ECOSYSTEM RESPONSES TO CLIMATE VARIABILITY, DISTURBANCES AND ENVIRONMENTAL FACTORS IN SOUTHWEST YUKON OF CANADA

by

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Abstract

The south-western part of the Yukon Territory of Canada has experienced an unprecedented spruce bark beetle outbreak and frequent forest fires beyond the historical trends. Accumulating evidence also suggests that the southwest Yukon has experienced the impacts of recent climate change: warmer winters and warmer and drier summers over the past 15 years have contributed to the severe spruce bark beetle infestation, affecting white spruce on approximately 340,000 hectares of the traditional territory of the Champagne and Aishihik First Nations in southwest Yukon. The mortality caused by the bark beetle outbreak has also increased the risk of wildfire severity and frequency in the region.

I studied the impacts of climate variability, disturbances and environmental factors on stand structure, forest regeneration and vegetation diversity within the CATT. The research was conducted in close collaboration with the Ministry of Energy, Mines and Resources of the Yukon Government and the Champagne and Aishihik First Nations Government. Data were collected in the summer of 2008 from the forested landscape of the Champagne and Aishihik Traditional Territory.

I found that stand structure varied significantly by edaphic and topographical factors with higher forest productivity at lower elevation and on lower slope positions where there was a higher soil moisture regime. Overall stand productivity and vegetation diversity were higher on warmer aspects and in mixed stands. Although regeneration of all tree species was higher in burned areas, broadleaved species prevailed in these areas, indicating that persistent disturbances associated with the predicted increase in temperatures in the region may promote broadleaved species. A higher diversity was found in moderately disturbed open areas with higher mean temperature and precipitation. Salvage harvested areas had the highest diversity and highest composition of

broealeaved trees. The undisturbed mixed stands had the ecosystem characteristics that would closely meet the ecological goals of the Strategic Forest Management Plan (2004) in the region. The vegetation distribution were closely linked with topographical, climatic and disturbance regime in the study area, which could be a basis for vegetation classification, which is still lacking in the study area.

Preface

Disturbance is an integral part of the boreal forest ecosystem, playing an important role in forest succession and helping to maintain ecosystem functioning when it occurs within historical limits. However, this is not the case of the south-western part of the Yukon Territory of Canada, where the forests have been affected by disturbances beyond the historical range of natural variability. The region has experienced a severe spruce bark beetle infestation since early 1990s, affecting white spruce on approximately 340,000 hectares of the traditional territory of the Champagne and Aishihik First Nations (CAFN), the study area of this research. The mortality caused by the bark beetle outbreak has increased the risk of wildfire severity and frequency. Between 1946 and 2003, 23 large fires and many small fires were recorded, burning approximately 100,100 ha of forest in the planning region. In 1998, there were two large forest fires near Haines Junction, affecting about 7000 ha of the forests. In the absence of active fire management, the average annual frequency of fire and total area burned in the Yukon Territory are projected to be doubled by the 2070s.

Climate change has been considered as the dominant factor for the increased forest disturbances in the Champagne and Aishihik Traditional Territories (CATT). An increase in mean annual temperature (MAT) of 0.6 ºC, with the greatest increase occurring in January (2.4 ºC) were recorded in the years between 1971–2000 compared to 1951–1980. The model projections indicated that the MAT in the region will be increased by 2 ºC by 2040 and 7 ºC by 2100, which poses greater uncertainty of future climate and forest disturbances in the region. The CAFN did not have prior forest management experiences except for limited forestry activities resulting in the widespread occurrence of old white spruce stands, which is also another reason for increased forest disturbances in the region.

The majority of the forestland is presently inaccessible due to the lack of a road network. Moreover, the local communities have very small populations (approximately 1200 people in the region), and there is no history of involvement in commercial forestry. Their economy is mainly based on traditional land-use practices. Forests provide significant socio-economic and cultural values to the local people; traditional practices include hunting, fishing, trapping and the collection of non-timber forest products (NTFPs). The major sources of income for local people are employment in service sector, wilderness-based tourism and small service businesses.

Forest disturbances have caused significant impacts on forest ecosystems in the region, specifically on forest composition, structure and vegetation diversity. About 80% of the dominant white spruce trees are dead, turning the landscape into a mosaic of dead conifer stands mixed with early successional broadleaved species. This situation may also significantly affect the local people's traditional use of the forests. In response to the forest disturbances, a Strategic Forest Management Plan was prepared and and has been implemented since 2004. The plan has four goals and 33 objectives aiming to balance ecological, economic and social values from the affected forests. However, the plan lacked baseline information on existing ecosystems and their variations in the landscape, a clear roadmap for future development and silvicultural systems to achieve its goals and objectives. The plan did recognize salvage harvesting as an important forest intervention in response to forest disturbances. However, questions have been raised over the effectiveness of salvage harvesting in mitigating forest disturbances and reducing ecosystem impacts.

This research was triggered due to pressing needs to fill the information and knowledge gap on existing ecosystem components, specifically on vegetation composition and diversity, forest productivity, and natural regeneration dynamics and their relationship with biogeoclimatic and disturbance factors. In addition, information was sought on how these natural phenomena would interact with the cultural and socio-economic systems within the area. This knowledge and information would lay the foundation for devising appropriate silvicultural systems in support of the SFMP. Accordingly, this research was conceptualized as per the agreement between Ministry of Energy, Mines and Resources, Government of Yukon and Faculty of Forestry, UBC, in order to assist the long-term management of the forests in the region. Over the course of the research, many changes occurred in the staff of the Ministry, and priorities changed. In addition, it soon became evident that the appetite amongst local people for more socio-economic surveys was very limited, and I was advised not to proceed with this part of the project. The following account reflects the research that emerged as a result of these changing circumstances.

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List of Abbreviations

ACIA: Arctic Climate Impact Assessment

ANOVA: Analysis of Variance

AIC: Akaike Information Criterion

CAFN: Champagne and Aishihik First Nations

CCA: Canonical Correspondence Analysis

CM = Centimeter

GIS: Geographical Information System

GLM: Generalized Model

IDH: Intermediate Disturbance Hypothesis

KNPR: Kluane National Park and Reserve

KM: Kilometers

MCA: Multivariate Canonical Correlation

MCoA: Multiple Co-inertia Analysis

MEMR: Ministry of Energy, Mines and Resources (Yukon Government)

MSL: Mean Sea Level

NCE: Northern Climate Exchange

PoC: Point of Commencement

SFMP: Strategic Forest Management Plan

SWY: Southwest Yukon

YG: Yukon Government

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1. Introduction

1.1 Setting: the boreal ecosystem

This research was undertaken in the landscape of the Champagne and Aishihik Traditional Territory (CATT), which is a part of Southwest Yukon's (SWY) boreal forest. The ecosystems of the region are currently facing the impacts of climate change and related disturbances. This triggered the current research, which aims to provide ecological knowledge and information to policy makers and forest managers in order to assist the long-term management of the forests in the region.

Boreal forests cover 1.2 billion hectares of land, extending across about 17% of earth's surface and comprising 30% of the global phytomass (Wein and MacLean, 1983; Stocks and Lynham, 1996). They play an important role in global climate, carbon and water cycles and the world economy (Johnson et al., 2003). About one third of the world's boreal forest lies in Canada and Alaska (Hare and Ritchie, 1972).

The boreal forest varies significantly in climate and disturbance regimes (Chen and Popadiouk, 2002), with climate in the Canadian boreal ranging from dry and cold, with a mean annual temperature of −8 ºC and a mean annual precipitation of 300 millimetres (mm), to warm and moist, with a mean annual temperature of 6 ºC and a mean annual precipitation of 1350 mm (Rowe, 1972). The characteristics and composition of the vegetation vary with climate, aspect, slope, soil type and moisture gradient (Meideniger and Pojar, 1991). The diverse physiographic and climatic factors have created diverse community types (Douglas, 1974). The forest composition is also strongly influenced by interactions between species regeneration capacity, longevity and the frequency and types of disturbance (Bergeron, 2000).

The overstory of the Canadian boreal forest is mainly dominated by trembling aspen (*Populus tremuloides* Michx.) or white birch (*Betula papyrifera* Marshall) in early successional stages, black spruce (*Picea mariana* (Mill.) B.S.P.) or white spruce (*Picea glauca* (Moench) Voss) in mid-successional stages and by balsam fir (*Abies balsamea* (L.) Mill.) in late successional stages (MacDonald, 1995). Understory vegetation plays an important role in ecosystem functioning by affecting canopy succession (Messier et al., 1998), and nutrient cycling (Weber and Van Cleve, 1981), by providing wildlife habitat (Okland and Eilertsen,1996) and by providing many valuable foods and medicines to human society (Penafiel et al., 2011).

1.2 Context: boreal forests in the Champagne and Aishihik Traditional Territory (CATT), southwest Yukon

1.2.1 Forest ecosystems in the CATT

The CATT is located in the southwest Yukon (SWY), covering 272,220 hectares (ha) of forest lands excluding the forest area in Kluane National Park and Reserve (SFMP, 2004). The region has 20% forested land suitable for forestry activities, 28.8% forested land unsuitable for timber production, 1.8% poorly regenerated, 42% alpine shrubs and 7.4% of remaining lands classified as rivers, settlements, lakes and wetlands (Ogden, 2006). The vegetation in the Kluane region has been divided into three ecological regions based on elevation, namely montane valley bottom forest (780–1080 m), subalpine forest (1080–1370 m) and alpine tundra (above 1370 m) (Krebs and Boonstra, 2001). Forests are mostly confined to below 1100 m in the river valleys. Due to soil, topographic and climatic constraints, the forests in the region are characterized as slow-growing with low productivity (NCE, 2006a).

Forest ecosystems in the southwest Yukon include a small number of tree and understory species. According to SFMP (2004), the major tree species are white spruce (*Picea glauca* (Moench) Voss, 235,000 ha), trembling aspen (*Populus tremuloides* Michx., 36,300 ha) and balsam poplar (*Populus balsamifera* L., 920 ha). Less common tree species include lodgepole pine (*Pinus contorta* Dougl. ex Loud.), black spruce (*Picea mariana* (Mill.) B.S.P.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Trembling aspen is generally found in pure stands on well-drained sites at moderate elevations and on south-facing slopes. The forest understory is mainly composed of deciduous shrubs such as ground birch (*Betula glandulosa* Michx.) and willow (*Salix s*pp.). The understory also includes a variety of herbs such as arctic lupine (*Lupinus arcticus* Wats.) and fireweed (*Epilobium angustifolium* L. s.l.) (NCE, 2006a).

Disturbances play a dominant role in forest succession and community dynamics in southwest Yukon forests (Ogden, 2006). Prior to the spruce bark beetle infestation (before 1994), 80% of the forests were classed as mature stands between 80 and 120 years old (SFMP, 2004). However, the spruce bark beetle (*Dendroctonus rufipennis*) infestation has affected the forest age class and stand height distributions in recent years. The infestation is expected to affect species composition over time in a large area of the planning region (SFMP, 2004). The current forest composition in the affected areas comprises an overstorey of dead white spruce with a variety of regenerating plant species. In general, the forest in the region is characterized by low productivity (with over 80% of the forest classified as poor) and slow growth rate (with an average of 10 to 14 m height attainment at 100 years of age) (SFMP, 2004).

1.3 Research rationale: climate change and forest disturbances in the CATT

1.3.1 Climate change and its impacts in the CATT

The IPCC 4th assessment report summarized that mean temperatures have increased globally; the warming is greater at higher latitudes where temperatures have increased at almost twice the global average rate in the past 100 years. Frugal and Prowse (2008) state that climate in the Canadian north is changing significantly, with increased temperature and precipitation being reported over the last 50 years. Model projections suggest that the increase in temperature will be higher in northern regions than in the rest of the world (Solomon et al., 2007), with the greatest winter warming (from 2 to 9 ºC) being projected in Alaska and northern Canada (Christensen et al., 2007; Anisimov et al., 2007). Annual winter precipitation is also expected to increase at higher latitudes (Christensen et al., 2007).

Climate change and its effects are apparent in the CATT (Ogden, 2006). The mean annual temperature in the region rose by 3 ºC between 1955 and 2005 (Field et al., 2007). The meteorological record from the Burwash Landing weather station reveals an increase in mean annual temperature of 0.6 ºC, with the greatest increase occurring in January (2.4 ºC) in the years between 1971–2000 compared to 1951–1980 (Ogden, 2006). In the future, the mean annual temperature in the region is projected to increase by 2 ºC by 2040 and 7 ºC by 2100 (ACIA, 2004). Moreover, increasing precipitation and shorter and warmer winters will decrease snowfall and snow cover in the region substantially through delayed snowfall and earlier spring snow melting (ACIA, 2004; Christensen et al., 2007). About a 10% decline in snow cover has been estimated in the past 30 years and a 10 to 20% decline has been projected by the 2070s (ACIA, 2004).

The impacts of climate change on natural and socio-economic systems are already apparent in southwest Yukon. Climate change has affected the extent of glaciers and permafrost, the frequency of floods and landslides, and has affected forests, wildlife and local communities. Permafrost is highly sensitive to disturbance and global warming (Smith and Burgess, 1999) especially during the winter season. Floods and fluvial erosion are apparent in the region due to snow and glacier ice melting precipitated by warmer weather (Ogden, 2006).

1.3.2 Spruce bark beetle outbreak

One of the most obvious problems related to climate change in the region is the spruce bark beetle outbreak (ACIA, 2004; NCE, 2006b). ACIA (2004) concluded that “the region is experiencing the largest and most intense infestation of spruce bark beetle ever recorded in Canada”, which is an apparent example of ecosystem response to recent warming (Frugal and Prowse, 2008). Beetles attained epidemic levels in the region after 1992 (SFMP, 2004), although the infestation began to subside in 2007. Approximately 340,000 hectares of forest were affected by the beetle outbreak (NCE, 2006; Government of Yukon, 2010), which is the second largest infestation after the infestation in south central Alaska, where white spruce has died over about 1.2 million ha (Berg et al., 2006). Using aerial mapping, it was determined that white spruce forests affected by spruce beetle in 2007 covered only 10,286 ha, compared to 41,170 ha in 2006 and 82,620 ha in 2005 (Garbutt, 2007; Garbutt, 2008).

The magnitude, intensity and severity of this infestation have been linked to recent climate change together with the presence of large areas of unmanaged, mature stands of white spruce (Barber et al., 2000; Berg and Henry, 2003; ACIA, 2004). As cold winters generally suppress the spruce bark beetle population, the recent mild winters are thought to be the main reason for the major increase in the beetle population (SFMP, 2004). In addition, already susceptible mature and weaker trees have lost their resistance to beetle attack due to warmer summers and moisture stress in the region (ACIA, 2004; Juday et al., 2005). If the climate trends continue, white spruce mortality is expected to continue because of the higher population of spruce bark beetle (Berg and Henry, 2003; Berg et al., 2006).

1.3.3 Forest fire hazards

Climate variability is considered to be one of the dominant factors affecting the occurrence of forest fires (Rosenzweig et al., 2007), and has contributed to an increase in forest fire hazard in the region. Because of weather patterns and fuel structures, fire is an important disturbance agent in the boreal forest (Johnson, 1992). Between 1946 and 2003, 23 large fires and many small fires were recorded, burning approximately 100,100 ha of forest in the planning region, excluding the Kluane National Park and Reserve (KNPR) (SFMP, 2004). Although, historically the region has been considered as an area of low wildfire probability compared to other areas in the boreal forest (NCE, 2006b), the situation has changed over the last decade due to the increased fire hazard in the forest caused by changes in climate, spruce mortality (thus increasing fuel loads) and changing forest structure (SFMP, 2004).

The white spruce mortality associated with the bark beetle infestation has contributed to an increase in the quantity and extent of fuel (Frugal and Prowse, 2008), which in turn has increased the possible severity of future forest fires (Flannigan et al., 2005). In addition, warmer and drier conditions have changed the characteristics of the fire regime (annual fire incidences, area burned and seasonal fire severity rating) in the region (McCoy and Burn, 2005). In the absence of active fire management, the average annual frequency of fire and total area burned in the Yukon Territory may double by the 2070s (McCoy and Burn, 2005). Moreover, the possibility of lightning strikes may increase, elevating lightning-caused fire incidents by as much as 44% (Price and Rind, 1994; NCE, 2006b). As a result, overall fire danger, fire intensity, fire severity, fire occurrence, length of the fire season, and annual areas burnt are all likely to increase (Stocks et al., 1998; Ogden, 2007), with significant ecological, social and economic impacts.

1.3.4 Salvage harvesting

The SFMP (2004) recognized salvage harvesting as an important forest intervention in response to the spruce bark beetle infestation and increased fire severity in the region. The plan recommended that although the sustainable harvesting of timber[1] should be the focus of SFM, salvage harvesting should be carried out to promote ecological recovery (SFMP, 2004), focusing especially on the beetle-infested area as timber quality will degrade over time. As part of the plan, the CAFN and Government of Yukon (GY) have accepted a recommendation for the salvage harvesting of up to 1 million m^3 of beetle-affected timber between 2006 and 2015. However, questions have been raised over the effectiveness of salvage harvesting in mitigating forest disturbances and reducing ecosystem impacts. Specifically, research is needed to understand how salvage harvesting affects forest dynamics such as the development of stand structure and regeneration and its effect on biodiversity. A part of the research presented in this

[1]Sustainable harvesting refers to harvesting of timber based on growth, yield and allowable cut.

thesis therefore focuses on assessing the potential effects of salvage harvest on the potential development of stand structure, biodiversity and regeneration.

1.4 Current understanding of boreal forest disturbances

1.4.1 Disturbance ecology

Disturbance ecology has become an important concept in forest ecology. White and Pickett (1985) define disturbance ecology as “...any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability or the physical environment”. However, Rogers (1996) suggests that the definition of disturbance ecology should not be bound by size and time, as these factors are relative to the systems under consideration. White and Pickett (1985) have also categorized disturbances as perturbations (small events with specific alteration in the system) and catastrophes (rare and large destructive events). Forest disturbances have also been discussed in terms of the temporal and spatial scale of equilibrium or non-equilibrium states that the disturbances may bring to the forest. It has been argued that when large-scale disturbances occur frequently, it is unlikely that the affected forest will reach equilibrium or a steady state (Bergeron and Dansereau, 1993; Romme et al., 1986). However, if disturbances are smaller in scale and occur rarely then a forest may reach a steady state (Bormann and Likens, 1979; Lorimer and Frelich, 1994). The recent theory of complex adaptive systems suggests however that non-steady and non-equilibrium conditions characterize forests (Levin, 2005), even when disturbance regimes are small-scale. This suggests that forest management needs to be based on heterogeneity, unpredictability and adaptability (Messier and Puettmann, 2011).

Disturbances can be explained in terms of cause, scale (temporal and spatial) and intensity (intense or weak) (Rogers, 1996). The causes of forest disturbances may be biotic (such as insects, disease, animals and human interventions) or abiotic (fire, wind, floods, drought, etc). According to Angelstam (1996), fire is the most important cause of stand-changing disturbances. However, forest harvesting has been considered a very important disturbance factor in the boreal forest of Europe and many parts of North America (Niemela, 1999; Loope, 1991). The heterogeneity and mosaics created by harvesting operations often differ significantly from those associated with natural disturbances such as fire (Niemela, 1999).

Disturbance affects forest ecosystems in various ways. One of the important implications of disturbances for forest ecosystems is gap dynamics and thereby changes in resource availability. This can significantly change the succession pattern, forest structure and biodiversity (McCarthy and Weetman, 2006; Lorimer, 1989). Gaps can be smaller, created by the mortality of a single tree or patches formed by the mortality of groups of trees, or they can be as large as entire stands (Rogers, 1996). Smaller gaps or patches generally create uneven-aged stands (Oliver, 1980), while stand replacement disturbances generally create even-aged stands (Romme and Despain, 1989). However, Lorimer (1989) has stated that the effects of small-scale disturbances will be limited or insignificant if large catastrophic disturbances occur at intervals shorter than the potential lifetime of the trees.

Shifting from the conventional paradigm, which has considered disturbance as a negative factor for ecosystem functioning and productivity, natural disturbance regimes have been recognized as an essential process to promote healthy and dynamic ecosystems. Consequently, suppressing them may be deleterious to the long-term healthy functioning of forest ecosystems (Rogers, 1996). An understanding of the specific ecosystem process is necessary if disturbance ecology is to be implemented in forest management. Disturbances should be monitored at both community and regional levels so that their extent, frequency, rotation period, intensity and severity can be better understood (Noss, 1990).

1.4.2 Impacts of disturbances in boreal forests

Disturbance is an integral part of the boreal ecosystem. Both natural and anthropogenic disturbances have played an important role in the succession of boreal forests (Kuusela, 1990), as the combination of these disturbances governs the dynamics of boreal forests (Engelmark, 1999). Fire has been considered as a paramount disturbing factor in the region, although other disturbances such as wind, floods, insects, climate variability and their interactions are equally important (Engelmark, 1999). Similarly, it is important to understand the variation in the disturbance regime through time as this can have a significant impact on forest composition. The impacts of climate variability and disturbances on regeneration, stand structure and biodiversity are reviewed separately in the following sections.

1.4.2.1 Impacts on tree regeneration

As my study area is dominated by three tree species, namely *Picea glauca* (Moench) Voss (white spruce), *Populus tremuloides* Michx. (trembling aspen) and *Populus balsamifera,* L. (balsam poplar), I will focus mainly on the regeneration of these species.

Impacts of climate change and disturbances on white spruce regeneration have been reported by several authors. Climate change may have significant effects on regeneration and growth of white spruce (Oswald and Brown, 1990; Barber et al., 2000; Wilmking et al., 2004; Nistchke, 2009). Variation in precipitation may reduce moisture availability or increase the frequency of drought, which would significantly affect the spruce regeneration of white spruce (Wang and Kemball, 2005; Johnstone and Chapin, 2006a).

Similarly, increased disturbances could also reduce seed sources through the extensive mortality of parent trees, which would affect total seed produced (Jasinski and Payette, 2005). Although fire is considered to be a very important factor for the establishment of white spruce seedlings as interactions between masting years and fire can result in abundant regeneration (Peters et al., 2005), intense and severe fire may kill seeds and reduce the probability of germination (Neary et al., 2005). In areas of the northern boreal forest, fire may play an important role for white spruce regeneration by removing organic layers, removing permafrost and increasing soil temperature (Yoshikawa et al., 2003).

Like white spruce, the regeneration of trembling aspen is also sensitive to dry climatic conditions (Hogg and Wein, 2005). Regeneration by suckering is the principal method of aspen regeneration following a major disturbance (Bartos, 2001; Frey et al., 2003). Its regeneration responds positively to increasing fire severity (Johnstone and Chapin, 2006a). However, both seed germination and vegetative reproduction are very sensitive to soil moisture stress (Perala, 1990). Moreover, severe fire can damage roots and suckers and significantly affect the density, height and diameter of the regeneration (Wang, 2003). Increased fire frequency resulting from warmer temperatures may favour the establishment of trembling aspen and other herbaceous woody species in the boreal forest (Flannigan and Van Wagner, 1991). Post-fire regeneration of aspen can be prolific and rapid where moisture is not limiting and the disturbance is followed by suitable climate conditions (Hogg et al., 2002; Hogg and Wein, 2005; Johnstone and Chapin, 2006a).

Balsam poplar has similar environmental requirements to trembling aspen for its regeneration. It requires adequate soil moisture and prefers higher temperatures (> 15 ^{o}C) for its germination (Zasada and Densmore, 1980; Krasny et al., 1988; Zasada and Phipps, 1990). Soil moisture deficits can reduce regeneration following disturbance, leading to a reduction in species abundance over time (Yarie, 2008). Fire is an important disturbance factor for its germination, provided that adequate moisture is available (Klinka et al., 2000).

1.4.2.2 Impacts on forest structure and composition

The magnitude and intensity of spatial and temporal disturbances shape the structural development of the landscape (McCarthy and Weetman, 2006) by creating periodic gaps (Lorimer, 1989) and by developing a mosaic of patches of varying age and size (McCarthy and Weetman, 2006). Variations in disturbance characteristics such as frequency, size and severity strongly influence forest structure and function (Johnstone and Chapin, 2006b). However, Johnson (1984) suggests that smaller gaps created by scattered disturbances are not of long-term significance. A gap of 500 m^2 or more will have a significant impact on stand structure (Lorimer, 1989).

Fire affects stand structure in various ways. The space and time variability of fire cycles (Payette et al., 1989; Bergeron, 1991) creates gap dynamics in such a complex way that stand mosaics are formed ranging from post-fire early successional deciduous species to mixed and pure coniferous stands in the older post-fire stands (Bergeron & Dansereau, 1993). Similarly, longer fire intervals increase the chance of a spruce budworm outbreak due to the increased proportion of late successional species such as spruce (Bergeron and Leduc, 1998). The increased mortality due to insect outbreaks alters the structure and composition of stands (Bergeron et al., 1995; Harvey et al., 2002). Hence, heterogeneity increases with increasing stand age (Cumming et al., 2000; Brassard and Chen, 2006). Frequent fires and longer fire intervals, would all have similar impacts on stand structure, namely the elimination of pure deciduous stands and the development of mixed stands (Bergeron and Dansereau, 1993).

Climate plays an important role in stand structure and tree growth variability (Lloyd and Fastie, 2002). There are many examples of how climate can affect stand structure variability. Climate directly affects the growth and behavior of individuals, modifies population size and structure, and affects ecosystem structure and function by affecting decomposition rates, nutrient cycling, water flows, and the distribution of ecosystems within landscapes (Gitay et al., 2002). One example of the impact of climate is the growth reduction associated with higher temperatures and drought stress (Barber et al., 2000). Higher temperatures can significantly reduce tree growth (Lloyd and Fastie, 2002). It was found that white spruce growth was negatively correlated when mean July temperature was more than 16 ^{o}C (Wilmking et al., 2004)). The mean July temperature in the study area was 13.2 ^{o}C which implies that increase in 3 ^{o}C temperature as predicted may affect white spurce growth in the study area. Species composition is also affected by species tolerance to shade and moisture stress. For example, aspen is a light-preferring species that occupies the early stage of succession when enough light is available for its growth, but it is eventually replaced by white spruce or other shade-tolerant species (Bergeron and Dubuc, 1989). Drought plays a direct role in shaping and limiting species distributions (Aber et al., 2001; Hannah et al., 2002) and is a key determinant of the distribution of boreal tree species (Chhin and Wang, 2008). Climate also affects forest structure and forest carbon by influencing fire regimes and the spread of insects and pathogens (Dale et al., 2001; Ma et al., 2012).

1.4.2.3 Impacts on biodiversity

Disturbances can have major implications for biodiversity (Nilsson and Ericson, 1997) by creating a mosaic of structures and processes that influence the variety and diversity of species present in a forest (Palik et al., 2002). Studies in the boreal forest suggest that the frequency and severity of disturbances can affect forest ecosystems by influencing vegetation dynamics, diversity patterns and ecosystem processes (Wardle et al., 1997). As most forestry operations such as logging involve some kind of disturbance, affecting both diversity and ecosystem functions, an understanding of the effects of natural disturbances and disturbance dynamics on diversity has become important for forest managers (Haila et al., 1994; Angelstam, 1997; Bengtsson et al., 2000). It is also important to understand the relationships between disturbance dynamics and biodiversity (Hughes et al., 2007).

Climate change influences forest biodiversity by affecting species interactions and ecosystem processes (Spittlehouse, 1996). It may change biodiversity, stand structure and species dominance by creating open stands that encourage a dense shrub cover (Hebda, 1998). Similarly, wildlife distributions and populations are expected to be affected due to changes in the quantity and quality of food availability, habitat structures and interactions between predators and prey (Ogden, 2006).

Community dynamics and their relationships with biodiversity are important elements that need to be considered in the study. Variation in diversity could be both a cause and a consequence of variation in community dynamics (Loreau et al., 2001). It is therefore important to understand how community properties contribute to the maintenance of biodiversity (Huston, 1979; Hughes et al., 2007). Similarly, the amount of course woody debris could also play a significant role in determining the presence or absence of several species, especially in boreal forests where many species are dependent on the density of dying and dead trees (Esseen et al., 1997; Nilsson et al., 2001).

