995; Gunderson, 2000) the three most common properties include resilience, resistance, and persistence (Marell, 2006). Where, resilience is the speed at which a system recovers to equilibrium, resistance is the tendency to remain unchanged by a disturbance, and persistence is the time a system lasts before it is changed (Marell, 2006). Fire is a natural disturbance in boreal forest ecosystems and helps maintain diverse landscapes in both time and space (Zackrisson, 1977). A forest ecosystem can therefore appear to be unstable at a small spatial scale or over a short period of time, while it is considered stable at large spatial scales and long time scales.

Crown fire caused by lightning is the primary large-scale disturbance in the boreal forest (Johnson *et al.*, 2001). In a study by Chipman and Johnson (2002), these crown fires tend to produce even-aged stands of all tree species except *Abies balsamia* (balsam fir). It is therefore understood that much of the boreal forest is a fire dependent ecosystem. There is a significant link between succession and ecosystem stability in the boreal forest. In ecosystems that encounter a high frequency of wildfires, many of the species that are vital to the functioning of the system become so well adapted that any alteration from the "normal" fire frequency regime can cause negative effects on the community (Weber & Flannigan, 1997). Following a disturbance such as fire, the ecosystem resets itself and permits a new or altered vegetative community to fill the

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niche left by the disturbance. In a typical boreal forest black spruce stand, large scale

ecosystem stability is maintained by a natural disturbance regime synonymous with fire

(Van Wagner, 1987). This is due to the adaptations of the plant communities to the fire

regime driven by succession.

Fire and Vegetation Dynamics

The occurrence of wildfire has four distinct yet interrelated requirements. Firstly,

it requires the accumulation of fuel in the form of plant material produced by

photosynthetic carbon fixation. The second requirement is a climate favourable for drying

plant material enough (at least seasonally) to encourage ignition. Third, the atmospheric

conditions must be suitable for combustion to occur. Fourth, some mechanism of ignition

is required for a wildfire to start. In order for a fire to begin, all four requirements must be

met (Cope & Chaloner, 1985). There are two limiting conditions for all wildfires to

spread. Firstly, the fire must transfer enough heat ahead of the fire to dry out the

unburned fuel. Secondly, it must raise the fuel to the required ignition temperature by the

time the flame arrives. In order for a fire to spread from tree to tree, equilibrium must be

maintained between all elements of mass and energy in and around the combustion zone

(Van Wagner, 1983).

Individual plants possess properties that influence fire behaviour, making them

more or less susceptible to burning. The most important property is the production of soft

tissues, or retention of water, within the organism. The moisture content in dead plants is

usually quite low, at around 5 to 15 percent water in dry weather, making them far more

flammable than living plants, where the moisture content can be greater than 50 percent

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water. An increase in the presence of dead material will result in an ecosystem that is more susceptible to fire (Bond & Van Wilgen, 1996).

The shape, size, and arrangement of plant parts are also major factors in determining an area's susceptibility to fire (Bond & Van Wilgen, 1996). The surface area to volume ratio is important for two reasons. Firstly, it influences the rate of moisture loss from the plant's surfaces. Secondly, it affects the ratio of fuel to air, otherwise known as the packing ratio. Plants with finely divided leaves are more prone to fire damage. This would include species such as pine, grasses, and sedges. Plants that are less susceptible to fire damage have broad, thick leaves, like those found in tropical areas and desert plants such as cacti. These plants are bulkier and able to retain moisture, two factors that render them less prone to fire damage (Bond & Van Wilgen, 1996).

In the northern boreal forest, there are four main type of fuel arranged in an infinite number of combinations (Van Wagner, 1983). First is a blend of dead foliage litter, bryophytes and fine shrubs with a component of fine twigs that may become quite dry. Second, it is common in the boreal forest to have a deep duff/organic layer that contains partially decomposed vegetative matter. This layer usually averages around 15 cm in depth and it can provide enough fuel to maintain slight combustion after the main front has passed (Van Wagner, 1983). The total extent to which the organic layer burns is usually referred to as the severity of the fire. The third type of fuel is composed of fallen or dead trees and accounts for a significant amount of combustible material in some forests. These dead trees or snags often occur in clusters known as blowdowns and can cause a fire to flare up. The fourth and most significant type of fuel is the live foliage that is present in the forest. This type of fuel is of particular importance in the northern

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coniferous forest, due in part to the low water retention capacity of the needles. Five main features of coniferous forests that have a bearing on crown fires are: total weight per ground unit area, bulk density within the crown space, moisture content, flammable (dead or dry) branches, and resin content (Rowe & Scotter, 1973). This idea that canopy fuel is perhaps more important to fire regimes in the boreal forest than fuel accumulation consisting of dead or fallen trees is supported in a study by Johnson *et al.* (2001) who contested that unnatural fuel accumulation due to fire suppression was not responsible for a change in the fire regime of a ponderosa pine ecosystem in the U.S. Midwest. Rather, the change in the fire regime was primarily caused by a change in the fuel structure. The change in fuel structure was determined to be a region of dead foliage in the mid-canopy enabling a connection between surface and crown fires.

In the context of vegetation dynamics in boreal forests, there are fundamental differences between burn intensity and burn severity. Generally, burn intensity is defined as the amount of energy, in the form of heat, released per unit length of fire edge. The intensity is proportional to the rate of advance perpendicular to the edge. Fire severity is commonly defined as the physical impact of fire, for example, the removal of the duff/organic layer in the soil (Albini, 1976). Rowe (1983) describes fire severity as the degree of organic removal and soil heating on sandy soils for fires of all intensities. A low release of energy may nevertheless be classified as severe, because of the organic cover removal and the damage to near surface root structures. It is intuitive that fires that occur during summer and fall tend to be more severe than spring fires when the duff/organic layer is usually moister. This seasonal change in the hydrologic regime is often enough for fire to have very different effects on local vegetative communities

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(Weber & Flannigan, 1997). This is confirmed by Miyanishi and Johnson (2002), who determined that the spatial correlation between burned patches and fire-killed trees were explained by the within-stand spatial variation in duff moisture.

The Influence of Fire on Succession

Understanding the diversity of the distribution of materials and organisms within ecosystems has lead to broader landscape theories that often integrate disturbances as major factors. For example, the intermediate disturbance hypothesis was developed by Connell (1978) by examining tropical rain forests in Africa as well as coral reefs in Australia. He developed the basic idea that ecosystems maintain their highest species diversity under conditions of moderate disturbance. The rate or interval of disturbance has a direct influence on the amount of biodiversity. Another model developed by Nobel and Slatyer (1980) also examined the role of disturbance frequency on species diversity. This model was aptly named the 'vital attributes model', as it linked the species traits and adaptations to the probable pathways of succession. This model, however, fails to incorporate the effects of ecosystem heterogeneity created by a disturbance such as wildfire. It is generally understood that post-fire habitat diversity is created by spatial fluctuations in burn severity and species regeneration strategies. These also play a significant role in determining species diversity as well as the rate and direction of succession (Mallik, 2003). The vital attribute approach also does not distinguish between different species to determine the progress and direction of succession from secondary species that are functionally redundant in the system (Mallik, 2003).

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In early studies of fire succession, traditional observations measured separate elements, or stands, out of a forest mosaic that were thought to represent various stages of succession. It was thought that eventually this succession would lead to some type of climax, or ultimate equilibrium of species (i.e., the Clementsian view). Using this assumption, short lived species like *Pinus banksiana* (jack pine) were seen only as stages in succession to a more stable shade tolerant fir, spruce, cedar, and birch forest in the absence of fire (Wright & Heinselman, 1973). A typical boreal forest community of northwestern Ontario and eastern Canada is a relatively simple ecosystem with low biodiversity consisting of primarily fire prone *Picea mariana* (black spruce), yet it remains a stable ecosystem. This stability provides an excellent comparison to the modern succession hypothesis. It also provides a suitable opportunity to test some of the more contemporary theories of community ecology and help to explain the theories involved in secondary succession. Following a disturbance such as fire, it is possible to observe the tendency for these communities to follow the successional pathways that result in the conversion of *Picea mariana*-dominated forests into areas of low-lying shrub growth dominated by such species as *Kalmia*. Mallik (2003) illustrated key factors that appear to play important roles in this retrogressive succession from forests to low shrub growth. The first significant factor is the dramatic increase in *Kalmia* cover after forest canopy removal. The second factor is the habitat-modifying ability of *Kalmia* litter, which is unfavourable for the reestablishment of species such as *Picea mariana*. It has been suggested that long term occupancy of *Kalmia* in a site changes the nutrient status of soil so much so that it can no longer support overstorey tree growth. The occurrence of a ground fire severe enough to remove this layer of *Kalmia* litter would also provide

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enough bare soil for *Picea mariana* to become re-established. In cases where the fire is not severe enough to remove the *Kalmia* litter, the regeneration of *Kalmia* is promoted. This provides an excellent opportunity for wildfire to clear the litter from the understorey promoting regeneration of overstorey species such as *Picea mariana*.

Fire also has a significant impact on the community composition, as different species respond to this disturbance in different ways. These differences are primarily due to variations in the location of seeds and rhizomes in the soil and to the colonizing habitat of the individual plant species. A model developed by Schimmel and Granstrom (1996) highlights these relationships. They depicted the initial responses of three different groups of species: rhizomatous sprouters, early successional seed bank species, and seed dispersers. Rhizomatous sprouters are the first species to regenerate, and they generally decrease in abundance with increasing depths of burn. They regenerate first, making the best use of the increased light from reduced overstorey vegetation. Seed bank species will generally regenerate better under situations where fire has removed some of the organic soils and exposed the previously buried seed banks. If the fire burns too deep, the seed bank can be destroyed leaving the seed dispersers to recolonize the burn. This is a very simple model, and it does not account for some of the underlying hydrologic and microbial factors that also act to impede or aid in species regeneration. Freedman (1995) describes an interesting successional model that is more specific to regeneration in the boreal forest. In this model, three successional stages based on tolerance of competitive stresses are highlighted. The early successional stage is dominated by competition intolerant species. These species are usually rare or absent after the overstorey canopy closes and the competitive stresses intensify. Some deciduous trees and woody shrubs,

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such as *Alnus* (alder), *Betula* (birch), *Prunus* (cherry), and *Populus* (poplar), are shade-intolerant species that cannot reproduce effectively after the canopy closes, although large individuals may persist for a while (Freedman, 1995). Semi-woody shrubs, such as *Rubus idaeus* (raspberry), *Sambucus* (elderberry), and the members of the Aster family comprise a great deal of the richness of annual and short-lived perennial species. The succession models of both Freedman (1995) and Schimmel and Granstrom (1996) complement each other since the success of a species is largely determined by the regeneration strategy employed by each species.

Species that have an intermediate tolerance to competitive stresses and have survived a wildfire are often present in small numbers among the ground vegetation of mature stands (Freedman, 1995). The individuals that survive the disturbance and are released from the understorey can become relatively abundant until a full canopy is established. These species can regenerate after disturbance by the establishment of seedlings, by vegetative regeneration, and/or by the growth of surviving individuals.

Species that are tolerant of competitive stresses may more easily survive the disturbance and eventually dominate the later-successional stages (Freedman, 1995). Some species in this group are present in all stands regardless of the current successional stage. Under shaded conditions, these species have a low light compensation threshold, a characteristic that enables survival under low light conditions. Examples of species in this type of group include *Abies balsamea* (balsam fir) and *Acer saccharum* (sugar maple). Small individuals of tolerant tree species may be present in mature stands as regeneration progresses. If these trees survive the disturbance, they may be ecologically released from

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the stress exerted by the previous canopy of trees and become important in the successional pattern.

Gutsell and Johnson (2002) challenge the validity of classifying tree species as early, mid, or late-successional based on height-growth rates or age. This concept contradicts Clements' initial theory of plant succession which indicates that different plant species recruit or become dominant in the canopy at different times after stand initiation. The results from Gutsell and Johnson's (2002) research showed that all tree species in the mixed-wood boreal forest of Saskatchewan recruit within the first 5-10 years after fire. Species with lower initial growth rates will remain shorter than species with high initial growth rates for most of their lifespan. This gives the false impression that the species with a lower initial growth rate is younger. The rapid recruitment of all tree species after fire and the short fire cycle means that any changes to the composition or abundance of species within a stand between fires are driven primarily by the mortality rates of the post-fire canopy trees (Gutsell and Johnson, 2002).

Chipman and Johnson (2002) indicated that the topography and microsite conditions might play a greater role in determining vascular plant diversity on the upland mixed-woods in Prince Albert National Park in central Saskatchewan. Chipman and Johnson (2002) suggested that surficial geology and hillslope position are more important in accounting for variations in species diversity, richness, and evenness than either canopy basal area or time since fire. They argue that surficial geology and hillslope position are of primary importance because they control the moisture and nutrient gradients which in turn determine the principal vegetation composition. The results from

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this study showed that on glacial till and glacial-fluvial hillslopes, richness and diversity increased parallel to the down slope increase in moisture (Chipman and Johnson, 2002).

Most species within the typical *Picea mariana* ecosystem are well-adapted to fire and are tolerant of the competitive stresses exerted by a closed canopy of trees. Many of these tolerant species exhibit relatively little release after removal of the overstorey. Such a response reflects a conservative strategy of slow growth rates and efficient use of resources to survive under competitive, stressful conditions (Freedman, 1995). As many of these species cannot tolerate full insolation, they may decrease greatly in abundance after disturbance and regenerate slowly or decolonize as the next forest canopy develops.

Research Objectives

My research explores two aspects of forest regeneration after fire in the upland *Picea mariana* (black spruce) boreal forest in northwestern Ontario. The first objective was to study the vascular plant community that regenerated in pre-fire *Picea mariana* stands after the Nipigon-10 fire in 1999 in northwestern Ontario. The aim of this study was to determine if there is an ecological relationship between variations in pre-fire spruce composition and burn intensity to the post-fire species composition. The intermediate disturbance hypothesis (Connell, 1978) suggests that moderately burnt sites should have the greatest biodiversity. There have been several studies which indicate that certain types of environmental conditions will favour distinct vegetation communities, highlighted by specific indicator species (Rowe & Scotter, 1973; Connell, 1978; White, 1979; Rowe, 1983; Petraitis *et al.,* 1989; Nguyen-Xuan *et* al, 2000; Peltzer *et al.,* 2000). This research will utilize a recent pre-fire GIS-based forest resource inventory and a burn

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map generated from satellite imagery to test if different species compositions can be observed among the different classes of burn intensity, pre-fire spruce composition, and the combined or mixed classes. Field data collected was used to examine the influences of pre-fire spruce composition and burn intensity on plant regeneration after fire in the Nipigon-10 burn.

The second objective was to examine the influences of many underlying environmental gradients on the post-fire regenerating species composition. This will be an unverifiable attempt to determine if common spatial analysis tools can be used to model environmental gradients and possibly further explain post-fire regeneration species composition. This research follows the Curtis (1959) concept that vegetation composition changes gradually in response to environmental gradients. Curtis demonstrated that individual species increased and decreased in richness along these gradients in a gradual way, as the richness values plot out as a series of overlapping curves. This study will utilize modern spatial analysis procedures, including Geographic Information System (GIS) and remote sensing to model environmental gradients in an attempt to examine how regenerating species composition varies along specific environmental gradients in the boreal forest. This thesis consists of two separate chapters each aimed at testing these two research objectives, respectively.

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CHAPTER 1:

Examination of Burn Intensity and Pre-fire Spruce Composition on Regenerating Species

Abstract

In the boreal forest of northwestern Ontario, the post-fire regeneration of understorey vascular plant species composition is at least partially influenced by the impacts of wildfire and pre-fire overstorey species composition. The aim of this study was to examine the relationship of burn intensity and pre-fire spruce composition on the composition of regenerating species in the boreal forest of northwestern Ontario. Three classes in each of the burn intensity and pre-fire spruce composition data were developed from GIS-based and remotely sensed data sources. Four hundred and eighty one-square metre total composition quadrats were sampled (ten at each site) using a radial sampling pattern spread out over an area of about forty square metres. A two-way analysis of variance (ANOVA), blocked multiple response permutation procedure (MRPP), discriminant function analysis (DFA), and indicator species analysis were used to characterize the differences in plant community structure among the three burn intensity classes, the three pre-fire spruce composition classes, and the combined nine classes comprised of both burn intensity and pre-fire spruce composition. Results indicate that burn intensity and pre-fire spruce composition classes showed significant differences in understorey species composition ($p < 0.001$). The combination of burn intensity and pre-fire spruce composition better explained the variance in understorey composition. The indicator species found in this study were used to determine which plant species are most influenced by burn intensity and pre-fire spruce composition.

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Introduction

Many previous studies of post-fire disturbance in forests have focused on the mechanics of regeneration and nutrient cycling. Regeneration of an area after fire is through a combination of the germination of buried seeds that have survived the disturbance, underground plant parts regenerating and/or seeds transported into the area using a variety of methods (i.e. evaders, endurers, and invaders respectively) (Rowe 1983). Moore and Wein (1977) showed that fires of low severity might remove only the top layer of litter, whereas a fire of higher severity may remove more organic matter and may even heat up the upper layers of mineral soil. The survival of viable seed populations is strongly dependent upon the depth of the burn, as shallow seeds would suffer from higher mortality, allowing for seeds buried deeper to regenerate. Burn intensity has been defined as the amount of energy, in the form of heat, released per unit length of fire edge (Moore & Wein, 1977). The intensity is proportional to the rate of advance perpendicular to the edge. The intensity of a fire is also related directly to the amount of forest canopy removed by the fire (Tanaka *et al.*, 1983; Jakubauskus *et al.*, 1990; Miller and Urban, 1999). The amount of fuel consumed would be greater as an intense fire increases. This results in an increase in the amount of light penetration to the understorey after the fire. A study by Ross *et al.* (1986) examined the successional changes that occur as a result of changing levels in light quality and quantity. The greater the openness of the canopy, the better shade intolerant species will be able to regenerate in that area. In the case of a post-fire landscape, higher burn intensity results in a greater opportunity for shade intolerant species to establish (French *et al.,* 1996; Keane *et al.,* 2004).

Many species in the boreal forest are inherently fire dependent. Wildfires act to reset the processes of succession and thus many species in the system are dependent on fire for regeneration. One of the most common species in the boreal forest is *Picea mariana* (black spruce), and it is well adapted to dealing with fire. The fire frequency for the boreal mixedwood forest is between 100 and 250 years (Heinselman, 1973; Wright & Heinselman, 1973; Rowe & Scotter, 1973), although this can become significantly longer in highly fragmented forest regions (Weir *et al.*, 2000; Miyanishi *et al.*, 2002). This fire frequency has meant *Picea mariana* has become well-adapted to fire, primarily through its reproduction using semi-serotinous cones. Although the cones are partially open when growing on the tree, the heat from a fire is required to fully release the seeds. *Picea mariana* begins to produce cones as early as 10 to 15 years old, but it is not until 50 to 150 years that cone production reaches its peak (Viereck, 1983). As this conifer grows, it tends to layer its branches causing the lower branches to die from lack of light. This layering habit is important to the tree's susceptibility to crown fire, as often a continuous layer of highly flammable, fine material forms from the ground to the crown. This is especially true in open spruce stands, and consequently the burn intensity is often much higher (Viereck, 1983).

The occurrence of wildfire in many forests systems is vital to the long-term health of the ecosystem, as opposed to the common perception that it is a single destructive event (Heinselman, 1973; Rowe & Scotter, 1973; Wright & Heinselman, 1973; Boerner, 1982; Viereck, 1983; Chen & Popadiouk, 2002). The ecological effects of disturbance caused by fire in the boreal forest ecosystem maintains species abundance and diversity and determines the outcome of succession (Rowe and Scotter, 1973; Connell, 1978;

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White, 1979; Rowe, 1983; Petraitis *et al.*, 1989; Barbour *et al.*, Chambers, 1993; Peltzer *et al.*, 2000; Dickinson and Johnson, 2004; Lee, 2004). Gilliam (1991) defined a general fire hypothesis, stating "For these ecosystems in which fire occurs predictably and frequently enough to result in a degree of fire-dependence, fire serves to increase and/or maintain the availability of essential resources which would without fire be growth-limiting for the organisms in the system". A positive feedback loop exists between fire and the vegetation, to such an extent that fire might be equally as important as climate in regulating species composition. Wright and Heinselman (1973) outlined six major influences of fire on an ecosystem, which comprise what is known today as the field of fire ecology. These influences include the impact of fire on the physical-chemical environment, as a regulator of dry organic matter accumulation, as a controller of plant species and communities, as a determinant of wildlife habitat patterns and populations, as a controller of forest micro-organisms (insects, parasites, fungi), and as a controller of major ecosystem processes and characteristics. The primary focus of this study is on fire as a controller of species and communities.

Rowe (1980, 1983) related the severity of fire to patterns in regeneration through the traits of the regenerating species. Using the vital attributes model (Noble & Slatyer (1980), Rowe established three 'modes of persistence' for plants in the context of fire. The first mode of persistence that Rowe (1980, 1983) highlights is the invading species. These are species that originate outside the disturbed area and reproduce by dispersing large numbers of short-lived propagules in the wind. These species tend to be shade intolerant pioneering species like *Epilobium angustifolium* (fireweed), *Betula* (birch), and *Salix* (willow). The second mode of persistence Rowe (1980, 1983) refers to is

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represented by the endurers. These species comprise nearly two-thirds of the boreal forest plant species (Rowe, 1980) and reproduce vegetative by dispersing roots or rhizomes below ground. The fate of these species is largely dependent upon the severity of the burn, which dictates the depth of the combustion zone into the soil. Schimmel and Granstrom (1996) demonstrate that as more organic material is removed by the fire, the chance these species have of surviving diminishes. The third and final mode of persistence (Rowe, 1980; Rowe, 1983) encompasses the species that evade disturbances (i.e. evaders). These species rely on long-lived seeds either in the canopy or in the soil to avoid the lethal temperatures of the fire. Species that store seeds in their canopies include *Pinus banksiana* (jack pine) and *Picea* (spruce). These species have cones that are serotinous or semi-serotinous, meaning that the germination of the seed is triggered by the high temperature of a fire. *Picea mariana* (black spruce) produces seed at an early age, produces good seed crops regularly, and has persistent cones that release seed slowly over a period of years.

Research Hypotheses

Many factors influence the species regeneration in *Picea mariana* stands after fire. Previous research has shown these factors to include burn intensity, seed availability, hydrologic regime, and pre-fire conditions (Moore & Wein, 1977; Rowe, 1983; Van Wagner, 1983; Bond & Van Wilgen, 1996; French *et al.*, 1996; Johnston and Elliott, 2000; Webber and Flannigan, 1997; Nguyen-Xuan *et al.*, 2000; Keane *et al.*, 2004). My goal was to examine two aspects of forest vascular plant regeneration in *Picea mariana*

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stands in northwestern Ontario, specifically burn intensity and pre-fire spruce composition.

According to the intermediate disturbance hypothesis (Connell, 1978), the maximum levels of biodiversity should be expected from intermediate levels of disturbance (in this case burn intensity). A fire must be severe enough to cause enough disruption and create environmental heterogeneity for the survival of species that could not persist in an undisturbed system, without being too severe as to remove the disturbance sensitive species (MacDonald & Thompson, 2003).

The intermediate disturbance hypothesis (Connell, 1978) suggests that moderately disturbed environments should have the greatest biodiversity. Species richness and evenness have been used to identify patterns in biodiversity (Barbour *et al.*, 1998). These two factors can therefore be used to examine understorey vegetation diversity in *Picea mariana* stands among the three pre-fire spruce composition and burn intensity classes. It is hypothesized that regions of moderate intensity will produce an understorey community of the greatest diversity. In addition, the greatest diversity in pre-fire spruce composition classes should be found in stands of low pre-fire spruce composition that had a higher pre-fire diversity in tree species. I will test if burn intensity, pre-fire spruce composition, and the combination of fire and pre-fire spruce composition affect regenerating plant biodiversity for the Nipigon-10 burn.

It is understood that the factors which influence species regeneration can define distinct communities of species (Rowe & Scotter, 1973; Connell, 1978; White, 1979; Rowe, 1983; Petraitis *et al.*, 1989; Peltzer *et al.*, 2000). I will also test if unique understorey vegetation communities can be defined within three pre-fire spruce

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composition classes, three burn intensity classes, and nine fire-intensity and pre-fire spruce composition combination (or mixed) classes.

The three modes of persistence outlined by Rowe (1980, 1983) indicate that communities affected by regular disturbances like fire can be identified by species that are adapted to disturbance-prone environments. It is hypothesized that for different levels of burn intensity and pre-fire spruce composition, specific species (indicator species) can define that class. I will test whether indicator species can be used to identify unique species communities within the three burn intensity classes and the three pre-fire spruce composition classes.

In this study, I will test the following research hypotheses:

- moderately burned forest stands will have the greater post-fire plant composition biodiversity as defined by species richness and evenness measurements;

- forest stands with higher pre-fire overstorey species composition diversity (i.e., lower pre-fire spruce composition) will have greater post-fire plant composition diversity; and

- indicator species can be used to identify unique regenerating species communities within the three burn intensity classes and the three pre-fire spruce composition classes.

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Methods

Study Area

The study area for this project is located approximately 80 km northeast of Thunder Bay, Ontario in the Black Sturgeon Lake region (Figure 1). The Nipigon-10 fire was accidentally started by Bowater forestry operations on April 30th, 1999, and it burned until May 5th, 1999. Several months passed before the fire was declared to be officially extinguished. The size of the fire was estimated at just over 50,000 hectares.