1.5 Research objectives and questions

This research arose from the Strategic Forest Management Plan (2004) for the Champagne and Aishihik First Nations traditional territory of southwest Yukon. It was intended to support the plan's goals and objectives by providing scientific information as agreed between the University of British Columbia and the Government of Yukon in November, 2007. In this connection, the research was designed and conducted to support one of the goals of the SFMP (2004), namely "to maintain ecosystem functioning" with the objectives to "maintain or restore or enhance forest regeneration and succession, species and ecosystem diversity".

Specifically, the research would contribute to one of the key indicators of the SFMP for monitoring its goal, which is "to assess the variation in pattern, composition and structure of the ecosystem" (SFMP, 2004). This would require the development of a sound understanding of the existing ecosystem structures and composition in the region. To achieve this, more research had been suggested to obtain a better understanding of the linkages between forest disturbances, ecological complexities/uncertainties and the ecological responses of the forests in the region. The NCE report (2006) also suggested that an understanding of the relationship between climate change and forest disturbances was essential for the better understanding of future ecosystems under future disturbance regimes.

The main objective of this research is to understand the recent responses of forest ecosystems of the CATT to bio-geoclimatic and disturbance variability. This is needed in order to understand better their variation and to develop possible scenarios of future ecosystem dynamics. Such an understanding would be extremely useful in developing forest management tools for sustainably managing the forests in the region in the context of predicted climate change and associated future uncertainties. Specifically the research;

I. studied the impacts and variation in forest ecosystems in response to bio-geoclimatic and disturbance factors.

II. assessed the implications of the research findings in relation to possible forest management strategies and activities to meet the ecological goals of SFMP (2004).

1.5.1 Research questions

The general research questions associated with these objectives were as follows:

- How does stand structure vary with environmental factors, climate and disturbance types?
- How does landscape topography interact with climate variability to affect stand structures and composition?
- What are the most important variables that explain the distribution and abundance of tree regeneration in the study area?

- What are the overall species richness, evenness and abundance in the study area and how do they vary by landscape and ecological variability?
- What are the forest management implications and strategies in response to the above ecosystem variability in the CATT?

1.6 Research framework and thesis structure

The research framework, linking the research issues, objectives and specific questions, is provided in Figure 1.1. The dissertation has seven chapters. The first chapter includes an introduction, literature review, justification of the research, research objectives and research questions. The 2nd chapter contains the research methodology, including the methods of data collection and analysis.

The 3rd, 4th and 5th chapters contain the main research sections. The third chapter deals with the variation in stand structure in response to climate variability, disturbances and geographical factors. The fourth chapter examines the distribution and abundance of regeneration of tree species in response to climate variability, disturbances, geographical variation and stand structure. The fifth chapter examines variation in vegetation diversity in response to bio-geoclimatic and disturbance factors. Chapter 6 is a synthesis of the previous chapters to assess forest management implications and to recommend appropriate management strategies and activities. A final chapter provides conclusions and recommendations.

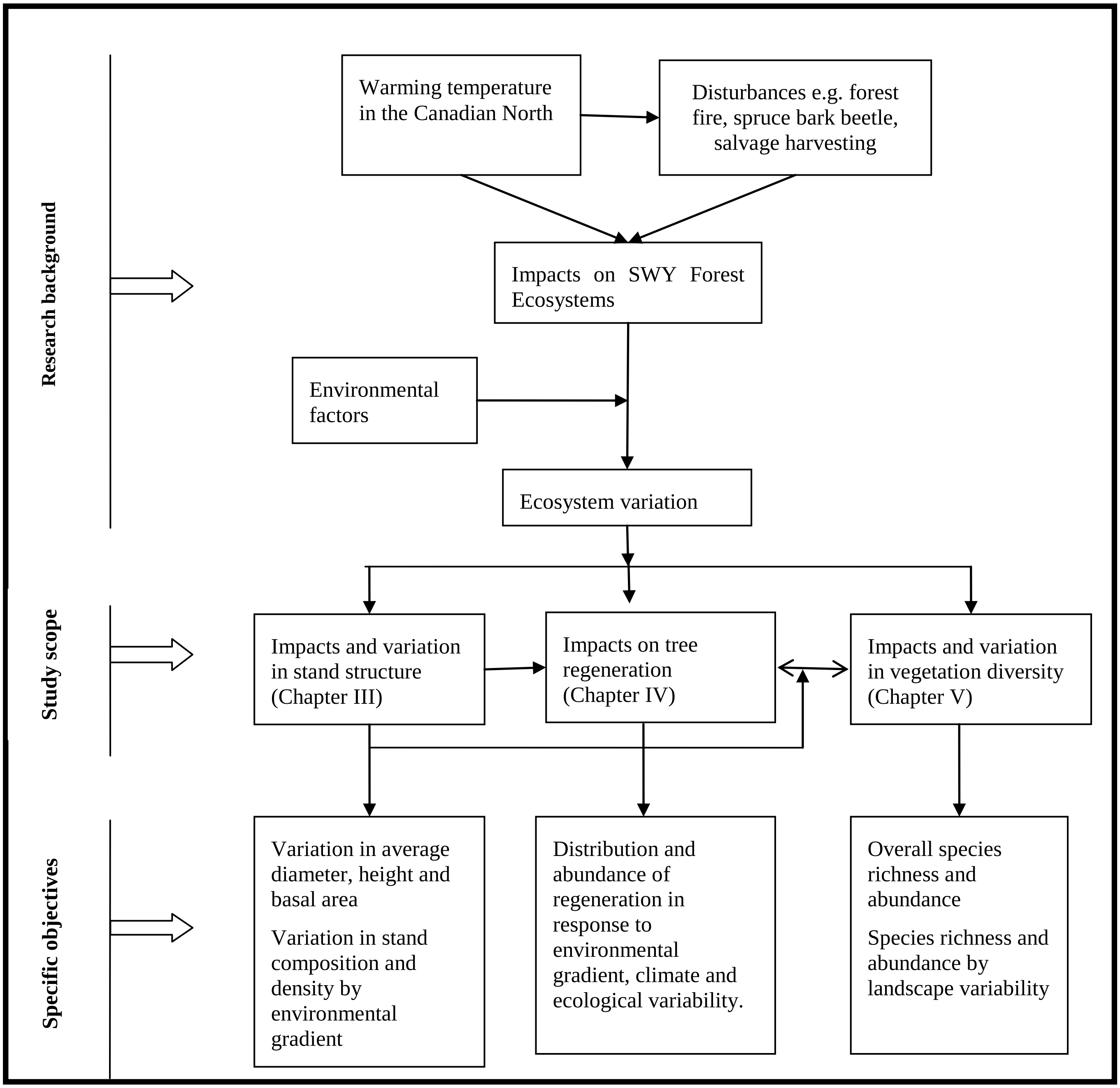

Figure 1.1 Research framework

[Note: The figure indicates the research background that justified the need for the research. The research scope corresponds to specific research chapters in the thesis. The last section in the figure highlights the research objectives that each chapter deals with]

2. Methodology

2.1 Study area justification: Why was the research important in the forest of CATT?

This research was undertaken in the Champagne and Aishihik Traditional Territory (CATT) within the southwest Yukon (SWY). The main reasons for carrying out this research in the CATT were;

- Issues of climate change: Model projections suggested that the increase in winter temperature in the region will be from 2 ºC by 2040 to 7 ºC by 2100 (ACIA, 2004). As the variation in mean annual temperature in the study area is 1.2 ^{o}C (Annex B-2), any variation in ecosystem attributes within 1.2 ^{o}C would suggest that there would be significant variation of ecosystems in the projected climate scenarios.
- Multiple forest disturbances: The forests of the CATT have been affected by multiple disturbances such as spruce bark beetle, fire and salvage harvesting. The region is suffering from the largest and most intense infestation of spruce bark beetle ever recorded in Canada, and with an increase in fire frequency in recent decades (SFMP, 2004). In the absence of active fire management, the average annual fire frequency and total area burned in the Yukon Territory is projected to double by the 2070s (McCoy and Burn, 2005). Although salvage harvesting has been initiated as a short-term management solution, the possible consequences of the salvage harvesting on the forest ecosystem have not been assessed yet.
- Value of forests to the First Nations: The forest has great socio-economic and cultural values to the Champagne and Aishihik First Nations who officially acquired their traditional territory in 1995 after signing land claim agreement. However, the increasing

forest disturbances have threatened the sustainability of those values derived from the forests.

- Forest management issues and initiatives: To manage forest disturbances and to achieve long-term forest sustainability, a forest management initiative was started with the approval of the SFMP in 2004. A detailed ecosystem assessment in response to bio-geoclimatic and disturbance factors was suggested by SFMP (2004), NCE (2006) and Ogden (2007) in order to support forest management decisions in the region. Accordingly, this research was conducted as a part of the research agreement made between the University of British Columbia and the Government of Yukon in November, 2007.

2.2 Study area description

The CATT extends across four eco-regions of Yukon: the St. Elias Mountains, the Ruby Range, the Yukon Southern Lakes and the Yukon Stikine Plateau; these characterize the landscape diversity and variability (SFMP, 2004). The study area occupies a latitudinal range between 60.63 and 61.20 ºN and a longitudinal range between -137.35 and -136.97 ºW (Figure 2.1). The climate of the study area is characterized by cold winters and warm/dry summers, with mean annual temperature -1.65 °C and annual precipitation of 319.5 mm. The elevation range of the study area is 651 to 1158 meters above Mean Sea Level (MSL). The soil texture varies from mixtures of sandy and silty fluvial deposits beside rivers and lakes in lowland areas to mixtures of sandy and silty clays in the remaining area. The study area is dominated by white spurce stands (about 87%), with majority of them age class between 80 to 120 years (SFMP, 2004).

Approximately 380,000 hectares of forest were affected by the recent beetle outbreak (SFMP, 2004). Most of the beetle-affected forests that were not harvested or affected by fire had the highest stand densities (1400 stem/ha) and 63.93% average crown cover (Table 2.1). Evidence of past fire is common in the study area. Between 1946 and 2003, the region experienced 23 large fires and numerous small fires (SFMP, 2004). Most of the areas in the region burned in the 1950s. Past fires were identified by the presence of burnt logs. These old fire sites mostly had mixed stands of white spruce and trembling aspen, with an average of 48% crown cover and 8.21 cm soil organic depth (Table 2.1), and had no evidence of spruce bark beetle activity. The most recent large fire occurred in 1998 about 15 kilometres (KM) east of Haines Junction along the Alaska Highway (research block D, Figure 2.1), severely affecting both the forest crown and the soil. Prior to the fire, these forests had been affected by spruce bark beetle. Plots[2] in the recent fire indicated low average crown cover (12%), organic depth (2.75 cm) and soil moisture (19%), indicating a higher fire severity (Table 2.1). Salvage harvesting of beetle-affected trees started in 2006 in research blocks 5 and 6 (Figure 2.1). Dead trees were removed, with severe impacts to both the soil and understory vegetation due to the operation of heavy equipment. The harvested plots also had lower average organic depth (5.19 cm) and soil moisture (18.59%). Based on the types and intensity of disturbances, the disturbed plots could broadly be categorized as (i) high severity: plots with a combination of either spruce bark beetle and fire (fire plots) or spruce bark beetle and salvage harvesting (harvested plots), (ii) medium severity: plots which had more than 50% spruce bark beetle infestation without fire and salvage harvest (beetle plots), and (iii) low severity plots: plots with traces of old fires and unaffected by spruce bark beetle (old fire plots).

[2] Explanation on plots and blocks are provided in the next section.

2.3 Data collection

2.3.1 Sampling methods

The selection of the most appropriate sampling method depends upon various factors, as there is no ideal technique for vegetation monitoring (Korb et al., 2003). The selected technique should have an acceptable level of precision, and be replicable, feasible, realistic and inexpensive (Sutter, 1996).

Stratified systematic sampling (Kindt and Coe, 2005) was applied for the collection of data in this research. Stratified sampling has been suggested for landscape-level vegetation assessment when the vegetation has heterogeneous characteristics (Kindt and Coe, 2005; Cooper et al., 2006; Rolecek et al., 2007). The stratified sampling technique captures the representative heterogeneity of landscape (Cooper et al., 2006), captures the major sources of variability and is useful for gradient analysis and comparing the results (Kindt and Coe, 2005). Similarly, a systematic lay-out of the plots has a comparative advantage over random sampling as it is easier, saves time, avoids the chance of too short or too great distances between the plots and is useful for assessing environmental gradients (Kindt and Coe, 2005).

Data were collected from 90 sample plots from six blocks (with five distinct strata types) in the forest landscape of the CATT (Figure 2.1, Table 2.2). The plots were classified into five strata based on the disturbance type i.e. (I) undisturbed forest (control), (II) an old fire area (>50 years old), (III) a recent fire area (<20 years old), (IV) a spruce bark beetle affected area, and (V) a salvage-harvested area. The plots were identified and mapped using the local knowledge of the Yukon Government's Ministry of Energy, Mines and Resources (MEMR) and Champagne and Aishihik First Nations (CAFN) government in the summer of 2008.

Vegetation, soil and fuel data were collected in a nested system based on 20 m x 20 m sample plots. The number of sample plots in each stratum depended on the size of the respective research area. A summary of the plot design is given below (Figure 2.2).

I. The landscape was divided into six blocks (with five strata as shown in table 2.2) based on discussion with YG and the CAFN government.

II. In each block, a point of commencement (POC) was chosen, which was generally a landmark located along the road.

III. A random bearing was selected using random numbers. The first plot was selected 100 meters (m) from the POC towards the direction generated by the random bearing selection. The subsequent plots were selected accordingly 100 m apart systematically following the dominant topographic gradient.

IV. A plot centre and four corners of the plots (20 m x 20 m) were marked with the help of compass and tape. GPS points and other various geographical parameters such as altitude, slope, aspect, vegetation types, and vegetation conditions were recorded.

V. With each 400 m^2 plot, three 5 m x 5 m (25 m^2) nested subplots were randomly selected and used to collect seedling, sapling, and shrub data.

VI. Regeneration density and herb/shrub/bryophyte cover were collected from three randomly selected 1 m x 1 m subplots located within the 25 m^2 subplots.

VII. One soil pit was dug in a randomly selected location within the 400 m^2 plot to determine soil characteristics.

VIII. There were a total of 90 plots, 270 subplots and 270 mini plots. The locations of the plots were recorded by GPS for future monitoring.

IX. Data collected from the 20m x 20m, 5m x 5m and 1m x 1m plots are given in Table 2.3.

2.3.2 Variables

The data were classified broadly into topographic, stand structure, edaphic, climatic and disturbance regime categories (Table 2.4). Basal area, slope, elevation, organic depth and average moisture were converted into categorical variables for the purpose of the analysis (Table 2.5).

2.3.2.1 Topographic variables

Topographic variables represent macro-scale factors and for this study consist of latitude, longitude, elevation, slope and aspect. Aspect was transformed into Cosine of aspect ($COS\alpha$ = *northness*) and Sine of aspect ($SIN\alpha$ = *eastness*). The northness value ranges from 1 to -1 (1 = northward, -1 = southward, 0 = either eastward or westward). Similarly a SINα value close to 1 represents east-facing slopes (1 = eastward, -1 = westward, 0 = either northward or southward) (Robert, 1986).

2.3.2.2 Stand structure variables

At each plot, tree[3] density (number of trees per ha), diameter at breast height (DBH) and height

[3]Tree: Vascular plant more than 1.3 meter height and 7 cm diameter.

(Ht) of trees (based on height dominance classes), crown cover (%), shrub[4] cover (%), herb[5] cover (%), seedling[6] density (number per ha) and sapling[7] density (number per ha) were recorded (Table 2.3), which represent the meso-scale factors. The definitions for tree, seedling, sapling, herb, and shrub followed the Yukon Monitoring Guideline (Ogden, 2008). Total and species-specific basal area (BA) per hectare were calculated. Average BA, DBH and Ht were calculated for each block to assess block effects. Tree and regeneration density were converted into a per hectare basis to standardize the data from plots and sub plots.

2.3.2.3 Ecological variables

Vegetation data were collected as percent cover in 270 nested mini plots (1 m x 1 m). The vegetation included all bryophytes, lichens, herbs, shrubs and tree regeneration by species within the mini plots. Due to the different height layers of the vegetation, in many cases the total percent cover for all vegetation was more than 100%. Species were identified using local flora (Cody, 2000; Johnson et al., 1995). Photographs were taken and specimens were collected to verify the species. The vernacular and scientific names of the species and their code names are provided in Appendix A.

The edaphic variables of soil depth, soil moisture and soil texture were used as micro-scale variables. Soil moisture was collected from different layers of the soil using a Vernier soil moisture sensor (accuracy +/- 4%), which measures the dielectric permittivity of soil to

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[4]Shrub: Woody plants higher than 15 cm height

[5]Herb: Any herbaceous species (irrespective of height) and any plant under 15 cm height

[6]Seedling: Tree species less than 1.3 meter tall

[7]Sapling: Tree species with more than 1.3 meter tall but less than 7 cm diameter

determine the volumetric water content. Soil moisture was taken in single snapshot within two months perod during field study. Multiple soil moisture readings were taken from each soil pit, and these were averaged for the purpose of the statistical analysis. Soil texture was segregated into percentage of sand and clay based on the classification of each sampled soil layer, and converted into soil texture classes in the field using a standard soil texture diagram.

2.3.2.4 Climatic variables

Climatic variables were used to represent large-scale factors. The ClimateBC model (Wang et al., 2006) was used to project mean annual temperature, mean annual precipitation, mean annual maximum temperature, mean annual minimum temperature, number of frost free days, number of days below 0 °C and number of days above 5 °C for each plot (Table 2.4). Climate normals were based on the years 1970 to 2000. The ClimateBC model uses longitude, latitude and elevation to project climate variables. The standard error of predictions for ClimateBC monthly temperatures and precipitation varies from 0.8–1.3 °C for temperature and 8 to 24 mm for precipitation (Wang et al., 2006). The variations in mean annual temperature and precipitation of the study area were 1.2 ^{o}C (range = from -2.4 ^{o}C to – 1.1 ^{o}C) and 80 mm (range = 290 mm to 370 mm), respectively.

2.3.2.5 Disturbance regime

Disturbance was considered as an explanatory variable and represented large-scale variation. The four types of disturbances considered in this study were old fire (> 50 years), new fire (<20 years), spruce bark beetle and salvage harvest.

2.4 Data analysis

Various simple and multivariate statistics were used to achieve the objectives of the research. Descriptive statistical analyses were undertaken for all the dependent and independent variables; these are presented in Appendix B. They helped to visualize the nature of data, their distribution and central tendency. The necessary data conversions were undertaken as per the requirement of each research question. This section provides only the names of the tools used in each research chapter. The details of each analytical tool are provided in the respective research chapters.

2.4.1 Stand structure analysis (Chapter 3)

Correlation coefficients, analysis of variance (ANOVA), proportionate ratio of regeneration versus parent trees, basal area ratio, density index, Shannon-Wiener structural diversity index, multiple co-inertia analysis, geographical information system (GIS) are used in chapter 3 to assess the stand structure variation in the landscape.

2.4.2 Regeneration analysis (Chapter 4)

Multivariate canonical correlation analysis, negative binomial generalized model and the most nearest neighbour imputation model are used in chapter 4 to analyse the distribution and abundance of regeneration in the study area.

2.4.3 Vegetation diversity analysis (Chapter 5)

Simpson's index, Shannon-Wiener index, richness, abundance and evenness analysis, Renyi's profile, species spatial distribution and range calculation, canonical corresspondence analysis (CCA), species accumulation curves and geographical information system (GIS) are used in chapter 5 to describe and analyse the vegetation diversity variation in the study area.

Table 2.1 Characteristics of disturbed plots

Disturbance Type	Soil moisture (%) p < 0.05	Crown cover (%) p < .001	Stand Density (tree/ha) p < .001	Organic depth (cm) p < 0.05	Shrub cover p < .001
Spruce bark beetle plots	25.96	63.93	1400	11.29	40.71
Fire plots	19.82	11.98	247	2.75	36.23
Harvested plots	18.59	29.00	591	5.19	40.08
Non-disturbed	19.42	44.48	789	8.98	61.11
Old fire plots	25.14	48.21	1039	8.21	55.59
Mean values	21.78	39.52	813.2	7.24	46.74

[Note: The above table shows the variation of soil moisture, organic depth, crown cover, stand density and shrub cover by disturbance types. The mean variation of above variables were significant at p <0.05]

Table 2.2 Research blocks and their characteristics

Blocks	No of plots	Elevation range (m)	Slope range (%)	Average white spruce age (years)	Major disturbances	Major species
A	13	933-967	3-24	60	Mostly undisturbed with the traces of old fires	White spruce (dominant), aspen and willow
B*	20	887-1158	3-65	102.8	Traces of old fire and beetle	White spruce (dominant) mixed with willow and aspen
C	10	754-786	4-20	121.8	Old fire	White spruce dominant with the scattered patches of aspen
D*	25	651-693	0-28	123	Recent fire and beetle	White spruce dominant with many patches of willow
E	13	778-791	0-13	93.13	Salvage harvested	White spruce dominant
F	9	773-781	0-22	118.5	Salvage harvested	White spruce and aspen mixed forest

[Note: The table provides the details of each research blocks including number of plots in each blocks, elevation range, slope range, the major disturbances observed and major tree species. The number of plots depends upon the size of the each research block. The block D had the highest number of plots and F had the lowest number. *Blocks B and D are divided into two sub-blocks (B, B1, D and D1) for the purpose of vegetation diversity study.]

Table 2.3 Plot sizes, types of data collected and brief methodology

Variable plot sizes	Data (variables)	Indicators	Methods
20 m x 20 m	Tree counts	By species By dominant class By dead or live	Total enumeration
20 m x 20 m	Crown cover	Total crown cover Crown cover by species	Ocular estimation. An average was considered after three field crewmembers estimated the cover
20 m x 20 m	Tree measurements	Tree height Tree diameter at breast height	Height and diameter of sampled trees of each dominant class were measured
20 m x 20 m	Tree age	Growth ring	Using tree ring borer
5 m x 5 m	Tree counts	By species By dominance class By status (dead or alive)	Total enumeration within the sub plot
5 m x 5 m	Sapling counts	By species By dominance class By status (dead or alive)	Total enumeration
1m x 1m	Shrubs estimation	By species By percentage of area cover in the subplot	Observation and ocular estimation
1 m x 1 m (mid-point)	Soil profile	Depth and texture of organic and mineral horizons (Ogden, 2008) Rooting depth Total depth Soil moisture Soil temperature	A soil pit was dug to the depth of the hard pan, and profiling the horizons using key. A moisture meter was used to measure soil moisture and temperature
1m x 1m	Regeneration count	By species	Total regeneration count for each species
1m x 1m	Herbs estimation	By species By % of area cover in the mini plots	Ocular estimation with proportionate area covered by each species

Table 2.4 Variables (with full and code names) collected and generated for analysis

Geographical variables and disturbance regime	Ecological Variables	Stand structure variables	Climate variables (1971-2000 mean) generated from BC climate model
Aspect {cosasp, sinasp}	Density of white spruce (STT)	Total basal area (ToBA)	Mean annual temperature (MAT)
Slope (slope)	Density of trembling aspen (ATT)	White spruce basal area (SpBA)	Mean annual precipitation (MAP)
Latitude (lat)	Density of balsam poplar (PTT)	Trembling aspen basal area (AtBA)	Maximum summer temperature (TMXsm)
Longitude (long)	Number of white spruce seedlings (SpsedTot)	Balsam poplar basal area (PoBA)	Minimum summer temperature (TMNsm)
Elevation (ele)	Number of trembling aspen seedlings (AtsedTot)	White spruce average height (Spavht)	Maximum winter temperature (TMXwt)
Disturbances	Number of balsam poplar seedlings (PosedTot)	Trembling aspen average height (Atavht)	Minimum winter temperature (TMNwt)
Old Fire (OLDFR)	Average soil moisture (AM)	Balsam poplar average height (Poavht)	Number of frost free days (NFFD)
New Fire (FR)	% of clay (CL)	White spruce average diameter (at breast height) (Spavdia)	Number of days above 5^0C (NDD>5)
Spruce bark beetle (BT)	% of sand (SA)	Trembling aspen average diameter (at breast height) (Atavdia)	Number of days below 0^0C (NDD<0)
Salvage harvest (SALV)	% of shrub (shrubcov)	Balsam poplar average diameter (at breast height) (Poavdia)	
No disturbances	% of herb (herbcov)		
	% of bryophytes		
	% tree regeneration		
	Total crown cover (TCC)		

Table 2.5 Categorized variables

Variables	Very High (E)	High (D)	Medium (C)	Low (B)	Very Low (A)
Trembling aspen basal area (m^2/ha)	> 8	6.1 to 8	4.1 to 6	2.1 to 4	< 2
Balsam poplar basal area (m^2/ha)	1.6 to 2	1.2 to 1.6	0.8 to 1.2	0.4 to 0.8	<.4
White spruce basal area (m^2/ha)	> 40	30.1 to 40	20.1 to 30	10 to 20	<10
Elevation (m)	>1050	951 to 1050	851 to 950	751 to 850	650 to 750
Slope (%)	-	>30	15.1 to 30	1 to 15	0
Soil organic depth (cm)	>24	18.1 to 24	12.1 to 18	6.1 to 12	0 to 6
Average moisture (%)	>40	>30 to 40	>20 to 30	>10 to 20	0 to 10

[Note: The variables were categorized for the purpose of ANOVA test and plotting the mean variation.]

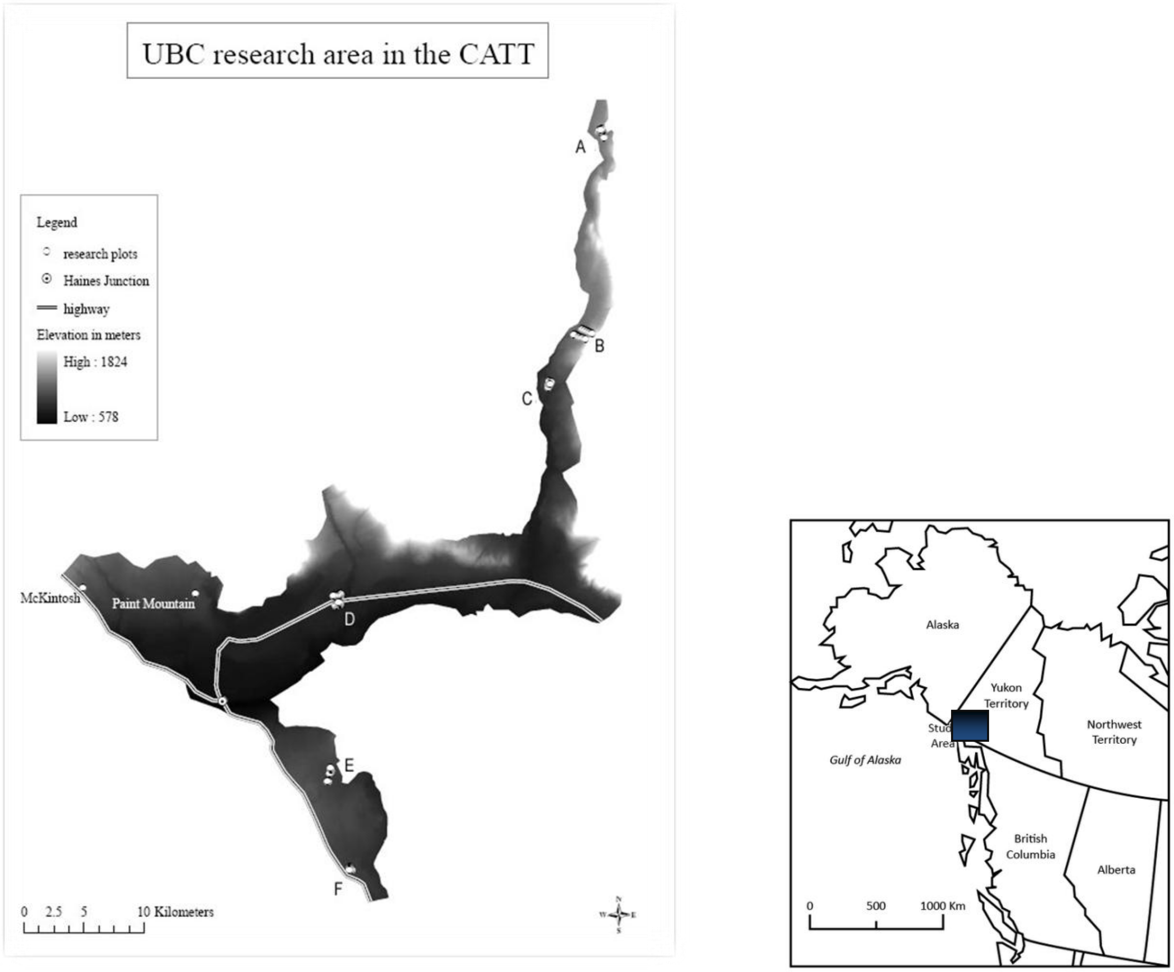

Figure 2.1 Map of the study area showing blocks and plots where the data were collected.