Picea Mariana Ecosystem

The study area is considered to be a part of the boreal mixedwood forest (Rowe 1980). This type of forest tends to occur on the more fertile regions of the boreal zone and can be distinguished by a diverse number of hardwood and conifer overstorey species in varying proportions (Borealforest.org 2005). This ecoregion encompasses around 50 percent of Ontario's productive forest (Natural Resources Canada 2005). Some of the predominant canopy species in the Black Sturgeon forest include: *Picea mariana* (black spruce), *Abies balsamea* (balsam fir), *Betula papyrifera* (white birch), *Populus tremuloides* (trembling aspen), and *Pinus resinosa* (red pine).

Each overstorey species has a different growth rate and tolerance to disturbance that results in a patchwork of stand types and compositions, making the boreal mixedwood extremely diverse (Boreal Forest Network, 2005). This diversity provides a variety of food and shelter for abundant wildlife.

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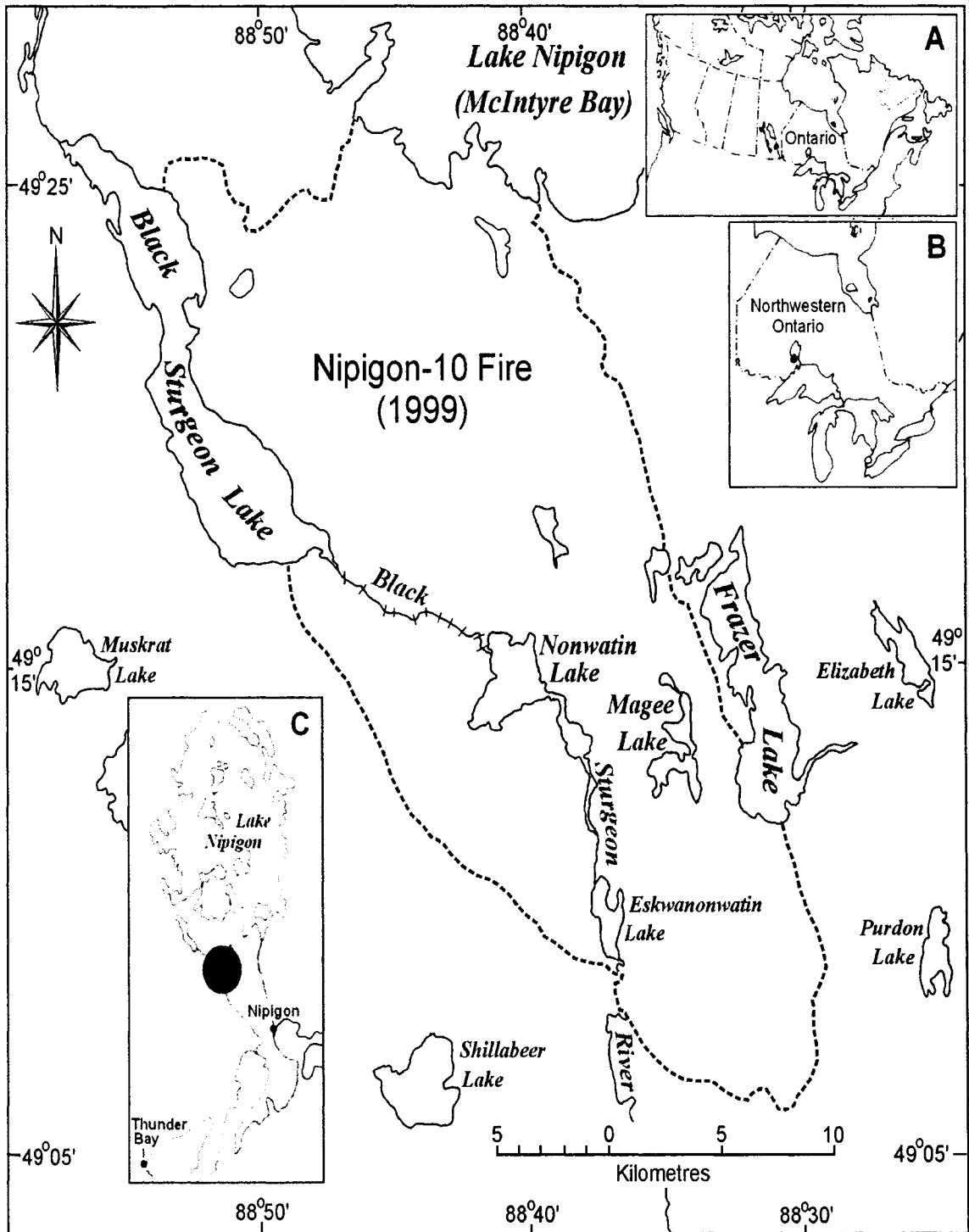
Figure 1: Black Sturgeon Forest Study Area. Red dot denotes location of study area on larger scale maps.

Climate

The climate of the study area is influenced by a modified continental climate similar to the nearest major city, Thunder Bay. Long, cold, dry winters and warm to hot, humid summers characterize this climate. Extremes in temperature are moderated to some extent by the close proximity of Lake Superior and Lake Nipigon. The annual mean daily maximum temperature for the study area is 7.6°C and a minimum daily temperature is -4.1°C; this gives a daily mean temperature of 1.8 °C. The average precipitation is 711.4mm. The length of the growing season for this region is between 150 and 160 days (Environment Canada, 2005).

Industry

Much of the region is second growth forest which dates back to the first harvest of virgin timber between 1939 and 1945. Logging was initially established by Great Lakes Paper. Horses were used to haul the virgin *Pinus strobus* (white pine), *Picea glauca* (white spruce) and *Pinus resinosa* (red pine) out of the bush where they were placed on the frozen lakes. As the lakes thawed, the logs were floated down the Black Sturgeon River into Lake Superior, and onward to Thunder Bay (Scarratt, 2001). The current Sustainable Forest Licence holder in the study area is Bowater, a pulp and paper company (Scarratt, 2001). After the Nipigon-10 fire, salvaging efforts by Bowater have been intensive, leaving little unsalvaged forests to study.

Other examples of human activity in the area include a few trap lines and associated cabins. There are also a few recreational camping and fishing locations that are commonly used by local residents. Outward-Bound operates an outdoor education facility

on the west shore of Black Sturgeon Lake. A few small gravel pits used in the construction of the region's major logging roads are also scattered across the landscape.

Digital Data

For this project, there were two controls derived from digital sources to represent burn intensity and pre-fire *Picea mariana* composition. Both controls were derived from different sources. The burn intensity map used in this study was created by digital image classification of satellite imagery acquired one and four months after the fire. Burn intensity classes were based on the amount of visible scarring left on the landscape shortly after the fire and on the areas that responded that same year with new growth (Freeburn, 2002). The burn intensity classification included three burn intensity classes: light, moderate and severe (see Figure 2). Visual inspection of the satellite images showed that severely burnt areas appeared very dark in colour, and no signs of vegetation regeneration had occurred in these areas even 4 months after the fire. The lightly burned areas had greened up significantly after 4 months but were obviously burnt in the air photography (acquired 1.5 weeks after the fire) and the Landsat TM imagery acquired one month after the fire. Moderately burned areas exhibited a blotchy pattern consisting of a mixture of the two previous classes. The spatial resolution of the raster classification map was 30m by 30m. The accuracy assessment for this burn map was completed by Freeburn (2002), with the aid of an experienced aerial photography interpreter from Bowater and consisted of the initial classification and post-classification accuracy assessments. The classification was created by comparing 1: 15 000 colour aerial photographs with areas in the image. A total of 477 sites were identified as belonging to

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one of ten classes identified within the aerial photographs. These classes include: water, roads, upland forest, lowland forest, mixed forest, burned area, clearcuts, lightly burned, moderately burned, and severely burned. The user's accuracy of the final burn map was 91.6% and a Kappa coefficient was 93.9% (Freeburn, 2002).

Figure 2: Nipigon-10 burn intensity map used in analysis (Freeburn, 2002)

The map of pre-fire spruce composition was extracted from a 1996 Forest Resource Inventory (FRI) supplied by Bowater Inc. This map was derived from air photo interpretation of large-scale colour and colour infrared photography. Stands with an

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overstorey composition of more than 50 percent *Picea mariana* were identified from the FRI and reclassified into three levels of pre-fire spruce composition: 50-60 percent, 70-80 percent, and 90-100 percent. The accuracy of the digital FRI was tested at each site to verify pre-fire forest composition. This was done by counting every burned overstorey tree within a 100 m^2 circular plot located at the centre of each sample plot. In these circular plots, the burned trees were identified by species. The composition of overstorey black spruce found at each site was compared to the FRI pre-fire spruce composition using an analysis of variance test. From this test it was determined that the accuracy of the FRI was sufficient when only the dominant species were examined (F = 66.8, p = 0.000), in this case *Picea mariana*. While this dataset might not be ideal, it was the only such dataset available at the time this study was conducted and was thus deemed acceptable despite the inherent uncertainties.

To get a clearer understanding of the combined effects of burn intensity and pre-fire spruce composition, a mixed group comprised of all nine classes in the 3 X 3 matrix was used in further analysis (Table 1).

Field Data Collection

Vegetation data was collected using the total composition by eye method in ten 1m^2 quadrats at each test site to determine local species composition (Barbour *et al.*, 1998). Appendix I is a sample of the data sheet that was used for all sampling. Every vascular plant species was identified using the *Forest of Central Ontario* (Chambers *et al.*, 1996) and the *Plants of the Western Boreal Forest & Aspen Parkland* (Johnson *et al.*, 1995) field guides. For any species that were not identifiable using these two field guides,

samples were taken to the Claude Gurton Herbarium at Lakehead University for further examination and comparison with preserved samples. Species that proved too difficult to identify, including the various willow species, certain grasses, bryophytes, and lichens, were identified to the genus level only. Appendix II indicates all the species found in the study.

The sampling design was developed to optimize the sampling of two factors, burn intensity and pre-fire spruce composition. It was suggested that an ideal sampling pattern of six sites should be sampled in each of nine classes (Table 1) (Mackereth *per com*, 2004). The ideal number of six sample sites could not always be achieved for each class due to intensive salvaging that occurred after the fire by Bowater Inc. In many instances, it was simply impossible to locate stands that were not salvaged and that were also far enough away from salvaged stands as to reduce the influence of edge effect on the samples.

Table 1. Sample size for each class. Each site is comprised of ten individual $1m^2$ quadrats. A minimum of four sites for each class was sampled.

	Severe Burn	Moderate Burn	Light Burn
>90% Spruce	4 sites x 10 plots	5 sites x 10 plots	6 sites x 10 plots
70-89% Spruce	7 sites x 10 plots	4 sites x 10 plots	4 sites x 10 plots
50-69% Spruce	6 sites x 10 plots	4 sites x 10 plots	4 sites x 10 plots

The sampling pattern used to measure the total composition of vascular plants is conceptually similar to the pattern used by Schmidtlein and Sassin (2004). It was established that 10 replicate plots within each site would be sufficient replication to eliminate as much variability as practical for such a study. The sampling design used in this study is based on a radial sampling pattern, whereby the centre of the plot was

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located using a Trimble GPS unit used in surveying (Figure 3). When in communication with sufficient satellites, this GPS unit is accurate to within one metre horizontal and two metres vertical, making locating and mapping the exact location of the site much easier. Each concentric ring in Figure 3 indicates a 5 metre distance between the previous ring. The inner ring is 10 metres away from the centre. Once the centre of the site was located using the GPS unit, two plots were always sampled along each azimuth. Two additional plots were sampled at 15 metres from the centre and rotated between the azimuths at every site to make a total of 10 samples per site.

To ensure the independence of the samples, a minimum distance of 100 metres was strictly maintained between sites. This value of 100 metres was selected to ensure that two plots could not occupy adjacent 30 metre Landsat TM pixels. Also, the salvaging efforts within the study area were quite widespread, which increased the chance of encountering edge effects. To mitigate the potential for edge effects, each plot was located a minimum of 40 metres from any cutovers, roads, and other disturbances that could adversely complicate the study. This distance was established based on the results previously stated, where the species composition was influenced by intensive harvesting up to a distance of 40 metres into the uncut stand (Stewart, 2004).

The aluminium framed $1m^2$ quadrat, used for all total composition measurements, was bisected by bungee cord grid dividing the square into 25 smaller areas, each representing 4 percent of the total area (Figure 4). This was a more accurate and convenient method of measuring species composition. An average of estimates by two observers was used to determine the total species composition.

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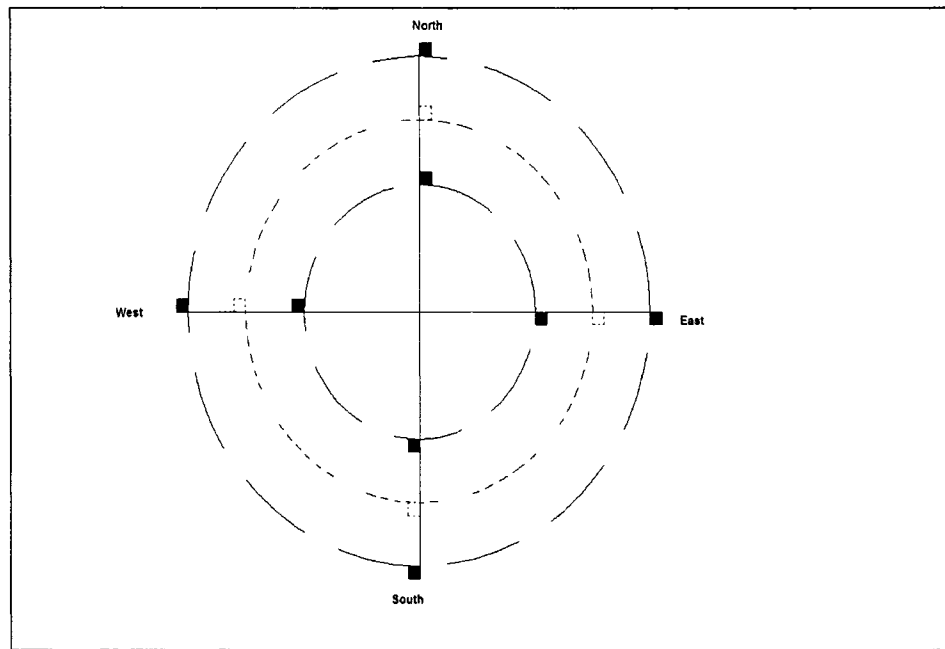
Figure 3: Sampling Pattern
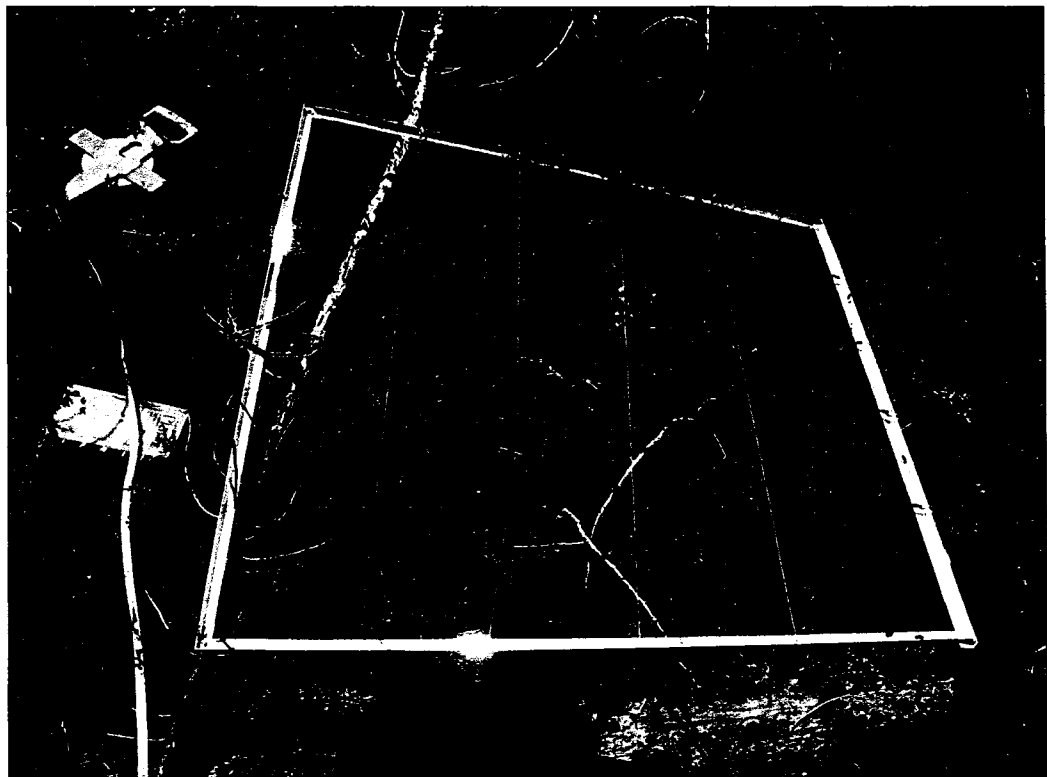
Figure 4: 1m^2 quadrat used to sample understorey vegetation

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Statistical Analysis

To examine the relationship between the post-fire species composition and the 3 burn intensities and the 3 pre-fire spruce composition classes, several statistical tests were performed. These include a two-way ANOVA, blocked multiple response permutation procedure (MRPP), discriminant function analysis (DFA), and indicator species analysis. The number of different species in each class was also calculated to determine how many species were common in each of the nine mixed groups.

To determine which level of pre-fire spruce composition or burn intensity had the greatest understorey species diversity; two population description indices were calculated and tested. These indices include evenness and species richness. By using these indices, a clearer indication of species composition differences may be observed.

Species richness (R), considered by Chipman and Johnson (2002) to be the most important indicator of diversity, is defined as the total number of different species in a defined area. The evenness index (E) calculates the relative distribution of individuals among the species present in a community. In this case, evenness was transformed logarithmically to ensure normality as required by the analysis of variance. Evenness is calculated by dividing the Simpson's diversity index by the natural logarithm of species richness ($E = H/\ln(D)$) (Freedman, 1995). Although these two indices do not directly measure diversity, they have been used by Chipman and Johnson (2002) to indicate relative levels of species diversity among species assemblages. It should be noted that this study uses species richness and evenness to measure components of diversity, diversity itself was not directly analysed in this study.

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A two-way analysis of variance (ANOVA) was run on species richness and evenness to determine if there was a difference in group means between burn intensity and pre-fire spruce composition. To illustrate the difference in means, means plots were utilized to show relative relationships of the classes. The two-way ANOVA also provides an interaction term between burn intensity and pre-fire spruce composition to determine whether one factor depends on the other. A one-way ANOVA and means plot was also run for the mixed groups to assess relative relationships between burn intensity and pre-fire spruce composition.

The blocked multiple response permutation procedure (MRPP) is a nonparametric method of testing for differences between groups. This test is ideal for ecological data as it has the advantage of not requiring homogeneity of variance or multivariate normality (Zimmerman *et al.*, 1985; McCune & Grace, 2002). The groups examined in the MRPP were defined by the sample design, defined by the 3x3 matrix classes (Table 1). The blocking variant of MRPP allows for a comparison between sites while retaining the spatial properties of the data (McClean *et al.*, 1998; McCune & Mefford, 1999). In this study, the ten replicates that made up a site were blocked together (1 = site 16, 2 = site 18, 3 = site 22, etcetera). Analysis was conducted for the three burn intensity and three pre-fire spruce composition classes. A combined grouping of both burn intensity and pre-fire spruce composition was also analyzed.

One of the key assumptions of the MRPP is that all groups have an equal sample size. This proved problematic as both burn intensity and pre-fire spruce composition classes had unequal number of replicates across the range (Table 1). This meant that to create an even number of samples, a random subset of study sites was selected. This was

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repeated six times to provide a minimum and maximum value. The random study sites were selected using a random number table corresponding to specific sites.

The blocked multiple response permutation procedure was conducted using PC-ORD software (McCune & Mefford, 1999). The default Euclidian distance was utilized as the distance measure, as suggested by McCune and Grace (2002). The output includes the three pertinent statistical values, the test statistic (T), the agreement statistic (A), and the significance statistic (p). These values provide an indication of group similarity. The test statistic (T) measures the separation between classes as indicated by a negative value, whereby the more negative the value the greater the separation between groups (McCune & Grace, 2002). The agreement statistic (A) indicates how similar the compositions of the groups are to each other. If the composition within the groups is identical, then A = 1; conversely, if heterogeneity within groups equals expectation by chance, then A = 0. However, if there is less agreement within the groups than expected by chance, then A will be negative (McCune & Grace, 2002). McCune and Grace (2002) indicate that for ecological data, an A value greater than 0.3 is fairly high; however, statistical significance may be achieved with very small "A" values, although the ecological significance may be limited.

Discriminate function analysis (DFA) was used to graphically illustrate the class separations found by the MRPP. DFA is an eigenanalysis technique that describes axes of maximum variance within large datasets (McCune & Grace, 2002). DFA differs from other ordination techniques in that it requires predefined groups. In this study, the input is an amalgamation of species variables organized by the DFA into axes which maximize

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the separation of the pre-fire spruce composition and burn intensity classes (McCune & Grace, 2002).

Unlike the MRPP, the discriminant function analysis does not require that all groups be of equal size. Therefore, the predictor variables utilized in the DFA were the nine mixed classes, the size of each being determined by the number of samples in each class (Table 1). For the purposes of this study, only the graphical output was examined (Mackereth *per com*, 2006).

One of the main goals of this study was to determine which plant species are influenced the most by burn intensity and pre-fire spruce composition. In this study, indicator species analysis is used to provide a means of characterizing each group established using the MRPP. This is done by combining information about species abundance, frequency, and regeneration strategies that occur within a particular group. It is suggested by McCune and Grace (2002) that the indicator species analysis is another good complement to the nonparametric MRPP test. The indicator values for each species range from 0 to 100, with 0 providing no indication and 100 providing perfect indication that a species belongs to a particular class. A perfect indicator of a particular group must always be present in that group alone without fail (McCune & Grace, 2002). A test of statistical significance was performed using the Monte Carlo randomization simulation technique using 1000 randomizations. This multivariate test was carried out using the PC-ORD program version 4 (McCune & Mefford, 1999).

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Results

Population Descriptions

The number of different species in each class was calculated to examine the number of common species for each of the nine mixed groups. Table 2 indicates the number and percent of all species in each of the nine mixed groups, burn intensity classes, and pre-fire spruce composition classes.

Table 2. Results from similarity analysis of the nine mixed groups, burn intensity classes and pre-fire spruce composition classes.

	Class	# of species	% of species
Mixed Groups	1	70	77.8
	2	68	75.6
	3	81	90.0
	4	73	81.1
	5	42	46.7
	6	45	50.0
	7	63	70.0
	8	47	52.2
	9	55	61.1
Burn Intensity	1	88	97.8
	2	79	87.8
	3	77	85.6
Spruce Composition	1	86	95.6
	2	74	82.2
	3	88	97.8

It can be observed that in the nine mixed groups, all the lightly burned classes (classes 1, 2, and 3) and one moderate burned class (class 4) have a large majority of the species present relative to the other more severely burned classes. This trend can also be seen in the burn intensity classification, where the number of species declines as the burn intensity increases. The moderate pre-fire spruce composition class (class 2) indicates an average of over 13% fewer similar species than in other classes. There appears to be little

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difference in numbers of species present in the low (class 1) and high (class 2) pre-fire

spruce composition classes.

According to the intermediate disturbance hypothesis (Connell, 1978), species

diversity should be highest for the intermediate disturbance classes. However, the results

indicated that the population descriptions were not the highest for the moderate burn

class. In fact, species richness was highest for the severely burned class (Figure 5a) and

was lowest for the moderate intensity classes ($F = 14.8$, $p = 0.000$). In contrast, species

evenness (Figure 5b) was highest for the moderate intensity classes and lowest for the

severe ($F = 10.5$, $p = 0.000$). The standard deviation bars indicate one standard deviation

from the mean. When the standard deviation bars are taken into account, there is little

difference in species richness and evenness for the low and moderate burn intensity
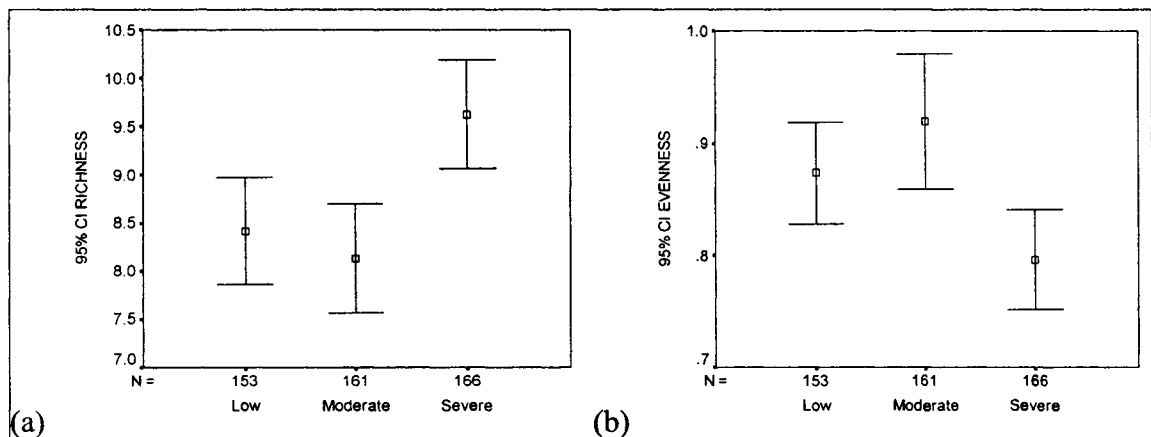
classes.

Figure 5: Species population descriptions for 3 levels of burn intensity *(low, moderate, severe)*. (a) richness; (b) evenness.

Regenerating understorey species diversity appears to be clearly influenced by the

three classes of pre-fire spruce composition. Results from the analysis of variance,

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shown in Figures 6a and 6b, illustrate a significant decrease in richness (F = 41.6, p = 0.000) as pre-fire spruce composition increases. This trend is also supported by a significant increase in evenness (F = 25.7, p = 0.000) as pre-fire spruce composition increases. It was hypothesized that the post-fire diversity should be lower for a more homogeneous pre-fire plant community (i.e. higher pre-fire spruce composition). The standard deviation bars indicate that species richness and species evenness of the three pre-fire spruce composition classes have very distinct groups.
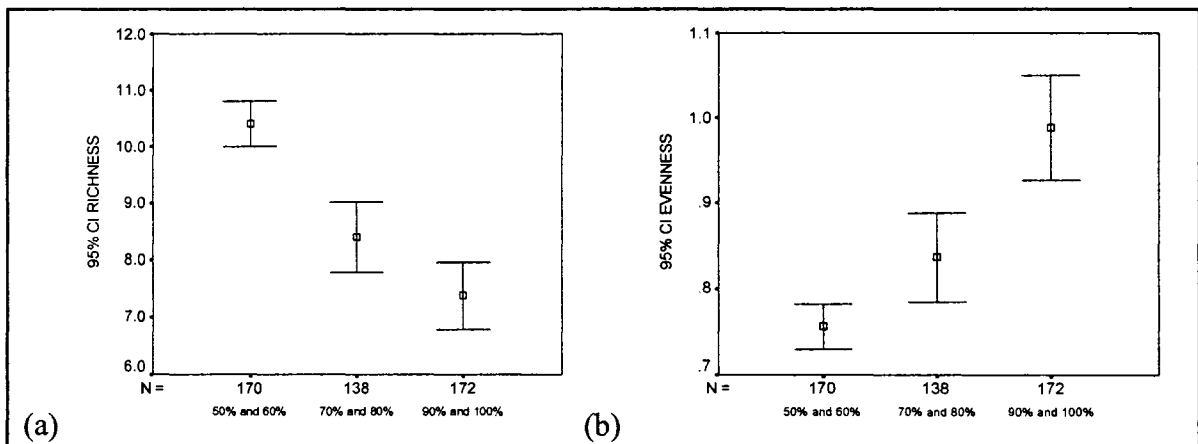
Figure 6: Species population descriptions for 3 levels of Pre-fire Spruce Composition *(50% and 60%, 70% and 80%, 90% and 100%)*.(a) richness; (b) evenness.

Figure 7 shows the results when both factors are combined. The low intensity classes provide the strongest indication that pre-fire spruce composition clearly influences the community structure. As the burn intensity approaches the severe class, there appears to be far greater variability from the influence of pre-fire spruce composition. These population descriptions also show that the three pre-fire spruce composition classes have significantly different community assemblages (Table 3). In general, it can be observed that species richness decreases and evenness increases in the

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moderate intensity classes. In both species richness and evenness, class 4 (moderate burn, 70-80% spruce) appears to be the only class that does not follow this general trend. From the standard deviation bars, it can be observed that the greatest variance in species richness and especially evenness for the nine mixed groups is in the moderate burn intensity classes (classes 4, 5 and 6).
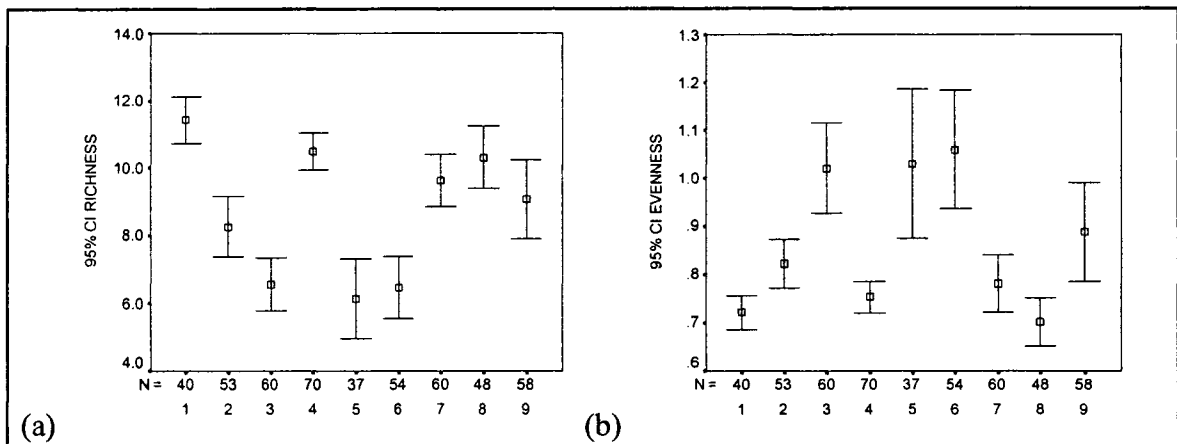
Figure 7: Species population descriptions for the 9 mixed classes (1 = Low: 50% and 60%, 2 = Low: 70% and 80%, 3 = Low: 90% and 100%, 4 = Moderate: 50% and 60%, 5 = Moderate: 70% and 80%, 6 = Moderate: 90% and 100%, 7 = Severe: 50% and 60%, 8 = Severe: 70% and 80%, 9 = Severe: 90% and 100%) (a) richness; (b) evenness.

Results indicate that the level of burn intensity is dependent upon the level of pre-fire spruce composition. This is shown by the interaction term (FIRE_INT * SP_COMP) in Table 3 that indicates an interaction on pre-fire spruce composition from burn intensity ($p < 0.0001$). This interaction term is present if the effect of one factor depends on the level of the other. The F statistic is an indicator of the contribution of each factor.

Table 3: Two-way analysis of variance of burn intensity, pre-fire spruce composition and mixed groups with species richness and log transformed evenness.

	Class	Sum of Squares	df	Mean Square	F	Sig.
Richness	Burn Intensity	305.380	2	152.690	14.767	0.000
	Spruce Composition	860.739	2	430.370	41.621	0.000
	FIRE_INT * SP_COMP	470.681	4	117.670	11.380	0.000
	Mixed Groups	1499.215	8	187.402	18.124	0.000
R Squared = .235 (Adjusted R Squared = .222)						
Evenness	Burn Intensity	0.0194	2	0.00462	10.544	0.000
	Spruce Composition	0.0473	2	0.02363	25.669	0.000
	FIRE_INT * SP_COMP	0.0194	4	0.00462	5.018	0.001
	Mixed Groups	0.0801	8	0.01002	10.883	0.000
R Squared = .156 (Adjusted R Squared = .142)						

Blocked Multiple Response Permutation Procedure

As hypothesized, the results from the blocked multiple response permutation procedure (MRPP) indicate that there is a significant difference in species composition between the three burn intensity classes based on species composition, with a significance value (p) less than 0.010 for the six repetitions (see Table 4). The test statistic (T) value indicates a slight separation between groups. T values in this study ranged from -2.786 to -6.513 which are not considered strong separation values by McCune & Grace (2002). The chance correlated within group homogeneity value (A) ranging from 0.009 to 0.021, indicating there is a high amount of variability within each group. These results complement the results from the analysis of variance above (see Table 3), which indicates that the three burn intensity groups differ significantly in species composition.

There was a significant difference in species composition between the three pre-fire spruce composition classes based on species composition as indicated by the T values

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of -11.495 and -7.326 (Table 4). As with the burn intensity classes, the pre-fire spruce composition classes also have a high amount of variability within each group as indicated by the A statistic (Table 4). These results complement the analysis of variance (discussed above) where it was found that the three pre-fire spruce composition classes had significantly different species richness and evenness values.

The results for the mixed groups test statistic, or T value, indicated there was separation between the nine mixed classes. The T value ranged from -35.91 to -27.59 (Table 4). The variability within each group was still high as indicated by the chance correlated within group homogeneity (A) values of 0.066 to 0.086 (Table 4).

Table 4. Results from Blocked Multiple Response Permutation Procedure (MRPP) for burn intensity, pre-fire spruce composition, and the mixed groups.

	Result #1	Result #2	Result #3	Result #4	Result #5	Result #6	Range Min	Max
Burn Intensity								
Test Statistic (T)	-2.785781	-6.207974	-6.318426	-6.207974	-6.51336	-6.51336	-2.785781	-6.51336
Chance-corrected within-group agreement (A)	0.008899	0.020089	0.021365	0.020089	0.021268	0.021268	0.008899	0.021365
Prob. of smaller or equal delta/ Significance (p)	0.010317	0.000021	0.000021	0.000021	0.000013	0.000013	0.000013	0.010317
Spruce Composition								
Test Statistic (T)	-11.495688	-9.070924	-11.422629	-9.186472	-7.32586	-8.78283	-11.49569	-7.32586
Chance-corrected within-group agreement (A)	0.037635	0.030071	0.037926	0.030062	0.024851	0.029741	0.024851	0.037926
Prob. of smaller or equal delta/ Significance (p)	0	0	0	0	0.000001	0	0	0.000001
Mixed Groups								
Test Statistic (T)	-35.383747	-35.919033	-30.703671	-33.104777	-27.5869	-31.1755	-35.91903	-27.5869
Chance-corrected within-group agreement (A)	0.086202	0.084844	0.074399	0.077974	0.06597	0.075148	0.06597	0.086202
Prob. of smaller or equal delta/ Significance (p)	0	0	0	0	0	0	0	0

<u>Discriminant Function Analysis</u>

The Discriminant Function Analysis (DFA) was used in this study as a graphical representation of the MRPP results used for further examination. The DFA indicated that there were distinct groups of plant communities found in the mixed class categories. The differences in these groupings can be highlighted by the loadings on each discriminant function axis. Since the DFA is intended as a graphical representation of the MRPP, only the first two of the three discriminant functions are interpreted in this analysis. Appendix III indicates the test of significance for each discriminant function and Appendix IV indicates all discriminant function coefficients.

Figure 8 is a graphical representation of all sites plotted on the first two discriminant function axes. From this graphical representation, it is possible to make observations on the relative difference between classes. *Vaccinium angustifolium* (low sweet blueberry), *Rubus idaeus* (wild red raspberry), *Cornus canadensis* (bunchberry), *Lycopodium dendroideum* (ground pine), and *Populus tremuloides* (trembling aspen) are all significantly correlated with discriminant function 1. Discriminant function 2 is primarily influenced by *Populus tremuloides* (trembling aspen), *Rosa acicularis* (prickly wild rose), *Maianthemum canadense* (Canada mayflower), *Ledum groenlandicum* (labrador tea), *Polygonum cilinode* (bindweed), and *Deschampsia flexuosa* (common hair grass).

As shown in Figure 8, Function 1 separates groups 2, 3, 5, and 6 from the remaining classes, possibly due to greater presence of *Vaccinium angustifolium* than the other classes. These groups represent the Low and Moderate, 50% to 80% spruce classes.

Canonical Discriminant Function Analysis
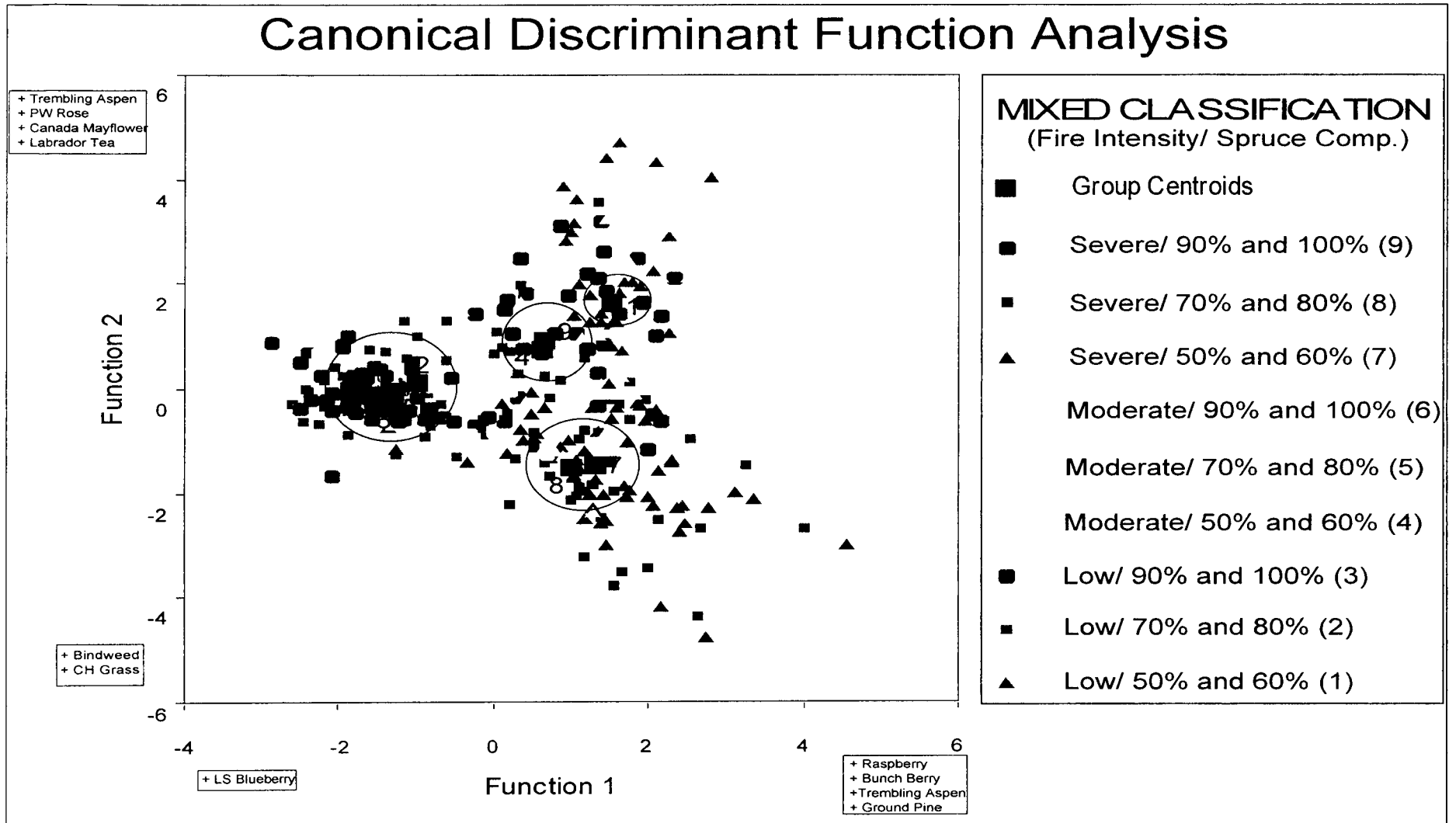
Figure 8: Discriminant Function Analysis, Mixed Classification. Ellipses manually drawn on chart to show clustering of group centroids from different classes.

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Function 1 does not sufficiently separate the remaining five classes, however, all of these classes were correlated with *Rubus idaeus*, *Cornus canadensis*, *Populus tremuloides*, and *Lycopodium dendroideum*.

Function 2 does a better job at separating classes 1, 4, 7, 8, and 9 from all other remaining classes, where Function 1 could not. Function 2 also tends to illustrate a more general pattern of a gradient in fire intensities with respect to species assemblages. Areas of low burn intensity tend to be associated with the occurrence of *Populus tremuloides*, *Rosa acicularis*, *Maianthemum canadense*, and *Ledum groenlandicum*. Areas of high fire intensities tend to be correlated with the occurrence of *Polygonum cilinode* and *Deschampsia flexuosa*, as indicated by the severely burned classes consisting of between 50% and 80% spruce (classes 7 and 8).

In Figure 8, the group of low intensity and low pre-fire spruce composition (Class 1) tends to show a greater tendency to be correlated with a high amount of *Populus tremuloides* in both Functions 1 and 2. This serves to separate this class from the remaining eight, indicating a unique community composition.

The classification results from the discriminant function analysis (DFA) of the three burn intensity classes indicate that 67.5% of the original groups and 58.4% of the cross-validated groups were correctly classified. The classification results for the three pre-fire burn intensity classes indicate 67.3% of the original groups and 60.9% of the cross-validated groups were correctly classified. This suggests that both the three burn intensity and pre-fire spruce composition classes are separated by a relatively distinct community of species. The results from the DFA classification (Figure 8) gave an idea of how unique each of the 9 mixed classes are. The results indicated that 57.5% of the original groups and 46.8% of the cross-validated groups were correctly classified. This

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increase in uncertainty is likely due to the increased variability faced when the same number of groups was classified into three times the classes.

Indicator Species Analysis

To determine which species were valid indicators of pre-fire spruce composition, burn intensity, and mixed group classes, an indicator species analysis was conducted (Appendix V). As indicated by the Discriminant Function Analysis, each group or cluster of groups has a few discrete sets of species associated with that group (Appendix V).

Results of the indicator species analysis for the three burn intensity classes showed species that were very strong indicators of low and severe fires, but very few indicator species of moderate fires. Species such as *Vaccinium angustifolium* and *Ledum groenlandicum* were strong indicators of low burn intensity classes, as shown by a high indicator value of 33.9 and 31.3. Severe intensity classes had four very strong indicator species: *Epilobium angustifolium* (fireweed), *Polytrichum* spp. (hair capped moss), *Cornus canadensis*, and *Rubus idaeus*. The strongest of these indicator species is *Epilobium angustifolium*, with an indicator value of 35.6. *Polytrichum* spp., *Cornus canadensis*, and *Rubus idaeus* had indicator values of 30.7, 28.9, and 27.7 respectively. These four species were significantly better indicators of severe burn intensity than any of the other statistically significant indicator species reported in the analysis. Classes of moderate intensity do not have strong indicator species, likely due to the high variability in species composition between severe and low intensity classes.

The results of the indicator species analysis for the three pre-fire spruce compositions highlighted seventeen species that were statistically significant indicators of low (50-60%) pre-fire spruce composition and only eight species that are statistically

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significant indicators of medium and high (70-80% and 90-100%) pre-fire spruce composition. However, only five of the indicator species are strong indicators of low pre-fire spruce composition, with *Rubus idaeus* being the strongest with value of 42.6. *Cornus canadensis* and *Populus tremuloides* also had significant indicator values of 35.6 and 32 respectively. As with burn intensity, the moderate (70% and 80%) pre-fire spruce composition class is not associated with very strong indicator species. The strongest indicator of the moderate classes is regenerating *Picea mariana* with an indicator value of only 18.3. Considering that all sites were sampled in stands dominated by *Picea mariana* prior to the fire, it was most surprising that *Picea mariana* only emerged as an indicator species in this class. Although the high pre-fire spruce composition class only had five species deemed statistically significant, indicator species *Vaccinium angustifolium* and *Ledum groenlandicum* both have quite high indicator values of 37.1 and 24.2.

With the pre-fire spruce composition and burn intensity classes combined to form the mixed groups, variability between classes can be further explained. Most of the indicator species were limited to the high and low classes for both burn intensity and pre-fire spruce composition. This same trend was noted when examining these classes as discrete groups. The low intensity and low spruce class (class 1) promotes a high abundance of *Populus tremuloides*, as shown by an indicator value of 48.5, the highest indicator species recorded. *Maianthemum canadense* is also a strong indicator of class 1 with an indicator value of 33.6. The severe intensity and moderate pre-fire spruce composition (class 8) also has relatively strong indicator species in *Polygonum cilinode* (25.6) and *Deschampsia flexuosa* (21.2).

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Discussion

Burn Intensity and Understorey Species Regeneration

Species community structure was unique for each of the three burn intensity classes where species richness and evenness showed distinct differences in post-fire species composition (Table 3). The levels of species richness and evenness varied significantly between burn intensity classes ($P < 0.05$). These results were confirmed by the blocked multiple permutation procedure (MRPP).

Contrary to the expectation of my research hypothesis that the highest diversity would be found in areas of intermediate disturbance, the results suggest that the highest diversity is found in regions of high intensity fire. This is illustrated by low species richness in the moderate intensity classes which is considered by Chipman and Johnson (2002) to be the most important indicator of diversity. Assuming the burn map is accurate and species richness adequately represents species diversity the results suggest that the environment created by a severe fire produces a more diverse ecosystem than that of low or moderate intensity fires. This might indicate that the severe burn intensity classes in the Nipigon-10 fire were not as severe as might be encountered elsewhere and might therefore only be considered a moderate disturbance from an ecological stand point. This could possibly be due to the fact that the Nipigon-10 fire was a canopy fire and perhaps the level of disturbance encountered on the forest floor might have been quite moderate. However, any interpretation along these lines is purely hypothetical but might warrant further investigation.

It is presumed that the more intense the fire, the greater the disturbance to the understorey vegetation and soils. This type of intense fire would remove many of the existing species and provide more opportunities for early successional species to

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colonize. For example *Polytrichum* spp. (hair capped moss), *Cornus canadensis* (bunchberry), and *Rubus* spp. (raspberry) all have the capability of regenerating vegetatively and are all indicators of severe burn intensities. It is presumed that severely burned stands would provide opportunities for endurer species to regenerate vegetatively with little competition from other species (Nguyen-Xuan *et al.*, 2000). The species that tend to be evaders and invaders are generally killed by the fire, or are out-competed following the fire. This indicates that several invading species might have taken advantage of the disturbance, suggesting that further investigation of the intermediate disturbance hypothesis is needed.

Indicator species can be a valuable method of describing key differences in community composition between different classes. Among the different burn intensity classes, several species were identified as indicator species. These species tended to be niche species favouring certain levels of burn intensity over another. The low and severe fires had very strong indicator species, whereas the moderate classes seemed to be affected by the high variability often associated with ecological data. *Vaccinium angustifolium* and *Ledum groenlandicum* are indicator species for the low burn intensity classes. *Ledum groenlandicum* is known as an indicator for acidic and nutrient-poor soil (Johnson *et al.*, 1995). These two shrub species have physical attributes that make them less likely to be damaged by low intensity ground fires and enable them to endure. The physical attributes that have enabled these species to endure light to moderate fires include bark that protects the plant tissue from being mortally damaged from the heat of the fire (Miller & Findley, 2001). *Epilobium angustifolium* was the highest indicator species for severe fire intensities. As its common name (fireweed) suggests, it is well adapted to regenerate after disturbances such as fire and is often found in recently burned

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areas. *Polytrichum* spp., *Cornus canadensis*, and *Rubus idaeus*, were also indicator species associated with severe fire. All of the species that have been found to be strong indicators for severe fires are known to be highly tolerant of fire and are propagated by seed dispersal (invaders), which aids in re-colonizing the area following a fire (USDA, 2005).

Pre-fire Spruce Composition and Species Regeneration

The results from the two-way ANOVA for pre-fire spruce composition illustrated a strong association between the plant community structure and the pre-fire spruce composition. The MRPP results confirm these findings and indicate that the species composition is different for each of the three pre-fire spruce composition classes. The analysis of variance indicated that species richness is negatively correlated with increasing pre-fire spruce composition, indicating that there are fewer understorey species overall in stands comprised predominantly of spruce. Both species richness and evenness had a significance of less than 0.05 (Table 3). A study by Legare *et al.* (2002) suggested that understorey richness and evenness were highly affected by surface deposits and that coniferous tree species are known to immobilize nutrients at a higher rate than deciduous species. This indicated that forest cover affects understorey composition through its influence on nutrient and light availability (Paré *et al.*, 1993; Brais *et al.*, 1995, Paré & Bergeron, 1996).

As hypothesized, species diversity, in this case measured using richness and evenness, increased as pre-fire spruce composition decreased. In stands dominated by spruce (high spruce), species diversity is lower than the mixedwood stands (low spruce).

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This is typical of the boreal forest ecosystem. For example, a study by Harper *et al.* (2003) highlights how late successional spruce-dominated stands lack the diversity seen in other early successional mixedwood stands. The reason for this lack of diversity in late successional spruce forests is likely caused by an underlying environmental gradient rather than any direct effects from the overstorey species composition (see Legare *et al.,* 2002). It was determined that the understorey plant biodiversity was strongly related to stand structural attributes such as light, basal area, and overstorey species composition. Messier *et al.* (1998) found that shade intolerant tree species such as *Populus tremuloides*, *Betula paprifera*, and *Pinus banksiana* transmit more light than shade tolerant tree species such as *Abies balsamea* and *Picea mariana*. This would indicate that light transmittance is one of the driving factors that differentiate understorey species composition in the three pre-fire spruce composition classes in this study.