[Note: Black A is mostly undisturbed forest predominantly consists of white spruce with small patches of Aspen and Willow; Block B has traces of old fires in 50% of its plots and consists of white spruce dominancy with scattered patches of Willow bushes; Blocak C has old burnt logs in the most of the plots and consists of White spruce and Aspen; Block D has been affected by spruce bark beetle and was gone through recent fire and has White spruce with scattered patches of Willow; Block E has beetle and harvesting and consists mainly White spruce trees; Block F is a harvested plot and has mixed of White spruce and Aspen trees.]

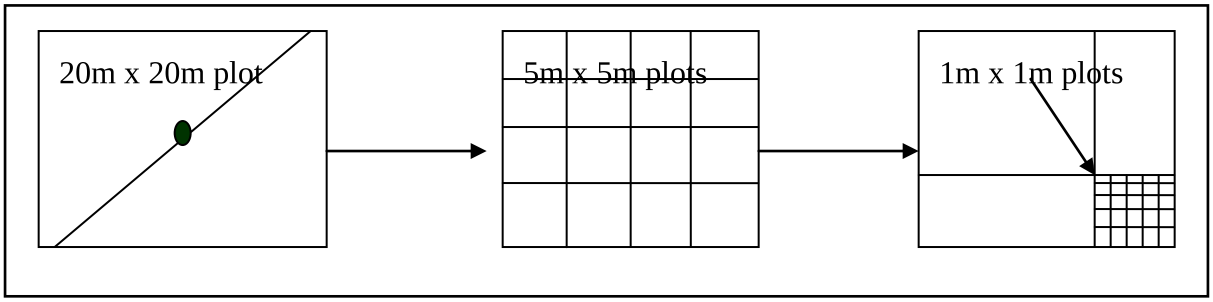

Figure 2.2 Plot design

[Note: The square plot with dimension of 20 m length and 20 m breadth was designed for the purpose of data collection. The 20 m by 20 m plot was divided into 16 sub-plots of 5 m x 5 m. Three sub-plots were further divided into 25 micro plots, each 1 m by 1 m in size for the purpose of micro site assessment including soil texture analysis, regeneration and herbs count]

3. Stand structure variability in response to bio-geoclimatic and disturbance factors in southwest Yukon

3.1 Introduction

Stand structure has important implications for forest ecosystem health, biodiversity conservation and forest management (Sturtevant et al., 1997; Kimmins, 1997; Kuuluvainen, 2002; Brassard and Chen, 2006). Although, forest composition and structure are generally affected by bio-geoclimatic factors and the temporal and spatial scales of disturbances (Bonan and Shugart, 1989), the resulting ecosystems may vary depending upon the extent and magnitude of disturbances and geo-climatic variations. Forest managers need to understand disturbance dynamics and their effects on ecosystem structure so that better management practices can be used, yet such an understanding is still lacking for many forest types in the boreal forest including in SWY (Martin and Gower, 2006). This chapter deals with the variation in stand structure and composition in response to bio-geoclimatic factors across multiple disturbance regimes in southwest Yukon.

Stand structure is defined as the “physical and temporal distribution of trees within a stand” (Oliver and Larson, 1996), including species dynamics such as spatial pattern, horizontal and vertical distribution, and size and age of trees (Stone and Porter, 1998). The change in stand structure over time refers to stand dynamics (Oliver and Larson, 1996). Climate, disturbance, permafrost, soil moisture, soil temperature, oceanic influence and complex interactions among physiographic patterns determine structure and composition in the boreal forest (Bonan and Shugart, 1989; Larsen, 1980). Bonan and Shugart (1989), Lawrence and Oechel (1983) and

Tryon and Chapin (1983) consider soil moisture and temperature as important factors for soil nutrition and tree growth as they can slow decomposition and lead to the high accumulation of organic matter. In Alaska and the Yukon, climatic and site factors influence the forest composition and future stand development by affecting post-fire recruitment (Johnstone et al., 2004).

Stand heterogeneity typically increases with increasing stand age indicating that the stand structure and composition are a result of gaps caused by disturbances (Cumming et al., 2000; Brassard and Chen, 2006). The magnitude and intensity of spatial and temporal disturbances shape landscape structural development by creating periodic gaps (Lorimer, 1989) and by developing a mosaic of development patches of varying age and size structure (McCarthy and Weetman, 2006). The variations in disturbance characteristics such as frequency, size and severity strongly influence ecosystem properties and processes (Johnstone and Chapin, 2006b). In the boreal forest, fire is considered to be the most important disturbance agent (Amiro et al., 2001). However, other disturbances such as insect and disease outbreaks, wind throw and salvage harvest are also important in shaping forest structure and composition (Blais, 1981; Bergeron et al., 1995).

Fire may affect stand structure in various ways. The spatial and temporal variability of fire cycles (Payette et al., 1989; Bergeron, 1991) creates a mosaic of stand compositions ranging from post-fire early successional deciduous species to mixed and pure coniferous stands in older post-fire stands (Bergeron & Dansereau, 1993). In eastern Canada, longer fire intervals increase the chance of a spruce budworm (*Choristoneura fumiferana* Clemens) outbreak due to increased proportion of late successional species such as spruce and fir (Bergeron and Leduc, 1998). Stand mortality due to insect outbreaks can alter stand structure and composition (Bergeron et al., 1995; Harvey et al., 2002). The absence of disturbance can also affect stand structure through the processes of competition and succession; these gradually change pure deciduous stands to mixed stands and then to coniferous stands in the boreal forest (Bergeron & Dansereau, 1993). As stand composition changes from pure to mixed stands, the forest productivity may also change significantly (Linder, 1998 & Brassard and Chen, 2006).

Climate can play an important role in stand structure and tree growth (Lloyd and Fastie, 2002). Climate directly affects the growth and behavior of individuals, modifies population size and structure, affects ecosystem structure and function by affecting decomposition rates, nutrient cycle, water flows, and distributing ecosystems within landscapes (Gitay et al., 2002). An example of a climate impact on growth is the observed growth reduction of trees associated with higher temperatures and drought stress as a result of recent climate change (Barber et al., 2000). Higher temperatures can significantly reduce tree growth at both altitudinal and latitudinal limits (Lloyd and Fastie, 2002). Species composition is also highly affected by species tolerance to shade and moisture stress. For example, as a light-requiring species, trembling aspen typically occupies the early stages of succession when light is sufficient for their growth; over time aspen is replaced by white spruce and/or other shade-tolerant species resulting in changes in stand structure and composition (Bergeron and Dubuc, 1989). Drought plays a key role in limiting species distributions (Aber et al., 2001; Hannah et al., 2002). Climate also affects forest structure indirectly by influencing fire regimes and the spread of insects and pests (Dale et al., 2001).

Topographic factors are also important in shaping vegetation structure and composition as they affect the availability of solar radiation, soil temperature, soil moisture and nutrient cycles (Van Cleve et al., 1983). Viereck et al. (1983) and Van Cleve et al. (1991) state that topography together with soil parent materials and disturbance regimes contribute to tree species composition. Similarly, site conditions also determine the species composition and structure.

Site variability can also influence stand structure (Brassad and Chen, 2006). Soil, water and nutrient availability influence tree growth in boreal and temperate forests (Stoeckeler, 1960; Lambers et al., 1998). Harper et al. (2005) found structural differences according to site type and moisture regime in the western boreal forest of Québec. Environmental variables such as slope angle, elevation, organic matter depth, and humus type affect site productivity, which in turn influences the diameter and height of stands (Boucher et al., 2006). Site type also influences stand composition, which in turn can determine the density and basal area of a stand (Chen and Popadiouk, 2002; Popadiouk et al., 2003).

3.2 Research problems, hypotheses and questions

The literature indicates that stand structure of boreal forests is affected by disturbances, climatic factors and site variability; however, as the boreal forest is a complex mixture of uneven-aged stands (Martin and Gower, 2006), its structure and composition can vary significantly from region to region depending upon specific disturbance regimes, site characteristics and climatic variability. As an increase in fire frequency is predicted to occur due to climate change (Bergeron and Flannigan, 1995; Flannigan et al., 1998), an understanding of how stand structure varies according to disturbance and climatic factors has been suggested as being important for improving management practices (Brassard and Chen, 2006). Specifically, it is important to understand which factors play a dominant role in shaping stand structure and how they affect the overall forest productivity. According to Martin and Gower (2006), such an understanding is still lacking for many forest types within the boreal forest including that of Southwest Yukon

(SWY). The main purpose of this chapter is therefore to assess how the structure and composition of the boreal forests of the CATT varies by bio-geoclimatic factors and disturbance regime. Specifically, this chapter will deal with the following hypotheses;

(i) I hypothesized that relationships among stand structure variables (diameter, density in stems per hectare, and basal area) vary significantly by stand type and are affected in my study area by edaphic factors. Specifically, I expect that mean stand diameter will decrease with increasing stand density, and this will be more pronounced in pure stand types and on sites with more fertile soils. I also expect higher stand productivity will occur in pure stands compared to mixed stands.

(ii) I hypothesized that forest composition, structural diversity, and forest productivity will vary significantly by disturbance type in the study area. Specifically, I expect that the density of white spruce would increase with any disturbance but that the proportion of broadleaved trees and regeneration would increase with disturbance severity, particularly following fire.

(iii) Climatic factors are expected to have significant impacts on current and future stand structure and composition. I hypothesized that stand structure and composition will vary significantly within climatic variability. I expect to observe higher mean diameter, height and stand productivity in warmer and wetter locations.

In addition, the research addressed the following research questions, which may be important to support the forest management decision making in the CATT.

- What are the overall stand structures and composition in the study area? How are the structural variables related?
- To what extend do stand structure variables such as diameter, height and density and their relationships significantly vary along environmental gradients?

3.3 Data analysis

The required data were collected from Southwest Yukon and are described in Chapter 2. This section deals only with the data analysis specific to this chapter.

3.3.1 Calculation of average diameter and height

Average height and diameter for each species were calculated. As DBH and Ht were measured for each dominance class, the average DBH and Ht values were normalized as follows;

Normalized average DBH = (DBH of Dominant tree *number of dominant tree + DBH of Co-dominant tree * number of co-dominant tree + DBH of intermediate tree x*number of intermediate tree + DBH of suppressed tree* number of suppressed tree)/total number of tree.

A similar formula was used for the normalization of height. Based on average diameter, average basal area was calculated using the formula [$BA = \pi r^2$] where, $\pi = 3.14$ and r = radius of the tree at breast height.

3.3.2 Calculation of stand structure and composition

Stand structure and composition were assessed using three different indices. The proportions (%) of the density (number of stems/ha) of tree, seedling, and sapling of each species with respect to the total density for that species were calculated. Similarly, average height and diameter of each species by dominance class were calculated to assess the species composition in the study area. Species composition was assessed using basal area ratio of a species with the total basal area (Huang and Titus, 1995), which can be calculated as "*species composition of specific species* =

basal area of the species/total basal area". The values range from 0 to 1 where a value of 0 indicates the absence of the species and 1 indicates a fully stocked species.

3.3.3 Density index

A density index was developed to compare the density of trees, saplings and seedlings of white spruce, trembling aspen and balsam poplar by disturbances regime with respect to average density on all 90 plots. To aid comparison, the average density of 90 plots was converted to 100% "as an index". The percentages of density of trees, saplings and seedlings with respect to total density by disturbance regimes were calculated as follows;

$\boldsymbol{D_i = \{D_d|D_t\}^{*}100}$ **..................................Equation 3-1**

where, D_i is the density index, D_d is the average density of tree, saplings or seedlings in a particular disturbance regime and D_t is the average density of the trees, saplings or seedlings in the 90 plots.

3.3.4 Calculation of variation of structural diversity index across disturbance regime

The Shannon-Wiener index (Shannon and Weaver, 1949) has been frequently used to assess structural diversity. The Shannon-Wiener index has also been applied to species size diversity by grouping the DBH and Ht values into classes (Staudhammer and LeMay, 2001; Lexerod and Eid, 2006). The diameter and height diversities of white spruce and aspen were calculated across disturbance regime by using the following formula (3.2):

$\boldsymbol{H' = -\sum(D_i * LnD_i)}$ **....................Equation 3-2** where, H' is the Shannon-Wiener Diversity Index and $D_{i,}$ is the proportion of each diameter class (N). The value ranges from 0 to Ln[8] (N) where N equals the number of diameter classes (Lexerod and Eid, 2006). The Shannon-Wiener diversity index is useful for assessing stand diameter/height structure when classifying forest structural types (Boucher et al., 2006). The index has previously been used in coniferous forests (Sarkkola et al., 2003).

3.3.5 Calculation of correlation coefficients and scatter plots

R^2 values were calculated for the variables related to stand structure. Scatter plots with fitted regression lines were constructed when both dependent and independent variables were numerical and plots of means were calculated for the nominal independent variables. The significance of the plots was tested using regression goodness-of-fit tests for scatter plots and ANOVA for the means of plots. R statistical software, version 2.12.0 (R Core Development Team, 2005) and MS Excel, version 2007 (Microsoft, 2007), were used to calculate ANOVA, R^2 values and to plot the relationship among variables.

3.3.6 Multiple co-inertia analysis (MCoA)

In addition to the above statistical tools, MCoA was used to assess the relationship between environmental variables and stand structure. MCoA has been recommended for the analysis of the response of community composition to environmental conditions (Dole'dec and Chessel,

[8] Natural Log

1994). It is a multivariate tool that analyzes the common structures of pairs of data tables and is more flexible than some other multivariate techniques, as it can utilize both qualitative and quantitative variables (Dray et al., 2003). It is a symmetric coupling method, which uses the co-inertia criterion on a set of orthogonal vectors (Chevenet et al., 1994). It aims to find vectors in species and environmental spaces with maximal co-inertia (Dray et al., 2003) and works on the co-variance matrix (Chevenet et al., 1994). Similarly, it is linked to partial least-squares regression (Dray et al., 2003).

MCoA is able to carry out the simultaneous ordination of several tables (Bady et al., 2004) and can simultaneously analyse the spatial and temporal variations in data (Dray et al., 2003). It optimises the variance within each individual and optimises the covariance between several individual ordinations (Bady et al., 2004). The method uses a pair of tables; if the number of tables is equal to one then the method corresponds to Principal Component Analysis (PCA) (Bady et al., 2004).

3.3.7 Geographical information system (GIS)

The GIS database developed by the Yukon Ministry of Energy, Mines and Resources (MEMR) was used to illustrate the species distribution, crown cover, forest types and average height in the study area. A shape file of the study area landscape was used as a mask to clip the database from the MEMR GIS database using ArcGIS software (ESRI, 2009).

3.4 Results

3.4.1 Stand composition

In this study, 2944 trees were sampled from 90 plots, each 400 m^2 in area (the total area sampled was 3.6 hectares). As expected, white spruce dominates the landscape with 87.5% stem cover followed by aspen and balsam poplar, which cover 12.2% and 0.3% respectively (Table 3.1). Mixed stands had higher stand density (1063 stems/ha) than pure aspen stands (300 stems/ha) or pure white spruce stands (848 stems/ha). Similarly, white spruce had the highest sapling cover with 67.8%, followed by aspen (31.4%) and balsam poplar (2.6%) (Table 3.1). Stand composition index analysis (Huang and Titus, 1995) indicated that white spruce has the highest index (0.907), indicating the highest stocks on the landscape, followed by aspen (0.09) and balsam poplar (.001) (Table 3.2). The species distribution is shown in Figure 3.1.

3.4.2 Average height, diameter and basal area of species by height class

An average height, diameter and basal area of white spruce and trembling aspen are provided in Table 3.3. The average stand height is plotted in Figure 3.2. The results indicated that the white spruce intermediate tree class was the most frequent on the landscape with 24.3% of the total cover. Its co-dominants, however, had the highest basal area, with 42.64% of the total in the landscape followed by white spruce co-dominant (20.6%) and dominant trees (18.3%). Similarly, trembling aspen had the highest number of co-dominant trees, covering 7.5% of the total cover, followed by intermediate trees (6.7%). Mixed aspen and white spruce stands had higher basal areas per plot (= 13.65 m^2/400 m^2) compared to pure white spruce stands (= 13.27 m^2/400 m^2).

3.4.3 Shannon-Weiner structural diversity Index across disturbance regime

Shannon-Weiner structural diversity indices for white spruce and trembling aspen across disturbance regime (Table 3.4) indicated that white spruce heights and diameters were more diverse in undisturbed plots. Similarly, trembling aspen heights and diameters were more diverse in undisturbed and old fire plots respectively. The results indicated that structural diversities were higher in undisturbed plots.

3.4.4 Analysis of stand structure variations using regression fit line (scatter plots) and ANOVA plots (plots of means)

3.4.4.1 Variation in stand diameters and heights by geo-climatic factors

The scatter plots with fitted regression lines (Figure 3.3 and Figure 3.4) showed an increasing trend of average diameter and height of white spruce with decreasing slope percentage and elevation, which indicated that overall white spruce productivity decreases with increasing elevation and slope. The average spruce height also increased with increasing soil moisture on northeast aspects (Figure 3.4). The variation in white spruce height and diameter by climatic factors was not significant. Similarly, the average white spruce diameter was positively correlated with average height ($r^2 = 0.89$, $p<0.05$) and tree density ($r^2 = 0.23$, $p<0.05$); however, average diameter decreased when the average density exceeded 500 trees per hectare (Figure 3.5).

Figures 3.3 and 3.4 indicate that white spruce average heights and aspen average diameters were significantly higher at lower elevation, in plots with loamy sandy soil and on eastern aspects. White spruce average diameter was positively correlated with stand density (r^2 = 0.2, p<.05) and basal area (r^2 = 0.3, p<.05) (Figure 3.5; Tables 3.5 and 3.6). The relationships between the average diameter and height of balsam poplar and the various environmental variables were not significant.

3.4.4.2 Variation in stand density and basal area by geo-climatic factors

The average stem density and basal area of white spruce varied significantly by climatic, topographical and edaphic factors in the study area (Figures 3.6 and 3.7). Average densities were higher on sites occupying lower slopes, with higher mean annual temperature, with higher moisture levels, and with greater organic depth. As with diameter, white spruce average basal area (BA) decreased with increasing elevation and slope but increased with increasing number of growing degree days > 5 ^oC (Figure 3.6). A higher BA was found on northeastern and southern aspects. Productivity graphs (Figure 3.5) and r^2 values (Table 3.6) indicate that average white spruce basal area was correlated with tree density and diameter, with r^2 values of 0.73 (p<.01), and 0.43 (p<.05), respectively. White spruce age did not show a strong correlation with diameter (r^2 = .04, P>.05) or height (r^2 = 0.1, P>.05).

The relationships between stem densities and basal areas of trembling aspen and balsam poplar and climatic and edaphic variables were not significant. However, plots of means (Figure 3.9) indicated that they were higher on NE and SW aspects and on sandy to loamy sandy soils. Similarly, the plots of means (Figure 3.8) indicated that balsam poplar is typically found on either southern aspects, sandy soils or a combination of the two. Productivity graphs (Figure 3.5) and r^2 values (Table 3.6) indicated that aspen basal area was loosely correlated with its diameter

($r^2 = 0.3$, $p<.05$) and height ($r^2 = 0.25$, $p<.05$); but was strongly related with its stand density ($r^2 = 0.76$, $p<.01$).

3.4.5 Impacts of forest disturbances on stand structures

The density index results (Table 3.7) revealed that the density of white spruce tree was higher than average (mean index value for 90 plots = 100) in beetle-affected plots (196) and old fire plots (120) and much lower in the recent fire plots (32). However, the number of white spruce seedlings was higher in fire plots (205), followed by beetle plots (157). Similarly, the density of aspen trees was higher than average in the old fire (197) and undisturbed plots (137) and less than average in recent fire plots (20). Aspen saplings and seedlings had higher than average densities in the harvested and recent fire plots. The densities of balsam poplar saplings and seedlings were higher than average in harvested plots (257 and 418, respectively), and its seedlings had higher than average densities in the fire plots (370).

The ratios of tree regeneration to parent trees across the disturbance regime showed an interesting trend (Table 3.8). With the exception of the fire and harvest plots, the ratios were less than one, indicating fewer seedlings and saplings than parent trees. However, with aspen, the ratio was higher than one in all the disturbance regimes, indicating greater numbers of regenerating trees than mature trees. The ratio was very high in fire plots (1:6 for white spruce and 1:45 for aspen). Although, the number of balsam poplar trees was negligible in the plots, regeneration (consisting of a few individuals) was found in both the fire and harvested sites.

Similarly, Figure 3.9 provides the plots of means that show the relationship between the types of disturbances and stand structure variables. The plots that were significant with 95%

confident level (p<.05) are discussed. The plots indicated that the density and basal area of white spruce were higher in beetle-affected plots than other plots. Similarly, both density and basal area of aspen were significantly higher in old fire plots. Density and basal area of balsam poplar were not significantly correlated with disturbance type.

3.4.6 Multivariate analysis of stand structure variables using multiple co-inertia analysis (MCoA)

MCoA was used to analyse the relationship between structural variables and geo-climatic factors. The output tables are provided in Appendix C. The output graphs provided a clear indication of the relationship between stand structure and environmental variables. In Figure 3.10, the average height of white spruce clearly increases[9] with increasing summer maximum mean temperature, eastern aspect (Sin aspect) and decreases with increasing slope, elevation and summer precipitation. Similarly, trembling aspen average diameter increases with increasing degree-days > 5 ºC but decreases with increasing depth of organic soil, elevation and slope. Balsam poplar diameter and height increase with increasing mean annual temperature, number of frost-free days and minimum average summer temperature.

The species/environment axis (Figure 3.11) shows a similar trend. However, it shows the relationship between environmental factors and white spruce average diameter and trembling aspen average height, which were unclear in Figure 3.10. White spruce average diameter

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[9] It is assumed that the mean age of white spruce is not significantly different in the study area as no management interventions were carried out in the past.

increases with increasing mean annual precipitation and trembling aspen average height decreases with increasing elevation and slope.

3.5 Discussion

3.5.1 Relationship between stand density, basal area, age and tree size

3.5.1.1 Stem density vs. tree sizes

I found an inverse relationship between tree sizes and stand density for spruce and trembling aspen, in agreement with my first hypothesis that diameter declines with increasing density. Although, the density of co-dominant white spruce was 4% less than that of the intermediate class, the basal area was 22% higher (Table 3.3), indicating that there is an inverse relationship between tree size and density of the stand and that the average diameter plays a greater role than density in increased forest productivity (basal area). The results also indicated that a decreasing trend in the average diameter of white spruce occurs when tree density exceeds 500 stems per hectare (SPH). Generally, stand density has an inverse relationship with tree size (Lee et al., 1997; Delong and Kessler, 2000; Martin and Gower, 2006), resulting in old growth stands having larger trees and lower densities due to self-thinning processes (Delong and Kessler, 2000). My results suggest that this relationship holds true below 500 SPH; at greater stand densities tree size may become limited by inter-specific competition, whereas at lower densities other factors are at play (Huang and Titus, 1995). The results suggest that thinning and selective harvesting could play an important role in increasing forest productivity in the region.

As with white spruce, the average diameter of aspen was higher when the density was less than 500 stems per hectare. Similar findings have also been reported by Perala (1991), Weingartner (1991) and Kabzem et al. (2007). I found a positive relationship between aspen density and basal area, contrasting with Perala (1984), who reported that basal area and biomass of aspen increase as stand density decreases due to self-thinning processes.

3.5.1.2 White spruce age vs. size

The ages of white spruce were poorly correlated with height and diameter, despite diameter being strongly correlated with height, density and basal area. McCarthy and Weetman (2006) obtained similar results in their study in Newfoundland, reporting that the age difference of trees with equal height and diameter could be more than 120 years. In my study, trees of similar size were found to be > 120 years apart, indicating that tree size is a poor indicator for defining old growth stands. The result suggests that size is more important than age when assessing stand dynamics and productivity in the region, a finding also supported by White (1980).

3.5.1.3 Stand type vs. species basal area and density

I found that the average density in mixedwood stand of trembling aspen and white spruce was 20% higher than in pure white spruce stands. This result contrasts with my expectation that productivity would be higher in pure than mixed stands. For example, Linder (1998) and Brassard and Chen (2006) reported higher densities in pure coniferous stands than in deciduous and mixedwood stands. In my study, however, the average basal area was 11.6% higher in mixed aspen and white spruce stands (13.65 m^2/400 m^2) than in pure white spruce stands (13.27m^2/400 m^2). Linder (1998) also reported similar findings in his study in central Sweden, namely that the BA was more than 21% higher in mixedwood stands compared to pure coniferous stands. In this regard, Kabzem et al. (2007) suggest that the presence of a small amount of aspen has a large effect on spruce productivity but that this effect diminishes when the aspen density is greater than 1000 stems per hectare. However, Stewart et al. (2003) reported that the basal area of pure coniferous stands was higher compared to mixedwood stands. Similarly, Hély et al. (2000) reported higher basal areas in deciduous forests followed by coniferous and mixed stands, but Linder (1998) and Stewart et al. (2003) found lower BA in deciduous stands than old mixedwoods or coniferous stands. The reason for the higher basal areas of mixedwood stands in this study may be due to their higher stand densities compared to pure stands in the study area.

3.5.1.4 Variation of stand structures by edaphic and topographic factors

(i) Stand density

The density of white spruce is generally affected by the interaction of a number of factors and it is therefore difficult to generalize (Wang et al., 1994). In my study, white spruce was more abundant and productive on lower slopes, on sites with higher moisture levels, on S to NE aspects and on soils with a thick organic layer. These findings agree with my expectation that relationships between stand structural attributes vary with edaphic factors, and that productivity increases with site fertility. This finding agrees with studies showing greater productivity of white spruce on silty, alluvial soils (Timoney and Robinson, 1996). White spruce was also found growing well on moderately well-drained clay loams in Saskatchewan (Kabzems, 1971; Qualtierem, 2008) and on decomposed organic matter or a shallow humus layer over mineral soil in Alaska (Purdy et al., 2002).

Similarly, trembling aspen was abundant in sandy to loamy sand soils on southern aspects within the fire plots, which were warmer sites and had the lowest moisture regime, although aspen generally colonizes mostly mesic sites (Gauthier et al., 2000; Brassard and Chen, 2006). Aside from soil moisture, slope position has also been reported as an important factor determining the distribution of aspen (Chen et al., 1998). However, this relationship was not significant in my study. Balsam poplar occurred under similar environmental conditions, mostly in harvested plots. However, the environmental factors affecting the distribution and density of balsam poplar are poorly understood (Bockheim et al., 2003). Floodplain locations with ample moisture have been reported as conducive to poplar growth (Viereck and Foote, 1970; Murray, 1980). Bockheim et al. (2003) reported that balsam poplar was mostly found in areas adjacent to rivers where favourable moisture conditions exist for the species.