The results of the indicator species analysis for the three pre-fire spruce composition classes highlighted several indicator species. Three species able to propagate vegetatively (endurers), *Rubus idaeus*, *Cornus canadensis*, and *Populus tremuloides,* were the three strongest indicators of low pre-fire spruce composition (50% and 60%). The occurrence of *Populus tremuloides* as an indictor species is expected in stands that may at one time have been heavily populated by mature *Populus tremuloides*. *Populus tremuloides* is often referred to as a pioneering species, as it can regenerate profusely after disturbance (Mitton & Grant, 1996; Madison, 1996). It does so by means of vegetative reproduction, whereby sucker shoots grow up from clonal roots following a disturbance. *Rubus idaeus*, *Cornus canadensis*, and *Populus tremuloides* are all known as early successional species, and they would be present in early successional stands that are not comprised fully of spruce or other coniferous trees (Shropshire *et al.,* 2001).

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Vaccinium angustifolium and *Ledum groenlandicum* are the two species that are strong

indicators of high pre-fire spruce composition. These species are often indicators of late

successional stands dominated by *Picea mariana* (Johnson *et al.,* 1995; Chambers *et al.,*

1996) and are able to propagate vegetatively. In the case of the Nipigon-10 fire, *Picea*

mariana dominated stands tended to be limited to a canopy fire and much of the

understorey did not burn. Figure 9 shows a typical *Picea mariana* dominated stand after

the fire. Much of the fire was limited to the overstorey, likely due to the lack of dry fuel

on the forest floor. This has enabled late successional species like *Ledum groenlandicum*

and *Vaccinium angustifolium* to persist after the fire in great numbers. The low number of

indicator species in this high pre-fire spruce composition class is likely a product of the

pre-fire low species richness normally associated with *Picea mariana* dominated forests.

Figure 9: Photo of typical study site. 100% spruce and severely burned
located in the Nipigon-10 fire.

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The Combined Impact on Understorey Species Regeneration

To better explain the response of understorey species associations between pre-fire spruce composition and burn intensity, nine individual classes were examined by combining the three pre-fire spruce composition classes and the three burn intensity classes. The results from the analysis of variance suggested that both burn intensity and pre-fire spruce composition played important roles in regenerating understorey species composition. The MRPP results indicate that the groups have a statistically different composition of species, suggesting that the combination of the pre-fire spruce composition groups and the burn intensity groups can explain more of the variability than either group alone.

The two species population description results agree with the intermediate disturbance hypothesis (Connell, 1978). Higher biodiversity was present in the moderate burn intensity class compared to either low or severe intensity. However, the moderate intensity class that had a 50-60% pre-fire spruce composition did not show high levels of diversity. This is likely due to the fact that deciduous species, like *Populus tremuloides* and *Betula papyrifera*, regenerate quickly after fire and may interfere with other species' ability to access sunlight and other resources (Connell, 1978). The low levels of species richness and abundance in the moderate burn intensity classes indicate fewer numbers of species persist in this moderately disturbed habitat. However, those species that do are not dominant and often exist in equal numbers as other species thereby increasing the relative biodiversity.

The difference in understorey species composition is most discrete between the three low burn intensity classes. In these three classes, there is a clear difference in

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species community structure along the pre-fire spruce composition classes. In the low burn intensity classes, the understorey community was likely unaltered by the effects of the fire. The discrete difference in species composition is probably governed by the successional stage of the stand. Earlier successional stands dominated by *Populus tremuloides* and other deciduous trees tend to have a much lower level of diversity and much higher species richness. In all of the sampled low pre-fire spruce composition sites (50% and 60%), there was very little difference in the community as the intensity of the fire increases; however, as the burn intensity increases the error also increases. This could be explained by the variability missed as a result of the larger spatial scale being used in the burn intensity and pre-fire spruce composition maps. The burn intensity map used in this study is unable to reproduce the inherent patchiness of fire at resolutions smaller than the defined 30 metre spatial resolution of the Landsat sensor. There could be several smaller patches of moderate and light intensity burns present within an area classified as intensely burned that could account for the variability found in the data (Jensen, 1996). Despite the variability missed by the Landsat sensor, it remains the ideal spatial resolution for landscape ecology. If an image of any greater spatial resolution is used, little of the variability would be incorporated. If the spatial resolution is too small, the variability would overwhelm the results.

To illustrate the results of the MRPP and the analysis of variance, a discriminant function analysis (DFA) was conducted. This analysis was able to illustrate graphically the distinct differences in community composition between several of the mixed burn intensity and pre-fire spruce composition groups. Several classes seem to have similar species compositions when plotted in species space. The low and moderate intensity classes and 70% to 100% spruce stands have similar species composition, identified in

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the DFA by a strong positive association to *Vaccinium angustifolium* and confirmed by the indicator species analysis.

The two severely burned 50% to 80% spruce classes are quite similar in species composition were identified by a strong association with *Polygonum cilinode* and *Deschampsia flexuosa*, identified by both the DFA and indicator species analysis. These species are known to be common indicators of highly disturbed areas with limited soil moisture (Chambers *et al.,* 1996). Understorey species associated with spruce-dominated stands tended to remain unharmed, whereas the understorey species in the 50% to 80% spruce stands were heavily impacted. This was likely due to fire causing mortality to the rhizomes of the species that tend to regenerate vegetatively (e.g. *Vaccinium angustifolium*, *Coptis trifolia*, and *Trientalis borealis*). This condition limits the understorey vegetation which reduces the shade and therefore increases the rate of evaporation and subsequent drying of the soil.

The low fire severity and low pre-fire spruce composition site tended to be strongly associated with *Populus tremuloides*, as indicated by both DFA and indicator species analysis. This is likely a product of the high amount of mature pre-fire *Populus tremuloides* present and their ability for very successful vegetative regeneration through suckering. Three other understorey species were identified in the indicator species analysis: *Maianthemum canadense*, *Aster macrophyllus* and *Cornus canadensis*. All three of these plants are shade tolerant species that can persist in the understorey beneath dense canopy cover. In this case, the cover from the regenerating *Populus tremuloides* has limited the amount of sunlight reaching understorey species, in turn limiting understorey species regeneration to those that are shade tolerant.

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Conclusions

The post-fire community structure differed from the intermediate disturbance hypothesis (Connell, 1978). This disparity could be a result of the new procedure used to create the burn intensity map as it is quite different from the established methods of mapping burn intensity. However, assuming the burn intensity map was relatively accurate, results show that burn intensity does influence the regenerative opportunities for some plants and that pre-fire spruce composition appears to be even a stronger influence on the regenerating species composition than the burn intensity. This was especially true in low intensity classes where the understorey species were strongly influenced by pre-fire spruce composition. This could have been the result of the burn intensity not being severe enough to change the understorey species composition significantly from its current successional stage. Although the results indicated some correlation between burn intensity and pre-fire spruce composition with understorey community composition, it is assumed that this is more a product of the microsite characteristics created by, or inherently present in, the environment. Although the results of this study are highly preliminary due to the nature of the spatial data used to segment the landscape into the nine classes, if they are accurate, they suggest that in each level of the pre-fire spruce composition and burn intensity classes there is a distinct ecological/microclimatic condition. Curtis (1959) suggested that species composition changes gradually in response to environmental gradients. Further research is necessary to determine if remote sensing and GIS based indices can be accurately used to model these environmental gradients and determine if regenerating species are responding to these gradients. Chapter 2 in this thesis will expand upon this question.

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Assuming that the FRI and burn maps are accurate, the results from the indicator species analysis suggest that unique vegetation communities can be identified by species that are uniquely adapted to the specific burn intensity or pre-fire spruce composition class. These species are adapted to living in the presence of fire and tend to demonstrate one of the three modes of persistence outlined by Rowe (1980, 1983).

Improvements to this research include the increased scrutiny and assessment of the two main datasets, the burn map and the FRI, which were used to segment the landscape into the desired nine classes. Increased confidence in these products would add confidence to the results, but it has proven difficult to be more rigorous within the confines of a master's thesis project.

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CHAPTER 2:

Using Landscape Indices to Model Environmental Gradients within the Mixedwood Boreal Forests of Northwestern Ontario, Canada

Abstract

Wildfire is a large-scale disturbance responsible for much of the structure, patterns, and forces associated with succession within the boreal forest. Past studies suggest that species composition of vascular plants respond to many different environmental gradients including wildfire. Some of the other gradients influencing plant community development include soil moisture, nutrients, light transmittance, and general productivity. The aim of this research was to examine variations in post-fire regeneration species composition with respect to remote sensing and GIS modeled environmental gradients. Due to the huge size of the study area (i.e., 50,000+ha), verifying the accuracy of all the modeled gradients was not possible making the results only speculative but may stimulate more scientific curiosity and effort in this area. A summary of the existing literature on modeling environmental gradients provides a basis for this research. Many of these studies have extensively verified their data and results and many practical applications exist.

Using spatial analysis procedures, I examined how post-fire regenerating species composition varied along specific modeled environmental gradients. Field data consisting of 481 square metre vegetation plots were sampled in the Nipigon-10 burn, 100 km northwest of Thunder Bay, Ontario. The species composition of these plots was examined with respect to spatial indices presumed to represent or be related to real underlying environmental gradients. All spatial indices were created using a Geographic Information

System (GIS) or derived from image analysis of Landsat TM satellite imagery. Canonical

Correspondence Analysis (CCA) was used to test which pseudo gradients (i.e., the

modeled gradients) were better predictors of the regenerating plant community. Results

suggest that modeled gradients derived from remote sensing and GIS can be used to

predict some degree of regenerating species composition.

Introduction

Numerous studies have utilized GIS and remote sensing techniques as viable methods of studying vegetation dynamics (Birth & McVey, 1968; Iverson *et al.*, 1989; Burke *et al.*, 1990; Chen, 1996; Jensen, 1996; Chen & Cihlar, 1996; Kimball *et al.*, 1997; Pitt *et al.*, 1997 and 2000; Blodgett *et al.*, 2000; Sriboonpong *et al.*, 2001; Chen *et al.*, 2002; Price, 2002; Melsse *et al.*, 2003; Tchir *et al.*, 2004). These methods provide an opportunity to study forest community ecology and monitor the environment at a landscape scale. These spatial tools have proven quite reliable and far more efficient for mapping large landscape features or assessing potential areas of concern. This ability to analyze many aspects of large tracts of land quickly and economically has meant that resource managers can include a wider variety of attributes in their analyses, which has often led to more holistic ecologically-based management policies (Boyce & Haney, 1997). For example, remote sensing and GIS in forest management is quite well established. Using traditional forestry and biology methods to examine forest dynamics is inherently difficult and time-consuming over a large scale. However, through the use of remote sensing, it has become possible to continually assess the characteristics of the forest communities by examining or comparing various indicators such as biomass and moisture, among others (Chen & Cihlar, 1996; Jensen, 1996; Chen *et al.*, 2002).

Chipman and Johnson (2002) suggest there are four primary environmental gradients that govern the success of vegetation species: soil moisture, nutrients, light transmittance, and general productivity. Remote sensing and GIS have both been widely used to produce maps and indices related to these and other environmental gradients.

The study by Dymond and Johnson (2002) is an example of the application of GIS and remote sensing to study landscape scale vegetation patterns. This study utilizes a

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GIS derived digital elevation model (DEM) and Landsat TM imagery to examine the relationship between the biophysical environment and species distribution. The study also maps the spatial pattern of trees, shrubs and herbaceous species. Using a CCA direct ordination method, temperature, moisture and radiation explained 17.2% of the species variance within the first ordination axis and 5.7% within the second axis. These results indicate that biophysical variables can explain as much or more variation in subalpine species composition than traditional environmental descriptors such as stand type. Therefore, Dymond and Johnson (2002) determined that simple mechanistic models of temperature, solar radiation and moisture can be used to improve vegetation maps in mountainous areas.

Figure 10 is a conceptual structural model illustrating possible pathways between environmental indices and corresponding environmental gradient. This model is intended to illustrate how a number of indices can be correlated to unique environmental gradients, represented by solid arrows. This illustration also shows how some indices might also have a secondary correlation to another gradient, represented by the dashed lines. For example, the Tasseled Cap Wetness index is strongly correlated to a moisture gradient but it is also slightly correlated to an insolation gradient. The following sections will describe how these tools can be used to model these spatial environmental gradients.

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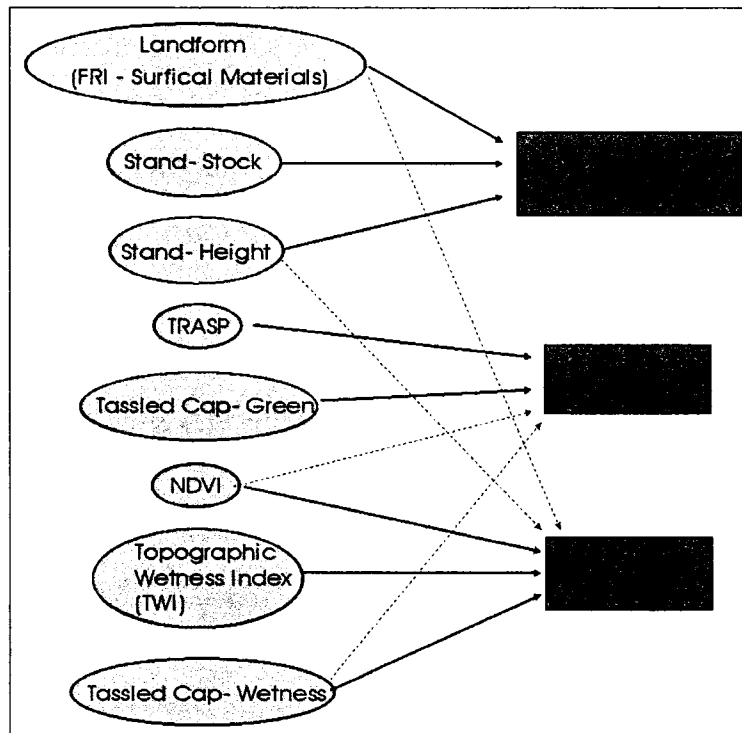
Figure 10: Structural model illustrating pathways between environmental indices and corresponding environmental gradients.

Research Hypotheses

The environmental gradients I attempted to model include soil moisture, soil properties, light transmittance, and green biomass. In a real ecosystem, these environmental gradients are known to influence vascular plant composition (Chipman and Johnson, 2002; Dymond and Johnson, 2002). Assuming that these modeled gradients are accurate representations of the conditions in the study area, I wish to test if the regenerating understorey species of the boreal forest respond to, or are related to, the pseudo gradients as would be expected for 'real' environmental gradients. Curtis (1959) and Whittaker (1956) proposed that floristic composition changes gradually in response to environmental gradients. In Chapter 1 of this thesis, I concluded that understory vegetation regeneration in the Nipigon-10 burn may be more a product of underlying

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environmental gradients than the direct influence of burn intensity or pre-fire spruce composition. In this chapter, I illustrate an analytical process that can be used to test the hypothesis that the understorey vegetation regeneration is more influenced by the modeled environmental gradients such as soil properties, insolation, and green biomass. For example, species regeneration in the three burn intensity classes might be affected by an insolation gradient due to the removal of the overstorey permitting greater sunlight to reach the forest floor. Likewise, species regenerating in the three pre-fire spruce composition classes might be influenced by the same moisture or soil gradient that helped define the composition of spruce prior to the fire. I hope to provide guidance for further research in forest regeneration using the methods highlighted in this chapter.

In testing the above hypothesis I have made a number of assumptions. Firstly, I am assuming the spatial indices used in the analysis are representative of 'real' natural variability in the environment, and therefore the among-site variability in the indicators can adequately be summarized by a few composite variables. If these two assumptions are true, then I am assuming that the principal component axes represent, or are associated with, environmental variability among the sample sites. If this is true, I am assuming that vegetation species composition is associated with environmental variability among sites. And finally, if the last two assumptions are true, then I am assuming that the CCA analysis can be interpreted as species response to environmental gradients.

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Literature Review

To date, only a few studies have examined the use of modeled spatial gradients. For example, Schmidtlein and Sassin (2004) used remote sensing to map continuous floristic gradients in the grasslands of southern Germany. This was done by extrapolating the axes of an unconstrained detrended correspondence analysis ordination of species data. Schmidtlein and Sassin (2004) were able to show a strong correlation between the remotely sensed vegetation gradients and the ground-based observations of floristic gradients. This method of detecting species composition gradients is more compatible with the field of vegetation ecology due to the incorporation of both spectral and vegetation information. However, floristic gradients are rather indefinable and abstract concepts relative to the simple idea that floristic composition changes gradually in response to environmental gradients (Curtis, 1959).

Spectral Response of Vegetation

The interpretation or analysis of remotely sensed data is largely dependent upon the optical properties of the item being studied, more specifically, the patterns of electromagnetic energy that the object reflects in different parts of the electromagnetic spectrum (i.e. spectral response). Remote sensing studies of vegetation use many types of imagery but can be generally separated into four portions of the spectrum: visible (400 - 700nm), near-infrared (750 - 900nm), the mid-infrared to far-infrared (1550 - 2350nm), and the microwave regions (1cm-100cm). In the visible portion of the spectrum, healthy leaves have high absorption for photosynthesis. Healthy leaves normally have a maximum reflectance in the yellow-green region (550 nm) of the electromagnetic spectrum, although most of the energy is still absorbed. In the near-infrared portion of the

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spectrum, reflectance can reach upwards of 50% depending on the structure of a leaf, specifically the number and orientation of the cellular layers (Guyot *et al.,* 1989; Jensen, 1996). The mid- and far-infrared portions of the spectrum are primarily sensitive to plant and soil moisture content, producing low reflectance if lots of water is available (Tucker, 1979; Jenson, 1996; Jackson *et al.,* 2003; Iverson *et al.,* 2004).

The optical properties of soils can vary greatly. The reflectance patterns of soils are highly dependent upon its mineral content and moisture level. Most soils often have reduced visible reflection as moisture content increases. The mid- and far-infrared wavelengths also decrease as soil or plant moisture increases (Guyot *et al.,* 1983).

Using these and other reflectance patterns for each ground cover type, it is possible to develop algorithms and classification techniques to analyze specific vegetative and landscape characteristics. Another factor in accurate detection can be the spatial resolution of the sensor. This aspect becomes critical when the objects being studied are smaller than the image's pixel size (Gholz et al., 1997).

Remote Sensing for Environmental Modeling

Spatial analysis tools, such as GIS and remote sensing, are now recognized as a legitimate methodologies in the field of landscape ecology (Perera *et al.,* 2000; Fortin *et al.,* 2002; Keane *et al.,* 2002; Gong & Xu, 2003; Wulder & Franklin, 2003; Van Wagtendonk *et al.,* 2004). Most studies of forest ecology using remote sensing generally use some form of vegetation index (i.e. a measurement of the amount of green-biomass). The benefit of using spatial analysis tools is its simplicity and the direct relationships with biophysical variables. As with most remote sensing operations, the repeatability of

using image-based indices allows for measurements to be easily duplicated at different dates and scales (Asner *et al.,* 2003). For example, vegetation indices are related to green-biomass amounts, productivity, leaf area, the amount of photosynthetic active radiation, and the amount of ground cover (Tucker, 1979; White, 1979; Chen & Cihlar, 1996; Goward & Dye, 1996; Jenson, 1996; Jackson *et al.,* 2003). Several algorithms have been developed to extract such information from remotely sensed data for different situations (e.g. areas with significant exposed soils like grasslands). For example, a study by Gould (2000) utilized the Normalized Difference Vegetation Index (NDVI) to estimate vascular plant species richness. By way of ground truthing, it was determined that variation in green biomass is positively correlated with measured species richness and mapped vegetation types, explaining 79% of the variance. Rey-Benayas and Pope (1995) utilized red, near-infrared (NIR), and mid-infrared bands of a Landsat TM image to produce vegetation diversity maps of Guatemalan national parks. They demonstrated that the NIR band alone provides an excellent tool in differentiating between different land-cover types (r = 0.67, n = 30, P < 0.0001). This study demonstrated the potential of remote sensing to provide valuable information on biodiversity patterns.

Remote sensing can also be used to examine spatial variation in an underlying moisture gradient. The Tasseled Cap Wetness index (Crist *and* Cicone, 1984) and the Moisture Stress index (Rock *et al.,* 1986) have been successfully used to measure moisture across vegetated landscapes.

The applicability of a Geographic Information System (GIS) in ecology is increasing every day. A GIS is able to deal with large amounts of spatial data in raster, point, line, or polygon form. Since the all these data types will have the same spatial or geometric properties, it becomes possible to examine spatial relationships between layers of data (Jensen, 1996). Furthermore, a GIS can provide a means of identifying spatially distinct information about a specific class or location. This information can include things like temperature, biomass, or other descriptive or temporal variables pertinent to that specific location. Many topographically-based gradients can be derived from high-resolution digital elevation models (DEM). These include common gradients such as elevation, slope, aspect, and slope-length.

A flow accumulation gradient is a measure of the upstream area for any given point in the study area and is related to soil moisture (Blaszczynski, 1999). Flow accumulation grids (i.e., raster datasets) are particularly useful in hydrologic modelling because they require inputs for a number of drainage delineation processes (Blaszczynski, 1999).

Another gradient that estimates soil moisture from topographic data is the topographic wetness index (TWI) (Spanner *et al.*, 1990; Treitz & Howarth, 1996; Freer *et al.*, 1997; Chen & Cihlar, 2002). Many studies utilize the topographic wetness index to model surface and subsurface flow of water. Sorensen *et al.* (2006) evaluated the effectiveness of the TWI in relation to field observations and indicated that the TWI was suitable for assessing the spatial moisture patterns on a landscape. They reported a significant correlation between wetness and the groundwater level (r = 0.96). Melsse *et*

al. (2003) examined methods of mapping watersheds using a digital elevation model within a GIS to model runoff. Several other ecological studies show that TWI is strongly correlated to underling moisture gradients (Beven & Kirby, 1979; Beven *et al.*, 1991; Thompson & Moore, 1996; Kim & Jung, 2003; Melesse *et al.*, 2003; and Iverson *et al.*, 2004).

Another topographic index which represents an insolation gradient is the topographic radiation index (TRASP) developed by Roberts and Cooper (1989). This transformation assigns a value of zero to land oriented with a north-northeast aspect, (typically the coolest and wettest orientation in the northern hemisphere), and a value of one to the hotter, drier south south-westerly slopes. This index is ideal for modeling the approximate amount of sunlight available to vegetation.

GIS also has the fundamental capability to store spatial data which might be used to represent other possible environmental gradients. For example, within a typical forest resource inventory (FRI) stand density information could logically be associated to insolation by determining the amount of sunlight reaching the forest floor. Similarly, the data found in the engineering survey map of surficial materials in Ontario (NOEGTS) can also be reclassified to represent particular a soil properties gradient like particle size.

The previous sections have described how remote sensing and GIS can be used to model environmental gradients at the landscape scale, but very few studies have been published using these types of gradients to study forest regeneration. My goal was to examine the potential of this methodology to study *Picea mariana* regeneration after fire in the boreal forest of northwestern Ontario and provide a framework for future studies.

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Methods

To examine variations in post-fire regeneration of understorey species, three methodological steps were implemented: spatial dataset creation, spatial analysis, and statistical analysis. The following section explains how the environmental gradients were modeled and explains their influence on forest regeneration.

<u>Study Site</u>

The study area for this project is the same as was used in Chapter 1. It is located approximately 80 km northeast of Thunder Bay, Ontario in the Black Sturgeon Lake region (Figure 1). The 50,000 hectare Nipigon-10 fire was accidentally started by Bowater forestry operations on April 30th, 1999, and it burned until May 5th, 1999.

The area is a part of the boreal mixedwood forest, which tends to occur on the more fertile regions of the boreal zone and can be distinguished by a diverse number of hardwood and conifer overstorey species in varying proportions (Borealforest.org 2005). Some of the predominant canopy species in the Black Sturgeon forest include: *Picea mariana* (black spruce), *Abies balsamea* (balsam fir), *Betula papyrifera* (white birch), *Populus tremuloides* (trembling aspen), and *Pinus resinosa* (red pine).

<u>Climate</u>

The climate of the study area is influenced by a modified continental climate much the same as the nearest city, Thunder Bay. Long, cold, dry winters and warm to hot, humid summers characterize this climate. Extremes in temperature are moderated to some extent by the close proximity of Lake Superior and Lake Nipigon.

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Field Data Collection

The same vegetation survey data utilized in Chapter 1 was also implemented in this study. Vegetation data was collected using the total composition by eye method in a $1m^2$ quadrat to determine local species composition (Barbour *et al.*, 1998). Appendix I is a sample of the data sheet that was used for all sampling. Species were identified using the *Forest of Central Ontario* (Chambers *et al.*, 1996) and the *Plants of the Western Boreal Forest & Aspen Parkland* (Johnson *et al.*, 1995) field guides.

The vegetation survey used in this study and Chapter 1 is conceptually similar to the pattern used by Schmidtlein and Sassin (2004) (Table 1). It was established that 10 replicate plots within each site would be sufficient replication to eliminate as much variability as practical for such a study. The sampling design used in this study is based on a radial sampling pattern, whereby the centre of the plot is located using a Trimble GPS unit used in surveying (Figure 3). Further details on the sampling routine can be found in the methods section of Chapter 1. To ensure the independence of the samples, a minimum distance of 100 metres was strictly maintained between sites. This value of 100 metres was selected to ensure that two plots could not occupy adjacent 30 metre Landsat TM pixels. Also, the edge effects caused by adjacent cutovers were mitigated, as discussed in Chapter 1.

Spatial Dataset Creation

This study required the acquisition or creation of several digital datasets, including a digital elevation model (DEM) to create various topographic indices. A soils and surficial materials dataset was obtained through the Ontario Ministry of Natural Resources (OMNR), of which only a few soil attributes were used. Other datasets were

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derived from satellite imagery for the study area or a pre-fire Forest Resource Inventory (FRI). The following sections describe the methods used to create the spatial datasets used in this study.

Digital Elevation Model

The digital elevation model (DEM) used in this study was interpolated from 1:20 000 scale Ontario Base Maps (OBM) contours using TOPOGRID, a topographic interpolation routine found in ArcINFO GIS software. A raster DEM grid cell size of 30 metres was selected to correspond with the pixel size from the Landsat TM imagery. To improve the DEM output, digital data of lakes and rivers were incorporated in the interpolation process. This prevents the interpolator from creating points below the surface level of lakes, thereby creating an artificial sink in the dataset. As well, the slope of a river is presumed to be continuously downhill throughout its length. This ensures that TOPOGRID only interpolates down slope along rivers and does not create artificial inclines where none exist. Figure 11 illustrates the DEM used in this study. Although interpolating a DEM from contour maps is a common practice, it is not without its limitations. It is important to note that although the DEM in this study is assumed to be an accurate representation of the Earth's surface, it is simply a model and like other models it is subject to error. Examples of these possible errors include: the inherent uncertainty of the elevation between the contour lines, data errors due to the age of the contour map, measurement error from the initial survey used to create the contour map, and computational errors (Wechsler, 1999).

The DEM in this study was assumed to be representative of actual topography and therefore used to calculate the previously described topographic indices. The

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topographically-based indices utilized in this study include flow accumulation, aspect, Topographic Wetness Index, Heat Load Index, and the Topographic Radiation Index (all described below).

The distance to water measurement was calculated by using an inverse difference weighted interpolation routine to create a raster file indicating the distance in metres away from the nearest body of water.

The Topographic Wetness Index (Figure 12) is commonly used to estimate the moisture content of a landscape based on a digital elevation model (DEM). It is based on the simple notion that the regions of the landscape that drain a large upstream area would logically be wetter. The index was developed by Beven and Kirby (1979). The equation used to calculate the Topographic Wetness Index (TWI) is as follows:

TWI = $ln(a/\tan\beta)$

*where;   a = the upstream contributing area.
               $\tan\beta$ = slope

The Topographic Radiation Index (TRASP), developed by Roberts and Cooper (1989) and shown in Figure 13, uses the average angle of the sun and the local topography to model the relative solar radiation hitting the surface of the Earth. Areas in red indicate regions of high solar radiation, and areas in dark blue indicate low radiation. Figure 13 is an example of the topographic wetness index used in this study. Areas in blue indicate wet or saturated soil and areas in dark brown indicate dry soil. The equation used to calculate the Topographic Radiation Index (TRASP) is as follows:

$$TRASP = \frac{[1 - \cos((\prod / 180)(\emptyset - 30))]}{2}$$
*where $\emptyset$ = aspect in degrees east of true north

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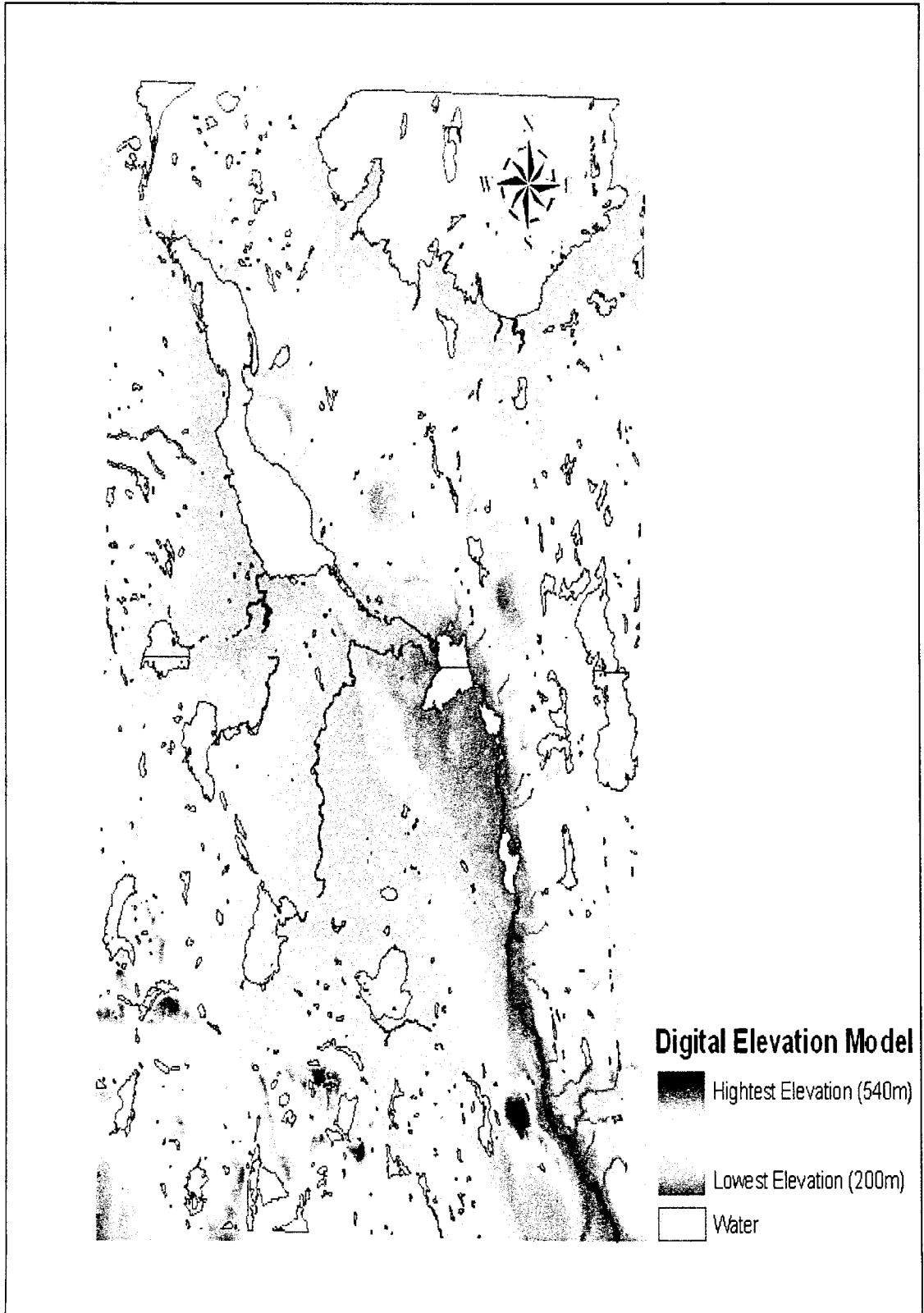
Figure 11: Digital Elevation Model (DEM) interpolated from 1:20 000 Ontario Base Maps

75
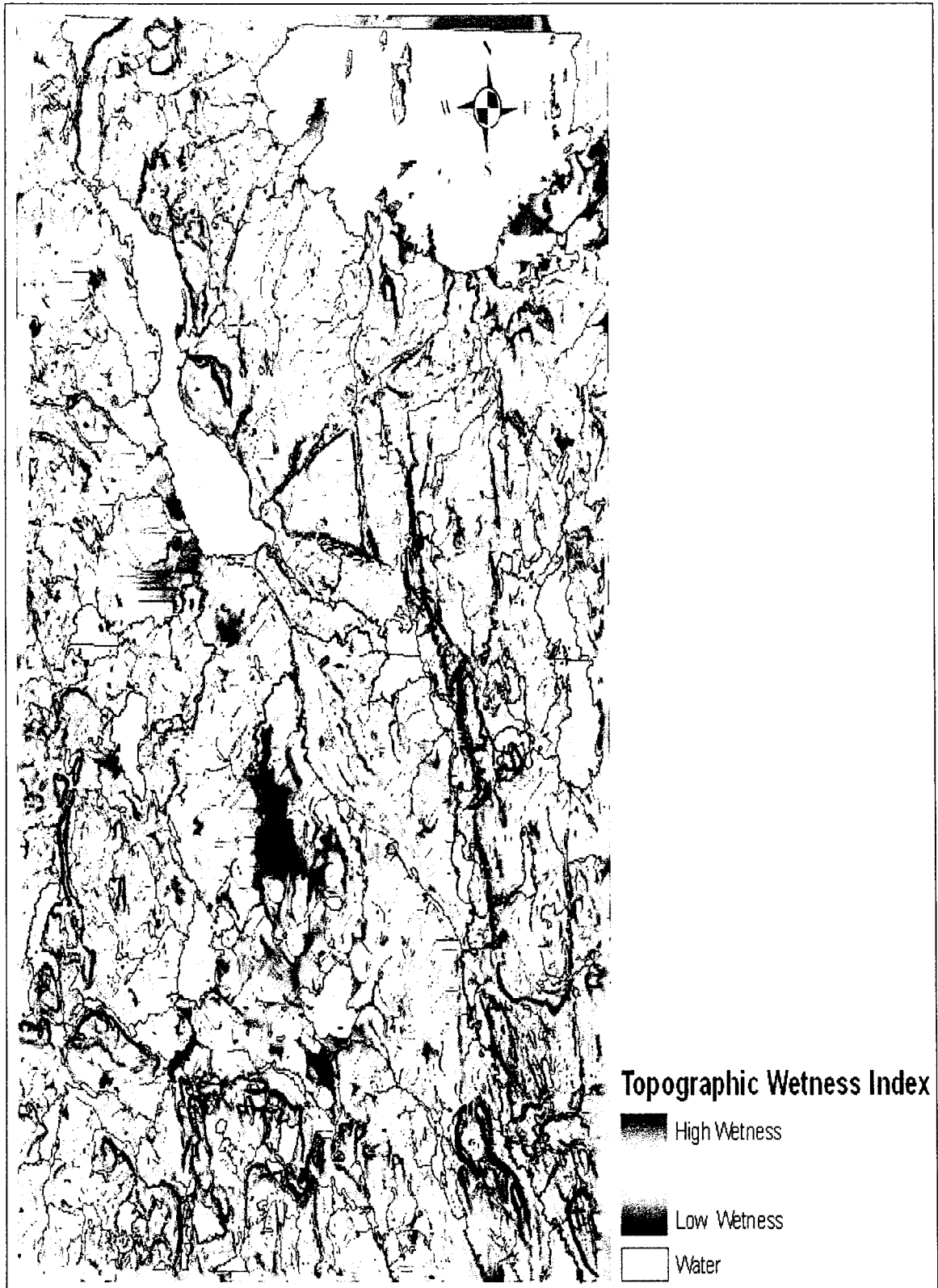
Figure 12: Topographic Wetness Index (TWI) calculated from DEM in ArcGIS

76
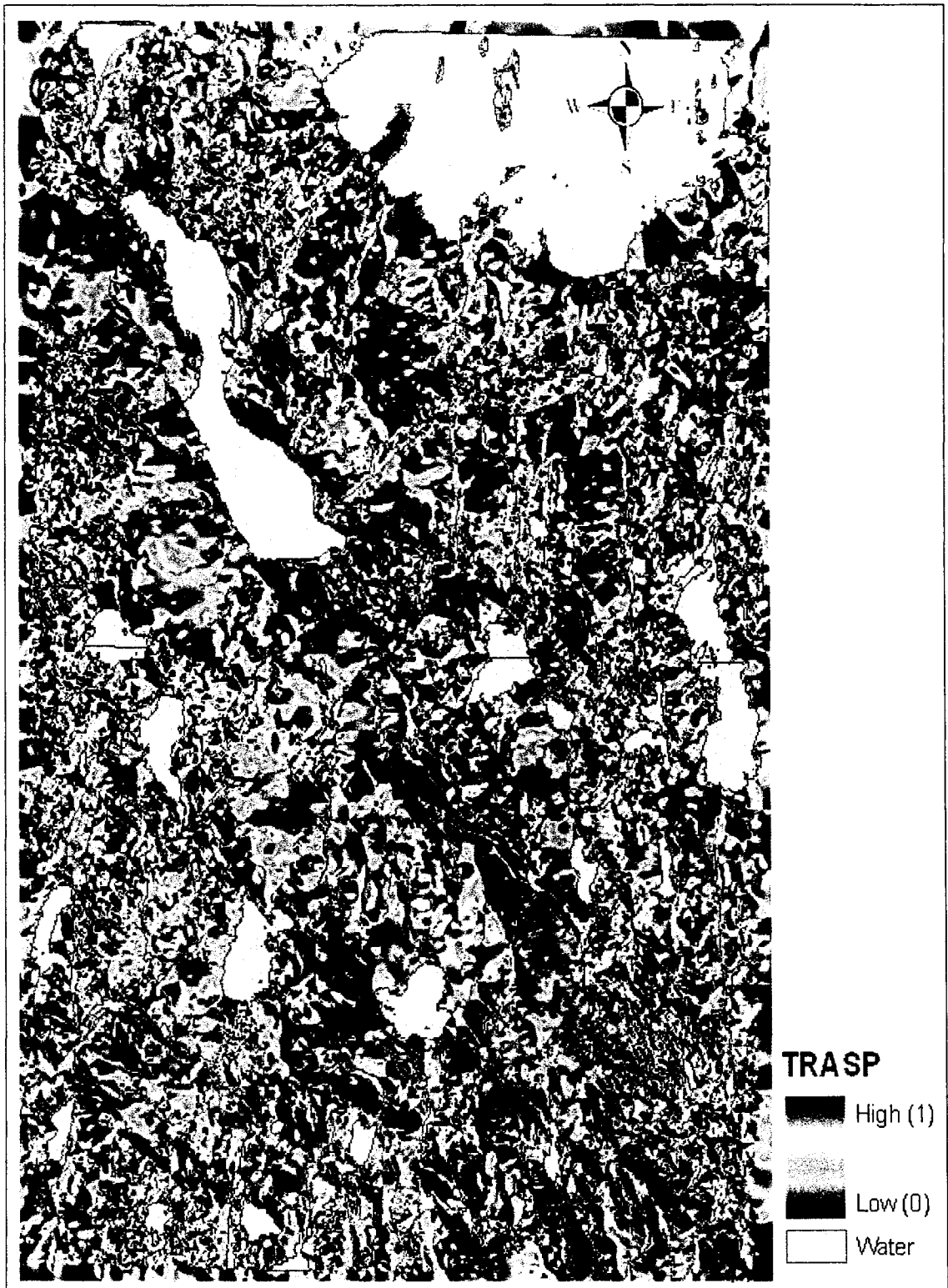
Figure 13: Topographic Radiation Index (TRASP) calculated from DEM in ArcGIS

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The final topographic index created in this study is the Heat Load Index. It is a topographic measure of the solar radiation hitting the surface of the Earth. It differs from the topographic radiation index only in calculations used to determine the angle of the sun, but conceptually they are the same. This index rescales aspect to a scale of zero to one. The coolest slope, northeast, is assigned a value of zero and the warmest slope, southwest, is assigned a value of one (McCune & Grace, 2002). The equation utilized to calculate this index is as follows:

$$\text{Heat load index} = \frac{1 - \cos (\emptyset - 45)}{2}$$

*where $\emptyset$ = aspect in degrees east of true north.

Soils and Surficial Materials Data

The digital surficial materials data that were used in this project were obtained from northern Ontario engineering geology terrain studies (NOEGTS) digital maps (1:250,000), provided courtesy of the MNR. This dataset consists of 103 original cartographic maps used for the study of near-surface geological conditions (Keane *et al.*, 2002; MNR, 2005). The data were transformed from NAD-27 to NAD-83 in order to register it with the other spatial data used. The data that were deemed appropriate for this study include drainage, and soil texture. Since the data were not comprised of ordinal or interval data, but rather qualitative descriptions of features (e.g. sand, wet, organic) the data were reclassified into appropriate ordinal or categorical classes. Appendix VI is a table illustrating the ordinal values given to each class in the two different categories (particle size, and drainage). This data, consisting of the two reclassified layers, were then transferred to the project file containing all the topographic indices.

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Forest Resource Inventory Data

The forest resource inventory (FRI) was obtained from Bowater Inc. and was derived from an interpretation of 1:20,000 colour aerial photographs. The confidence level for the species map of the FRI was not provided at the time of acquisition. Bowater staff have indicated verbally on several occasions that this database was very useful for their applications and they have great confidence in its overall accuracy, but our requests for accuracy assessment data have not been met. Forest resources inventories have been successfully used in several other forest ecology studies (Tomppo, 2000; Lehtonen, 2005).

This GIS data were transformed from NAD-27 to NAD-83 in order to co-register it with the other spatial data used in this study. To obtain the three pre-fire spruce composition classes, all non-spruce dominated stands were cut from the dataset and the remaining spruce stands were reclassified into the three specific classes used in this study (50% and 60%, 70% and 80%, 90% and 100%). The site selection was done by intersecting this pre-fire spruce composition layer with the burn intensity layer as described in Chapter 1.

There are some significant benefits as well as limitations associated with the use of GIS derived spatial datasets for use in landscape scale ecological research. Of key importance are the sources of possible error inherently associated the DEM previously mentioned. As stated, it was produced from the contour lines of a 1:20,000 OBM and results in a modeled landscape rather than true representation. It is therefore true that all spatial indices derived from this DEM share this initial source of error. Furthermore, each of these indices are models of the landscape feature calculated using algorithms rather than being direct measures of the environmental gradient in question. Therefore, the

accuracy of the results is partially dependent upon the accuracy of the spatial data being utilized in the study. Although the above noted errors are likely associated with the data in this project, the study was conducted under the assumption that the GIS derived spatial indices are accurate representations of the gradients they represent.

Satellite Image Derived Data

The first image that was chosen for this project was taken using the Landsat 7 Enhanced Thematic Mapper (ETM+) sensor on July 4th 2001 and was obtained through the Natural Resources Canada *GEOGRATIS* online database. This date was chosen to correspond as closely as possible with the date of the field data collection. Due to the failure of the Landsat ETM sensor in recent years, it was impossible to obtain an image nearer the date of the fieldwork. The image obtained had been crudely georectified but required a further image to map geometric correction to ensure the data overlaid with the spatial data already obtained. The geometric correction was done using 26 ground control points resulting in a RMS error of less than 30 meters. The image was delivered with an atmospheric correction already performed.

As described in Chapter 1, the burn intensity map used in this study was created by digital image classification of satellite imagery acquired one and four months after the fire. Burn intensity classes were based on the amount of visible scarring left on the landscape shortly after the fire and on the areas that responded that same year with new growth (Freeburn, 2002). The accuracy assessment for this burn map was completed by Freeburn (2002), with the aid of an experienced aerial photography interpreter from Bowater and consisted of the initial classification and post-classification accuracy

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assessments. The classification was created by comparing 1: 15 000 colour aerial photographs with areas in the image. A total of 477 sites were identified as belonging to one of ten classes identified within the aerial photographs. These classes include: water, roads, upland forest, lowland forest, mixed forest, burned area, clearcuts, lightly burned, moderately burned, and severely burned. The user's accuracy of the final burn map was 91.6% and a Kappa coefficient was 93.9% (Freeburn, 2002).

The process of calculating spectral indices using digital remotely sensed imagery is conceptually similar to the topographically-based indices. For example, the Landsat 7 ETM sensor is capable of detecting seven distinct wavelengths of electromagnetic energy emitted from the surface of the Earth: blue, green, red, near-infrared, mid-infrared, thermal infrared, and far-infrared. Many spectral indices compare the amount of energy being emitted in different wavelengths and have been consistently related to many surface characteristics (Birth & McVey, 1968; Hardisky *et al.,* 1983; Huete, 1988; Chen & Cihlar, 1996; Trishchenko *et al.,* 2002). The spectral indices for examination in this study include the normalized vegetation index (NDVI) (Rouse *et al.,* 1974), soil adjusted vegetation index (SAVI) (Chen & Cihlar, 1996), simple vegetation index (SVI) (Tucker, 1979), the fraction of photosynthetic radiation (fPAR) (Ahern *et al.,* 1977), the tasseled cap transformation (wetness, greeness, and brightness) (Kauth & Thomas, 1976; Crist & Cicone, 1984), infrared index (IR) (Jensen, 1996), and leaf area index model(LAI) (Ahern *et al.,* 1977).

The basic premise behind vegetation indices is that healthy vegetation absorbs much of the visible light it intercepts but reflects much of the near-infrared light. A larger difference between these two spectral regions indicates more green-biomass. The

Normalized Difference Vegetation Index (NDVI) (Rouse *et al.*, 1974) was utilized in this study and has the following equation:

$$NDVI = \frac{nearinfrared - red}{nearinfrared + red}$$

Another index that was utilized in this study is the geomatics model of the Leaf Area Index, henceforth referred to as simply the Leaf Area Index (LAI). This index used was developed by Lanzl and Richter (1991), Richter (1991), Richter (1990) and Ahern *et al.* (1977) to closely represent the common ground measure of the Leaf Area Index which is the average density of vegetation covering the ground.

The spatial variation of this index was calculated in PCI Geomatica. It uses the Soil Adjusted Vegetation Index (SAVI) to calculate the Leaf Area Index Model (LAI). The equation is used to calculate the LAI model:

$$SAVI = a0-a1*exp(-a2*LAI),$$

*where; $a0 = 0.75$

$a1 = 0.65$

$a2 = 0.6$

The Fraction of Photosynthetic Active Radiation (FPAR) index used in this study is another geomatics variation of common ground measured index (Ahern *et al.*, 1977). This index uses the Leaf Area Index noted above and was calculated in PCI Geomatica using the following equation:

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$$FPAR = c \, [1\text{-}a^{(-b*LAI)}],$$

*where;   a = 1.0

                     b = 0.4

                     c = 1.0

                     LAI = Leaf Area Index (as calculated above)

The Tasseled Cap transformation is a group of three indices that uses a modeling equation that multiplies constants with each Landsat TM spectral value (Kauth & Thomas, 1976; Crist & Cicone, 1984). It uses a modeling equation to transform the spectral bands of Landsat TM data into three indices. It has been used successfully in analysis of forest ecology and other related disciplines (Blodgett *et al.*, 2000; Owens *et al.*, 2003; Ager & Owens, 2004; Wulder *et al.*, 2004). The three separate indices that make up the tasselled cap index include the brightness index, the green vegetation index and the wetness index. The three equations for these indices utilize the seven Landsat TM sensor bands (i.e., TM1 is Landsat TM band 1 (blue band)) as follows:

Brightness   = 0.2909TM1 + 0.2493TM2 + 0.4806TM3 + 0.5568TM4 +
                        0.5568TM5 + 0.1706TM7

Greenness   = -0.2728TM1 − 0.2174TM2 − 0.5508TM3 + 0.7221TM4 +
                        0.0733TM5 − 0.1648TM7

Wetness   = 0.1446TM1 + 0.1761TM2 + 0.3322TM3 + 0.3369TM4 −
                        0.6210TM5 − 0.4186TM7

Figure 14 shows a colour infrared display of the Landsat imagery and two spectral indices, specifically the tasseled cap brightness (upper right) and NDVI (lower right). The extent of the Nipigon-10 fire is indicated by the light pink and white regions in the centre

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of the image. The tasseled cap brightness index illustrates variations in exposed soil with brighter areas containing less ground cover. The NDVI image shows brighter tones for regions with higher biomass.

There are several limitations commonly associated with the implementation of spectral datasets. One of these potential sources of error is related to the temporal variations in the image acquisition. In the case of this study, the images utilized to create the burn map and spectral indices were simply chosen based on financial resource limitations. It is not known if these images were acquired during an ideal period to most accurately capture vegetation patterns. For example, it might have been more appropriate to utilize an image nearer the date of the fire, in a different time of the year, or under different climatic conditions. Any of these variables might influence the vegetation community and thus the image.

Perhaps the most significant source of error for this project is a result of the logistical impossibility to accurately ground truth the spectral indices used in this study. It is therefore unknown how well they model environmental conditions in this environment. An effort was made to use only those indices with prior history of success in similar environments to the study area. However, the actual relationship between the spectral index and the environmental feature being assessed cannot be determined due to the size of the study area (i.e. over 50,000 ha). This study was conducted under the assumption that these indices are reasonably accurate measures of the intended environmental feature being modeled. Therefore the results of this chapter are considered unverifiable and highly preliminary, but they will hopefully stimulate more interest in this area.