(ii) Stand height and diameter

Both multivariate and univariate analyses confirmed that the average heights and diameters of both trembling aspen and white spruce were higher at sites at lower elevation, and on lower slope positions, agreeing with the expectations in my first hypothesis. Site productivity has been suggested as one of the main factors influencing the diameter structure of coniferous stands (Boucher et al., 2006). As soil properties can significantly affect the height growth of boreal trees (Martin and Gower, 2006), lower rates of decomposition and high rates of leaching can cause lower nutrient availability at higher elevations and on steep slopes (Vitousek et al., 1988; Cole, 1995), and these factors may have affected lower height and diameter growth in this study.

White spruce average heights responded positively to soil moisture, and this has been reported to be one of the important factors affecting the height growth and site index of white spruce (Wang, 1995), which also controls the southern limit of white spruce in western Canada (Chhin and Wang, 2008). Similarly, higher average spruce diameters and heights were found on

NE and south aspects and the lowest on N or SE aspects. The reduced diameter growth on the N aspect can be explained by lower temperature, reduced availability of light and thereby shorter growing seasons. Conversely, the reduced diameter on SE aspects could be due to temperature-induced drought (Barber et al., 2000; Juday et al., 2003). Generally hot, dry, summer conditions are exacerbated on S and SE aspects, and may reduce radial growth (Chapin et al., 2004; Barber et al., 2004). Temperature induced summer droughts in the western boreal region were recorded by Barber et al. (2000).

(iii) Stand productivity

I found that forest productivity (basal area per hectare) varied significantly by geographical position with higher basal area at lower elevation and on lower slopes. This could have important, implications for deciding silvicultural system in the study area. A similar trend was found in interior and northern British Columbia (Klinka et al., 1996), and northwestern Quebec (Chen et al., 1998 and Boucher et al., 2006). However, white spruce basal area was not correlated with stand age, which differs from the findings of Popadiouk et al. (2003), who reported increasing basal area with stand age in eastern boreal mixedwoods.

3.5.2 Variation of stand structures by disturbance regime

I found that stand structure and composition varied significantly by disturbance type, leading me to accept my second hypothesis. Disturbances had significant effects on forest composition including species densities and their regeneration, and promoted the development of a broadleaved forest in the region.

A higher density of white spruce trees and their regeneration was found in plots with some kind of past disturbance such as fire or spruce bark beetle, meeting my expectation that white spruce density would increase with any type of disturbance. The higher density of white spruce in old fire plots is indicative of the later stages of succession, which is generally dominated by shade-tolerant species such as white spruce (Brassard and Chen, 2006). The higher density of trembling aspen in old fire and undisturbed plots indicated that these plots are at an intermediate stage of secondary succession (Chapin et al., 2004). The higher regeneration of trembling aspen in recently harvested fire plots indicated that fire promotes aspen regeneration and that the gap dynamics created by these disturbances (harvested plots had 29% mean crown coverage) were sufficient to promote the regeneration of this light-demanding species (Cumming et al., 2000; Kuusela, 1990). Similarly, balsam poplar and its regeneration were also higher in disturbed forests, particularly in harvested plots. Balsam poplar, like trembling aspen, is a shade-intolerant species and prefers open areas to regenerate and grow (Alexander et al., 1990). The increased proportion of broadleaves following disturbance met my expectation that proportion of broadleaved trees and regeneration would increase with disturbance.

3.5.3 Variation of stand structures with climatic factors

I partially accept the third research hypothesis, that one or more climatic variables (e.g. MAT, MAP, TMXsm and NFFD) would significantly affect stand structure of all three species. I only partially accept the hypothesis, as some of the climatic variables were not significantly correlated with the densities of white spruce and balsam poplar, or variation of height, basal area and density of trembling aspen.

I found higher basal area of white spruce on sites with a higher accumulation of growing degree-days and higher soil moisture. Similarly, the results of the multivariate analysis suggested that average diameter increases with increasing mean annual precipitation. These two results agree with my expectation that stand productivity would be greater on warmer and wetter locations. This expands the understanding of Wang and Klinka (1996) in their study in British Columbia, who suggested that the site productivity of white spruce was mostly influenced by edaphic factors rather than climate. In contrast, Chavardes et al. (2012), who undertook their study in the same research plots as my study, found that precipitation was important determining the growth of white spruce, although the relationship varied month to month, with a negative relation found with April precipitation. Barber et al. (2000) reported that the radial growth of white spruce has decreased with increasing temperature in their study sites in Alaska, although this could be connected to soil moisture. Chavardes et al. (2012) also indicated that although white spruce growth was negatively related to maximum temperatures in general, increased precipitation accompanied by warmer temperature were correlated with increased tree growth in the last 30 years. It seems feasible that precipitation is a key factor affecting tree growth in the area but it may interact negatively with increasing temperature. The mean annual precipitation in the study area is of 319.5 mm (ClimateBC, 2006), which is projected to be increased by 20% (ACIA, 2004), which may favor spruce growth if temperature is not a limiting factor.

The multivariate analysis used in this study suggested that the average height of white spruce increased with increasing summer maximum mean temperature. Climatic factors are considered more important than edaphic factors for white spruce height growth as height variations have been found in different climatic regions with the same edaphic site index (Wang et al., 1994). However, it has also been reported that summer drought caused by increased temperature and hence evapo-transpiration may limit the growth of white spruce (Barber et al., 2000). A similar result was found by Wilmking et al. (2004) in their study in Alaska.

The relationships between trembling aspen/balsam poplar structural variables and climatic factors were not significant in this study, contrary to my expectations. Climatic factors are frequently reported to be important in determining the productivity and height growth of aspen (Hogg et al., 2002). However, the multivariate analysis indicated that the average diameter of aspen increased with increasing number of degree-days above 5 ^{o}C. This may explain why warmer temperatures favour the growth of this species (Fralish and Loucks, 1975), if no drought condition exits.

3.5.4 Overall stand composition and structural in the study area

As expected, white spruce dominated the study area with the highest composition index (0.9) and stem density. Generally, the old growth sere is dominated by shade-tolerant species in the boreal forest succession unless there is a catastrophic disturbance (Bergeron and Dubuc, 1989; Brassard and Chen, 2006), as it can establish under shade in the absence of major disturbance (Takahashi et al., 2001). The continuous loss of light-demanding species such as aspen has been reported in the absence of major periodic disturbances (Rogers, 2002). The density of white spruce were greater within the intermediate height class (Delong and Kessler, 2000), as generally stem density is generally higher in younger stands than old growths.

I found the maximum density of aspen within pure aspen plots to be 1575 trees per hectare, very close to what Bates (1989) has suggested as the ideal density of aspen within mature stands after natural thinning (1000 to 1730 per hectare). Generally, aspen density is lower in mature stands due to natural thinning processes (Bates, 1989). I found that the average regeneration density of aspen was more than 40,000 stems per hectare, enough to fully stock stands of aspen after natural thinning (Bates, 1989), given that a regeneration density of about 2500 to 3000 stems per hectare has been suggested as sufficient to produce fully stocked aspen stands at maturity (Ek and Brodie, 1975; Sorensen, 1968; Bates, 1989). The maximum number of balsam popular recorded in the research plots was 100 trees per hectare (in mixed stands), lower than the ideal density of 1127 stem/ha reported by Douglas (1974) in balsam poplar dominant stands.

The Shannon-Wiener diversity indices indicated that there was higher structural diversity in undisturbed or old fire plots. Structural diversity is one of the characteristics of old growth boreal forest (Brassard and Chen, 2006). Diversity generally differs with tree species dominance, stand age and with changing proportions of shade-tolerant and intolerant species (Varga et al., 2005).

3.5.5 Chapter conclusions

The increasing forest disturbances and the changing climate have important implications for ecosystem structures and forest management in SWY. I hypothesized that the forest structures and composition were affected by bio-geoclimatic and disturbance factors in the region. My results showed that although white spruce dominates the landscape in terms of its density, basal area, average height and DBH, its regeneration was proportionately less than that of trembling aspen, especially in disturbed plots, suggesting broadleaved species may become more common if disturbance persists in the region. I also found that mixed stands of aspen and white spruce had higher basal areas per hectare than pure stands of trembling aspen or white spruce and that average stand diameter was positively correlated with tree density up to 500 trees per hectare, beyond which the average diameter decreased. Average density and basal area of white spruce increased with decreasing elevation and were higher in lower slope positions. These findings suggest that forest management should promote mixed stands in boreal region for higher productivity with regular thinning or selective harvesting to enhance regeneration and forest productivity.

Table 3.1 Total number of trees, seedlings and saplings of the species sampled

Species	**Number of trees (400 m^2)**	**% of total**	**Number of saplings (25 m^2)**	**% of total**	**Number of seedlings (1 m^2)**	**% of total**
White spruce	2577	87.5%	645	67.8%	2426	65.8%
Trembling aspen	360	12.2%	292	30.7%	1173	31.4%
Balsam poplar	7	0.3%	14	1.5%	95	2.6%
Total	2944	100%	951	100%	3694	100%

[Note: The above table shows that white spruce has the highest density of tree, seedling and sapling. However, compared to tree density, the % of its seedling and sapling are lower. In case of trembling aspen, tree stem cover is 12.2% only but it has more than 30% seedling and sapling cover.]

Table 3.2 Stand composition index

Species	**Basal area (m^2)**	**Index**
White spruce	1253.4	0.907932
Trembling aspen	124.74	0.090356
Balsam poplar	2.34	0.001698
Total	1380.5	

[Note: The above table shows the stand composition index for each species (Huang and Titus, 1995). White spruce has the highest composition followed by trembling aspen and balsam poplar]

Table 3.3 Average height, diameter and basal area of the sampled tree species by dominance class

Species	Dominance class (height class)	Total trees sampled (no)	% of total sampled	Average height (m)	Average diameter (cm)	Total basal area (m^2)	% of total Basal Area
White spruce	Dominant	63	18.3	15.9	25.7	12.8	23.2
	Co-dominant	71	20.6	12.5	19	23.6	42.6
	Intermediate	84	24.3	7.3	9.9	11.3	20.4
	Suppressed	45	13	6.6	8.4	2.5	4.6
Trembling Aspen	Dominant	19	5.5	11.4	19	1.2	2.1
	Co-dominant	26	7.5	8.6	14.1	3.2	5.7
	Intermediate	23	6.7	5.9	7.4	0.7	1.2
	Suppressed	7	2.0	3.3	4.3	0.1	0.1
Balsam Poplar	Dominant	2	0.6	7.4	15.1	0.1	0.1
	Co-dominant	0	0	0	0	0	0
	Intermediate	5	1.4	4.6	6.7	0.02	0.1
	Suppressed	0	0	0	0	0	0

[Note: The above table shows that white spruce intermediate height class has the highest density (24.3%) but its co-dominant height class has significantly highest basal area (42.64%)]

Table 3.4 Shannon-Weiner structural diversity indices by disturbance types (Bold fonts indicate the highest values by species)

Shannon-Weiner Indices	White spruce height	White spruce diameter (cm)	Trembling aspen height (m)	Trembling aspen diameter (cm)
Beetle affected plots	1.5	1.7	1	1
Recent fire plots	1.6	1.6	0.6	0.6
Old fire plots	1.5	1.7	1.1	**1.3**
Undisturbed plots	**1.9**	**2.2**	**1.2**	1

Table 3.5 Stand structure variables that were significant with environmental variables

	White spruce	Trembling aspen	Balsam poplar
Height	Elevation (F = 7.4; P < .001)	Elevation (F = 4.6; P =.02)	Not significant
	Slope (F = 4.6; P =0.037)	Aspect (F =3.8; P <.05)	
	Soil moisture (F = 4.1; P =0.33)	Soil texture (F = 2.7; P <.001)	
	Disturbance type (F = 5; P<0.001)	Mean annual prep (F = 6.5; P<.01)	
Diameter	Elevation (F = 3.7; P = 0.046)	Elevation (F = 4; P = 0.039)	Not significant
	Slope (F = 3.7; P <0.05)	Soil texture (F = 2.4; P <.001)	
	Aspect (F = 3.2; P<0.05)	Aspect (F = 4.6; P<0.05)	
		Mean annual prep (F = 5.7; P<.01)	
Density	Aspect (F = 2.2; P = 0.035)	Aspect (F = 4.6; P<.05)	Aspect (F=3.4; P<.05)
	Slope (F = 3.4; P = 0.44)	Soil texture (F =3.8; P<.05)	Soil texture (F =2.4; P<.05)
	Mean annual temp. (F = 3.6; P <.05)		
	Mean annual prep. (F = 4.5; P =0.03)		
	Soil moisture (F = 3.6; P<.05)		
	Soil texture (F = 4.3; P < 0.05)		
	Disturbance type (F = 6.1; P<0.0001)		
Basal area	Aspect (F = 4.7; P<.05)	Aspect (F = 4.2; P<0.05)	Not significant
	Elevation (F = 3.1; P <.05)	Soil texture (F =3.8; P<.05)	
	Slope (F = 5.4; P = 0.03)		
	Number of days>5 ^{0}C (F =3.4; P = 0.042)		
	Disturbance type (F = 10.5; P <0.001)		

[The above table shows the relationship of structural variables of white spruce, trembling aspen and balsam poplar with climatic, topographical, edaphic and disturbance variables. The categorical independent variables were tested using ANOVA (with means of plots) and numerical variables were tested by fitting regression lines. The only variables which were significant at p<0.05 are listed above. The table indicated that white spruce structures varied significantly with several factors. Trembling aspen diameter and height also varied significantly with edaphic and topographic factors.

Table 3.6 R^2 values between stand structure variables and other ecological variables

	STT	ATT	PTT	TT	TCC	AtBA	PoBA	SpBA	ToBA	Spavht	Spavdia	Atavht	Atavdia	Poavht
ATT	0.01	1												
PTT	0.01	0.01	1											
PTT	0.89	0.07	0.01	1										
TCC	**0.40**	0.02	0.01	**0.44**	1									
AtBA	0.01	**0.75**	0.01	0.05	0.03	1								
PoBA	0.01	0.02	**0.91**	0.05	0.07	0	1							
SpBA	**0.72**	0.03	0.02	**0.63**	0.36	0.01	0	1						
ToBA	**0.67**	0.08	0.02	**0.68**	**0.44**	0.03	0	**0.93**	1					
Spavht	**0.29**	0.01	0.07	**0.24**	**0.24**	0	0.01	**0.48**	**0.47**	1				
Spavdi	**0.28**	0.07	0.09	0.19	0.19	0	0.02	**0.43**	**0.42**	**0.89**	1			
Atavht	0.02	0.18	0.02	0.06	0.06	**0.25**	0.01	0.01	0.05	0.05	0.03	1		
Atavdi	0.02	0.18	0.02	0.04	0.06	**0.29**	0.01	0.01	0.06	0.06	0.04	**0.96**	1	
Poavht	0.06	0.04	**0.98**	0.07	0.06	0	**0.9**	0.01	0.01	0.01	0.02	0.01	0.01	1
Poavdia	0.08	0.04	**0.99**	0.008	0.01	0	**0.95**	0.01	0.01	0.01	0.02	0.01	0.01	**0.98**

[Note: R^2 values greater than 0.2 have been highlighted. Abbreviation of names: STT = spruce density, ATT = aspen density, PTT = poplar density, TCC = total crown cover; AtBA = aspen basal area (m^2), PoBA = poplar basal area (m^2), SpBA = spruce basal area (m^2), ToBA = total basal area (m^2), Spavht = spruce average height, Spavdia = spruce average diameter, Atavht = aspen average height, Atavdia = aspen average diameter, Poavht = poplar average height, Poavdia = poplar average diameter]

Table 3.7 Comparing density index by disturbance type

Species	Mean index for 90 plots	Beetle Plots	Fire plots	Harvested plots	Old fire plots	Undisturbed plots
White spruce tree	100	192	32	71	120	92
White spruce sapling	100	141	70	74	157	83
White spruce seedling	100	157	205	73	67	70
Trembling aspen tree	100	30	20	80	179	137
Trembling aspen sapling	100	2	104	177	59	111
Trembling aspen seedling	100	18	322	94	96	64
Balsam poplar tree	100	0	0	257	92	83
Balsam poplar sapling	100	0	58	418	0	0
Balsam poplar seedling	100	7	370	204	0	24

[Note: The above table shows index values of trees, saplings and seedlings in each disturbance type compared to the mean values for 90 plots. It indicates that white spruce tree density was higher in beetle-affected and old fire plots. Both trembling aspen and balsam poplar regeneration were higher in fire and harvested plots]

Table 3.8 Ratio of tree regeneration to parent trees by disturbance types (values are averaged per plot)

	STT	Spsed	STT:Spsed	ATT	Atsed	ATT:Atsed	PTT	Posed	PTT:Posed
Beetle (16 plots)	55	52	1:0.95	1	2	1:2	0	0	0
Fire (10 plots)	9	59	1:6.6	1	45	1:45	0	4	0:4
Harvest (20 plots)	20	25	1:1.25	3	18	1:6	2	3	1:1.5
Old fire (16 plots)	34	29	1:0.85	7	15	1:2.1	0	0	0
Undisturbed (28 plots)	26	25	1: 0.96	5	12	1:2.4	0	0	0

[Note: The table shows that trembling aspen had much higher ratio of trees to regeneration in disturbed plots than that white spruce. Abbreviation of names: STT = white spruce tree density; Spsed = white spruce seedling density; ATT = apsen tree density; Atsed = aspen seedling density; PTT = balsam poplar tree density; Poseed = balsam poplar seedling density.]

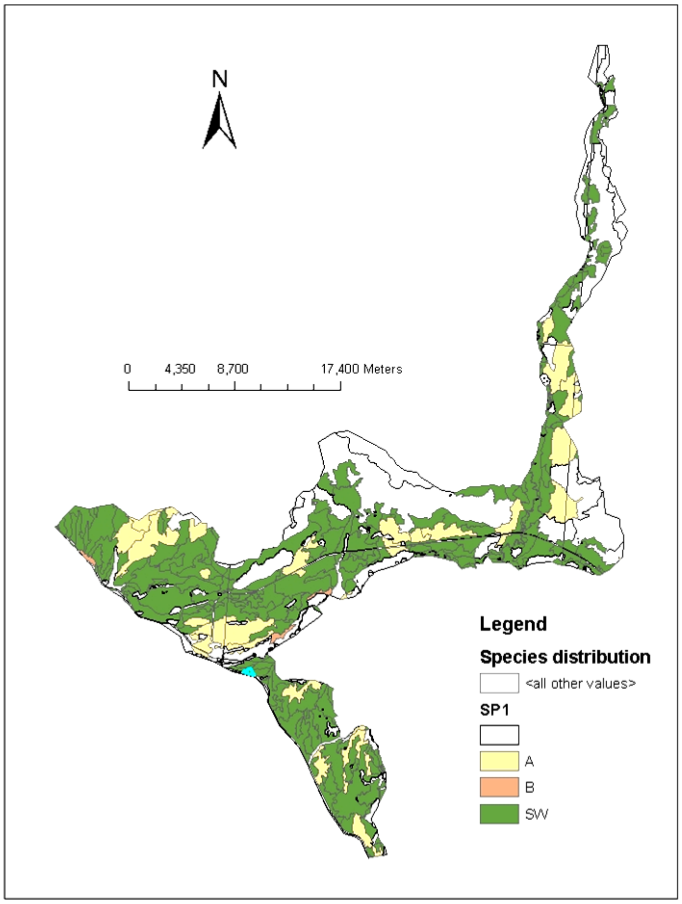

Figure 3.1 Species distribution in study area

Note: White spruce data were received from Ministry of Eneery, Mines and Resources, Government of Yukon. Abbreviation: A = Aspen; B = Balsam poplar, SW = White spruce, Blank = no species recorded.]

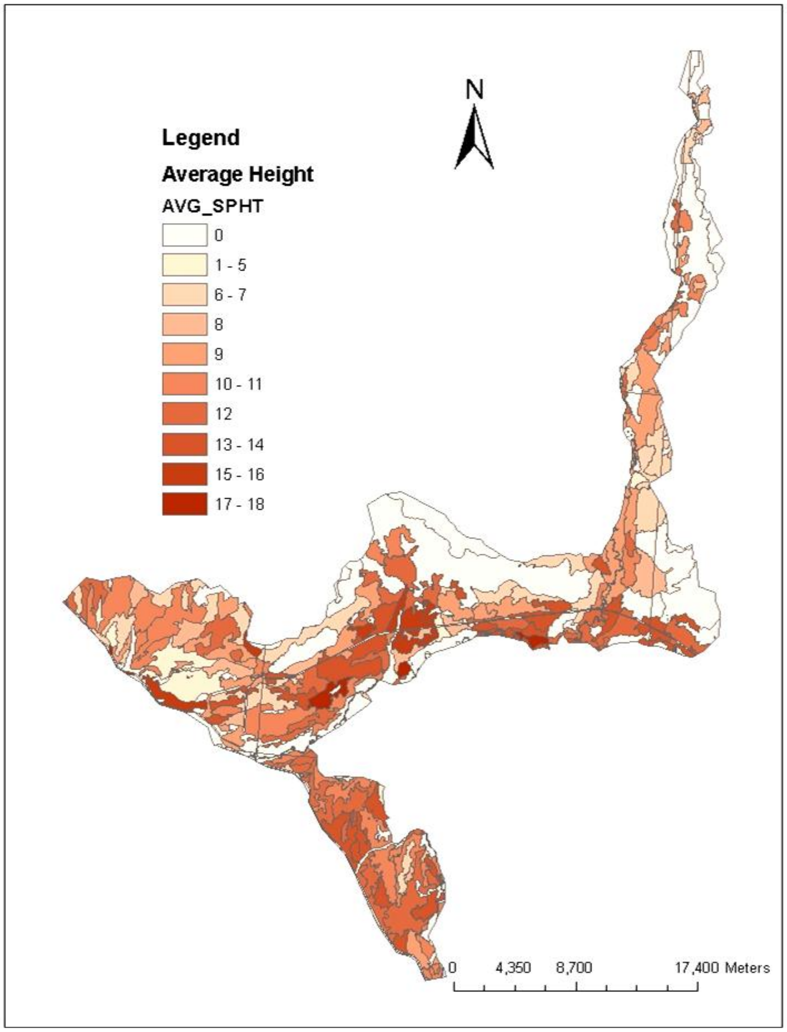

Figure 3.2 Distribution of average height (m) in the landscape

[Note: The average height was higher in research blocks D, E and F, which were characterized by lower elevation, lower slope position or flat and exposed sites. Data were received from MEMR, Yukon Government]

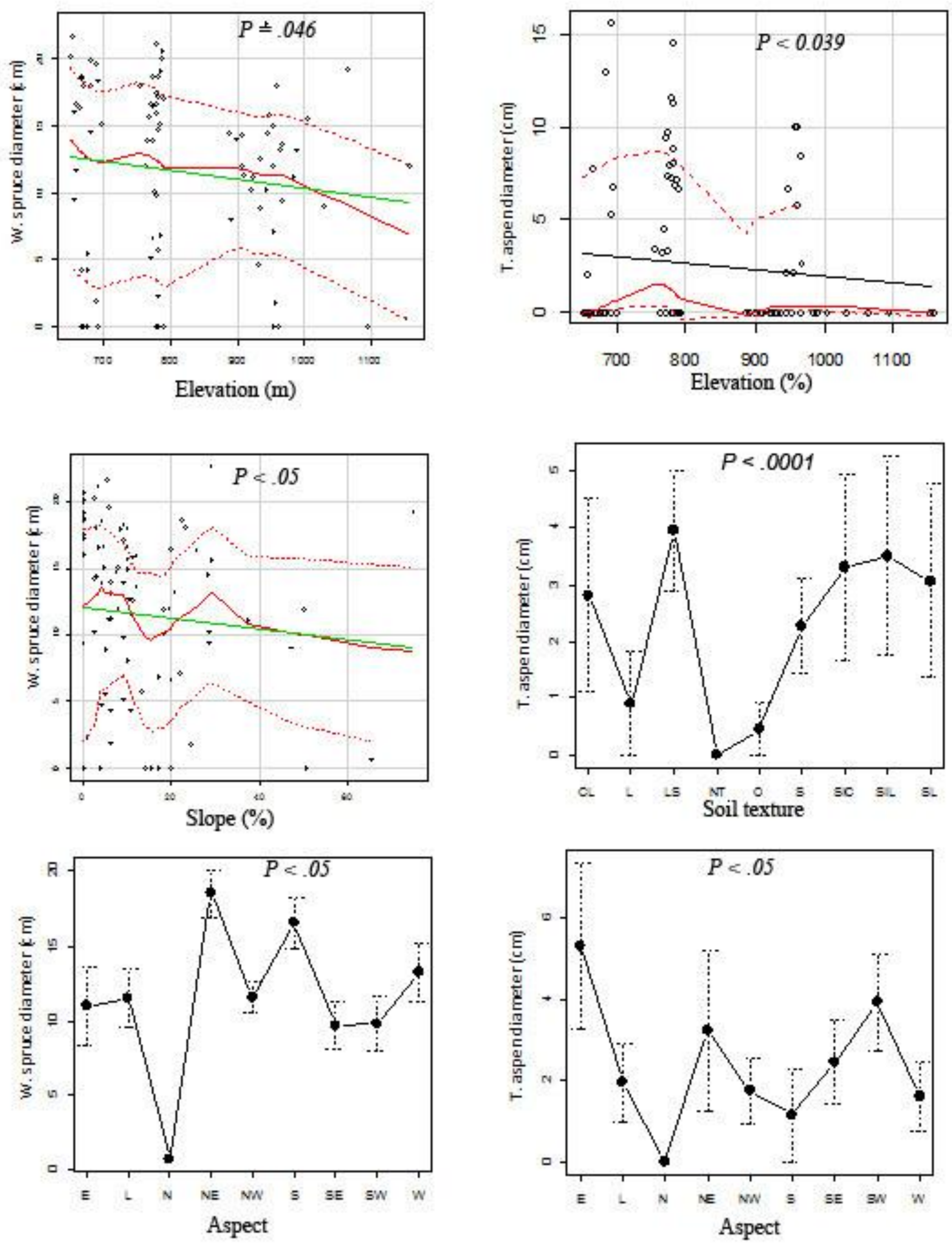

Figure 3.3 Stand diameter Vs environmental factors

[Note: The figures indicate that white spruce diameter varied significantly with elevation, slope and aspect. Similarly trembling aspen diameter varied with slope, soil texture and aspect. The variations were significant at p<0.05]

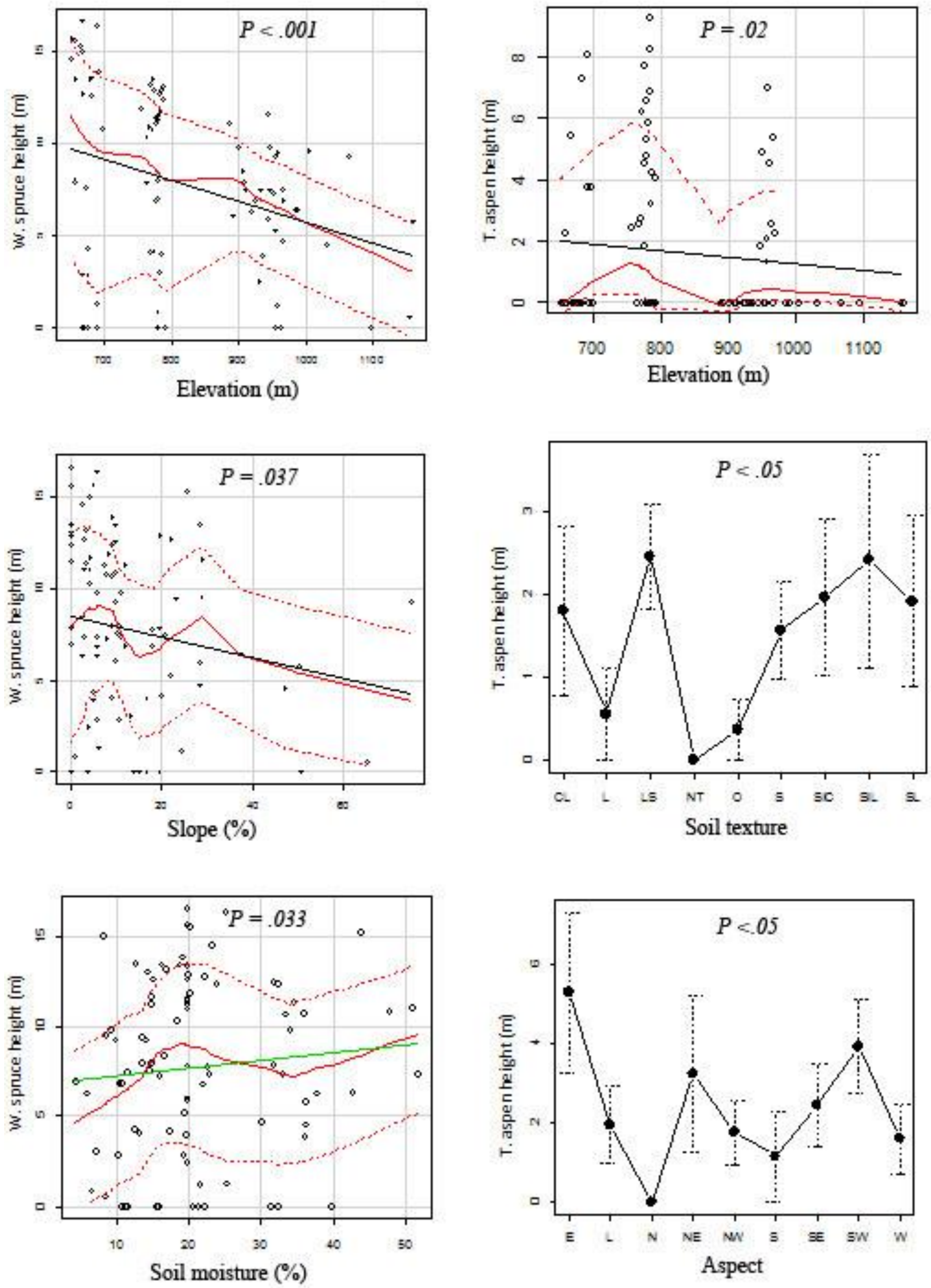

Figure 3.4 Stand heights vs. environmental variables

[Note: The figures indicate that white spruce average height decreased with increasing elevation and slope, but increased with increasing moisture level. Trembling aspen height also decreased with increasing elevation. Average heights of aspen were higher in loamy soil and on eastern aspect.]

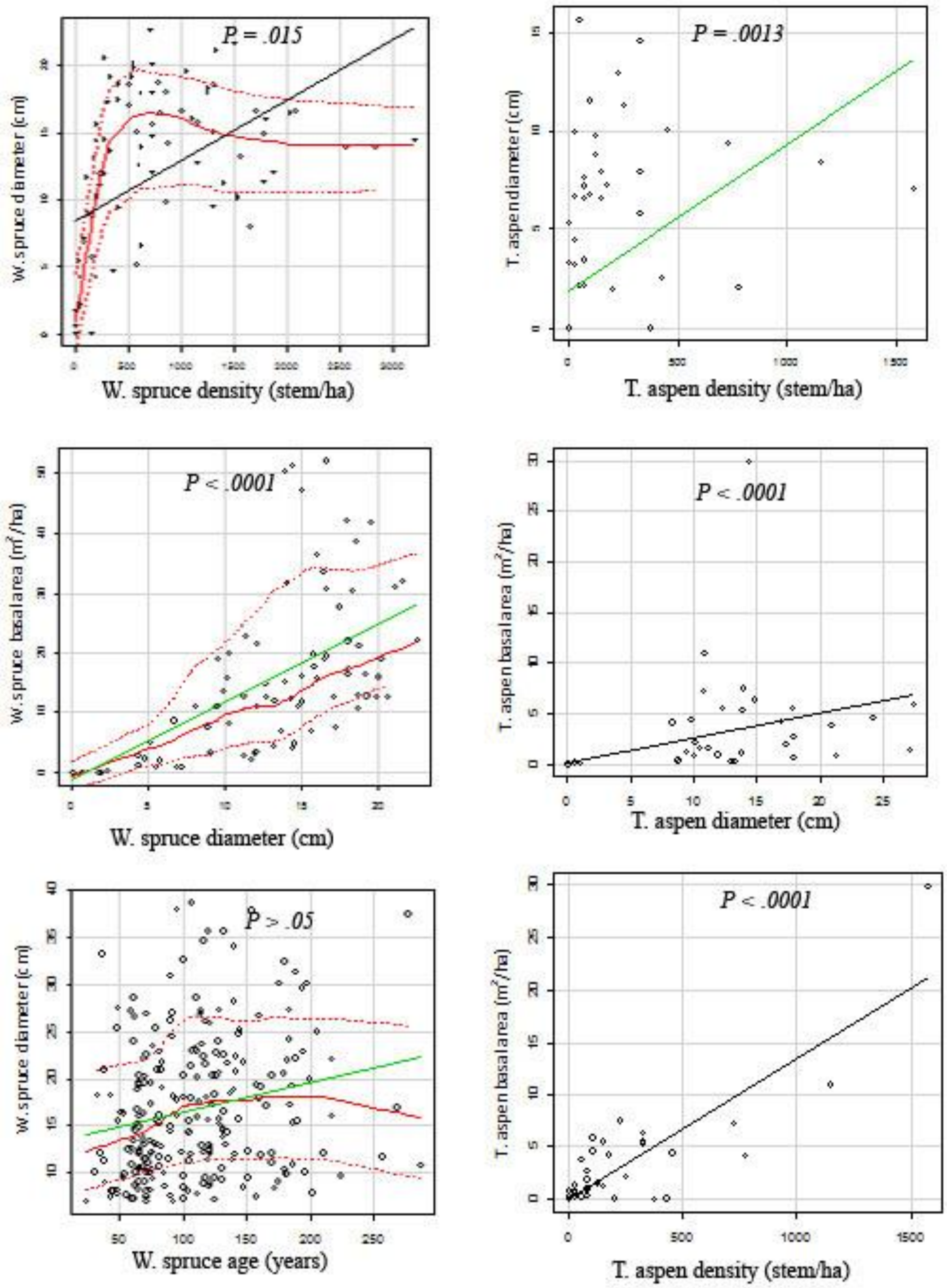

Figure 3.5 Stand productivity vs. environmental variables

[Note: Stand productivity indicates basal area per hectare. The figures indicated that diameters of both white spruce and trembling aspen were positively correlated to its density and basal area, though average diameter decreased once density reached 1000/ha. Relationship between white average age and diameter was not significant. The colours of the lines are the default outputs from R. Red colour lines indicate the general distribution of the data and green and black colours straight lines are the regression fit lines.]

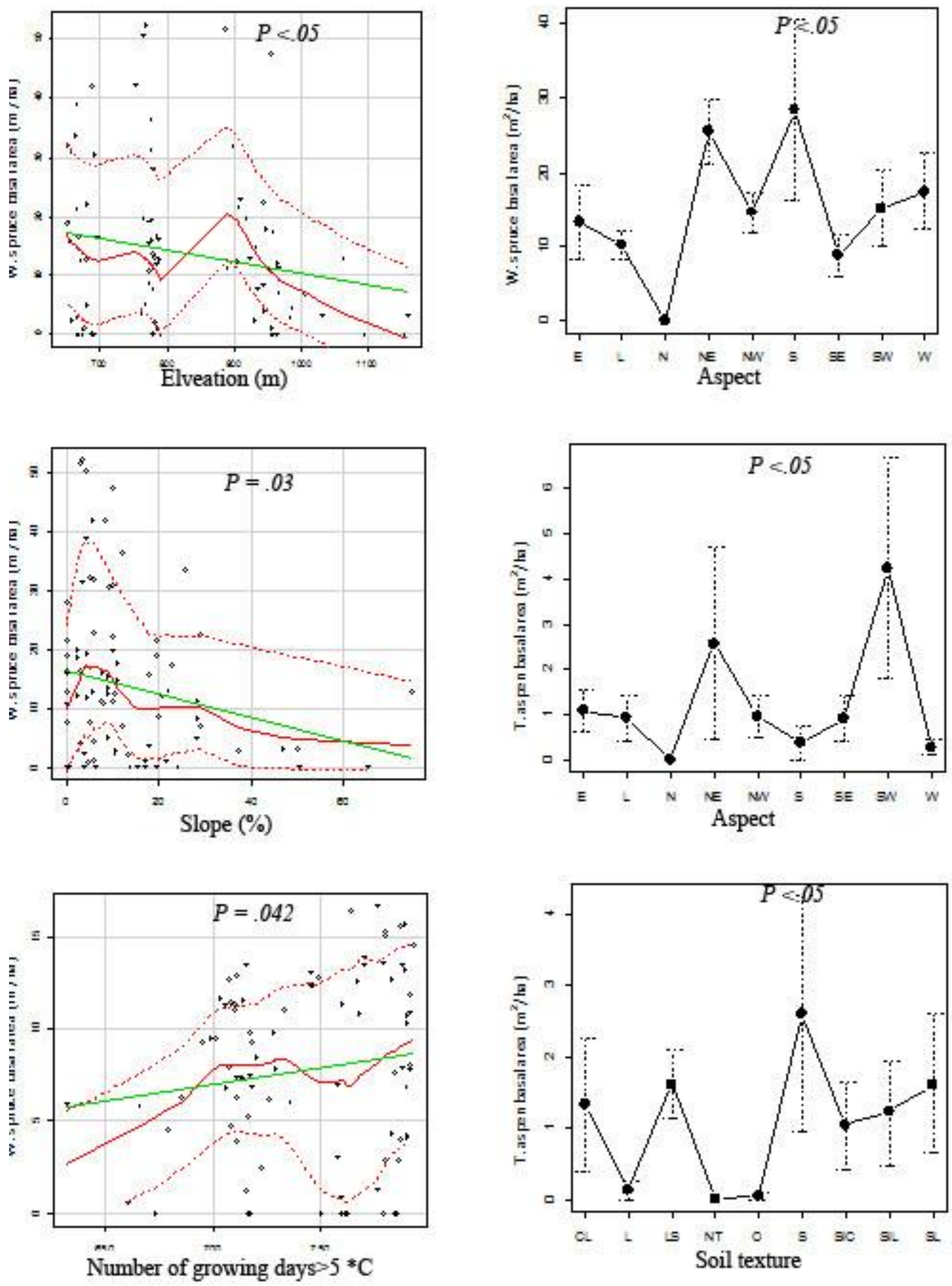

Figure 3.6 Stand basal area vs. environmental variables

{Note: White spruce basal area was greater at lower elevations and slope positions with higher growing number of days > 5 ^{o}C. Trembling aspen basal area and density followed similar trends]

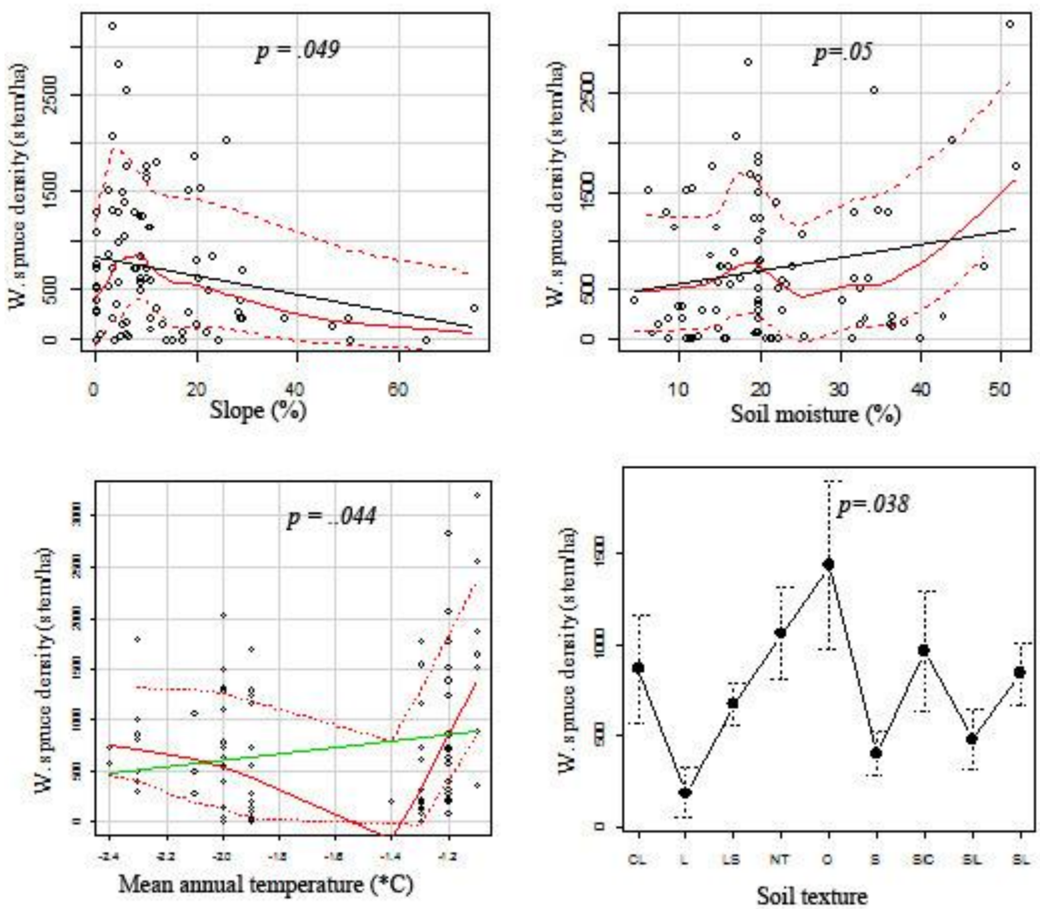

Figure 3.7 White spruce average density vs. environmental variables

[Note: The average densities of white spruce were higher in lower slope positions with higher mean annual temperature and higher soil moisture. Organic soils were present in dense spruce stands]

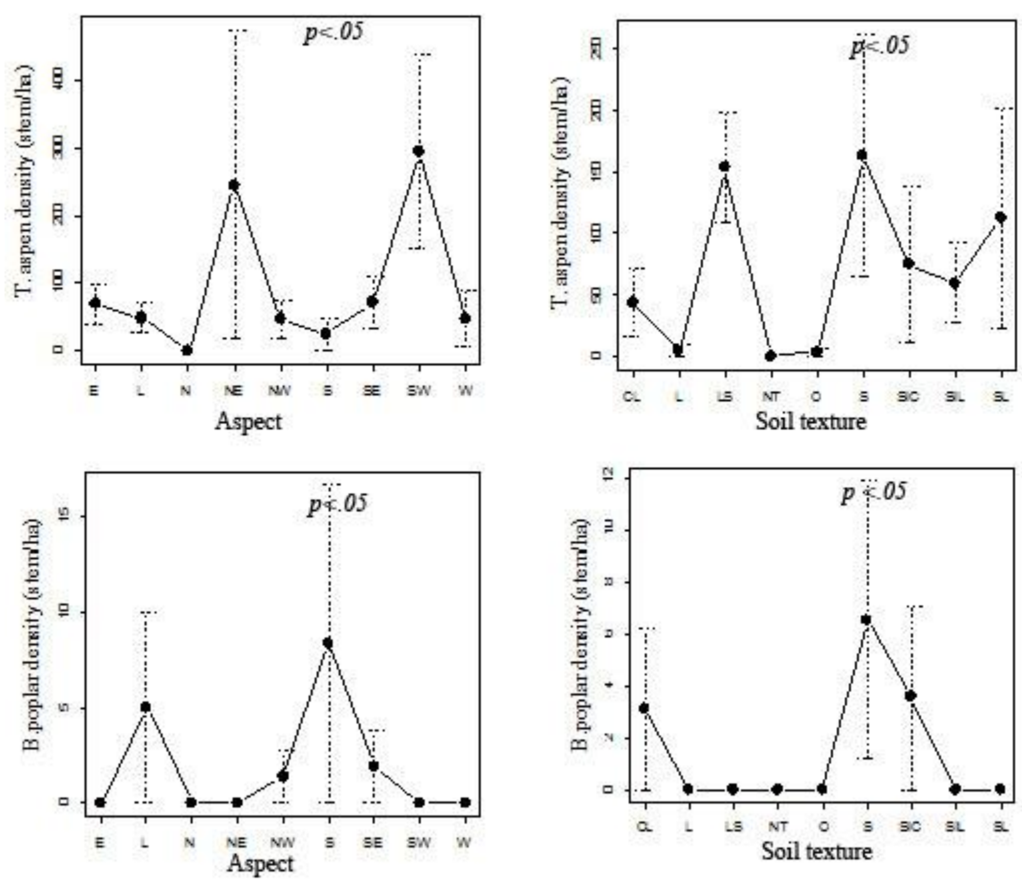

Figure 3.8 Trembling aspen and balsam poplar average density vs. environmental variables

[Note: The densities of trembling aspen were higher in exposed sites on NE and SW slopes. The species was abundant on sandy and loamy sand soils]

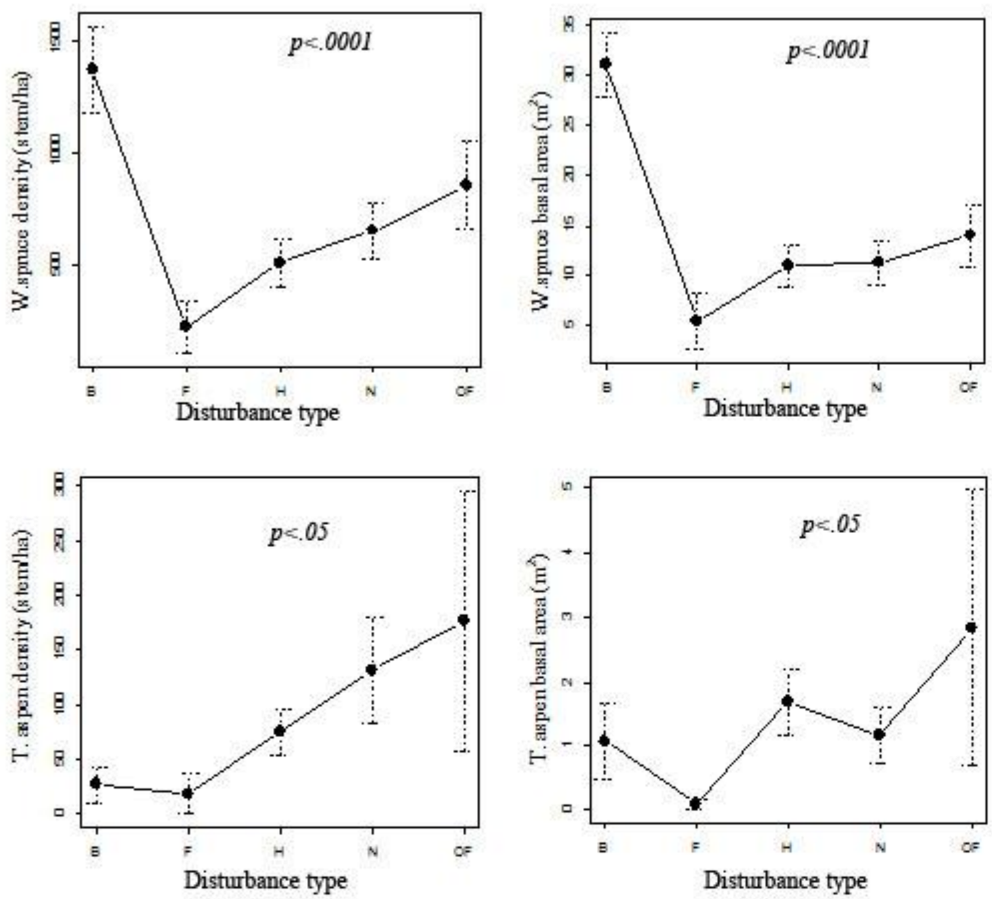

Figure 3.9 Variation of stand density and basal area by disturbance type

[Note: White spruce density and basal area were higher in beetle affected plots whereas for trembling aspen, density and basal area were higher in old fire plots]

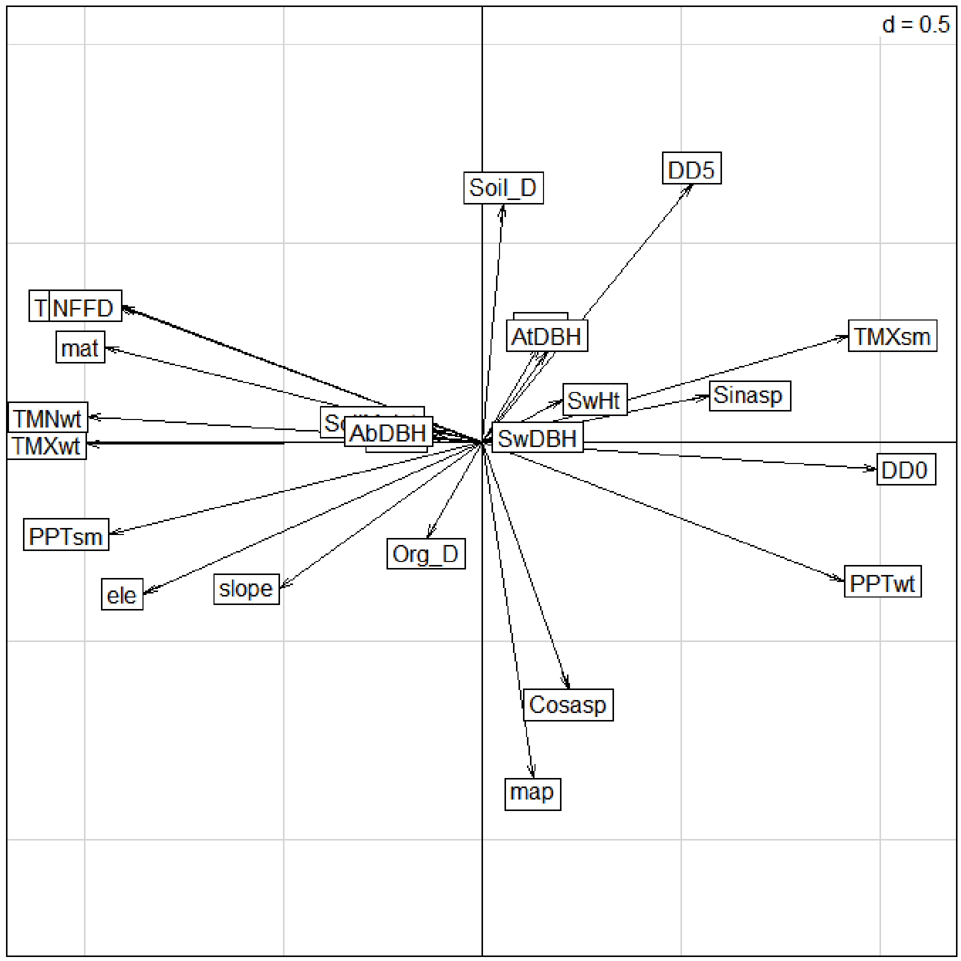

Figure 3.10 Axis I - Environmental/structure variables

[Note: Figure 3.10 was the ouput of the Multiple Co-intertia analysis. It shows that the average height of white spruce increases with increasing summer maximum mean temperature, eastern aspect and decreases with increasing slope, elevation and summer precipitation. Similarly, trembling aspen average diameter increases with increasing degree-days more than 5^{0}C but decreases with elevation and slope. Abbreviation of names: NFFD = number of frost free days; mat = mean annual temperature; TMNwt = minimum winter temperature; TMXwt = maximum winter temperature; AbDBH = average DBH of balsam poplar; PPTsm = average precipitation; ele = elevation; Org_D = organic depth; Soil_D = soil depth; DD5 = degree days above 5; AtDBH = Average DBH of aspen; TMXsm = Maximum summer temperature; map = mean annual precipitation; SwHt = white spruce average height; SwDBH = white spruce average diameter; Sinasp = Sine of aspect; Cosasp = Cosine of aspect; DD0 = degree days< 0 ^{o}C; PPTwt = Winter precipitation].

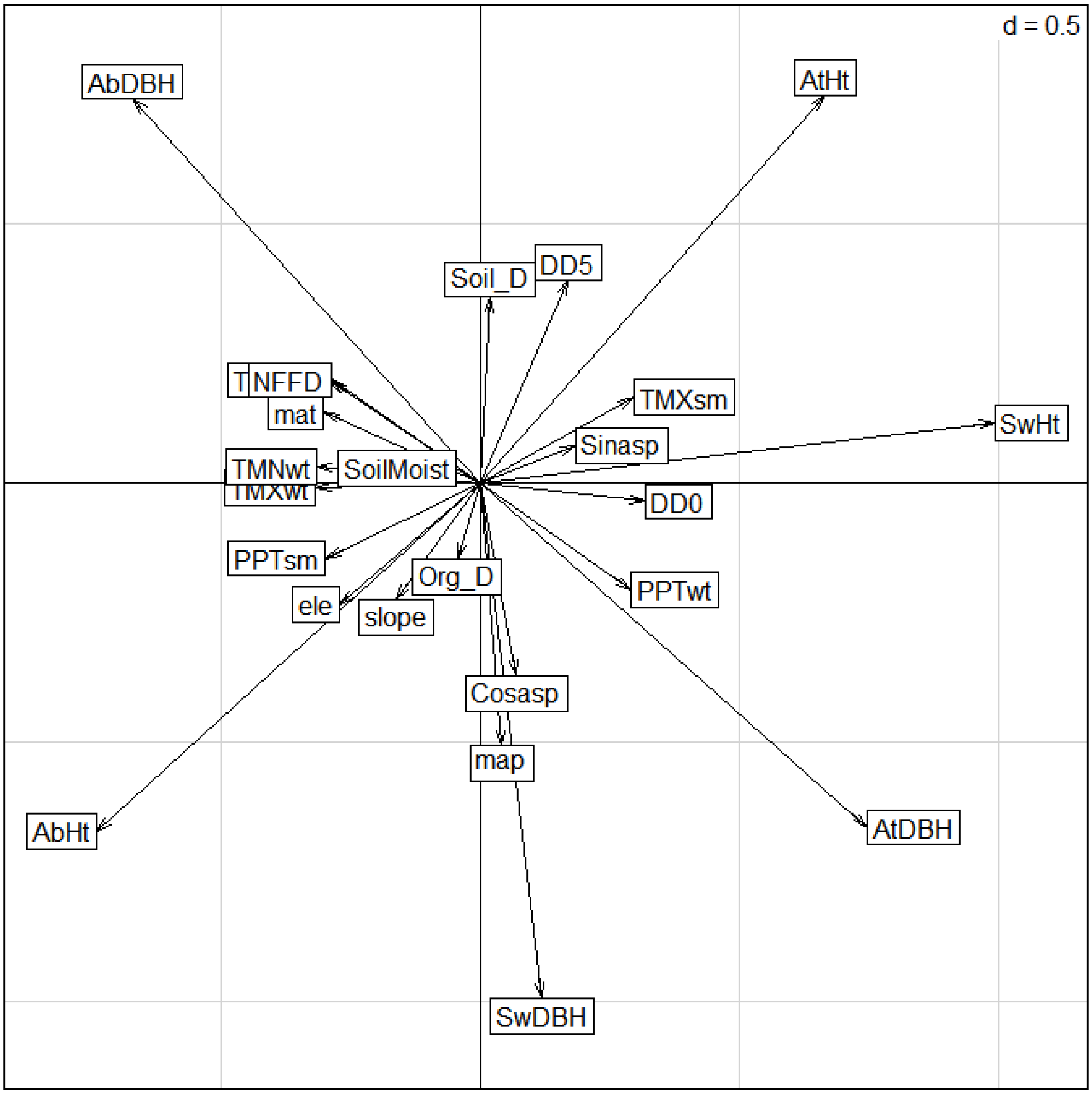

Figure 3.11 Axis II - Species environmental axis

(Note: Figure 3.11 (output of the Multiple Co-inertia Analysis) provides additional information. It indicates that white spruce average diameter increases with increasing mean annual precipitation and trembling aspen average height decreases with increasing elevation and slope. Abbreviation of names: same as Figure 3.10)

4. Tree regeneration in response to bio-geoclimatic and disturbance factors in the southwest Yukon of Canada

4.1 Introduction

The boreal forests of southwest Yukon (SWY) have been experiencing the consequences of climate change, particularly through increases in disturbance. These perturbations strongly affect the ecosystem properties and processes that shape community structure and composition (Johnstone and Chapin, 2006b). They are particularly important in determining the recruitment of boreal tree species and their abundance and distribution (Johnson et al., 2003) and have significantly affected species regeneration in the region. This chapter deals with the distribution and abundance of tree species regeneration in SWY in response to bio-geoclimatic and disturbance factors.