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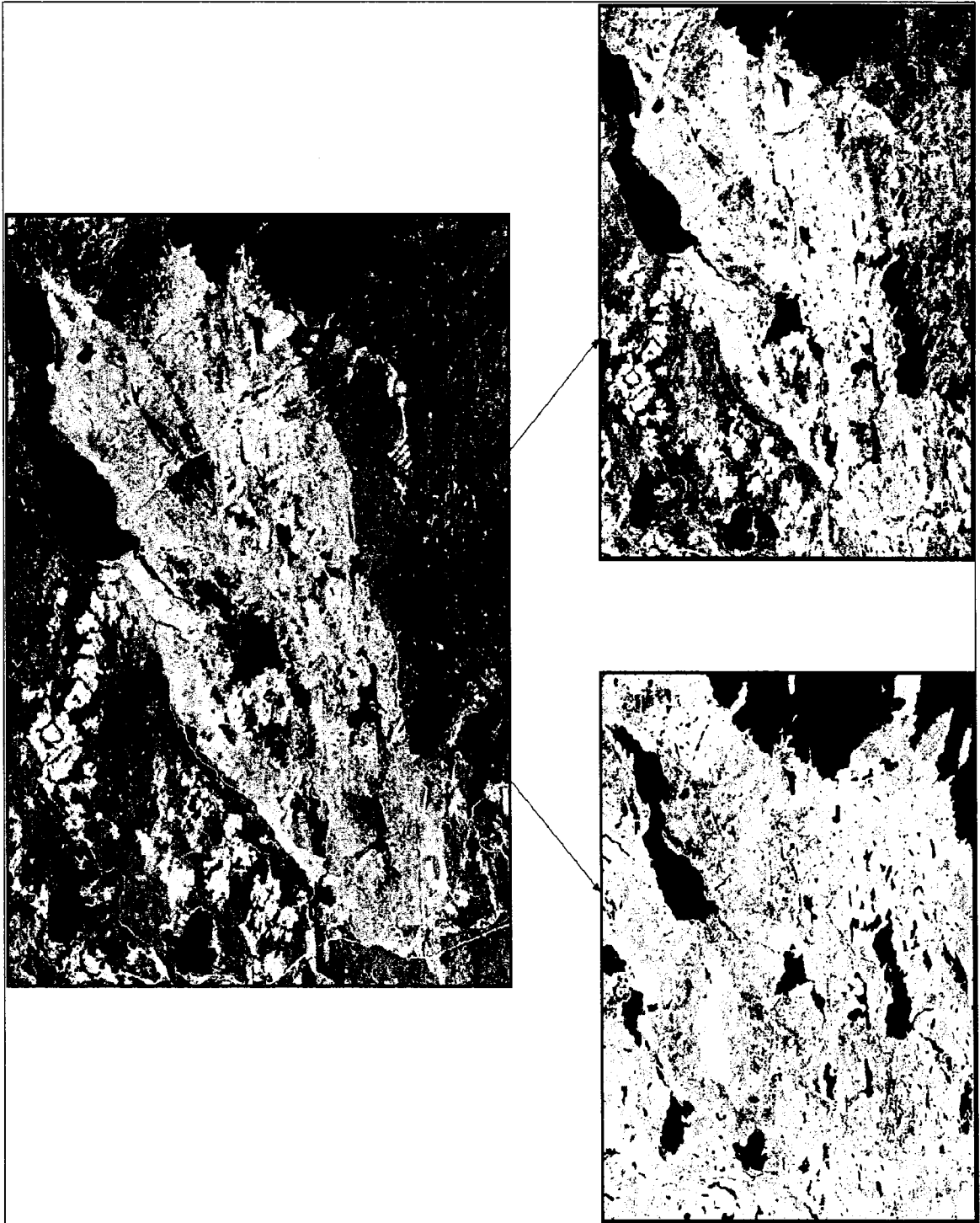
Figure 14: Left: Landsat 7 ETM+ imagery (near-infrared colour infrared). Top-Right: Tassled Cap Brightness index. Bottom-Right: Normalized Difference Vegetation Index (NDVI).

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Data Extraction

To extract the values for each modeled gradient, pertaining to each study site, all the spectral indices were integrated with the topographic indices by importing them into a GIS. Every one of the 480 field site locations was entered into the GIS. This created a point file in the GIS including a template of the plot pattern (Figure 3). Figure 15 illustrates how the plot pattern shown in Figure 3 was transposed onto the satellite data. The red dots on the right image represent the centre of a sampled plot.
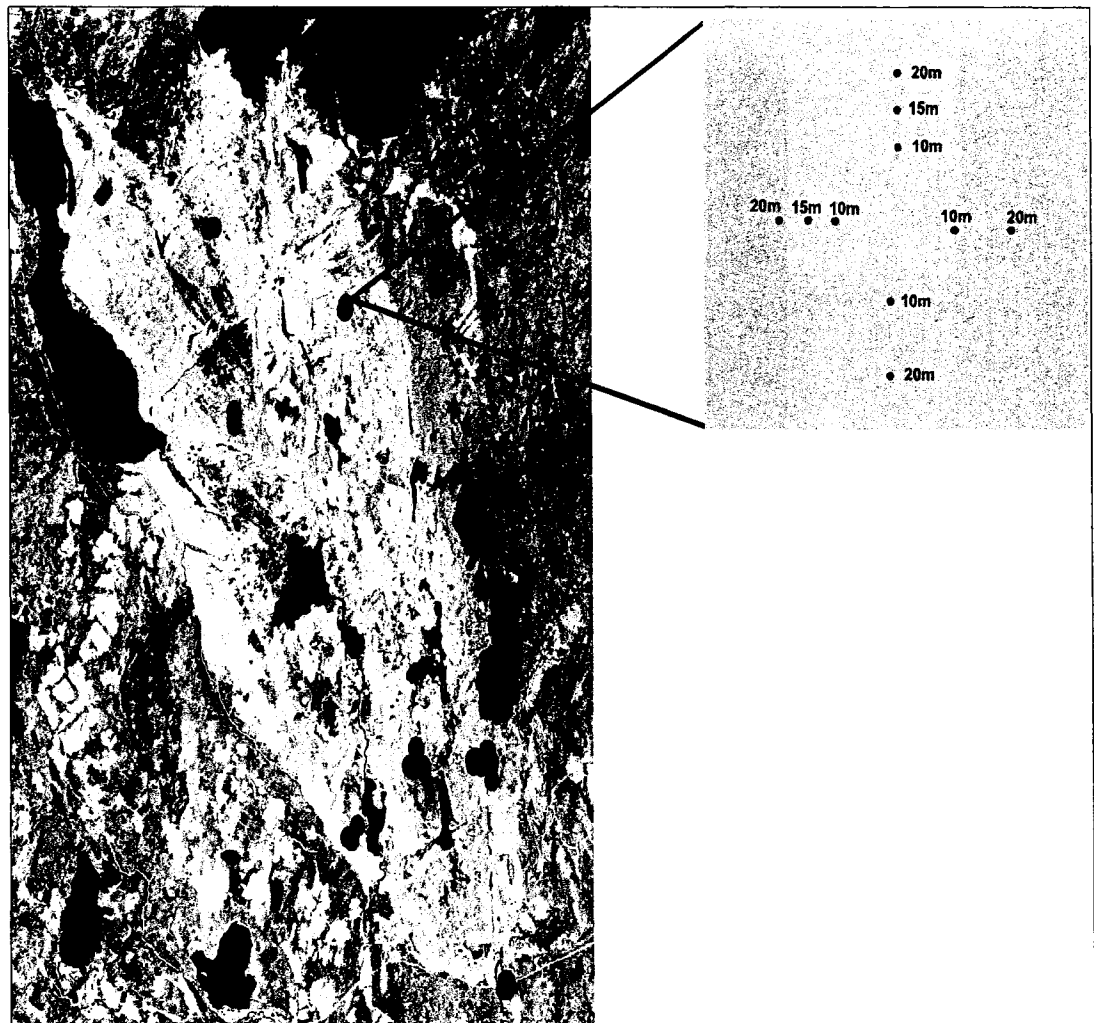
Figure 15: Plot pattern transposed on to a true colour satellite image. The values from each red point were used to create a database of index values.

The values of every plot were determined for each index by intersecting the 480

plots with the cell value for each of the spatial indices. The result was a file consisting of

all 480 plots with each index value associated with each plot as an attribute. This file was

converted to a spreadsheet for statistical analysis. The following table lists all created

spatial indices:

Table 5: List of Indices

Index Type	Indices
Topographic	Topographic Radiation, Solar Radiation, Topographic Wetness index, Heat Load
Satellite Image	Normalized Difference Vegetation Index (NDVI), Soil Adjusted Vegetation Index, Simple Vegetation Index, Infrared Index, Leaf Area Index, Fraction of Photosynthetic Radiation, Tasseled Cap – Wetness, Greenness, and Brightness
Soils	Surficial Materials, Drainage, Soil Texture

Although, spatial analysis techniques are becoming increasingly common, there

are still some significant limitations associated with scale when performing landscape

ecology research using a plot level sampling design. The issue of scale is fundamental to

all ecological research (Weins, 1989). GIS and remote sensing provide the field of

ecology the tools to study ecology at the landscape scale. However, such benefits do not

come without limitations. The most significant of these is the problem of extrapolation, a

concern in most spatial studies where the geospatial data is calibrated against ground-

based measurements at a few locations and used to infer the properties at other locations

(Rastetter, 1999). This study utilizes data in three different spatial scales; plot level ($1m^2$),

Spectral Data ($30\ m^2$), and Topographic Data derived from 1:20,000 OBMs. Although

combining spatial scales is not particularly uncommon (Pitt *et al.*, 1997; Schmidtlein and

Sassin, 2004), it is still important to acknowledge this as a possible source of error.

Statistical Analysis

My objective was to determine if spatial indices can be used to model environmental gradients that govern vascular plant regeneration after fire in a *Picea mariana* ecosystem. The preceding section highlighted the process used to develop the digital database of indices and extract the values of that data to the corresponding ground vegetation plot locations. Upon completion of the database table created in the GIS, the data was formatted and imported from Microsoft Excel into the PC-ORD software package for statistical analysis. The analysis primarily consisted of a Principal Components Analysis (PCA) and a Canonical Correspondence Analysis (CCA) ordination.

Data Reduction

To eliminate any indices that were highly correlated, a correlation coefficient matrix was used to assess correlations between indices and reduce correlated data. When highly correlated datasets are found, the index chosen for use in further analysis was based on its performance in the supporting literature. This was especially true for the vegetation indices, as these indices were all ratios derived from the visible and infrared wavelengths of the Landsat TM image. Therefore, the Normalized Difference Vegetation Index was chosen based on its performance in the supporting literature relative to the other indices. Other indices that were found to be redundant were also removed from further analysis. This includes the Heat Load index, the distance to water index, and the raw DEM. The Stand Age index was also removed as there was little evidence in the literature that stand age was an influencing factor to species regeneration. The remaining

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indices were grouped into a single database table ready to be used in the Canonical Correspondence Analysis.

One of the common problems when examining ecological data is the influence of rare species on the statistical tests. Rare species contribute a great deal of 'noise' to the ordination and only contribute marginally to the effective ecological significance (McCune & Grace, 2002; Work *et al.*, 2004). The conventional rule of removing those plant species that occupied less than 5 percent of the sample was followed. This meant that from a list of the 64 species originally sampled, 36 species were utilized in the MRPP and other analyses. The other 28 species were removed. Appendix II is a table of the species that were sampled in the field. Those species that were not considered rare (i.e. >5%) are shown by the highlighted values.

A principal components analysis was used to create pseudo variables (environmental gradients) that represent most of the information from the original 11 indices. It is therefore possible to reduce the number of variables from 11 to 6. It is important to note that principal components analysis assumes multivariate normality; however this is rarely possible with ecological data and for the purpose of this study this assumption is broken. However, principal components analysis is a convenient statistical method for data reduction and in this capacity it is will be used to establish which principal component axis best characterizes the environmental gradients found in real world environments.

Canonical Correspondence Analysis (CCA)

Canonical Correspondence Analysis (CCA) was used to determine whether species composition (matrix 1) responds to the principal components of the various spatial indices (matrix 2). The principal components were interpreted to represent pseudo environmental gradients to determine if the principal components correspond to the underlying environmental gradients influencing species composition. The data inputs include the total composition of vascular plants used in Chapter 1 and the principal components developed from the remote sensing and GIS indices. This data was imported into PC-ORD with the total composition data as the main matrix and the environmental indices as the second matrix. One of the key assumptions of CCA is that it is a direct gradient analysis and assumes all important environmental gradients have been measured in some capacity. This assumption was accounted for as best as possible. However, since remote sensing and GIS indices are not direct measures of individual gradients, but rather a detection of possible indirect responses to the gradient, it was not possible to ensure all aspects of every gradient were measured.

The optimization of the species and site scores was done using a compromise between the site scores as weighted mean species scores and the species scores as weighted mean sites scores (McCune & Grace, 2002). The Axis Scaling method used was the Centered with Unit Variance, the PC-ORD default. The four ordination diagrams used in this study utilize the linear combination (LC) scores in environmental space for each axis. Palmer (1993) indicated that for most applications in ecology, the linear combination (LC) score is the most suitable means of plotting an ordination. To test the results of the CCA, a Monte Carlo simulation was conducted to test the null hypothesis

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that no structure exists in the species matrix and therefore there is no linear relationship between the species and environmental variable matrices (McCune & Grace, 2002). The total number of randomizations used in the Monte Carlo simulation was the standard 1000.

One of the key outputs in the CCA analysis is the intraset correlations matrix. This matrix indicates which of the principal components was most influential in the structuring of the ordination (McCune & Grace, 2002). In this case, the intraset correlation matrix indicates which of the principal components was most correlated with each of the three axes examined in this study. The highest absolute value indicates a high correlation between the principal components and the axis. The biplot scores are used when graphing the environmental variable vectors in species space. They give the coordinates for the tips of the radiating lines. The values of these lines are interpreted in the same way as the intraset correlations: the higher the absolute value the longer the environmental variable vector and the stronger the relationship with that community. The direction of the environmental variable vector gives an indication of how exclusive the association is with the axes. For example, if the vector is parallel to axis 1 then there is a very strong association with axis 1 relative to the other axis being displayed. Conversely, if the vector is perpendicular to axis 1 then a very weak relationship is presumed. Using this method, it may be possible to determine which of the principal components, presumed to represent environmental gradients, have a close association with a particular axis. This will indicate which environmental gradient is most influential over the understorey species assemblages.

The final species scores matrix gives an indication as to which species was most closely correlated with each axis of the CCA. Once again, it was interpreted much the same as the intraset correlation matrix, or the biplot scores, where the highest absolute value indicates a high correlation between the species and the corresponding axis. Since the associations of the principal components with a particular axis may indicate an underlying environmental gradient, the species that are associated with this axis also respond to the underlying environmental gradient.

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Results

To help assess if spatially derived environmental indices might be used by others to model underlying environmental gradients, the following procedures were performed. A correlation analysis was conducted to identify correlated indices to remove redundancy. A Principal Components Analysis was conducted to reduce dataset and limit the impact of non-normal data. Finally, a Canonical Correspondence Analysis was conducted to test if the resulting principal components responded or were related to regenerating understorey species composition in a similar way as they would be expected to in real underlying environmental gradients.

Correlation Analysis

Twenty-three landscape level spatial indices were derived from GIS data and remotely sensed Landsat ETM+ images. The correlation matrix results for the spatial indices in Appendix VII shows that eleven of the indices were determined to be appropriate for further analysis, as indicated by the highlighted columns. These eleven indices were chosen based on their occurrence and performance in the literature. When two or more indices were highly correlated, the index most commonly used in ecological analysis was used. Several indices were omitted from the analysis to reduce their interdependence, as often occurs when two indices are derived from the same source using slightly different algorithms.

Of the indices that were derived from the Landsat ETM+ image, the various vegetation indices proved to be the most highly correlated with each other. This was likely caused by these indices all being derived from, or being ratios of, the visible and near-infrared portions of the electromagnetic spectrum. Only one vegetation-related index

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could be selected, so NDVI was chosen to represent vegetation abundance based on its long history as the standard vegetation index as observed in the published literature (Miura *et al.*, 2001; Trishchenko *et al.*, 2002). Although other vegetation indices might give better results, it was determined that the NDVI was to be used in this study for the simple reason that it is well proven.

Principal Components Analysis

To reduce the dataset and eliminate the impact of non-normal data on the Canonical Correspondence Analysis (CCA), a Principal Components Analysis (PCA) was conducted. Assuming the indices selected from the correlation analysis results are accurate representations of real world environmental conditions, it may be feasible to interpret the Principal Components as possible environmental gradients. The results from Table 6 are far from conclusive, but they do show a tendency of the groupings of the spatial indices along possible underlying environmental gradients. For example, Principal Component 1 (PC1) is supported by high negative correlations to, the Normalized Difference Vegetation Index (-0.3996), Leaf Area Index (-0.3832), Tasseled Cap Greenness (-0.4241) and FPAR (-0.3829). These four indices were developed to assess some facet of vegetation biomass (Jenson, 1996). Therefore it is hypothesized that PC1 is negatively correlated to a theoretical green biomass gradient, whereby the higher the PC score the lower the level of biomass. Similarly Principal Component 2 (PC2) is negatively correlated to Flow Accumulation (-0.3846) and the Topographic Wetness Index (-0.5437), and positively correlated to Solar Radiation Index (0.5300). This group of indices would indicate a negative correlation to a moisture gradient where the higher the PC score the drier the landscape. This is illustrated by TWI and Flow accumulation

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indicating moisture and the Solar Radiation Index indicating solar radiation, and

intuitively increased evaporation and thus less moisture. Similarly, Principal Component

3 (PC3) is thought to represent a soil properties gradient as highlighted by a negative

correlation to stand height (-0.6025) and a positive correlation to soil particle size

(0.4499). Principal Component 4 (PC4) is thought to represent an insolation gradient

illustrated to by the positive correlation to the Topographic Radiation Index (0.5507) and

a negative correlation to Stand Density (-0.5419). The first four PC axes were interpreted

and accounted for 74.7% of the variance in the model with 39.4% of the variance

attributed to PC1 alone (see Table 6). Principal Component 5 and 6 were not analyzed in

this analysis as they describe very little variance and are not included in the Canonical

Correspondence Analysis discussed below.

Table 6: Principal Component Variances and PC Scores for Environmental Indices.

Presumed Association	PC1 (Biomass)	PC2 (Moisture)	PC3 (Soil Properties)	PC4 (Insolation)	PC5 ?	PC6 ?
Eigenvalue	5.118	1.859	1.518	1.211	0.964	0.832
% of Variance	39.369	14.301	11.675	9.314	7.415	6.401
Cumulative Variance	39.369	53.670	65.345	74.659	82.073	88.474
Flow Accumulation	0.0691	**-0.3846**	0.0599	0.2272	0.5582	0.4229
Stand Height	-0.1333	0.2231	**-0.6025**	-0.1304	-0.0736	0.3734
Stand Density	0.0282	0.3595	-0.0022	**-0.5419**	0.3583	-0.4468
Topographic Radiation	0.0007	0.0969	-0.393	**0.5507**	0.4491	-0.3924
Solar Radiation Index	0.1705	**0.5300**	0.2121	0.1444	-0.1189	0.3541
Normalized Difference VI	**-0.3996**	-0.0665	0.0093	0.1743	-0.2651	-0.0666
Leaf Area Index	**-0.3832**	0.1799	0.2293	0.0042	0.2565	0.018
FPAR	**-0.3829**	0.1809	0.2275	0.0047	0.2601	0.0199
Topographic Wetness	-0.1774	**-0.5437**	-0.1307	-0.3531	-0.035	-0.1311
TC Wetness	-0.304	0.0803	-0.1699	0.2683	-0.2544	-0.2107
TC Greenness	**-0.4241**	-0.0195	0.0861	0.1248	-0.1494	-0.0508
TC Brightness	-0.3525	-0.0348	0.2718	-0.1135	0.155	0.1926
Soil Particle Size	0.2577	-0.0981	**0.4499**	0.2408	-0.1509	-0.3103

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Canonical Correspondence Analysis (CCA)

A Canonical Correspondence Analysis (CCA) was performed to test if the principal components, presumed to represent underlying environmental gradients, respond to understorey species composition. Results from the CCA indicated that 4 of the principal components were closely associated to 3 of the CCA ordination axes. Principal Components 5 and 6 had low eigenvalues (i.e., below 1) and were not assessed since they only explained 7.4% and 6.4% of the variance (Table 6).

Figure 16 illustrates that the species which are associated with axis 1 fall along PC2 and to a lesser extent PC3. As noted above, I am assuming that these principle components are linked to possible soil moisture (PC2) and soil properties (PC3) gradients. The results of the principal components analysis suggest that PC3 (soil properties) had high intraset correlations with axis 2 and 1 of the CCA (-0.694 and 0.591). The species associated with axis 2 falls along PC4, or what could be an insolation gradient. The results from Table 7 shows an intraset biplot score for PC4 of -0.712.

Table 7: Intraset Correlations and Biplot scores for modeled gradients used in CCA. Values in bold indicate variables highly correlated to Axis.

Principal Components	Intraset Correlations			Biplot Scores		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
PC1	-0.061	-0.375	**0.769**	-0.041	-0.195	**0.377**
PC2	**-0.578**	-0.182	-0.448	**-0.389**	-0.095	**-0.220**
PC3	**0.591**	**-0.649**	-0.304	**0.398**	**-0.338**	-0.149
PC4	0.375	**0.712**	-0.104	0.253	**0.370**	-0.051
PC5	-0.374	-0.041	0.174	-0.252	-0.022	0.085
PC6	-0.157	-0.197	-0.141	-0.106	-0.102	-0.069

Figure 17 suggests that the species which are associated with axis 3 of the CCA fall along PC1 and to a lesser extent PC2. As indicated above, these principal components could be a response to an underlying environmental gradient represented by a

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combination of a biomass (PC1) and moisture (PC2). These two variables have biplot scores of 0.769 and -0.448 respectively. It is also important to highlight that both PC1 and PC2 are negative gradients, whereby the higher the PC score the lower the gradient. For example, Table 7 illustrates a PC2 (moisture) score of -0.578 along CCA axis 1 this would indicate a low moisture level in the positive region of CCA axis 1.

To illustrate the possible relationship between species assemblages in various pre-fire spruce composition classes and the underlying environmental gradients, ellipses were manually drawn on the biplot to show the general dispersion patterns of pre-fire spruce composition (Figure 16 and 17). Results suggested that some pattern may exist between regions of high to low pre-fire spruce composition with respect to axis 1 (Figure 16). It is observed that high pre-fire spruce composition (90% and 100%) is negatively correlated with PC2 (moisture) and positively correlated to PC3 (soil properties). Likewise, low pre-fire spruce composition class (50% and 60%) has a negative correlation to PC4 (insolation).

Figure 17 illustrates the relationship between PC1, presumed to be a response to a biomass gradient as noted above, and pre-fire spruce composition. There appears to be a strong positive correlation between high pre-fire spruce composition and PC1 (biomass). The strong correlation observed in Figure 17 is supported by the relatively high intraset correlation of 0.769 (Table 7). It can also be seen in Figures 16 and 17 that due to the high variability in species composition of the intermediate (70% and 80%) pre-fire spruce composition classes, no clear group can be identified.

Along axis 1, PC2 (moisture) and PC3 (soil properties) did a reasonable job at separating the high intensity classes from the low intensity classes (Figures 18 and 19).

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Axis 2 which is highly correlated to PC4, does not show any capacity to separate the species associated with the high intensity classes with those found in low intensity classes (Figure 18). Along axis 3, results suggest that PC1 (Biomass) does appear to have a slight capacity to separate low intensity species from high intensity species (Figure 19).

A Monte Carlo simulation was run to test the null hypothesis that there is no relationship between the spatial indices and species assemblage matrices (Table 8). Results indicate that a linear relationship exists between all three CCA axes and species assemblages ($p < 0.05$). The percent of the variance explained by each axis indicates 'goodness of fit' of the proposed environmental gradients to the species assemblages. The results from the CCA indicate that 11.9% of the variance can be explained by axis 1, 4.3% of the variance can be explained by axis 2, and 3.3% explained by axis 3. With a cumulative percent variance of 19.5% for the first three axes, the CCA does a poor job at summarizing the species variability associated with the PC variables. This indicates that over 80% of the natural variability is not captured by the PC variables. This would suggest the key assumption of the CCA has been broken by not including all of the underlying gradients in the analysis.

Table 8: Monte Carlo Tests for Eigenvalues and Species-Environmental Correlations.

Axis	Real Data Eigenvalue	Mean	Monte Carlo Test, 999 runs Minimum	Maximum	p	Cumulative % Variance
1	0.206	0.077	0.042	0.146	0.001	11.9
2	0.073	0.053	0.031	0.094	0.026	16.2
3	0.058	0.040	0.021	0.060	0.006	19.5
	Spp-Envt	Mean	Minimum	Maximum	p	
1	0.821	0.708	0.541	0.858	0.019	
2	0.726	0.678	0.511	0.820	0.210	
3	0.531	0.648	0.479	0.803	0.980	
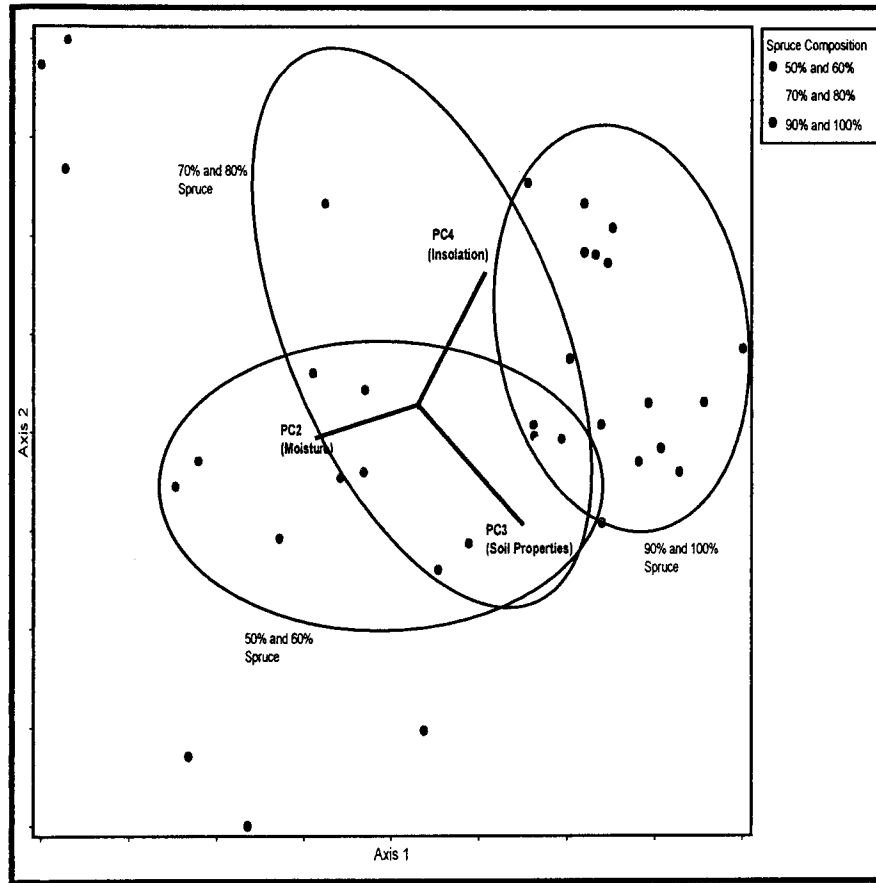
Figure 16: CCA biplot of Axis 1 and Axis 2. The graph indicates the three pre-fire spruce composition levels (50% and 60%, 70% and 80%, and 90% and 100%) and associated vectors. Ellipses are manually drawn to represent the approximate distribution of the sample plots associated with varying levels of Spruce Composition.
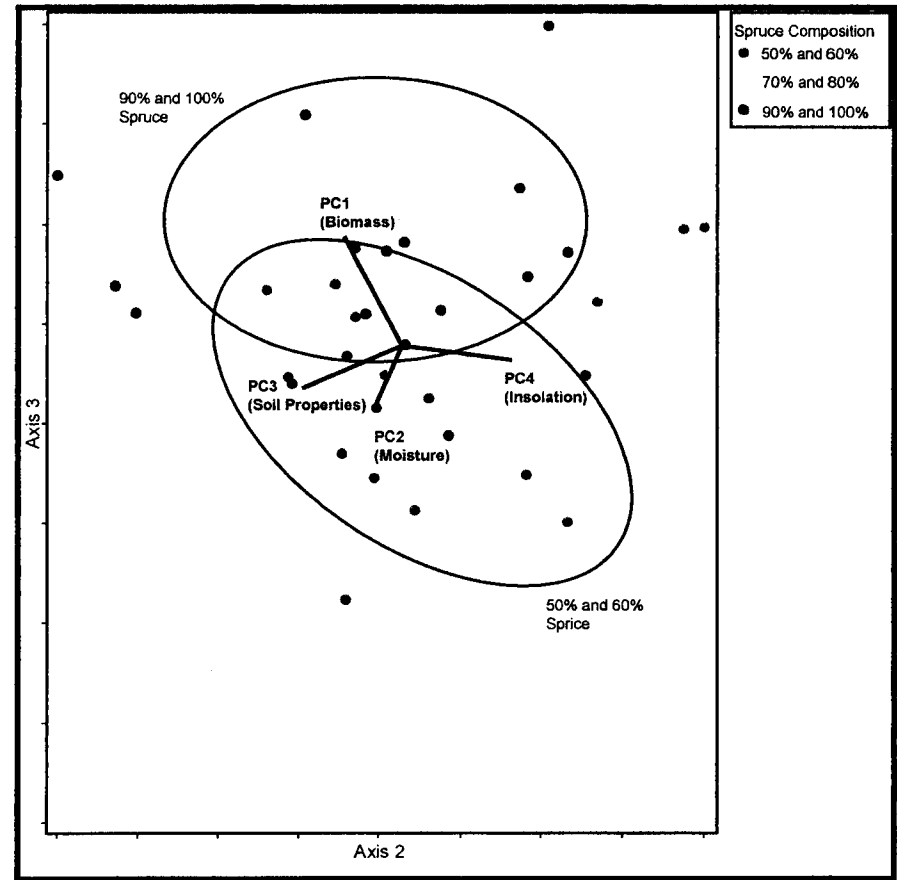
Figure 17: CCA biplot of Axis 2 and Axis 3. The graph indicates the three pre-fire spruce composition levels (50% and 60%, 70% and 80%, and 90% and 100%) and associated vectors. Ellipses are manually drawn to represent the approximate distribution of the sample plots associated with varying levels of Spruce Composition.

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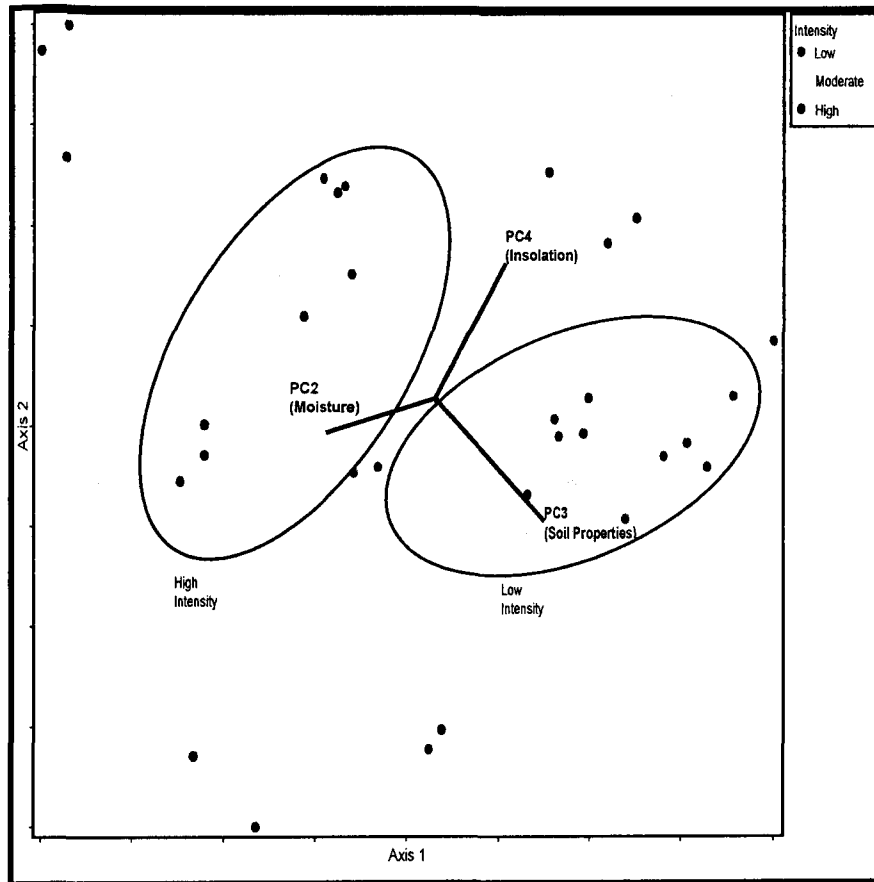
Figure 18: CCA biplot of Axis 1 and Axis 2. The graph indicates the three burn intensity levels (Low, Moderate, and Severe) and associated vectors. Ellipses are manually drawn to represent the approximate distribution of the sample plots associated with varying levels of burn intensity.
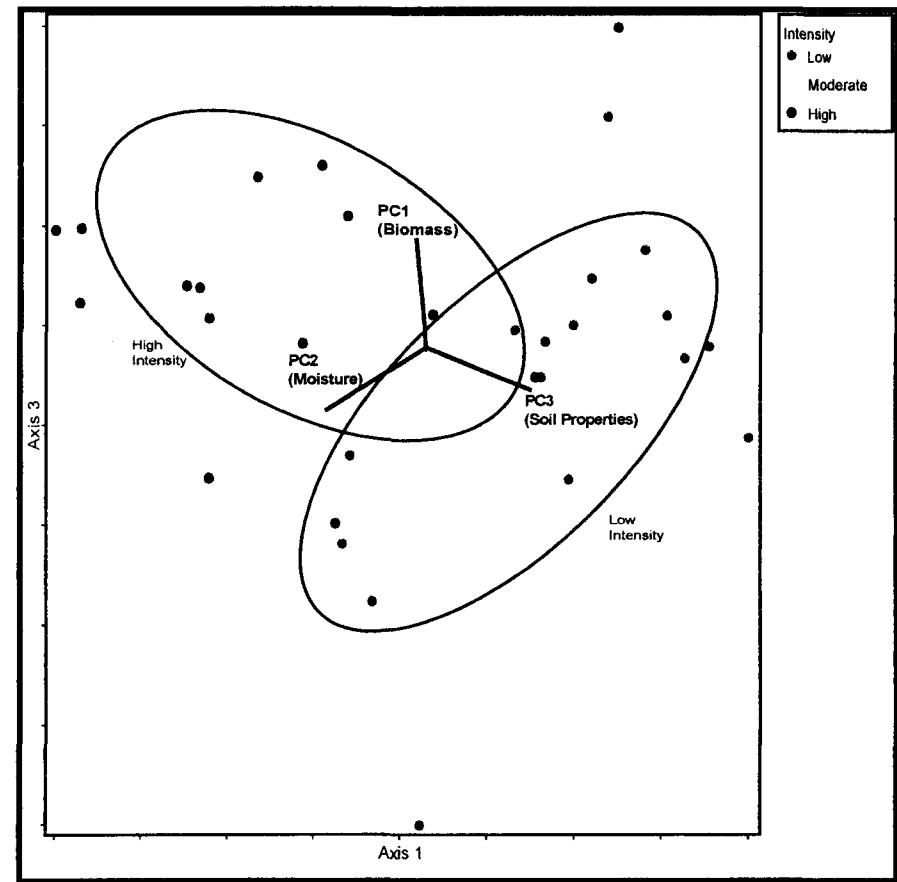
Figure 19: CCA biplot of Axis 1 and Axis 3. The graph indicates the three burn intensity levels (Low, Moderate, and Severe) and associated vectors. Ellipses are manually drawn to represent the approximate distribution of the sample plots associated with varying levels of burn intensity.

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Assuming the indices used in this study do accurately model the environmental gradient for which they were developed, it can be concluded that species appear to be correlated to many underlying environmental conditions. For example, species associated with the three pre-fire spruce composition classes are inversely correlated with PC2, thought to represent an underlying moisture gradient. PC3, thought to represent an underlying soil properties gradient, appeared to be positively correlated with species assemblages in different pre-fire spruce composition classes. Likewise, PC1, thought to represent a biomass gradient, appears to separate the three pre-fire spruce composition classes quite well. Species assemblages associated with high (90% and 100%) pre-fire spruce composition tended to be associated with PC4 along axis 2, thought to represent an insolation gradient.

The species compositions associated with the three burn intensity classes are correlated with PC3, thought to indicate the presence of a soil properties gradient (Figure 18). PC1, thought to represent a biomass gradient, also appears to separate low burn intensity species assemblages from high burn intensity species along axis 1 (Figure 19).

Species Response

In this study, three key environmental gradients are thought to correspond to the three ordination axes: soil structure, insolation, and moisture. Each environmental factor has a number of species that were highly correlated to the high and low end of the gradient. Table 9 indicates the final species scores for each of the three axes of the canonical correspondence analysis. The values in bold represent those species are highly

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correlated to that axis. If the bold value is positive then there is a positive correlation, inversely if the value is negative there is an inverse association.

Table 9: CCA Scores for Select Understory Species.

Species	Axis 1	Axis 2	Axis 3
Picea mariana	-0.78658	**1.040298**	-0.97782
Betula papyrifera	-0.12352	-0.80602	0.346845
Populus tremuloides	0.665845	-0.57804	-0.86234
Amelanchier ssp.	0.60918	0.252074	-0.50125
Sorbus americana	-0.42466	0.700591	**-1.08635**
Vaccinium myrtilloides	0.052105	-0.29081	0.69533
Vaccinium angustifolium	0.859519	0.253105	0.307185
Rubus ssp.	-0.7892	-0.33406	-0.28282
Rosa acicularis	0.146539	**-1.17518**	-0.21049
Prunus pensylvanica	-0.52955	0.108533	0.190434
Gaultheria hispidula	-0.50991	0.980269	**-1.71737**
Ledum groenlandicum	0.545026	-0.37816	0.017321
Alnus viridis ssp.	-0.32177	-0.08856	-0.47141
Salix ssp	**1.473629**	0.024724	0.043601
Cornus canadensis	-0.81548	-0.14952	-0.14735
Epilobium angustifolium	**-1.19221**	-0.17478	0.819449
Polygonum cilinode	**-1.52659**	**1.075669**	0.439301
Coptis trifolia	-0.39663	**-1.72585**	0.015384
Maianthemum canadense	-0.41746	-0.85052	-0.54608
Calamagrostis canadensis	**-1.49485**	0.766249	0.385585
Deschampsia flexuosa	-0.47712	0.532649	-0.1333
Poaceae fam.	0.19321	**-1.38827**	0.612173
Cyperaceae fam	0.047765	-0.91773	-0.49684
Cladonia chlorophaea	-0.13911	-0.19204	0.396638
Pleurozium schreberi	**-1.05986**	0.720502	0.051908
Tortella ruralis	-0.30531	0.951827	**1.258021**
Polytrichum ssp.	-0.60846	-0.81471	0.324212
Sphagnum ssp.	0.173167	**1.079548**	-0.3552
Linnaea borealis	-0.85571	**-1.67707**	-0.26439
Clintonia borealis	-0.35334	0.642725	-0.28569
Equisetum sylcaticum	-0.50609	-0.54929	0.118317
Lycopodium dendroideum	-0.92852	0.835535	0.492609
Pteridium aquilinum	**-1.5922**	**1.154232**	0.567939
Viola ssp	-0.74207	-0.50809	-0.00492
Aster macrophyllus	-0.01239	0.321445	**-1.1181**

Discussion

This research examines if vascular plant community structure responds to principal components which could represent corresponding underlying environmental gradients. Although the results should be considered highly preliminary due to the inability to assess the accuracy of many of the spatial indices, the CCA results do suggest that understorey plant community structure in the Nipigon-10 burn is correlated with the representative principal components which may be linked to real underlying environmental gradients. These results are similar to those reported by Chipman & Johnson (2002), Frelich *et al.* (2003) and Iverson *et al,* (2004). All of these studies identified the same or very similar influential gradients in several forested environments including the boreal forest. The results from this study suggest that understorey vegetation regeneration in the Nipigon-10 burn may be more a product of the main underlying environmental gradients than the direct influence of burn or disturbance intensity or pre-fire tree composition.

The first four axes in the PCA were interpreted and had a cumulative explanation of variance of 74.7%. This indicates that roughly three quarters of the variance in species composition was accounted for by the first four principal components with the first principal component accounting for a substantial 39.4% of the variance in the model. As noted in above, results suggest that PC1 may represent an underlying green biomass gradient. PC1 has a high inverse association to the NDVI, LAI, and the Tasseled Cap Greeness Index. In this case, an inverse relationship indicates the higher the PC score the lower the level of green biomass. These indices were all developed to measure different

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aspects of green-biomass (Rouse *et al.,* 1974; Kauth & Thomas, 1976; Ahern *et al.,* 1977; Crist & Cicone, 1984) and could be well-adapted to form a biomass gradient.

PC2 is assumed to represent a moisture gradient and is highlighted by a negative correlation to common indices developed to model variation in soil or vegetation moisture. Similar to PC1, this negative correlation suggest that the higher the PC2 score the lower the moisture level. This gradient was heavily weighted to the topographic wetness index and the flow accumulation index (Spanner et al, 1990; Treitz & Howarth, 1996; Freer *et al.,* 1997; Chen & Cihlar, 2002; Sorensen *et al.,* 2006). The solar radiation index is also negatively correlated to the moisture gradient, which indicates that the areas that have lower solar radiation due to topography are associated with regions of higher moisture.

PC3 is thought to represent some form of soils gradient and is identified by the negative correlation to stand height and a positive correlation to soil partial size. The attributes related to the soil, such as soil partial size, are inherently correlated to nutrient content within the soil. Stand height are products of the overstorey species composition and age. Species regenerating in high burn intensity classes appear to be negatively correlated to PC3, presumed to represent a soil property gradient. This result might suggest that newly regenerating species following a severe disturbance are strongly influenced by an underlying soil gradient. A similar result was reported by Foster (1985) who indicated that following a severe disturbance, ground cover undergoes compositional change which represents contrasting substrate requirements of regenerating species. Frelich *et al.* (2003) also suggest that fine-scale environmental variation in soil nitrogen is a large factor in species composition and distribution. *Picea mariana*, generally a

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shorter species which tends to favour poorly drained regions, often inhabits areas that have surficial material consisting of organic substrate and bedrock. These materials are not conducive to growing tall trees due to the lack of nutrients and a lack of a good foothold for the roots of tall trees (i.e. leads to blowdown). This reasoning gives a strong indication that, as stated by Chipman & Johnson (2002), the primary environmental gradient for regeneration is commonly associated with soil properties. However, since the direct measurements of forest soils are inherently impossible using the techniques employed in this study, the specific soil properties that contribute to species composition could not be measured. Therefore, any suggestion that PC3 represents an actual soil gradient is highly speculative.

PC4 is comprised primarily of a very strong negative correlation to the Topographic Radiation Index (TRASP). The positive region of axis 2 is characterized by hotter and drier topography. Corresponding studies by Chipman & Johnson (2002), Urban *et al.* (2000), and Frelich *et al.* (2003) have found that insolation is a common and important environmental gradient in plant regeneration.

The results also suggest that several of the spatial indices appear to be inter-correlated by some significant margin with one or more components. This suggests that none of these environmental gradients are completely discrete from each other. Urban *et al.* (2000) approached this dilemma by suggesting that the interpretation of gradients using an ordination procedure is "confounded by a fundamental lack of independence among environmental factors". They note that the primary physical gradients are inherently correlated with each other. The lack of independent variables that Urban *et al.* (2000) spoke to can be clearly seen in this model. It is likely for this reason that, although

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the results from the CCA were significant, a great deal of the total variance was left unexplained by these three ordination axes.

The relationships between the first four principal components, presumed to be related to underlying environmental gradients, and the pre-fire spruce composition and burn intensity were examined using a CCA. It was hypothesized that species regeneration is more a product of underlying environmental gradients rather than the direct influence of burn intensity or pre-fire spruce composition, as shown in Chapter 1. The presumption that the correlation in species composition, observed in Chapter 1, is more a product of the environmental gradients that govern both burn intensity and pre-fire spruce composition levels rather than a direct result from either of these.

PC1, presumed to have an inverse relationship to a biomass gradient (Figure 16, 17 and 19), has some association with the regenerating understorey species composition in the three spruce composition classes as well as the three pre-fire spruce composition classes. Results suggest that the 90% and 100% spruce composition class is negatively correlated with green biomass. This is indicated by a high positive association to axis 3 of the CCA biplot which in turn is positively correlated to PC1 indicating an association with low biomass. Likewise, regions of high fire intensity appear to have a positive correlation to PC1 along axis 3. This would indicate that the regenerating understorey species communities in severely burned 90% and 100% pre-fire spruce stands had the lowest green biomass as indicated by PC1 which, as indicated, is inversely related to biomass.

As noted above, PC2 is presumed to represent an underlying moisture gradient defined in this model by the Topographic Wetness Index (TWI), Solar Radiation Index

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(TRASP), and Flow Accumulation. The presumed negative correlation that this moisture gradient has with biomass was reported by Iverson *et al.* (2004) who indicated that a combination of the TWI and hillshade model had the highest correlation with measured soil moisture variables. This suggests that the TWI can be a strong indicator of a moisture gradient. Species regenerating in regions of 90% and 100% pre-fire spruce tend to be associated with a wetter environment with lower biomass than those species regenerating in low spruce compositions. This is indicated by PC2 having a negative correlation to axis 1 of the CCA biplot, and by PC1 having a positive correlation to axis 3 of the CCA biplot.

PC3, assumed to represent a soil properties gradient (Figure 16, 17, 18, and 19), appears to be correlated with understorey species regeneration in the three pre-fire spruce composition classes (Figures 16 and 17). This relationship with soil conditions is likely a product of a feedback loop in which soil structure influences plant community structure and, inversely, the plant community can influence the soil structure. The influence of soil structure on plant communities is well known. For example, *Picea mariana* tends to favour soil types with high acidity (Lauriault, 1989). The mechanisms by which tree species can influence soil structure, specifically soil acidity, include differences in the uptake of cations and anions, nitrogen fixation and ensuing nitrification, and the production of litter high in organic acid content (Finzi *et al.*, 1998).

It was observed that PC3 also appears to be correlated with understorey species regeneration in the three burn intensity classes (Figure 18 and 19). Species communities regenerating in severely burned regions tend be negatively correlated with the soil properties gradient (PC3). The combination of high stand height and density creates an

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ideal environment for high intensity fires to take place which creates an opportunity for fire resistant regenerating species. This produces a unique species composition in the severe classes compared to the low and moderate burn intensity classes. As observed in Chapter 1, species regenerating in the low or moderate intensity classes are primarily species that endured the impact of fire and are largely artefacts of the species community that existed before the disturbance.

PC4, assumed to represent an underlying insolation gradient, was able to separate the species regenerating in the 50% and 60% pre-fire spruce composition classes from the remaining pre-fire spruce composition classes. The Topographic Radiation Index had a strong positive correlation to PC4 (0.5507) and Stand Density had a strong negative correlation to PC4 (-0.5419). The 50% and 60% pre-fire spruce composition class is negatively correlated to the insolation gradient indicating that shade tolerant understorey species tend to be associated with the more mixed forests of the 50% and 60% pre-fire spruce composition classes, likely to have a greater abundance of shady deciduous overstorey species.

Using the concepts established by Curtis (1959), the highest species densities occur in regions where optimum environmental conditions exist. Specialist or indicator species, which have a narrow tolerance to environmental changes, are often restricted to narrow distributions on an environmental gradient and therefore have a defined niche (MacDonald & Thompson, 2003). The results from the CCA identified individual species that were associated with the extremes along many of the proposed environmental gradients (Table 9). An association between an individual species responding as predicted to an indirect measure of an environmental gradient supports my hypothesis that pseudo

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environmental gradients can adequately represent real underlying environmental gradients. However, due to the inability to determine how well the environmental indices represent real world environmental conditions, the ability to accurately examine species response to any pseudo environmental gradients should be considered highly preliminary.

The two species that had strong negative correlation to PC1 (biomass), as indicated by high negative species scores along axis 3, were *Sorbus Americana* (American mountain ash), and *Aster macrophyllus* (large leafed aster) (Table 9). This suggests that these two species are associated with sites that have appropriately higher biomass. The USDA (2005) Plant Characteristic Table confirms that *Sorbus Americana* and *Aster macrophyllus* are shade tolerant species and can therefore survive in more densely vegetated communities which have inherently higher biomass.

Two species that have a strong positive correlation to PC2 (moisture), as indicated by positive species scores along axis 1, were *Sphagnum* spp. (sphagnum moss) and *Picea mariana* (black spruce) (Table 9). A positive correlation along axis 1 of the CCA biplot corresponds to a negative correlation with PC2, which in turn is inversely correlated to moisture. The USDA (2005) plant characteristic tables confirmed that both species are well-adapted to high moisture sites with *Picea mariana* stands often found in lowland environments with wet soil.

The species that appear to have the strongest association to PC3 (soil properties), as indicated by high negative species scores along axis 1 and high positive scores along axis 2, were *Pteridium aquilinum* (bracken fern), *Polygonum cilinode* (bindweed), and *Calamagrostis canadensis* (blue joint grass) (Table 9). The USDA plant characteristics categories also indicate that these species are largely dependent upon soil. (USDA, 2005).

These categories suggest *Polygonum cilinode* is well adapted to fine and medium textured soils with little organic material. This species is shade intolerant and is commonly associated with the severe disturbances classes (USDA, 2005).

The species that appear to have a strong association with PC4 (insolation) include *Rosa acicularis* (prickly wild rose), *Coptis trifolia* (goldthread), and *Poaceae* spp. (grass species) (Table 9). These species have a strong negative association with CCA axis 2 and *Sphagnum* spp. (sphagnum moss) indicated by a positive association with CCA axis 2. *Rosa acicularis* and *Poaceae* spp. are both shade intolerant species and *Sphagnum* spp. is a moss that is light intolerant (USDA, 2005). These results indicate that the species assemblages are responding to the expected pseudo insolation gradient, as they do naturally.

These results suggest that individual species might be associated with the modeled environmental gradients, in a manner similar to direct measures of actual environmental gradients found in the literature. For example, *Polytrichum* spp., *Sorbus Americana*, *Poaceae* spp., and *Polygonum cilinode* showed similar associations with PCA derived pseudo gradients as they did with the preferred environmental conditions outlined in the USDA (2005) plant characteristics tables. However, as no assessment was done to compare the principal components derived gradients with real world environmental gradients, the results from this study should be considered theoretical at best. Assuming the principal components do represent underlying environmental gradients these results support the research hypothesis that understorey vegetation regeneration is associated with the environmental gradients created by, or inherently present in, burn intensity and/or pre-fire spruce composition classes. This is because the

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pre-fire forest stand composition would be subject to similar environmental gradients to which the regenerating species respond. It is not the stand composition but rather the underlying environmental gradient that determines the composition of both the pre-fire stand composition and the species regeneration composition.