4.1.1 Tree species and their regeneration in the southwest Yukon

The southwest Yukon has only three major tree species i.e. white spruce, trembling aspen and balsam poplar. The regeneration potential of these species depends upon various factors including seed sources and viability, the condition of substrates, climatic condition and disturbances. White spruce regenerates from seed (Qualtierem, 2008); and therefore, its regeneration is primarily dependent on annual seed fall and masting events (Nienstaedt and Zasada, 1990). The condition of the soil substrate is very important for white spruce regeneration. Burned substrates with rotten logs and exposed mineral soils following the disturbances provide better environments for recruitment (Simard et al., 2003; Stewart et al., 2001; Peters et al., 2005; Wirth et al., 2008), provided that there is sufficient moisture availability within the mineral substrates (Wang and Kemball, 2005; Johnstone and Chapin, 2006a). However, white spruce may also establish on an organic substrates provided that moisture is not a limiting factor (Wirth et al., 2008). In addition, this species typically prefers coarse-textured, well-drained sandy to loamy textured soils rather than clay-dominated soils (Galipeau et al., 1997; Lindbladh et al., 2007).

Both trembling aspen and balsam poplar require similar geoclimatic conditions for their regeneration, but with aspen more prevalent on upland sites and balsam poplar on lowland sites. They both regenerate vegetatively and by seeds (Perala, 1990; Zasada and Phipps, 1990). Suckering is the principal mode of regeneration however for both species following a major disturbance (Frey et al., 2003; Bartos, 2001; Zasada and Phipps, 1990). The seeds of both species are small and light and can be dispersed by wind over many kilometres (Perala, 1990; Zasada and Phipps, 1990). Once dispersed, the seeds remain viable for 2 to 4 weeks for aspen (Perala, 1990) and 4 to 6 weeks for balsam poplar (Zasada and Phipps, 1990). Soil moisture is very important factor for their germination of both species (Zasada and Densmore, 1980; Krasny et al., 1988; Perala, 1990). Both prefer exposed sites with high light conditions and mineral substrates, typically provided following major disturbances, (Zasada et al., 1981; Klinka et al., 2000; Johnstone and Chapin 2006a).

4.1.2 Climatic and disturbance factors and tree species regeneration in SWY

Climate variability and disturbances can have a significant impact on the recruitment and survival of all three species. White spruce is very sensitive to fire because of its thin bark and lack of an aerial seed bank (Kuusela, 1990; Messaoud et al., 2007). Intense and severe fire may kill seeds and reduce the probability of germination due to loss of nutrients by vaporization and combustion of organic matter (Neary et al., 2005). Increases in temperature and changes in soil moisture following fire may prevent or delay regeneration of white spruce (Oswald and Brown, 1990). Fire, however, a very important factor for white spruce seedling establishment and the interaction between masting years and fire can result in abundant regeneration of white spruce (Peters et al., 2005). In areas of the northern boreal forest that are dominated by cold, wet, organic soils and/or permafrost, fire plays an important role by removing organic layers and causing the degradation of permafrost (Yoshikawa et al., 2003). Similarly, fire is important for aspen regeneration (Wang, 2003). Severe fire can however damage roots and suckers, which can significantly affect the density, height and diameter of aspen regeneration (Wang, 2003). Increased fire frequency resulting from warmer temperatures could favour the establishment of aspen and other broadleaved woody species in the boreal forest (Flannigan and Van Wagner, 1991).

Pests and diseases are important disturbance agents that can affect the ability of species to regenerate. A reduction in seed availability due to the extensive mortality of maternal trees can affect the regeneration and establishment of white spruce (Jasinski and Payette, 2005). Annual variation in precipitation is an important factor for the regeneration of both balsam poplar and trembling aspen as these species are sensitive to dry climatic condition and moisture stress, which can limit their regeneration leading to species reductions over time (Perala, 1990; Hogg and Wein, 2005; Yarie, 2008).

4.1.3 Research problems, hypotheses and questions

Disturbances affect community structure and composition, which in turn can affect ecosystem properties and processes (Johnstone and Chapin, 2006b). Post-disturbance recruitment plays an important role in shaping the landscape patterns of boreal forest vegetation, providing opportunities for the recruitment of boreal tree species, which in turn impacts upon species abundance and distribution (Johnson et al., 2003). In the Champagne and Aishihik Traditional Territory (CATT) of the Southwest Yukon (SWY), >90% of the forest has been affected by the recent spruce bark beetle (SBB) outbreak in addition to the 100,100 ha of forest that have burned in the region between 1946 and 2003. Given the documented changes in climate over the last 50 years and the large areas of forest affected by the SBB outbreak and fires over the last five decades, I sought to identify what relationships exist between tree recruitment, climate and disturbance.

In response to the recent spruce bark beetle epidemic, salvage harvesting has been proposed within the study region to generate economic growth opportunities for local communities, with forest re-establishment to be dependent upon natural regeneration (SFMP, 2004). However, factors that have determined past recruitment success in the region have not been quantified, which the SFMP (2004) recognized as an important research issue in the study area. The following research hypotheses were developed in connection to disturbances and climate variability in the region and their effects on tree regeneration;

i. Post disturbance recruitment is important in shaping boreal forest composition. As the CATT has experienced four types of disturbance and has three major tree species, the regeneration response of each species was expected to differ according to type and severity of disturbances. I hypothesized that the extent and scale of regeneration of each species to vary significantly by disturbance type. Specifically, I expected higher regeneration abundance of all three species following recent fire than the other disturbance types. I also expected that any disturbances would favor the regeneration of broadleaved species over coniferous species.

ii. Similarly, climatic factors, specifically temperature, have been reported to have very important effects on the regeneration success of boreal species. I hypothesized that the distribution and abundance of tree recruitment should be associated with climatic factors. I specifically expect that the regeneration of all three species would respond positively to higher temperature and precipitation.

Besides reporting on my tests of the above hypotheses, this chapter also deals with following research questions that could have important implications for forest management decision making.

- What is the role of disturbance in the success of tree regeneration in SWY?
- How do climate variability and environmental factors affect the density and distribution of regeneration in SWY?
- What edaphic factors limit the distribution and density of regeneration in the landscape in SWY?

4.2 Data analysis

I used both univariate and multivariate statistical tools to assess the responses of tree regeneration to environmental and disturbance factors. Analysis of Variance (ANOVA) was performed to examine the mean variation of regeneration by disturbance type. The ratio of species regeneration to their parent trees was calculated by disturbance type to see the effect of disturbance on the regeneration of each species. The analytical tools used in this chapter are described separately below.

4.2.1 Multivariate canonical correlation (MCA)

MCA was used to investigate the multivariate correlation between dependent (regeneration abundance) and independent variables (climate, topography, stand structure, soils, and disturbance). MCA defines a multivariate relationship between two or more sets of variables and can accommodate multiple dependent variables. It identifies the sets of weights for the dependent and independent variables that provide the highest possible correlation between composite variates (McGarigal et al., 2000).

4.2.2 Negative binomial generalized model

The regeneration abundance of white spruce, trembling aspen and balsam poplar were modelled using a Negative Binomial Generalized Model (PROC Genmod), which uses the Maximum Likelihood method for estimating parameters (SAS Institute Inc, 2008; McCullagh and Nelder, 1989). Poisson and negative binomial probability distributions are generally used for count data modelling. A negative binomial distribution is generally preferred to Poisson when the variance is higher than the mean value; this was the case in this study so the former was utilised. Negative binomial distributions have frequently been used for modelling forest regeneration (Venables and Ripley, 2002; Fyllas et al., 2008). The overall model to estimate regeneration density was:

R_D = *f (Topographical variables +ecological variables +climatic variables +disturbance regime) + residual error*

$$\mathbf{Log\ (R_D) = b_0 + b_1{*}X_1 + b_2{*}X_2 + ... + b_n{*}X_n,}$$

$$\mathbf{R_D = exp^{(b..... + b1*X1 + b2*X2 + ... + bn*Xn).}} \text{.............................}\textbf{Equation (4-1)}$$

where R_D is the regeneration count for each plot, b_0 is the intercept of the slope of the model and X_1 to X_n are explanatory variables that represent topographic, ecological and climatic variables, as well as the disturbance regime. I used a stepwise modelling process to remove insignificant variables. I tested the goodness-of-fit of the model by comparing the Akaike Information Criterion (AIC) values of full models to the final reduced model. The smaller the AIC value, the better I judged the model to be. Similarly, the model's significance was tested using a Chi square test.

F-calculated = *2*(log likelihood of full model – log likelihood of reduced model)*

If the calculated F value was larger than the critical F value at an alpha of 0.05, then I considered the model to be significant. I used SAS Inc. software to develop the models (SAS, 2008).

4.2.3 The most nearest neighbor imputation model (MSN Imputation)

The most nearest neighbourhood imputation model was as a complementary model for estimating regeneration abundance in the study area. This model has frequently been used for estimating regeneration abundance (Ek et al., 1996; Hassani et al., 2002; Froese, 2003; LeMay et al., 2007). Imputation is defined as "replacing missing or non-sampled measurements for any unit in the population with measurements from another unit with similar characteristics" (Ek et al., 1997). Imputation methods include tabular imputation, most similar neighbour, nearest neighbour, k-nearest neighbour, and geo-statistical estimation (Hassani, et al., 2002).

The imputation method splits original data into "reference" and "target" variables. Data that have Y variables are classified as reference data and without Y variables are termed as target data (Ek et al., 1997). Programme "yImpute" in R statistical (R Core Development Team, 2010) was used for this purpose.

The imputation method has several benefits. It gives the result as estimates within the bounds of biological reality as it provides an estimate from existing Y variables (Moeur and Stage, 1995; Haara et al., 1997). It also allows any form of data, so no assumptions or data transformations are required for the variables (Haara et al., 1997; LeMay et al., 2007). In addition, the method can estimate multiple Y variables simultaneously (Katila and Tomppo, 2002). The root mean square error (RMSE) and correlation (R) between imputed and observed values of each species were calculated. The lower the RMSE the better the predictive power of the model, and when RMSE equalled zero the model was judged perfect (Tabachnick and Fidell, 1996).

$$\text{RMSE} = \sqrt{\sum_{i=1}^{1} \frac{(y_i - \hat{y}_i)^2}{n}} \quad \text{…............................Equation (4-2)}$$

Where y_i = observed variables; $\hat{y}_i$= predicated variables; and **n** = number of sampling plots.

4.3 Results

4.3.1 Regeneration in response to disturbances, and climatic and environmental factors

Regeneration of white spruce, trembling aspen and balsam poplar varied significantly ($p < 0.05$) by disturbance type (Table 4.1). Although the regeneration of all three species was highest in the recent fire plots, trembling aspen and balsam poplar had higher ratios of regeneration to their parent trees than spruce. The fire plots were characterized by thin organic humus layers (= 2.75 cm; sd = +/- 2.09), the lowest crown covers (= 12%; sd = +/- 25.5), lower soil moistures (= 19.82%; sd = +/- 11) and the least shrub cover (36.23%) compared with the other disturbances (Table 2.1). Both non-disturbed and old fire plots had the lowest regeneration density for all tree species. These plots were characterized by about 50% crown cover, thick organic humus layers (>8 cm) and higher shrub covers (> 50%) (Table 2.1).

The multivariate canonical correlation (MCA) categorized the total landscape into four axes (gradient). In MCA, each axis was correlated to several environmental variables with maximum variance (Table 4.2, Appendix, D). Axis 1 was defined by the variables balsam poplar basal area (PoBA) and total tree density (PTT), which were found to describe the occurrence of balsam poplar regeneration (Table 4.3). Axis 2 correlated positively with fire and negatively with total crown cover (TCC), organic depth, white spruce tree density and soil moisture. This habitat type was suitable for trembling aspen regeneration but was negative for white spruce saplings. Axis 3 was mostly influenced by lower elevations (650 m to 750 m), lower slopes (less than 15%), higher mean annual temperatures, higher growing degree days, and the occurrence of fire, which favoured spruce regeneration (both seedling and sapling). Axis 4 was influenced negatively by elevation and positively by slope, summer maximum temperature and the occurrence of spruce bark beetle, which also favoured the occurrence of both seedlings and saplings of white spruce. The main differences between habitat types 3 and 4 were the slope (%) and disturbance type, indicating that white spruce was present in fire plots on lower slopes and beetle-affected plots on higher slopes.

The plots of regeneration density against specific environmental factors (Figure 4.1, Figure 4.2 and Figure 4.3) all showed similar results to that of the MCA. Figure 4.1 indicated that white spruce exhibited a positive relationship with sites at lower elevations and lower slope positions that have higher growing degree-days and higher mean summer temperature and with soils that had lower soil moisture and had been subject to disturbance. Both trembling aspen and balsam poplar showed similar responses to environmental factors. I found regeneration of these two species at sites affected by fire and harvesting, indicating their preference for disturbed sites. They also responded positively to sites with exposed aspects (flat, east to south to west), indicating a preference for sites with higher solar radiation inputs. Trembling aspen regeneration responded negatively to increasing mean annual temperature, crown cover, organic depth and responded positively to the presence of loamy to silty loam soil texture. Regeneration of balsam poplar was greater in sandy and silty clay soil.

4.3.2 Negative binomial regeneration abundance model

Altogether, 38 explanatory variables were used to predict the regeneration abundance of white spruce, trembling aspen and balsam poplar (Table 2.3). The negative binomial dispersion parameters were estimated by the maximum likelihood method. The stepwise modelling method resulted in many variables being dropped ($p>0.05$) with eight, 14 and nine variables retained for white spruce, trembling aspen and balsam poplar, respectively. Table 4.4 provides the criteria for assessing goodness of fit of the models including AIC and log likelihood. The algorithms of all three models were converged and the results are provided for white spruce, trembling aspen and balsam poplar in Tables 4.5, 4.6 and 4.7 respectively. The dispersion values were higher than zero in all the models, justifying the application of the negative binomial model. The majority of the climate variables and the total basal area were significantly correlated with regeneration for all three species. Variables related to disturbance were significant for trembling aspen and balsam poplar only. The AIC values of full models of white spruce, trembling aspen and balsam poplar were 2207.32; 1302.42 and 346.73, respectively, which were reduced to 2164.98, 1273.94 and 340.68, respectively, by the stepwise method (Table 4.8). The reduced AIC signifies the model fitness. F-tests were performed for all three models using log likelihood values of full models and null models. The calculated F values for models were larger than the F table values at $p \leq 0.05$ (Table 4.9). The F-tests demonstrated that all three models were statistically significant.

4.3.3 MSN imputation model

An imputation model was used on all explanatory variables to impute the results from reference to target variables. The results of the heads and tails of imputed and observed values of the models are shown in Table 4.10. The full results have been provided in Appendix E. The model significances were tested using the correlation between observed and imputed values and the RMSE of the imputed values. The correlation between observed and imputed regeneration abundance of white spruce, trembling aspen and balsam poplar were 0.618, 0.656, and 0.874, respectively. The relationships between the imputed and observed regeneration abundance for each species are illustrated in Figure 4.4. The RMSE of the models for the three species were 89014, 79974 and 10114, respectively. The correlation and RMSE values indicate that the abundance of balsam poplar regeneration was better predicted than the other two species.

4.4 Discussion

4.4.1 Disturbances vs. regeneration

I found that disturbance had positive effects on the successful regeneration of all three species in the study area, supporting my first hypothesis that this factor plays important role in tree recruitment by creating a favourable environment for regeneration. As expected, regeneration was particularly evident in recent fire plots, which had a thin layer of organic matter and low moisture content compared to other plots. Fire helps white spruce regeneration by removing cold wet organic soils and degrading permafrost, creating a suitable seedbed by exposing mineral soil (Peters et al., 2005; Yoshikawa et al., 2003; Purdy et al., 2002). However, time elapsed since last fire was an important factor as the old fire plots had significantly less regeneration than recent fire plots. In other studies, white spruce regeneration was greatest within first seven years after a fire but declined after that, with the decline becoming significant after 10 to 14 years (Johnstone et al. 2004; Purdy et al., 2002; Macdonald et al., 2001). The changes in micro-habitat conditions in the old fire plots were the main reason for lower regeneration; these plots were characterized by thicker organic layers, higher crown cover and the presence of a dense shrub layer. However, regeneration success after fire also depends upon the co-occurrence of masting events with fire events (Peters et al., 2005). I found the highest abundance of white spruce regeneration in beetle-affected plots, although the micro-sites within these plots were quite different to recent fire plots, with a thicker layer of organic matter (= 11.29 cm; sd = +/- 9.5), higher crown cover (63.93%; sd = +/- 17.5), higher average moisture (= 25.96%; sd = +/- 11.8), lower shrub cover (40%), and the presence of abundant decayed logs, suggesting that spruce bark beetle disturbance had little effect on understory vegetation. The abundant presence of decayed logs may be the reason for the higher regeneration in these plots, as regenerations were densely concentrated on and around the decayed logs, which provide a favourable seedbed for white spruce regeneration (Vernon et al., 2006; Purdy et al., 2002). The regeneration of white spruce in intact forest or old fire forests was generally less than elsewhere since the mineral seedbed deteriorates with time since disturbance (Simard et al., 1998; Nienstaedt and Zasada, 1990), restricting regeneration to decayed logs with sufficient moisture availability (Coates et al. 1994).

Open light conditions created by disturbances had a positive impact on trembling aspen and balsam poplar regeneration and their regeneration was more abundant in fire plots than for white spruce, partially supporting my second expectation. Both species are shade-intolerant and unable to regenerate in the understory of mature stands (Landhäusser and Lieffers, 2001). Johnstone et al. (2004) obtained similar results in their study in the southeast Yukon, finding that seedling establishment of trembling aspen was highest after fire. Due to its ability to sucker, trembling aspen has a high tolerance to fire, making it better than white spruce at re-colonizing fire-disturbed areas (Purdon et al. 2002). Fire can benefit regeneration of balsam poplar by promoting vegetative reproduction (Rood et al., 2007). Regeneration of both broadleaved species was also higher in salvage-harvested plots. Harvested plots had similar micro-site conditions to the recent fire sites, with thinner layers of organic matter, lower moisture content, and lower crown and shrub cover. Similar results were obtained by Kurulok and Macdonald (2004; 2007) in their study in Alberta, although they concluded that salvage logging might negatively affect aspen regeneration, as the salvaged stands tend to have higher abundances of shrubs and grasses. The higher regeneration of both broadleaved and conifer species on disturbed plots therefore contradicted my expectation that any disturbance would favor the regeneration of broadleaved species over coniferous species.

4.4.2 Climate variability vs. regeneration

This research identified a strong relationship between climatic variables and white spruce and trembling aspen regeneration in the SWY, supporting my hypothesis that climatic factors significantly affect boreal tree recruitment and influence its abundance and spatial distribution. White spruce was found to prefer sites with higher summer temperatures and a higher number of growing degree-days, partially agreeing with my expectations. This is supported by the work of Andalo et al. (2005) in Quebec, who reported that temperature is the key factor for the germination of white spruce. Contrary to my expectations, precipitation did not significantly affect white spruce regeneration in my models. According to Archibold et al. (2000), the base germination temperature of white spruce is significantly correlated with average June precipitation as the optimal temperature for germination of white spruce is 20 °C, which can occur in June. However, drought and moisture limitations induced by higher temperatures and evapo-transpiration can significantly affect white spruce regeneration (Barber et al., 2000; Hogg and Wein, 2005).

The results of both the regeneration model and the MCA identified that temperature was negatively and precipitation positively correlated with aspen regeneration, suggesting that available moisture is an important factor for regeneration of aspen. It also suggests that this species is sensitive to the drought conditions that can be associated with higher temperatures (Frey et al., 2003). These finding are consistent with those of Hogg et al. (2005), working in northeast British Columbia, who found that aspen is sensitive to drought conditions. Dry soil conditions and/or drought can also significantly affect regeneration and growth of aspen (Frey et al., 2003). Thus, climatic factors favouring aspen regeneration contrasted strongly with those for spruce.

The model coefficients also suggested that balsam poplar was sensitive to high temperature and soil moisture. The species was significantly affected by changes in soil moisture. According to Tyree et al. (1994), this species is very sensitive to drought stress, which can be induced by high temperatures and low soil moisture regimes. I found that the number of growing degree-days > 5 °C had a positive influence in the model, indicating that the species prefers a warm growing season with sufficient soil moisture for regeneration. This is supported by Kalischuk et al. (2001), who found seedling growth was positively correlated with the accumulation of growing degree-days in their studies in southeastern BC and southern Alaska.

4.4.3 Edaphic/topographic factors vs. regeneration

Besides climate variability and disturbances, all three species distinctly responded to diverse edaphic and topographic factors and their abundance and distribution varied significantly with those factors. I found that trembling aspen regeneration prefers loamy to silty loam soils, a finding supported by Perala (1990) and Hogg et al. (2008), who found that aspen prefers well-drained loamy soils. Balsam poplar regeneration was significantly higher on sandy or silty clay soils, which are the major soil types found on alluvial and flooded sites where this species is commonly observed (Viereck et al., 1993; Cordes et al., 1997). Variation of white spruce regeneration abundance with soil texture was not significant in this study, although it does grow well on loamy to clay loam soils (Kabzems, 1971).

The abundance of white spruce regeneration decreased with increasing soil moisture content, with a greater abundance found on soils with moisture content between 10 to 20%. Purdy et al. (2002), working in mixed boreal forest of Alberta, also found that increasing soil moisture can limit white spruce regeneration, although the threshold for an impact of soil moisture was not mentioned. Similarly, trembling aspen regeneration decreased with increasing organic depth. These findings are in accordance with their higher abundance in fire plots, which had no or thin organic layers that contribute to lower soil moisture content (Johnstone and Chapin, 2006a). The negative relationship between organic depth and regeneration was explained by Jonhstone and Chapin (2006); it correlates with the positive response to fire that removes the organic layer, exposes the mineral soil and enables warmer soil temperatures (Purdy et al., 2006). Exposed mineral soil is generally warmer than soil with a high organic content (Kirschbaum, 1995) and it is considered as a good seedbed for white spruce regeneration (Youngblood and Zasada, 1991; Lieffers et al., 1996). The reduced aspen regeneration on soils with a thicker organic layer and higher moisture is supported by Johnstone et al. (2004) in their study in southwest Yukon. The abundance of aspen regeneration on sites with low soil moisture indicates that it can tolerate moisture stress, something also reported by Lieffers et al. (2001).

The results indicated that white spruce regeneration is poor on north-facing slopes. This is supported by Danby and Hik (2007) who found that the growth of seedlings on north-facing slopes is limited by low soil temperature in southwest Yukon. Similarly, in my study area, both broadleaved species and white spruce occupied sites at medium to lower elevation with gentle slopes and east to southeast aspects or level ground, confirming that they are light and temperature-demanding species (Frey et al., 2003). However, Elliott and Baker (2004) found aspen growing at higher elevations on south-facing slopes, suggesting that this species can survive at higher elevations on south-facing slopes because of the longer growing season and warmer temperatures on these sites. Balsam poplar was found in riparian areas in the study area, confirming its preference for moist sites close to permanent water sources and floodplain areas (Bockheim et al., 2003; Viereck et. al., 1993). Floods can promote balsam poplar regeneration by scarifying shallow roots, thereby promoting suckering (Rood et al., 2007). In this study, the density of mature trees and poplar basal area were important factors for balsam poplar regeneration, which suggests that vegetative reproduction may be the dominant mechanism for regeneration within the study region.

4.5 Chapter conclusions

Both multivariate analysis and maximum likelihood models suggested that the distribution and abundance of regenerations of white spruce, trembling aspen and balsam poplar could be explained by disturbances, climatic and edaphic factors supporting my hypotheses that these trends existed in the region. I found that the regeneration of all three species benefitted from some form of disturbance. Spruce regeneration was favoured by salvage logging following bark beetle infestations. However, regeneration of trembling aspen and balsam poplar were higher than white spruce regeneration in fire-disturbed plots, supporting the hypothesis that broadleaved forest may dominate and prevail for a long time if fire disturbances occur persistently. This will be particularly important if the region faces the drier summers predicted by the IPCC (Christensen, et al., 2007), which would contribute significantly to increasing fire disturbances in the region. Although applying forest management practices under the uncertain climate and disturbance circumstances is a challenging task, applying both pro-active and reactive management practices have been suggested to maintain the regeneration composition of both white spruce and broadleaved species. I would suggest carrying out selection or group harvesting to create gaps in undisturbed plots to enhance regeneration, as these plots had the lowest abundance of regeneration. I would also suggest to carry out salvage harvesting in phases with high retention (more than 30%) to maintain or enhance white spruce regeneration in beetle affected plots. Similarly, prescribed fire after salvage would be useful to create favourable substrate for the regeneration of all three species.

Table 4.1 Mean density (number/ha) of trees and their regeneration by disturbance types

Disturbance Type	White spruce regeneration p < 0.001	White spruce tree density	Ratio	Trembling aspen regeneration p = .020	Trembling aspen tree density	Ratio	Balsam poplar regeneration p =.056	Balsam poplar tree density	Ratio
Beetle plots	142295	1373	1:11	7629	27	1:29	238	0	0:24
Fire plots	163394	230	1:71	106812	18	1:59	13042	1	1:13
Harvested plots	66337	511	1:13	43600	75	1:58	7253	5	1:14
Undisturbed	63273	656	1:96	28331	131	1;22	860	2	1:43
Old fire plots	61743	861	1:72	41924	177	1:24	0	2	2:0
Mean density	99408	726	1:14	45659	85.6	1:53	4278	2	1:21

[Note: The variations of mean regeneration density were significant at $p<0.05$. The ratio columns indicate the ratio of density of regeneration to density of their parent trees. The table indicates that broadleaved trees had significantly higher ratios compared to white spruce.]

Table 4.2 Axes and their association with environmental data (MCA) (correlation coefficient)

Axis 1	Axis 2	Axis 3	Axis 4
PTT (.9156)	STT (-.4883)	Ele (-.4580)	Ele (-.3133)
PoBA (.9923)	FR (0.4852)	Slope (-.3031)	Slope (.3895)
Lat (-.1514)	AM (-.4142)	TMXsm (.4073)	DD5 (.3213)
SALV (.231)	TCC (-.3114)	DD5 (.4812)	TMXsm (.2968)
SA (.134)	OD (-.3870)	FR (.5213)	BT (.2810)

[Note: The table wasgenerated by multivariate canonical correlation analysis. The analysis has classified landscape into four habitats based on disturbance, edaphic and climatic factors. Abbreviation of names: PTT= Balsam poplar density; PoBA = Balsam poplar basal area, Lat = Latitude. SALV = Salvage harvest, STT = White spruce density, FR = Fire, AM = Average soil moisture, TCC = Total crown cover, Ele = Elevation, TMXsm = Mean summer maximum temperature, DD5= Degree-days above 5^0C, SA = Sand, OD = Organic layer depth, BT = Beetle affected forests.]

Table 4.3 Synthesis of canonical correlation analysis (correlations between the tree regeneration and the canonical axes of environmental data

	Axis 1	Axis 2	Axis 3	Axis 4
Spsed	0.0418	0.1954	0.3562	0.3734
AtSed	-0.0362	0.7464	0.1697	-0.0184
Popsed	0.8748	0.0504	0.2375	-0.1172
Atsap	-0.0291	0.2757	0.1991	-0.3689
Spsap	-0.0208	-0.4111	0.3798	0.3600
Popsap	0.9975	-0.0001	-0.0124	-0.0008

[Note: The table shows the correlations between tree regeneration and habitat factors. It indicates that Habitat 1 and 2 are related to balsam poplar and trembling aspen, respectively, and that Habitat 3 and 4 are related to white spruce regeneration. Abbreviation of names: Spsed = White spruce seedling, Atsed= Aspen seedling, Popsed = Balsam poplar seedling, Atsap = Aspen sapling, Spsap = white spruce sapling, Popsap = Balsam poplar sapling]

Table 4.4 Criteria for assessing goodness of fit

Criterion	Balsam poplar		Trembling aspen		White spruce	
	DF	Value	DF	Value	DF	Value
Deviance	80	30.0744	75	75.4884	81	109.6360
Scaled Deviance	80	30.0744	75	75.4884	81	109.6360
Pearson Chi-Square	80	27.4311	75	27.0187	81	43.1213
Scaled Pearson X2	80	27.4311	75	27.0187	81	43.1213
Log Likelihood		3157610.9		44002776.3		90016345.7
Full Log Likelihood		-159.3446		-620.9703		-1072.4911
AIC(smaller is better)		340.6891		1273.9405		2164.9823

Table 4.5 Analysis of maximum likelihood parameter estimates of white spruce

Parameter	DF	Estimate	Standard error	Wald 95% confidence limits		Wald Chi-square	Pr>Chi-sq
Intercept	1	-35.8779	21.5492	-78.1135	6.3576	2.77	0.0959
Ele	1	0.0168	0.0051	0.0068	0.0268	10.93	0.0009
Slope	1	-0.0705	0.0127	-0.0954	-0.0456	30.83	<.0001
mat	1	9.5482	0.5310	4.5876	14.5088	14.23	0.0002
Map	1	-0.0222	0.0100	-0.0418	-0.0027	4.96	0.0260
TMXsm	1	5.0724	1.0646	2.9858	7.1591	22.70	<.0001
TMNsm	1	-6.8105	2.3985	-11.5115	-2.1096	8.06	0.0045
Spavdia	1	0.0629	0.0294	0.0053	0.1205	4.58	0.0323
ToBA	1	-0.0421	0.0140	-0.0697	-0.0146	9.02	0.0027
Dispersion	1	1.4336	0.1907	1.0599	1.8073		

[Note: Algorithm converged. Stepwise modelling process retained only eight variables that were significant at p<0.05. Abbreviation of names: Ele = Elevation, mat = Mean annual temperature,Map = Mean annual precipitation. TMXsm = Mean summer maximum temperature, TMNsm = Mean summer minimum temperature, Spavdia = Average white spruce diameter, ToBA = Total basal area.]

Table 4.6 Analysis of maximum likelihood parameter estimates of trembling aspen

Parameter	DF	Estimate	Standard error	Wald 95% confidence limits		Wald Chi-square	Pr> chi-sq
Intercept	1	1615.75	350.29	929.1772	2302.32	21.28	<.0001
Map	1	-7.29	1.49	-10.2264	-4.35	23.65	<.0001
DD0	1	-0.98	0.22	-1.4014	-0.56	20.81	<.0001
DD5	1	-0.63	0.13	-0.8903	-0.37	22.72	<.0001
TMXwt	1	-108.07	23.39	-153.904	-62.23	21.36	<.0001
PPTwt	1	15.51	3.16	9.3140	21.69	24.11	<.0001
PPTsm	1	9.72	2.06	5.6829	13.75	22.29	<.0001
BT	1	4.14	2.06	0.0940	8.18	4.02	0.0449
FR	1	5.87	2.41	1.1354	10.59	5.91	0.0151
TD	1	0.12	0.03	0.0600	0.18	15.38	<.0001
OD	1	-0.58	0.15	-0.8803	-0.29	14.75	0.0001
CL	1	-0.16	0.06	-0.2764	-0.05	7.55	0.0060
SA	1	-0.06	0.03	-0.1111	-0.0033	4.33	0.0375
ATT	1	0.01	0.001	0.0020	.0091	09.43	0.0021
ToBA	1	-0.14	0.05	-0.2388	-0.05	9.21	0.0024
Dispersion	1	6.53	1.08	4.4062	8.65		

[Note: Algorithm converged. Stepwise modelling process retained only 14 variables that were significant at p<0.05. Abbreviation of names: Map = Mean annual precipitation, DD0 = Number of degree day below 0, DD5= Number of degree above 5, TMXwt = Mean maximum temperature in winter, PPTwt = Mean winter precipitation, PPTsm = Mean summer precipitation, BT = Beetle, FR = Fire, TD = Total soil depth, OD = Organic Depth, CL = % of clay, SA = % of sand, ATT = Aspen density (per ha), ToBA=Total Basal Area per hectare.]

Table 4.7 Analysis of maximum likelihood parameter estimates of balsam poplar

Parameter	DF	Estimate	Standard error	Wald 95% confidence limits		Wald Chi-square	Pr> Chi-sq
Intercept	1	2320.86	634.83	1076.63	3565.10	13.37	0.0003
Mat	1	-104.54	23.31	-150.24	-58.85	20.11	<.0001
TMXsm	1	-182.00	42.50	-265.30	-98.71	18.34	<.0001
DD5	1	2.11	0.50	1.13	3.09	17.75	<.0001
NFFD	1	-6.86	2.51	-11.77	-1.95	7.50	0.0062
BT	1	17.19	4.63	8.12	26.26	13.80	0.0002
FR	1	22.02	4.86	12.49	31.55	20.49	<.0001
AM	1	0.53	0.13	0.28	0.77	17.74	<.0001
PoBA	1	5.44	1.92	1.68	9.21	8.04	0.0046
ToBA	1	-0.44	0.12	-0.67	-0.21	13.92	0.0002
Dispersion	1	11.06	2.87	5.43	16.69		

[Note: algorithm converged. Stepwise modelling process retained only nine variables that were significant at p<0.05 Abbreviation of names: Mat=Mean annual temperature, TMXsm = Mean summer maximum temperature, DD5= Number of degree above 5, NFFD = Number of frost-free days, BT = Beetle, FR = Fire, AM = Average Moisture, PoBA = Balsam poplar basal area, ToBA = Total basal area.]

Table 4.8 AIC and variables dropped in the models

Species	Full model AIC values	Reduced model AIC Values	Number of insignificant variables dropped (P >.05)
White spruce	2207.3221	2164.9823	29
Trembling aspen	1302.4169	1273.9405	23
Balsam poplar	346.7387	340.6891	28

[The AIC values of reduced models are smaller than full models, which signifies the goodness of fitness of the models]

Table 4.9 Chi-square tests of the models

Species	Log likelihood of final model (l)	Log likelihood null model (l_0)	F calculted value $2*(l-l_0)$	F table value at p< .05
White spruce	90016345.79	90016322.49	46.59	15.51 (df =8)
Trembling aspen	44002776.31	44002740.60	71.42	23.69 (df = 14)
Balsam poplar	3157610.9	3157585.21	25.7	16.92 (df = 9)

[The tests showed that the calculated F value is higher than the tabulated value for all the species indicating that the models are statistically significant at p<0.05]

Table 4.10 Imputed and observed regeneration abundance for the first and last six plots

Observation	White spruce seedling imputed	Aspen seedling imputed	Poplar seedling imputed	White spruce seedling observed	Aspen seedling observed	Poplar seedling observed
1	933	0	0	21733	0	0
2	40133	15867	0	14000	13467	0
3	106667	0	0	6800	166267	0
4	248400	113200	0	84000	260133	0
5	6933	13600	0	17200	24933	0
6	13333	147733	0	40133	15867	0
85	17200	24933	0	10667	23600	0
86	17200	24933	0	6933	13600	0
87	133	0	0	20000	13333	0
88	6800	10000	0	60133	16667	0
89	40133	15867	0	73333	14733	0
90	3333	0	0	13333	36667	0

[Note: the table shows the top six and bottom six observed values and imputed values. The correlation between observed and imputed regeneration abundance of white spruce, trembling aspen and balsam poplar were 0.618, 0.656, and 0.874, respectively; suggesting imputed and observed values were highly co-related.]

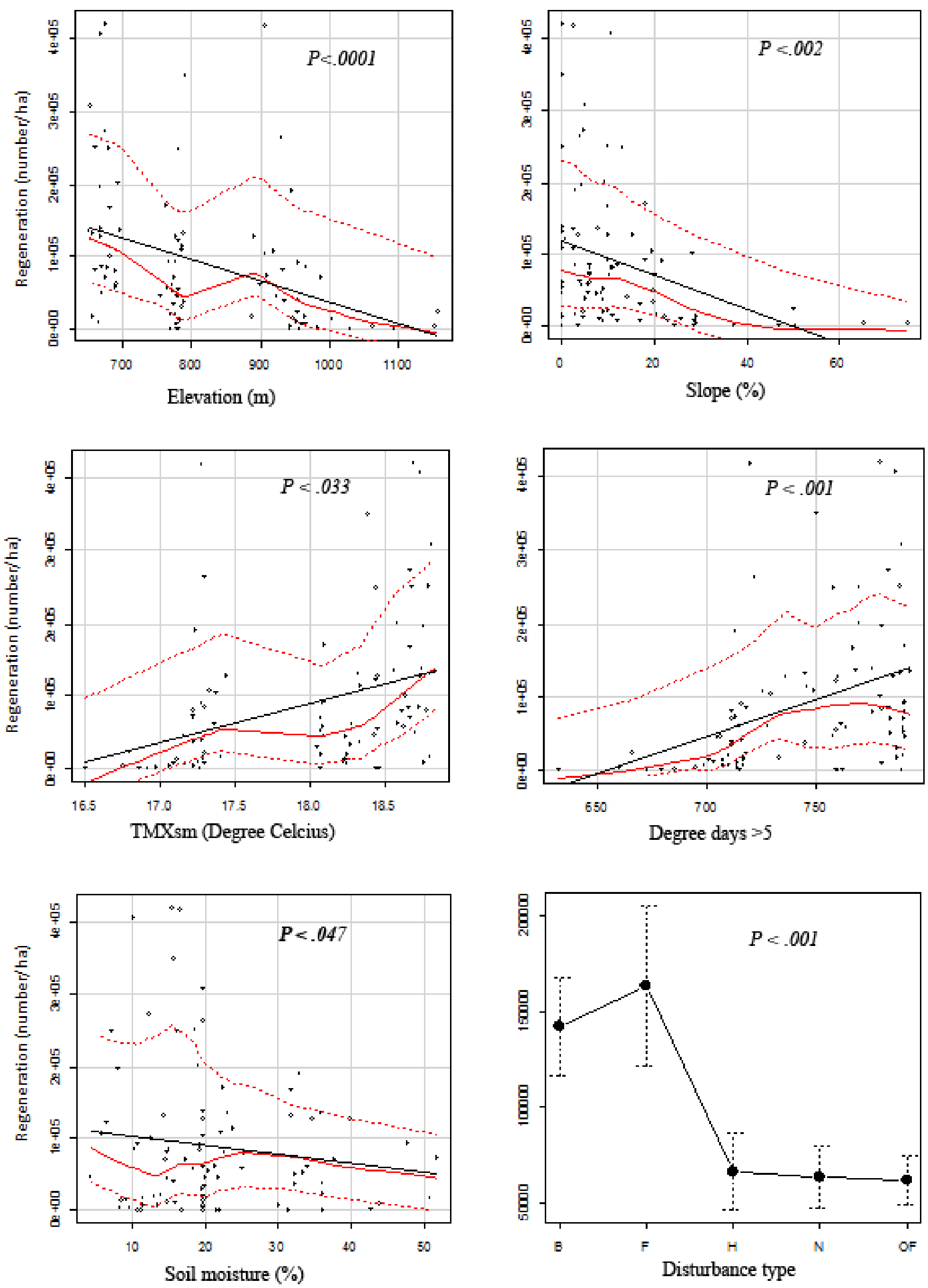

Figure 4.1 Responses of white spruce regeneration (number/ha) to environmental factors

[Note: Scatter plots indicating that white spruce responded negatively to increasing slope, elevation and soil moisture and positively to increasing summer temperature and number of growing days at significance level p<0.05. Means of plots (ANOVA; p<0.05) indicated regeneration variation by disturbance regime with its higher abundance in fire and beetle plots. Abbreviation of names: Beetle affected forests (B) Recent fire F), Salvage harvest (S); No disturbances (N) and Old fire (OF)]

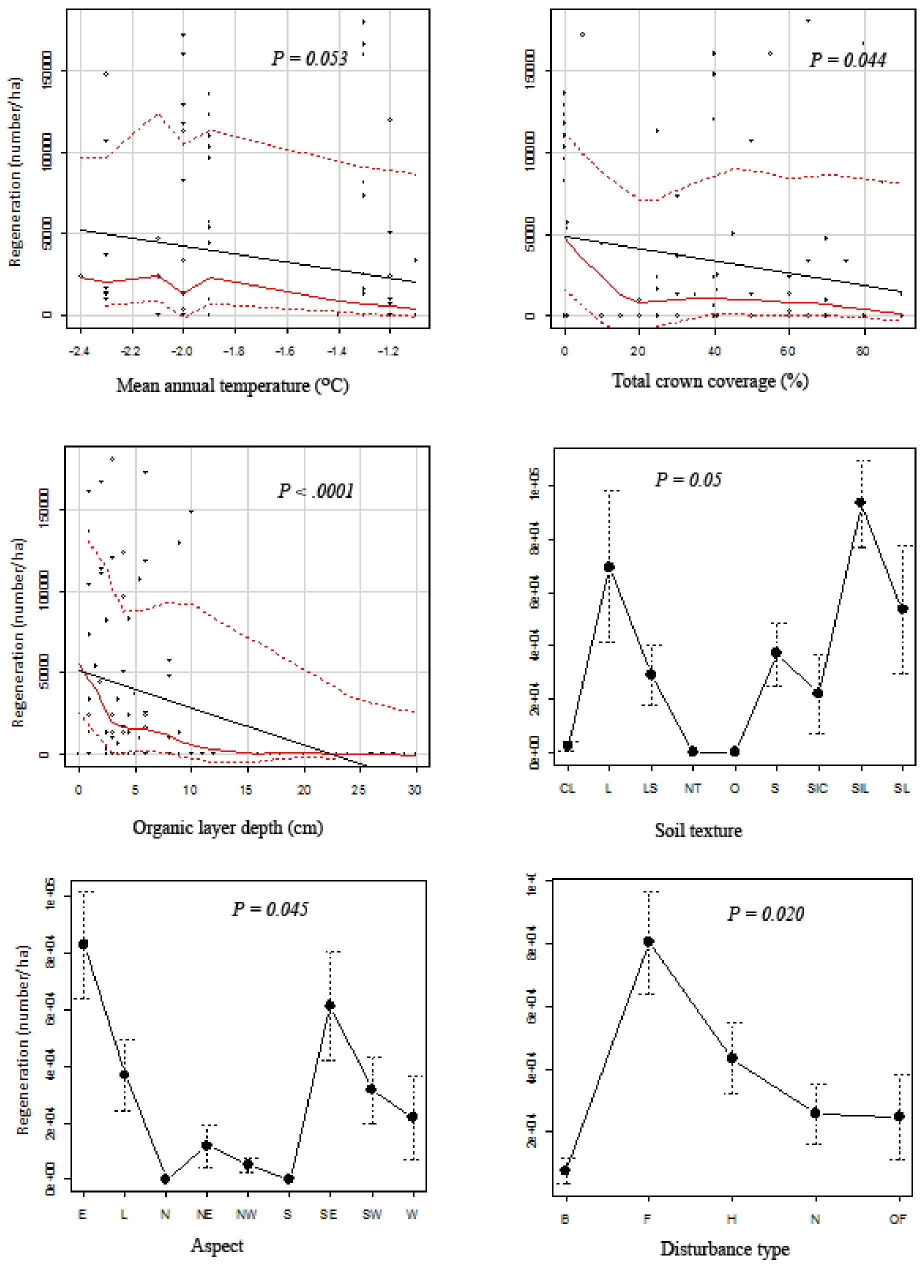

Figure 4.2 Responses of trembling aspen regeneration (number/hectare) to environmental factors

[Note: Scatter plots indicating that trembling aspen responded negatively to increasing mean annual temperature, total crown cover and organic depth layer at significance level p<0.05. Means of plots (ANOVA; p <.05) indicated higher abundance of regeneration in loamy to silty loam soil on eastern aspects and in fire plots. Abbreviation of names: Beetle affected forests (B), Recent fire (F), Salvage harvest (S), No disturbances (N) and Old fire (OF). Clay (CL), Loamy (L), Loamy sand (LS), No texture (NT), Organic (O), Sandy (S), Silty clay (SiC), Sandy loam (SL).Silty loam (SiL), Beetle affected forests (B) Recent fire F), Salvage harvest (S); No disturbances (N), Old fire (OF), East (E), Level (L), North (N), Northeast (NE), Northwest (NW), South (S), Southeast (SE), Southwest (SW) and West (W).]

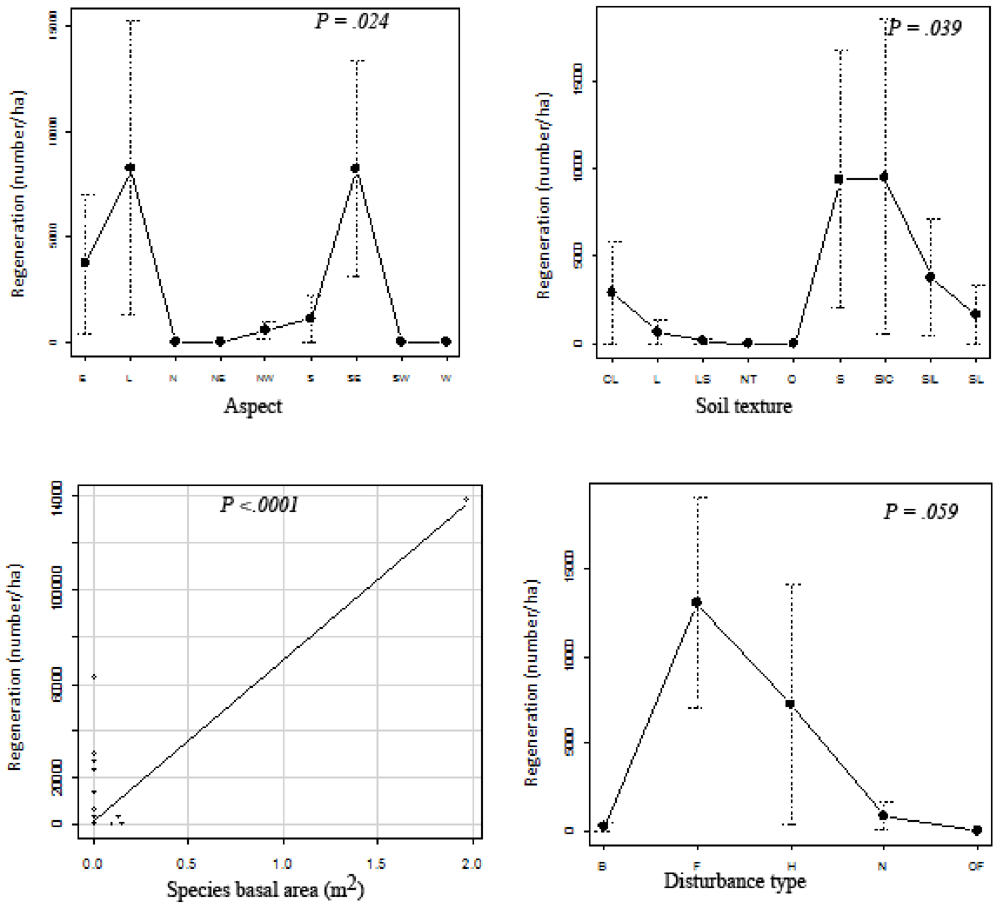

Figure 4.3 Responses of balsam poplar regeneration (number/hectare) to environmental factors

[Means of plots (ANOVA; p<.05) indicated balsam poplar's higher abundance in level or south-eastern facing sites, in sandy to silty clay soils and in fire plots. Abbreviation of names: Beetle affected forests (B), Recent fire (F), Salvage harvest (S), No disturbances (N) and Old fire (OF). Abbreviation of names: Clay (CL), Loamy (L), Loamy sand (LS), No texture (NT), Organic (O), Sandy (S), Silty clay (SiC), Sandy loam (SL).Silty loam (SiL), Beetle affected forests (B) Recent fire F), Salvage harvest (S); No disturbances (N), Old fire (OF), East (E), Level (L), North (N), Northeast (NE), Northwest (NW), South (S), Southeast (SE), Southwest (SW) and West (W).]

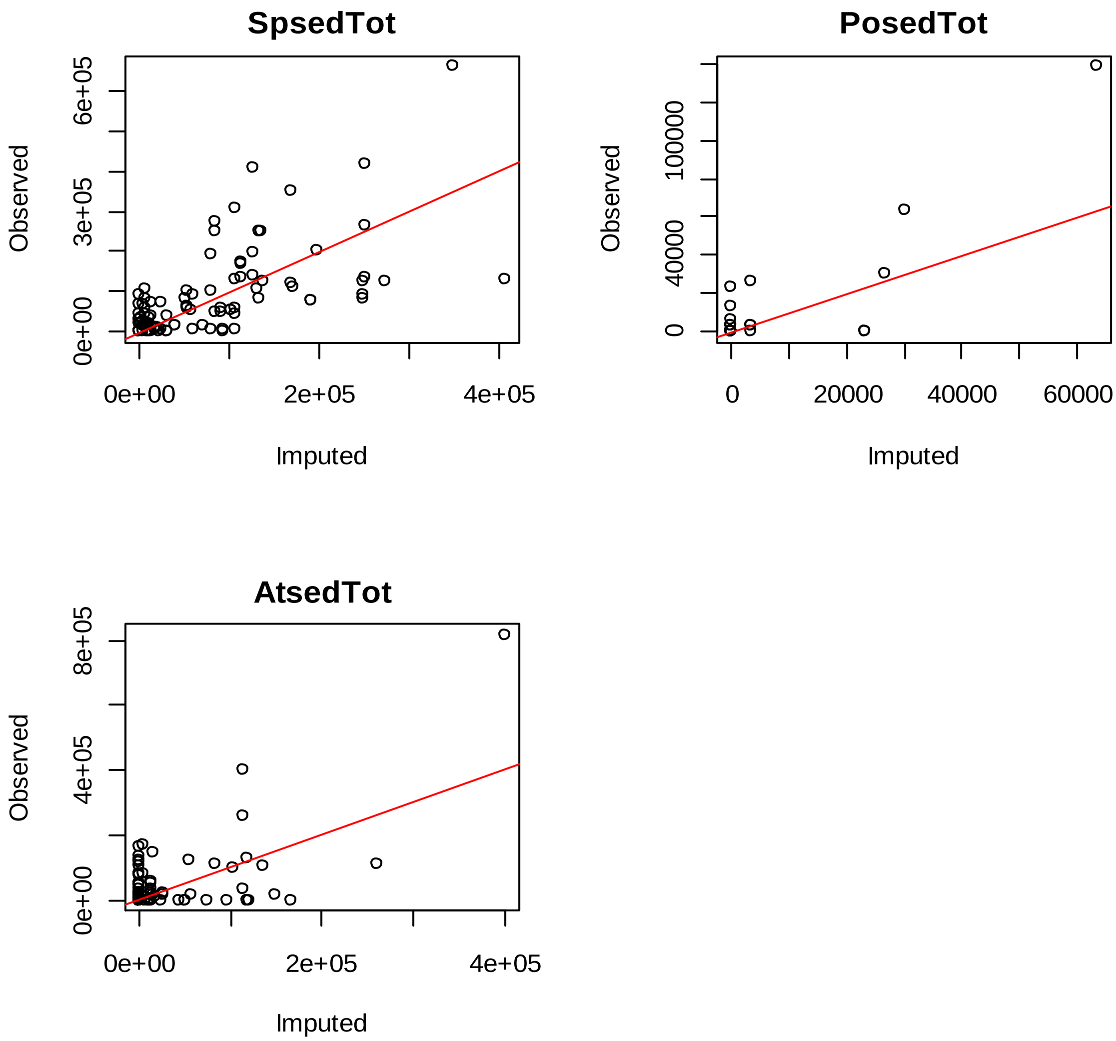

Figure 4.4 Relationship between imputed and observed values

[Note: The straight line in the figures indicates a correlation between imputed and observed values. For correlation coefficients close to 1, all the values would be along the line. Abbreviation of names: AtsedTot = Aspen seedling total; SpsedTot = White spruce seedling total; PosedTot = Balsam poplar seedling total.]

5. Vegetation diversity in response to landscape variability, disturbances and community dynamics in Southwest Yukon

5.1 Introduction

The southwestern region of the Yukon Territory, Canada, has experienced an unprecedented spruce bark beetle outbreak and an increase in forest fires; both are greater than historical trends. Such disturbances can cause significant impacts on ecosystems by shaping plant community structure and composition (Johnstone and Chapin, 2006b), and can have major implications for biodiversity and sustainable forest management (Nilsson and Ericson, 1997). A Strategic Forest Management Plan (SFMP, 2004) for the Champagne and Aishihik Traditional Territory (CATT) has been implemented since 2004 in response to the spruce bark beetle infestation in the region. The plan promoted the use of salvage harvesting as a short-term measure to achieve long-term goal of sustainable forest management. One of the goals of the SFMP is to "maintain ecosystem functioning" in the region, with the specific objectives being to maintain, restore or enhance forest succession, species and ecosystem diversity. This requires an understanding of the plant communities in the region. Such an understanding is still lacking, and this chapter presents the research that was undertaken in an attempt to fill this gap in knowledge.

5.1.1 Biodiversity and its importance

Hebda (1998; p. 195) defines biodiversity as "...a living legacy with a unique history developed in situ; not simply the number of species, not simply a collection of genes kept in a zoo, or frozen in a bottle, and not simply rarity or strangeness". According to Chapin et al. (2000) species diversity can be described by the number of species present (species richness), their relative abundances (species evenness), species composition (proportion of each species) and temporal and spatial variations in the above properties. Haila and Kouki (1994) refer to biodiversity as the overall heterogeneity in nature that is a necessary property of an ecological system. Similarly, Palik et al. (2002, p. 384) define "biodiversity as the variety and spatial patterns of physical structures, processes, species, and genotypes in a forest". Both species and genetic diversity generally depend on structural and process diversity (Franklin, 1988).

Species diversity influences ecosystem processes and functions and thus has important implications for the long-term sustainability of forests (Chapin et al., 2000). It plays an important role in ecosystem functions such as primary productivity, carbon storage, nutrient cycling and water retention, all of which are vital for ecological stability, determining for example, resistance or resilience after disturbances (Peterson et al., 1998; Naeem, 1998; Tilman et al., 1996; Bengtsson et al., 2000).

Increased species richness also increases the efficiency and stability of ecosystem functions (Tilman, 1996; Peterson et al., 1998). It is particularly important during succession, as the higher diversity ensures that enough species survive or persist to maintain ecological functions if a species disappears from the system due to a large-scale disturbance and may as well prevent successional retrogression (Folke et al., 1996; Chapin et al., 2000). Rich diversity increases the probability of including more disturbance-resistant species and can compensate for the loss of vulnerable species (Tilman, 1996; Hughes et al., 2007). Species diversity also reduces the probability of insect outbreaks by diluting the availability of their host species (Chapin et al., 2000).

Biodiversity also affects the distribution and abundance of wildlife in boreal forests as much of the vegetation provides important habitat and food for animals such as moose (*Alces alces*), wood bison (*Bison bison* ssp. *athabascae*), grizzly bear (*Ursus arctos* ssp. *horribilis*), American marten (*Martes americana*), Canadian lynx (*Lynx lynx*), snowshoe hare (*Lepus americanus)*, woodland caribou *(Rangifer tarandus* ssp. *caribou*), red fox (*Vulpes vulpes*), and muskrat (*Ondatra zibethicus*). Some of these species have important socio-economic significance for northern communities (Mulder et al., 2000).