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Conclusions

The speculative results from this study suggest that understorey species of the boreal mixedwood forest respond to underlying environmental gradients to a greater extent than to the direct influence of pre-fire spruce composition or burn intensity. This conclusion is consistent with the findings of Curtis (1959) and Whittaker (1956) who proposed that floristic composition changes gradually in response to these same important environmental gradients. Four environmental gradients interpreted from a PCA were assessed in this study. These gradients included a biomass gradient (represented by PC1), a moisture gradient (represented by PC2), soil properties (represented by PC3), insolation (represented by PC4). The ability for these gradients to represent real world environmental gradients is entirely dependent upon the accuracy of the environmental indices used in this study to represent the desired environmental conditions. However, due to large study area and the inability to assess the true accuracy of these environmental indices, the applicability of the environmental gradients derived from the PCA is suspect. As frequently indicated, the results of this study are highly preliminary due to the inability to assess how well the spatial indices represent actual underlying environmental gradients. Despite the inherent deficiencies, this study highlights a unique framework on which future fire ecology studies can be based. Much of the current research in the field of vegetation ecology has been at the community scale. This is due to the limitations of sampling techniques to adequately interpolate vegetation gradients over a large landscape. With the development of information technologies like GIS and remote sensing, scientists now have the ability to develop methods of studying spatial trends in vegetation dynamics with the understanding of limitations due to scale. This thesis is an

example of how such technologies can be implemented in a traditional ecological study to give insight into the relationship between understorey vegetation and environmental attributes at a landscape scale. The results from this research can be summarized by the following conclusions.

The key conclusion from the first study (Chapter 1) is that both burn intensity and pre-fire spruce composition are associated with some distinct groups of regenerating understorey species. Contrary to the intermediate disturbance hypothesis (Connell, 1978), the results suggest that the highest diversity is found in regions of high intensity fire. Biodiversity was highest in regions of low pre-fire spruce composition and lowest in regions of high spruce composition which was expected. Specific indicator species can be used to identify unique groups of regenerating species in the three burn intensity and pre-fire spruce composition classes.

The key conclusion from the second study (Chapter 2) is that spatial analysis procedures have the potential to be used to model environmental gradients and examine related species assemblages, although verification of the spatial datasets is a daunting task. The three most significant environmental gradients potentially influencing regeneration in this study were interpreted as soil properties, insolation, and a biomass/moisture gradient. Species in the fire intensity classes showed a strong association with CCA axis 1, presumed to represent a soil properties gradient. Likewise, species in the three pre-fire spruce composition classes showed the strongest association with axis 3, presumed to represent a combination of biomass/moisture. However, species were also associated with both axis 1 (soil properties), and axis 2 (insolation). Results from the CCA species biplot scores indicated that the relationship between specific

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species and the pseudo environmental gradients showed the same relationship as with reported actual underlying environmental gradients.

Recommendations for Further Research

The primary revision required to improve this study would be to ground-truth or perform accuracy assessments of the environmental indices used in this study. These indices should be compared to real world measures of environmental conditions. For example the results from the Topographic Wetness Index should be compared to measured soil moisture through out the study site measured with a soil moisture probe. This would enable the selection of only the most applicable indices to represent the desired gradients rather than use a statistical process like PCA to extract an environmental gradient from a number of suspect indices. The difficulty of performing this task for a large wildfire such as the one under study here cannot be underestimated.

The application of GIS and remote sensing in forest ecosystem research and management is still in its infancy. Until recently, the vast majority of research that utilized GIS and remote sensing did not incorporate basic ecological methods as the primary research principal. More research is needed on the implementation of ecological modeling in resource management. This study is intended to provide an analytical process that can be followed and be a preliminary step toward the ultimate goal of producing a species regeneration prediction model. One possibility is to use the results of this study to predict regeneration in the Nipigon-12 fire, near Beardmore, Ontario using GIS and remote sensing. This fire burned on the same date as the Nipigon-10 fire and would make an ideal candidate for comparison.

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The potential steps involved to complete a comprehensive ecologically-based regeneration prediction model include developing a structural equation model to test how well the remotely sensed modeled gradients explain the hypothesized underlying environmental gradients. This structural equation model is a mathematical analysis of the pathways in the flowchart in Figure 10. A vegetation prediction model would then be created for the Nipigon-12 fire using a neural network classification scheme. This is similar to a study by Valadan Zouj (2003) who estimated a variety of forest parameters through fuzzy classification, which is conceptually similar to neural network classification. Improvements upon the basic methods outlined in this thesis will provide a means of conducting predictive vegetation mapping based on environmental gradients.

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APPENDICES

Appendix I

Total Composition Data Sheet – 2004

Site # _____   Date_____   Time_____

UTM (NAD 83)_____

Polygon filename_____

Digital Camera File Numbers

Field Plot Data

10m North	20m North	10m East	20m East	10m South	20m South	10m West	20m West	15m _____	15m _____

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Microsite Factors

	15m North	15m East	15m South	15m West
Densiometer North				
Densiometer East				
Densiometer South				
Densiometer West				
Soil Moisture/PH				
Depth of Organic				

Basal Area for Pre-fire Overstory species (15m Radius)

SPECIES	DBH	SPECIES	DBH	SPECIES	DBH

Notes:_____

_____

_____

_____

_____

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Appendix II

List of species observed in the study area.

Scientific Name	Common Name	Species Code
Abies balsamea	Balsam Fir	B Fir
Acer spicatum	Mountain Maple	MM
Achillea millefolium	Yarrow	Yarrow
Alnus viridis ssp.	Green Alder	G Alder
Amelanchier ssp.	Serviceberry	S.Berry
Anaphalis margaritacea	Pearly Everlasting	P. Ever
Apocynum androsaemifolium	Spreading Dogbane	S.DogBane
Aquilegia canadensis	Wild Columbine	Columbine
Aralia hispida	Bristly Sarsaparilla	Br. Sarsap
Aralia nudicaulis	Wild Sarsaparilla	W. Sarsap
Aster macrophyllus	Large Leafed Aster	LLA
Aster ssp.	Aster (unknown)	Aster ssp
Athyrium filix-femina ssp.	Lady Fern	Lfern
Betula papyrifera	White Birch	BirchW
Calamagrostis canadensis	Blue Joint Grass	BJG
Campanula rotundifolia	Northern Bluebell	N.BlueBell
Cirsium arvense	Canada Thistle	C. Thistle
Cladina ssp.	Reindeer Lichen	RD lichen
Cladonia chlorophaea	Fire Moss	FM
Clintonia borealis	Bluebead Lily	BBL
Coptis trifolia	Goldthread	Goldthread
Cornus canadensis	Bunchberry	BB
Cornus stolonifera	Red Osier Dogwood	Red ODW
Corylus cornuta	Beaked Hazel	B.Hazel
Cyperaceae fam.	Sedge (Unknown)	sedge
Deschampsia flexuosa	Common Hair Grass	CH Grass
Epilobium angustifolium	Fireweed	FW
Epilobium glandulosum	Purple Leaved Willowherb	Purple Leaved willowherb
Equisetum pratense	Meadow Horsetail	MHT
Equisetum sylcaticum	Woodland Horsetail	W HT
Fragaria virginiana	Common Strawberry	Strawberry
Fraxinus nigra	Black Ash	Bl Ash
Galium asprellum	Rough Bedstraw	BedStraw
Gaultheria hispidula	Creeping Snowberry	Snowberry
Hieracium ssp.	Hawkweed	Hawk W
Kalmia polifolia	Bog Laurel	Bog L.

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Appendix II - Continued

Scientific Name	Common Name	Species Code
Lactuca	Wild Lettuce	Lettuce
Ledum groenlandicum	Labrador Tea	LT
Lichen ssp.	Lichen (unknown)	lichen ssp
Linnaea borealis	Twin Flower	Twin Fl
Lonicera dioica var.	Twinning Honeysuckle	Twin. Honey
Lycopodium dendroideum	Ground Pine	G PINE
Maianthemum canadense	Bush Honeysuckle	Mi Can
Marchantiaceae	Green-tongue Liverwort	GTLW
Mentha arvensis ssp.	Wild Mint	Mint
Osmunda claytoniana	Interrupted Fern	Int. Fern
Osmundaceae Fam	Fern (unknown)	Fern ssp
Oxycoccus microcarpus	Smallbog Cranberry	S.Bog Cran
Parmelia sulcata.	Waxpaper Lichen	WP lichan
Picea mariana	Black Spruce	BS
Pinus banksiana	Jack Pine	JP
Plagiomnium ellepticum	March Magnificent Moss	MM MOSS
Pleurozium schreberi	Schriber's Moss	Shribers
Poaceae fam.	Unknown Grass	Grass spp
Polygonum cilinode	Bindweed	BindWeed
Polypodium ssp.	Rock Polypody	Rk Poly
Polytrichum ssp.	Haircaped Moss	HC MOSS
Populus balsamifera	Balsam Poplar	B. Poplar
Populus tremuloides	Trembling Aspen	POT
Prunus pensylvanica	Pin Cherry	PC
Pteridium aquilinum	Bracken Fern	Br FERN
Ptilium crista-castrensis	Plume Moss	Ptilium CC
Pyrola ssp.	Pyrola (unknown)	Pyrola
Ranunculus ssp.	Smallflowered Buttercup	S.F Buttercup
Rhamuns alnifolia	Alderleaved Buckthorn	Alderleaved buckthorn
Rhytidiadelphus triquetrus	Shaggy Moss	Shaggy M.
Rosa acicularis	Prickly Wild Rose	PW Rose
Rubus ssp.	Raspberry ssp.	Raspberry
Salix ssp	Willow	willow ssp
Solidago ssp.	Goldenrod	Goldrod
Sorbus americana	American Mountain Ash	AMA
Sphagnum ssp.	Sphagnum Moss	SphM
Streptopus roseus	Rose-twisted stalk	RTStalk

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List of species observed in the study area.

Scientific Name	Common Name	Species Code	Shannon-Wiener Diversity Value
Taraxacum officinale	Dandelion	Dandelion	0.04
Thalictrum ssp.	Meadow Rue	meadow rue	0.20
Thuja occidentales	Eastern White Cedar	Cedar	0.19
Tortella ruralis	Hairy Screw Moss	HS MOSS	4.52
Trientalis borealis	Starflower	StarFL	1.23
Vaccinium angustifolium	Low Sweet Blueberry	LSB	85.37
Vaccinium myrtilloides	Velvet-leaved Blueberry	VLB	22.00
Viburnum edule	Low Bush Cranberry	LBC	2.21
Viburnum trilobum	High Bush Cranberry	HB. Cran	0.60
Vicia ssp.	Common Vetch	Vetch	0.57
Viola ssp.	Violet (unknown)	Violet ssp.	4.99

Appendix III

DFA – Test of Significance

Test of Significance for each Discriminant function for the mixed groups

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.418450	36.274950	36.274950	0.765841
2	0.945868	24.189298	60.464248	0.697202
3	0.722558	18.478435	78.942683	0.647663
4	0.321814	8.229960	87.172643	0.493421
5	0.244654	6.256686	93.429330	0.443355
6	0.117667	3.009184	96.438514	0.324468
7	0.080014	2.046253	98.484767	0.272188
8	0.059250	1.515233	100.000000	0.236507

a: First 8 canonical discriminant functions were used in the analysis.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 8	0.058643	1181.313258	288.000000	0.000
2 through 8	0.141825	813.490904	245.000000	0.000
3 through 8	0.275973	536.223465	204.000000	0.000
4 through 8	0.475380	309.726540	165.000000	0.000
5 through 8	0.628364	193.520930	128.000000	0.000
6 through 8	0.782095	102.366875	93.000000	0.238
7 through 8	0.874122	56.033829	60.000000	0.621
8	0.944064	23.974120	29.000000	0.730

Appendix IV

Discriminant function Coefficients

Standardized Canonical Discriminant Function Coefficients								
	Function							
	1	2	3	4	5	6	7	8
BS	-.060	-.053	.016	.073	.093	-.121	-.245	-.667
BIRCHW	-.024	.148	.025	-.149	.352	.011	-.011	-.117
POT	.275	.562	-.280	-.069	.118	.075	.164	-.038
S.BERRY	.081	.005	-.062	-.032	.020	.237	-.327	.340
AMA	.153	.086	-.172	.050	.041	.201	-.310	.277
VLB	-.080	.052	.241	-.089	.122	.194	-.186	-.111
LSB	-.534	.083	.087	.127	.230	.728	.173	.011
RASBERRY	.169	.180	.334	-.240	.178	.010	.218	-.072
PW_ROSE	-.047	.168	.083	.130	-.175	-.067	-.058	-.298
PC	.151	-.099	.014	-.161	.166	.103	.151	-.027
SNOWBERRY	-.093	-.060	-.039	-.093	.115	.122	-.093	.197
LT	-.170	.317	-.052	.045	.263	-.212	.271	.221
G_ALDER	.042	.126	.182	-.039	.434	.067	-.112	-.041
WILLOW_SSP	-.031	.043	-.037	.019	-.149	.091	.353	.036
BB	.253	.149	-.024	-.008	-.091	.167	-.035	.044
FW	.235	-.338	.129	.147	-.018	.142	-.105	.262
BINDWEED	.204	-.272	-.135	.405	.150	.164	.099	-.127
GOLDTHREAD	.012	.071	.370	.246	-.112	.145	.033	.072
MI_CAN	-.021	.136	.272	.003	.382	.053	-.097	.146
BJG	.189	-.193	.058	-.014	.059	.120	.079	.013
CH_GRASS	-.055	-.056	-.076	.126	.291	-.159	.184	.325
GRASS_SPP	.000	.162	.114	.266	-.449	.191	.114	-.031
SEDGE	-.003	.153	-.001	.259	-.126	-.200	-.116	.042
FM	.040	-.005	.229	-.096	.084	.606	.234	-.305
SHRIBERS	.254	-.222	.146	-.451	-.170	.178	-.058	.024
HS_MOSS	-.020	-.139	.010	.218	.081	-.103	.172	.012
HC_MOSS	.186	.031	.083	.374	.208	.054	-.010	.104
SPHM	-.229	-.113	-.035	.017	.167	.261	-.165	-.046
TWIN_FL	.042	.221	.327	.329	-.138	-.046	-.049	.048
BBL	-.032	-.023	.001	-.064	.398	.217	.147	-.102
W_HT	.167	-.084	.241	-.218	-.148	.252	.117	.196
G_PINE	.200	-.192	-.219	.173	-.198	.051	-.196	.099
BR_FERN	.159	-.213	.128	-.194	.106	.060	.018	-.006
VIOLET_SSP	-.064	.088	.022	.102	.075	.147	.294	-.025
B._HONEY	.169	.129	-.200	-.070	.005	.326	-.005	-.131
LLA	.171	.223	-.251	.235	.243	.262	.016	-.034

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Appendix V

Indicator Species Analysis

Indicator species of the different classifications for each class type. Class codes are indicated in the Table below. Relative frequency and abundance of each species within each class is summarized by the observed indicator value. The mean randomized indicator value is determined through 1000 Monte Carlo runs with randomized data. The p-value is the proportion of randomized trails with an indicator value equal or exceeding the observed indicator value (sig.≤0.01).

Classification Type	Indicator species	Class	Observed indicator value (IV)	Mean randomized error	p-value (sig.≤0.01)	Class codes
Burn intensity	S.BERRY	1	18	9.3	0.001	1 = Low
	LSB	1	33.9	25	0.001	2 = Moderate
	BOG_L.	1	3.3	1.2	0.001	3 = Severe
	LT	1	31.2	15.7	0.001	
	ASTER_SS	1	6.3	2.1	0.001	
	POT	1	12.8	7.5	0.002	
	MM	1	5	1.9	0.002	
	B.HAZEL	2	5.5	2	0.001	
	S.BOG_CR	2	5.7	1.9	0.001	
	RTSTALK	2	7.1	2.1	0.002	
	RASBERRY	3	27.7	17.6	0.001	
	FW	3	35.6	11.8	0.001	
	BINDWEED	3	19.9	5.8	0.001	
	BJG	3	15.5	7.1	0.001	
	CH_GRASS	3	16.4	8.8	0.001	
	HC_MOSS	3	30.7	19.5	0.001	
	WP_LICHE	3	4.2	1.3	0.001	
	G_PINE	3	14.2	6.7	0.001	
	LFERN	3	9.4	2.4	0.001	
	BR_FERN	3	9.5	4	0.001	
	W_HT	3	12.1	7	0.002	
	PC	3	13.2	8.3	0.004	
	BB	3	28.9	21.1	0.004	
	BS	3	16.4	9.7	0.005	
	SHRIBERS	3	12.4	7.2	0.006	
	VIOLET_S	3	10.9	7	0.007	

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Appendix V - Continued

Classification Type	Indicator species	Class	Observed indicator value (IV)	Mean randomized error	p-value (sig.≤0.01)	Class codes
Spruce Composition	POT	1	32	7.6	0.001	1 = 50% and 60% Spruce
	RASPBERRY	1	42.6	17.6	0.001	
	PC	1	16.2	8.3	0.001	2 = 70% and 80% Spruce
	BB	1	35.6	21.1	0.001	
	BJG	1	16.3	7.1	0.001	3 = 90% and 100% Spruce
	SHRIBERS	1	17.1	7.2	0.001	
	G_PINE	1	15.5	6.6	0.001	
	LFERN	1	7.3	2.3	0.001	
	B._HONEY	1	25.7	8.1	0.001	
	RTSTALK	1	6.7	2	0.001	
	BBL	1	22.2	14.4	0.002	
	LLA	1	14.6	8.3	0.002	
	B.HAZEL	1	5.1	2	0.004	
	WP_LICHE	1	4.1	1.3	0.004	
	BEDSTRAW	1	6.5	2.5	0.004	
	BL_ASH	1	3.5	1.2	0.005	
	LBC	1	4.7	2.1	0.007	
	BS	2	18.3	9.7	0.001	
	SPHM	2	12.3	7.4	0.006	
	BINDWEED	2	10.1	5.8	0.009	
	LSB	3	37.1	25	0.001	
	LT	3	24.2	15.7	0.001	
	MHT	3	3.2	1.3	0.003	
	GRASS_SP	3	12.8	6.9	0.004	
	BOG_L.	3	2.9	1.2	0.01	

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Classification type	Indicator species	Class	Observed indicator value (IV)	Mean randomized error	p-value (sig.≤0.01)	Class codes
Mixed Groups	POT	1	48.5	4.4	0.001	1 = Low/ 50% and
(Intensity and	S.BERRY	1	10.6	5.1	0.001	60%
Composition)	PW_ROSE	1	12.5	3.8	0.001	2 = Low/ 70% and
	GRASS_SP	1	15.9	4.7	0.001	80%
	B._HONEY	1	33.6	4.8	0.001	3 = Low/ 90% and
	LLA	1	19.1	4.8	0.001	100%
	BB	1	16	9.5	0.002	4 = Moderate/ 50%
	BOG_L.	3	8.3	1.8	0.001	and 60%
	LT	3	17.1	7.3	0.001	5 = Moderate/ 70%
	RASPBERRY	4	18.2	8.2	0.001	and 80%
	B.HAZEL	4	12	2	0.001	6 = Moderate/ 90%
	RTSTALK	4	16.2	2.2	0.001	and 100%
	S.BOG_CR	4	7	2	0.004	7 = Severe/ 50%
	S.DOGBAN	4	5.7	1.7	0.006	and 60%
	RED_ODW	5	8.6	2.1	0.001	8 = Severe/ 70%
	LSB	6	19.5	10.2	0.001	and 80%
	FM	6	14.8	11.7	0.01	9 = Severe/ 90%
	BJG	7	14.2	4.6	0.001	and 100%
	SHRIBERS	7	14.9	4.3	0.001	
	WP_LICHE	7	11.7	1.7	0.001	
	G_PINE	7	11.3	4.1	0.001	
	RK__POLY	7	7.9	2	0.001	
	LFERN	7	18.7	2.2	0.001	
	BEDSTRAW	7	7.2	2.4	0.004	
	MEDOW_RU	7	6.7	1.8	0.005	
	W_HT	7	9.2	4.2	0.007	
	PC	7	9	4.8	0.009	
	RD_LICHA	7	5.6	1.7	0.01	
	FW	8	15.8	6.2	0.001	
	BINDWEED	8	25.6	3.9	0.001	
	CH_GRASS	8	21.2	5.1	0.001	
	HC_MOSS	8	15	9.4	0.004	
	BS	8	12.6	6.3	0.008	
	MI_CAN	9	12	4.4	0.001	
	TWIN_FL	9	12.1	3.8	0.002	
	LETTUCE	9	6.9	1.5	0.002	
	GOLDTHRE	9	9.8	4.2	0.008	

Appendix VI

Landform Class Value Assignment

PARTICAL SIZE	Value
Peat, Muck	1
Silt	2
Clay	3
Sand	4
Gravel	5
Till	6
Rubble	7
Boulders	8
DRAINAGE	**Value**
Suspected high water Table	1
Wet	2
Mixed wet and dry	3
Dry	4

Appendix VII
Correlation Matrix of Modeled gradients

	FLOWACC	HEATLOAD	DEM	STAND_AGE	STAND_HIGH	STAND_STOC	TRASP	SOLAR RADIATION INDEXIO	SAVI	DIR_RED_IN
FLOWACC	1.0000									
HEATLOAD	0.0095	1.0000								
DEM	0.0195	0.0500	1.0000							
STAND_AGE	-0.0777	0.1696	-0.2067	1.0000						
STAND_HIGH	-0.0921	0.1832	-0.0048	0.6507	1.0000					
STAND_STOC	-0.1103	-0.0413	0.1482	-0.1268	0.0878	1.0000				
TRASP	0.0424	0.1110	-0.1063	0.1762	0.1427	-0.0662	1.0000			
SOLAR RADIATION INDEXION	-0.0692	0.0317	0.0353	0.0875	-0.0116	0.1623	-0.1185	1.0000		
SAVI	-0.0839	0.0513	-0.2253	0.2506	0.1722	-0.1529	-0.0288	-0.2964	1.0000	
DIR_RED_IN	-0.0913	0.0633	-0.1999	0.2650	0.1973	-0.1398	-0.0276	-0.2769	0.9835	1.0000
NDVI	-0.0851	0.0767	-0.1639	0.2313	0.1908	-0.2055	-0.0043	-0.3038	0.9757	0.9806
NIR_IR_IND	-0.0711	-0.0039	-0.1936	0.2251	0.2151	-0.0476	-0.0404	-0.2244	0.8764	0.8887
LAI	-0.0511	0.0035	-0.2996	0.2812	0.1318	0.0963	0.0017	-0.1085	0.7679	0.7594
IR_INDEX	-0.0724	0.0335	-0.1527	0.2270	0.2088	-0.1789	0.0333	-0.2464	0.9328	0.9347
FPAR	-0.0507	0.0026	-0.2988	0.2821	0.1334	0.0964	0.0043	-0.1079	0.7658	0.7570
TWI_GOOD	0.2110	-0.0756	0.2216	-0.2154	0.0170	-0.0716	-0.2253	-0.7175	0.2976	0.2896
TCWETNESS	-0.0575	-0.0005	-0.0334	0.1604	0.2312	-0.0479	0.1191	-0.0794	0.6436	0.6915
TCGREEN	-0.0826	0.0582	-0.2208	0.2492	0.1646	-0.1438	-0.0219	-0.2887	0.9976	0.9844
TCBRIGHT	-0.0350	-0.0509	-0.3254	0.1616	0.0256	-0.0829	-0.1446	-0.2711	0.7035	0.5927
LANDFORMS	0.0170	0.0391	-0.1018	0.0054	-0.4751	-0.0767	0.0946	0.1475	-0.1292	-0.1080
DRANAGE	0.1278	-0.0402	-0.2075	-0.2373	-0.2921	-0.4483	-0.3075	-0.1762	-0.0867	-0.0891
TEXTURE	0.0514	0.0300	0.0123	-0.2666	-0.5149	-0.0693	-0.0998	0.1936	-0.3484	-0.3218

Appendix VII -- Continued

	NDVI	NIR_IR_IND	LAI	IR_INDEX	FPAR	TWI_GOOD	TCWETNESS	TCGREEN	TCBRIGHT	LANDFORMS	DRANAGE
FLOWACC											
HEATLOAD											
DEM											
STAND_AGE											
STAND_HIGH											
STAND_STOC											
TRASP											
SOLAR RADIATION INDEXION											
SAVI											
DIR_RED_IN											
NDVI	1.0000										
NIR_IR_IND	0.8581	1.0000									
LAI	0.6452	0.7252	1.0000								
IR_INDEX	0.9399	0.8910	0.6502	1.0000							
FPAR	0.6428	0.7235	0.9999	0.6489	1.0000						
TWI_GOOD	0.3054	0.2502	0.1186	0.2905	0.1172	1.0000					
TCWETNESS	0.6810	0.8003	0.4498	0.8546	0.4496	0.1627	1.0000				
TCGREEN	0.9743	0.8930	0.7706	0.9379	0.7685	0.2942	0.6658	1.0000			
TCBRIGHT	0.5622	0.5126	0.7071	0.5308	0.7064	0.2309	0.1235	0.6804	1.0000		
LANDFORMS	-0.1109	-0.2071	-0.0638	-0.1676	-0.0651	-0.3034	-0.1751	-0.1207	-0.1486	1.0000	
DRANAGE	-0.0468	-0.0830	-0.2420	-0.1020	-0.2451	0.1961	-0.1597	-0.0923	-0.0324	0.1494	1.0000
TEXTURE	-0.3070	-0.3424	-0.3121	-0.3590	-0.3137	-0.2024	-0.3053	-0.3409	-0.3058	0.7174	0.4139

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