5.1.2 Importance of studying vegetation diversity in SWY

Several studies have been undertaken on the distribution and ecology of vegetation in the Canadian boreal forest and within Yukon Territory. Some of the more comprehensive studies include La Roi (1967), Hultén (1968), Murray (1971), Douglas (1974), Wali & Krajina (1973), Douglas and Vitt (1976), Stanek et al. (1981), Bornor and Oswald (1985), Oswald and Brown (1986), Looman (1987), Meideniger and Pojar (1991), Johnson et al. (1995), Scudder (1997) and Cody (2000).

The distribution of vegetation in Yukon typically follows temperature gradients along both latitudinal and elevation gradients, creating a complex mosaic of vegetation types (Hughes et al., 1983; Douglas and Vitt, 1976). The characteristics and composition of the vegetation vary with climate, aspect, slope, soil type and moisture gradient (Meideniger and Pojar, 1991). The dominant vegetation types in the Yukon are arctic tundra, alpine tundra, taiga or subarctic forest, boreal forest and subalpine-shrub forest (Scudder, 1997). Arctic tundra is the dominant vegetation type in the low arctic Yukon Coastal Plain, which is treeless but with a continuous vegetative cover (Scudder, 1997). The subalpine zone is dominated mainly by the spruce-willow-birch ecosystem (Meidinger and Pojar, 1991). Deciduous communities dominated by species such as Scouler's willow (*Salix scouleriana* Barratt), trembling aspen and common bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.) are the results of disturbances such as fire and occur throughout the region (Douglas and Vitt, 1976).

The boreal understory vegetation plays an important role in ecosystem functioning by influencing canopy succession (Messier et al., 1998), nutrient cycling (Weber and Van Cleve, 1981), providing wildlife habitat (Okland and Eilertsen,1996) and providing many valuable foods and medicines to human society (Penafiel et al., 2011). However, forest management generally considers the overstory composition and structure, giving least priority to understory vegetation diversity (Hart and Chen, 2006).

Besides maintaining ecological function, the biodiversity of the boreal forest provides many social, economic and cultural services for local people (Chen and Popadiouk, 2002). Although timber harvesting is considered to be economically profitable in a quarter of the boreal forest in Canada (CCFM, 2006), the shrub vegetation (non-timber forest products, NTFPs) provides many socio-economic and cultural benefits to the people. Working in Yukon, Holloway and Alexander (1990) found that 48 species of native plants were used by local communities as medicines (40%) and as food or beverage (56%). Wild fruits and mushrooms comprised the greatest proportion of edible plants. According to Holloway and Alexander (1990), mountain cranberry (*Vaccinium vitis-idaea* L.) accounts for 90% of the berries and mushrooms account for 70% of the food harvested in the Porcupine River region of Yukon. Duchesne et al. (2000) estimated the total value of NTFPs to be equivalent to $240 million (Canadian dollar) in 1997, although this figure did not include locally traded and used products. Wild berries and other wild food accounted for $21 million annually. It has been estimated that the potential for NTFPs harvest in Canada is about $1 billion, which could provide viable economic opportunities for many rural communities (Mohammed, 1999).

5.1.3 Research Issues: impacts of landscape variability, climate and disturbances on vegetation diversity

A landscape is an ecological unit with a unique or distinguishable character and structure where its components or units interact with each other as an ecological function (Forman and Godron, 1981). Landscapes are constantly changing due to geomorphologic processes, climatic change, human interference and disturbances (Noss, 1983; Bengtsson et al., 2000), which is one of the main reasons for biodiversity change (Noss, 1983). Change may influence diversity both negatively and positively. Bengtsson et al. (2000) suggested however that there is little or limited research on the effects of large-scale landscape changes on diversity, as most research has been conducted at relatively small scales, which may not be relevant for predicting large-scale dynamics of ecosystems.

Community dynamics resulting from disturbances are natural features of the boreal forest (Niemela, 1999). Disturbances can have major implications for biodiversity and sustainable forestry (Nilsson and Ericson, 1997). Disturbances create a mosaic of structures and processes that influence the variety and diversity of species (Palik et al., 2002). Studies in the boreal forest also suggest that the frequency and severity of disturbances can affect forest ecosystems by influencing vegetation dynamics, diversity patterns and ecosystem processes (Wardle et al., 1997). As most forestry operations such as logging involve some kind of disturbance that can affect both diversity and ecosystem function, the understanding of natural disturbances and disturbance dynamics on diversity has become an increasingly salient issue for forest managers (Haila et al., 1994; Angelstam, 1997; Bengtsson et al., 2000). Therefore, it is important to understand the relationship between disturbance dynamics and biodiversity if forest management practices are to conserve and sustain biodiversity (Hughes et al., 2007).

According to the intermediate disturbance hypothesis (IDH), local diversity is maximized when disturbances are neither too frequent nor too rare. In other words, higher diversity is maintained when the intensity and frequency of disturbances are intermediate (Grime, 1973; Connell, 1978). The hypothesis states that species diversity is low when there are frequent disturbances as only a few tolerant species can survive, or when there is no disturbance so that the ecosystem is dominated by a few, highly competitive species. Frequent disturbances can lead to the creation of bare patches, such that competitive exclusion does not occur in the landscape (Connell, 1978; Wilson, 1994).

Climate change may impact forest biodiversity by affecting species interactions and ecosystem processes (Spittlehouse, 1996). It may change both the biodiversity of an area and the stand structure and species composition (Hebda, 1998). Climate change may influence biodiversity directly by affecting individual organism, population, species distribution and ecosystem composition and function, and/or indirectly by the modification, loss or fragmentation of species habitats, increased frequency and severity of disturbances and introduction of non-native species (IPCC, 2002). More than 40% of Canada's protected areas are projected to be affected by biome change as a result of climate change (Lemieux and Scott, 2005).

Similarly, community dynamics and their relationship with biodiversity are also an important element. Variation in species diversity can be both a cause and a consequence of variation in community dynamics (Loreau et al., 2001). It is therefore important to understand how community properties contribute to the maintenance of biodiversity (Huston, 1979; Hughes et al., 2007). Similarly, the amount of coarse woody debris may play a significant role in determining the presence or absence of some species, especially in boreal forests where many species are dependent on the density of dying and dead trees (Esseen et al., 1997; Nilsson et al., 2001).

5.1.4 Research problems, hypotheses and questions

Plant diversity is an important aspect of forest management, both for maintaining, restoring or enhancing forest succession, species and ecosystem diversity and to fulfil the socio-economic needs of people. This has been recognized in the CATT (SFMP, 2004). However, a full understanding of the processes involved is still lacking in the region, which sets the scene for the major research questions asked in this chapter. I examined the variation in vegetation diversity in response to bio-geoclimatic factors and the disturbance regime in the CATT. My aim was to increase the knowledge of vegetation diversity in the region in order to help forest managers make more informed management decisions, thereby enabling the conservation and management of biodiversity. I hypothesize that:

(i) Canopy gaps created by harvesting and forest disturbances will increase vegetation diversity.

(ii) Vegetation diversity will increase with increasing stand structure and decrease with increasing stand density.

(iii) The highest diversity will occur at intermediate levels of disturbance (in terms of severity) *sensu* the IDH (Connell, 1978).

To address the above hypotheses and to understand the overall diversity pattern in the study area, this chapter deals with the following broad research questions;

- What is the overall diversity and distribution of vegetation in the study area?
- What stand structure and disturbance factors affect the variation of vegetation diversity in the study area?
- How do vegetation patterns vary with edaphic and climatic factors?
- Are the results of different diversity indices consistent?

5.2 Data collection and analysis

Vegetation data were collected from 90 randomly selected plots as explained in Chapter 2. Species were identified using local flora (Cody, 2000; Johnson et al., 1995). Specimens of each species were collected and photographs were taken to verify genus and species at the lab. However, despite my best efforts, some plants could not be identified to the species level and are therefore listed only at the genus level.

For data analysis, as a single index of diversity or evenness may result in an incorrect interpretation as some communities cannot be ranked by diversity or evenness (Taillie, 1979; Ricotta, 2003), complementary techniques have been suggested to produce diversity and evenness profiles (Kindt et al., 2006). In this case, vegetation diversity has been assessed using both alpha and beta diversity indices. Species richness, abundance and evenness were calculated. Similarly, Simpson and Shannon-Wiener indices were calculated for each of the 90 sites (alpha diversity) as well as for the variation along the environmental gradient (beta diversity). Species ranges and distribution were also calculated. Detailed descriptions of each method are provided in the following section.

5.2.1 Richness, abundance and evenness analysis

Species richness, abundance and evenness were calculated since these are common indicators of diversity (Kindt et al., 2006). Richness is a measure of the total number of different species in a particular area or in a community. Abundance is the total number of all the species in an area, and is expressed as a total count or percentage of cover. Evenness is a measure of the relative abundance of the different species in proportion to the total species assemblage in an area, which gives homogeneity or relative diversity (Kindt and Coe, 2005). Evenness is considered as important as species richness. Evenness has a more direct relationship with total forest productivity than species richness (Naeem et al., 1994) and a reduction in evenness may negatively affect plant productivity (Wilsay and Potvin, 2000).

5.2.2 Diversity indices

Shannon-Wiener index, Simpson index and Renyi's profiles were calculated; these are briefly described in the following sections.

5.2.2.1 Shannon-Wiener and Simpson indices

Shannon-Wiener and Simpson indices have been frequently used for assessing species richness (Shannon and Weaver, 1949; Simpson, 1949). The Shannon-Wiener index has been widely used for comparing diversity between different habitats (Clarke and Warwick, 2001) and has been used for both categorical and continuous variables (McRoberts et al., 2008). The Simpson index is the preferred method for comparing diversity between different species assemblages because of its ability to rank assemblages consistently when sample size varies (Magurran, 2004). It is also preferred to the Shannon-Wiener index due to its better performance as a general purpose of diversity index and as a measure of evenness (Magurran, 2004). The Simpson index is considered a dominance index as it is weighted towards the abundance of the most common species while being less sensitive to species richness (Whittaker, 1972; Smith and Grassle, 1977).

Although the Shannon-Wiener index is less dependent on the dominant species than the Simpson index (see below), it gives little weight to rare species (Zahl, 1977). The Shannon-Wiener diversity index (H') is calculated as (Shannon and Weaver, 1949):

$$\boldsymbol{H' = -\sum_{i=1}^{n}(P_i * LnP_i)} \text{………..……} \textbf{Equation (5-1)}$$

where, H’ is the Shannon-Wiener diversity index and P_i is the proportion of each species (N). The value ranges from 0 to Ln (N). The value of the Shannon-Wiener diversity index is usually between 1.5 and 3.5 and only rarely surpasses 4.5.

The Simpson index can be calculated by (Simpson, 1949):

$$\mathbf{H = \sum_{i=1}^{s} \frac{n(n-1)}{N(N-1)}} \text{…………….……….} \textbf{Equation (5-2)}$$

where H is the Simpson index, n is the numbers of individuals in each species, and N is the total number of individuals. The Simpson index is expressed either as H (where higher value means lower diversity) or 1-H or 1/H (where higher values means higher diversity) (Kindt and Coe, 2005).

5.2.2.2 Renyi's profile

A single diversity index such as the Shannon-Wiener Index or the Simpson Index can provide misleading results (Kindt et al., 2006). As a result, Renyi's profiling was used as a complementary method. This is a direct method for comparing diversity and evenness (Ricotta, 2003). Renyi's profile provides many kinds of indices for species richness and diversity including modified Simpson and Shannon-Wiener indices (Kindt and Coe, 2005). Tothmérész (1995) suggests that the Renyi's profile is one of the most useful methods for diversity ordering. In addition, as the sample size significantly affects the diversity index (Kindt et al., 2006); Renyi's values can reduce the sensitivity to sample size (Magurran, 1988). Renyi's profile is calculated as:

$$\boldsymbol{H_\alpha = \frac{ln\left(\sum_{i=1}^{s} P_i^{\alpha}\right)}{1-\alpha}} \text{.................}\textbf{Equation (5-3)}$$

where H_α is Renyi's diversity profile and P_i is the proportion of each species. It provides eight different α values (varying from 0 to infinity); each gives different index. For example alpha = 0 provides the logarithm of species richness, alpha = 1 provides Shannon-Wiener diversity index and alpha = infinity provides the information on the proportion of the most abundance species (Kindt and Coe, 2005).

The evenness profile can be derived from the diversity profile and orders communities in evenness (Smith and Wilson, 1996; Kindt et al., 2006). The evenness profile is calculated as:

$$\boldsymbol{LnE_{\alpha,0} = H_{\alpha} - H_{0}} \text{……………………..….}\textbf{Equation (5-4)}$$

Renyi’s profile was used in this study to assess the variation of species richness and evenness of the communities along the disturbance, environmental (slope, elevation, climatic variations, moisture etc.) and ecological gradients (tree density, crown cover and regeneration density).

5.2.2.3 Diversity curves

Species accumulation curves and Renyi’s profiling curves were used in this study to show variation in diversity at the landscape-level. Species accumulation curves show the species richness for combinations of sites or pooled species richness (Kindt and Coe, 2005). The curves indicate how many new species are added when one new site is added to the analysis. It also provides the average standard deviation of species richness with each new site added. Species accumulation curves are very useful for comparing species richness for subsets in the data when sample sizes of subsets are different.

Renyi’s profiling quantifies the variation of diversity and species richness along an environmental gradient. Each assessment provides H-alpha and E-alpha metrics for showing diversity and evenness of the communities, respectively. The curves that start and end at higher points indicate higher diversity or evenness of the communities (Kindt and Coe, 2005). One of the advantages of Renyi’s profile is that sites can be ordered from higher to lower diversity.

As suggested by Kindt and Coe (2005) and Kindt (2004), Biodiversity-R (R, 2005) and the Vegan package (Oksanen et al., 2005) software programme were used for the data analysis. As required by the Biodiversity-R programme, the community and environmental data were separately prepared in Excel sheets as community, environmental and community stacked data.

5.2.3 Species spatial distribution and range

The vegetation range in the landscape was analyzed by showing the presence or absence of particular species in each block. The range table also shows the abundance of each species in each block. This value indicates the type of habitat that each particular species may prefer. Similarly, distribution and abundance of understory vegetation by disturbance type were also assessed in order to identify the dominant and unique species related to specific disturbance type.

5.2.4 Canonical correspondence analysis (CCA)

As environmental variables are often highly correlated, it is better to see the combined effects than their independent effects (Ter Braak and Verdonschot, 1995). When the number of influential environmental variables is more than two or three, it becomes increasingly difficult to infer results for several species together. Canonical correspondence analysis (CCA) is designed to fulfil this need by analysing and visualizing the relationships between many species and many environmental variables (Ter Braak and Verdonschot, 1995).

Canonical ordination techniques were developed to detect the patterns in variation in species data that can be best described by a combination of environmental variables (Jongman et al., 1995). This method was introduced by Ter Braak (1986) and has been widely used in ecological analyses (Birks et al., 1996). CCA is considered as a simple ordination method for arranging species along environmental variables, constructing linear combinations of environmental variables along which the distributions of the species are maximally separated (Ter Braak, 1986). Its application is mainly for detecting species-environment relations and for investigating specific questions about the response of species to environmental variables (Ter Braak, 1986).

CCA was used to detect the relationship between species distribution and combinations of environmental variables. Out of 69 species recorded, the 25 most widely distributed species (species covering at least 1% in average in each plot or more than 90% in 90 plots) were considered for the analysis. CCA has also been used to detect the relationship between environmental variables and major diversity indices such as the Shannon-Wiener and Simpson indices, and species richness and abundance, as it may provide information on how those indices are affected by or related to environmental variables.

5.2.5 Diversity index mapping

A Geographical Information System (ArcGIS, 2009) was used to map Shannon-Weiner indices in the study area. Fisher Discriminant Analysis (Fisher, 1936) was used to develop a model for Shannon-Weiner indices against independent variables; slope, elevation and aspect. The model output was used to extrapolate the indices over the raster pixels of the landscape using ArcGIS (2009).

5.3 Results

5.3.1 Characteristics and severity of disturbed plots

The disturbed plots varied significantly in terms of moisture content, depth of organic layer and crown cover (Table 5.1). The analyses of these variations were important as they indicated the disturbance characteristics and severity.

With some exceptions, the beetle-affected forests that were not harvested or affected by fire had the highest crown cover (= 63.93%; sd = +/-17.5), soil moisture (= 26%; sd = +/-11.8) and soil organic depth (= 11.29 cm; sd= +/- 9.5). The old fire plots were mainly comprised of mixed stands of white spruce and trembling aspen with an average of 48% (sd = +/- 24.4) crown cover, an average soil organic layer depth of 8.2 cm (sd = +/-6.2) and 25% (sd = +/-11.8) soil moisture. The most recent large fire occurred in 1998 in a portion of the research area, severely impacting both forest crowns and soils. These plots were affected by spruce bark beetles prior to the occurrence of fire. These recent fire plots had low average crown cover (=12%; sd = +/- 25.5), organic depth (= 2.75 cm; sd = +/-2.09) and soil moisture (= 19%; sd = +/-11). In response to these disturbances, the salvage harvesting of beetle-affected stands commenced in 2006 and has had noticeable impacts on both soil and understory vegetation, with harvested plots having lower average organic depth (= 5.2 cm; sd = +/-4) and soil moisture (= 18.6%; sd = +/- 5.3). Undisturbed plots had the thickest organic depth (= 8.98 cm; sd = +/-7.8) and moisture content (= 19.4%; sd = +/-10.8).

5.3.2 Species richness, abundance and spatial distribution

In the study area, 63 genera and a minimum of 69 species were recorded (Table 5.2) of which four species were trees, 47 species were shrubs and herbs, 10 species were bryophytes and eight species lichens (Appendix A).

The average richness in each plot was 13.8 (~ 14), with maximum and minimum richness values of 21 and 4, respectively. Similarly, the average cover in the subplots was 114.7% (~115%), with maximum and minimum abundance of 18% and 269%, respectively. The abundance and richness data for each site are provided in Appendix F. Plot numbers 404, 106, 409, 502, 503 and 613 had the highest numbers for richness, with more than 20 species recorded in each plot. Similarly, 56 plots had more than 100% cover, with more than 200% cover in plot numbers 216, 217, 220 and 504 (appendix F). With the exception of research blocks C and F, which had an average abundance of about 80%; the blocks had more than 100% cover (Appendix H-1). The Shannon-Weiner indices have been plotted in the landscape using GIS (Figure 5.1) which shows higher diversity in research blocks four (recent fire), five and six (salvage harvested). However, the correlation analysis indicates that the richness and abundance data are weakly correlated ($r = 0.25$).

Species distribution and abundance comparisons among the research blocks are provided in Appendix G. The five most abundant higher plants (trees, shrubs and herbs) were willow (*Salix* spp.), white spruce *(Picea glauca* (Moench) Voss), bearberry (*Arctostaphylos uva-ursi* (L.) Spreng. s.l.), and soapberry (*Shepherdia canadensis* (L.) Nutt.), trembling aspen *(Populus tremuloides*, Michx.) with total proportionate covers of 9.86%, 8.17%, 7.3% 6.54% and 4.5% respectively. Similarly, common dandelion (*Taraxacum officinale* Weber ex Wiggers), common juniper (*Juniperus communis*, L.s.l), black snakeroot (*Sanicula marilandica* L.), yellow monkey flower (*Mimulus guttatus* DC.), hook-spur violet (*Viola adunca* J.E. Smith) and pink-flowered wintergreen (*Pyrola asarifolia* Michx.) were among the least abundant herbs and shrubs, with less than 0.05% proportionate cover. Among the bryophytes and lichens; red stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.) was highly abundant with more 12% coverage and broom moss (*Dicranum scoparium* Hedw.) and glow moss (*Aulacomnium palustre* (Hedw.) Schwagr) and sugary beard lichen (*Usnea hirta* (L.) F.H. Wigg.) were the least abundant in the study area.

In terms of the spatial distribution of the species, red stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.), *Salix* spp., *Picea glauca* (Moench) Voss, *Arctostaphylos uva-ursi* (L.) Spreng. s.l., *Shepherdia canadensis* (L.) Nutt., pixie cup lichen (*Cladonia* spp.), curled snow lichen *(Flavocetraria cucullata* (Bellardi) Karnefelt & A. Thell), freckled lichen (*Peltigera aphthosa*, (L.) Willd.), prickly rose (*Rosa acicularis* Lindl. s.l.), and Indian paint-brush (*Castilleja* spp.) were recorded in all blocks, indicating their wider distribution in the research area. In contrast, meadow barley (*Hordeum brachyantherum* Nevski), clear moss (*Hookeria lucens* Hedw. Sm.), fescue (*Festuca* spp.), cranberry (*Oxycoccus microcarpus* Turcz.), *Taraxacum officinale* Weber ex, broom moss (*Dicranum scoparium* Hedw), hook-spur violet (*Viola adunca* J.E. Smith), glow moss *(Aulacomnium palustre* (Hedw.)Schwagr.), sugary beard lichen (*Usnea hirta* (L.) F.H.Wigg.) and common juniper (*Juniperus communis* L.s.l.) were recorded from only one research block, indicating their limited distribution in the research area.

The species accumulation curve (Figure 5.2) rises steeply up to pool of 40 sites that includes almost 60 plant species while the remaining 50 sites added only 12 more species, flattening the curve out. This indicates that about 50% of sampling plots could accommodate 80% of the vegetation diversity in the study area.

5.3.3 Vegetation diversity in response bio-geoclimatic and disturbance factors

The mean richness, mean abundance, Shannon-Wiener and Simpson indices were calculated and the results of the indices are provided in the tables within Appendix H. Variation in vegetation diversity was assessed using Renyi's profile independently by eco-geographical gradient (blocks, slope, aspect, elevation and soil moisture), disturbance type, stand dynamics (stand density, stand type and crown cover) and climatic factors (mean annual temperature, mean annual precipitation and number of growing degree-days > 5 ºC)

Renyi's profile (Figure 5.3) provides variation in diversity by eco-geographical gradient and disturbance types. Figure 5.3 does not reveal a clear variation in vegetation diversity with aspect, although the Shannon-Wiener index, which gives more weight to species richness, was higher on eastern aspects and, conversely, the Simpson Index was higher on northern aspects (Appendix H-4). Vegetation diversity was higher at low elevations and on flat ground and lowest on southwest aspects and steep slopes. The Shannon-Wiener and Simpson indices provided similar results. Indices were higher at lower elevations, on flat areas and on northwest, north and east aspects.

Renyi's profile also illustrates the variation in species diversity by research blocks, disturbances and moisture gradient. The results suggested that diversity was higher in the harvested Block E, which has the driest soil moisture regimes, and lower in beetle-affected stands, which had higher soil moisture. The blocks with the lowest diversity were D and A, which were not differentiable. The evenness profile also showed a similar result to that of the diversity analysis.

The Renyi's profile did not reveal a clear variation in vegetation diversity with disturbance types as index lines cross each other. However the Shannon-Weaver and Simpson indices (Appendix H-5) indicated higher diversity in harvested plots (Shannon-Weaver Index = 2.16; Simpson Index = 7.19). The median diversity was found in fire plots (Shannon-Weaver Index = 196; Simpson Index = 5.5). The least diversity was found in old fire plots (Shannon-Weaver Index = 2.16; Simpson Index = 7.19), in spruce bark beetle plots (Shannon-Weaver Index = 1.84; Simpson Index = 4.67) and undisturbed plots (Shannon-Weaver Index = 1.79; Simpson Index = 4.85). Both harvested and fire plots were characterized by low crown cover, lower moisture content, thinner organic depth layer and the lowest shrub cover (Table 5.1). These findings indicate that medium soil disturbances (harvested plots in this study as indicated in section 5.3.1) favour higher vegetation diversity compared to highly disturbed (fire plots) or less/non-disturbed areas, suggesting that the diversity pattern is consistent with that expected under the Intermediate Disturbance Hypothesis (IDH).

Figure 5.4 provides the variation in diversity by climatic factors and stand dynamics. Diversity was higher in stands with lower stand density, lower crown cover and in mixed stands. The lowest diversity was recorded in stands with high stand density, high crown cover and in stands dominated by trembling aspen. Renyi's profile matched with Shannon-Wiener and Simpson indices for crown cover. The variations among some of the climatic factors were mostly unclear as in most cases the curves intersect each other. Diversity was higher with increasing mean summer maximum temperature, higher mean annual temperature and precipitation and lowest in plots with colder temperatures and lower annual precipitation. The Shannon-Wiener and Simpson indices provided the similar results.

Table 5.3 shows the top 10 most abundant plants. Distributions of these species varied significantly with disturbance type. Nine species were restricted to present in specific types of disturbance. *Arctostaphylos rubra* (Rehd. & Wils.) Fern. and *Peltigera canina* (L.) Willd. were only present in beetle-affected plots. Similarly, *Betula glandulosa* Michx., *Dicranum scoparium* Hedw., *Epilobium angustifolium* L.s.l., and *Equisetum arvense* L. were only present in recent fire plots. *Festuca* spp. and *Alnus incana* (L.) Moench were only present in harvested and undisturbed plots. In contrast, *Cladina mitis* (Sandst.) Hustich, *Pleurozium schreberi* (Brid.) Mitt. and *Shepherdia canadensis* (L.) Nutt. were absent from specific disturbance types namely old fire, recent fire and beetle affected plots respectively. Out of these 10 species, six of them are locally used species (Table 5.3); implying disturbances may affect availability of these species.

5.3.4 Canonical correspondence analysis (CCA)

The CCA results were similar to the results described in the previous section, although the analysis did provide some new information. It indicated how the independent variables are related in terms of vegetation distribution and diversity indices. The full results are provided in Appendix I. Most of the species were clustered around the centre of two axes (Figure 5.5), indicating no major influences of particular environmental variables. However, a few species showed a strong relationship to sandy soil, increasing density of trees, increasing slope and increasing degree days below and over 5 ºC.

The species distribution in Figure 5.6 indicates that willow and white spruce are clustered in the centre indicating they are widespread at most of the sites. White spruce showed a similar trend in the multiple co-inertia analysis in Chapter 3. *trembling aspen*, Michx., *Shepherdia canadensis* (L.) Nutt., and *Arctostaphylos uva-ursi* (L.) Spreng. s.l. were centered in one cluster, indicating that they prefer similar environmental conditions. Similarly, Labrador-tea (*Ledum groenlandicum* Oeder), dwarf blueberry (*Vaccinium caespitosum* Michx.), crowberry (*Empetrum* *nigrum* L.) and western rye grass (*Elymus glaucus* Buckl.) are on the same axis, indicating their similar environmental requirements. By overlapping the information in Figure 5.5 and 5.6, it can be inferred that these species mostly prefer sites that have a higher slope position, higher mean annual temperature and higher number of frost-free days.

5.4 Discussion

5.4.1 Variation in vegetation diversity by bio-geoclimatic and disturbance factors

5.4.1.1 Canopy gaps vs. vegetation diversity

The findings support my hypothesis that higher diversity is associated with canopy gaps in the study area. Diversity was higher in harvested and fire plots, which had 29% and 12% canopy cover, respectively, the lowest of any of the disturbance types. Higher understory diversity in harvested areas was also observed by Whittle et al. (1997) and Bergeron and Dubuc (1989). The higher diversity in these blocks (with larger canopy gaps compared to other blocks) is likely due to exposure to sunlight as light is considered to be the most limiting resource affecting understory vegetation establishment and considered to be one of the most important environmental factors (Chen et al., 1996; Legare et al., 2002). However, the understory vegetation may change over time as the overstory vegetation changes, and light availability to the understory can decline to less than 15% (Okland et al., 2003), causing a shift in understory vegetation from shade-intolerant to shade-tolerant species (De Grandpré et al., 1993). The increased abundance of white spruce seedlings under the closed canopy of aspen stands is one of the examples of the type of vegetation shift described in Chapter 3. Disturbances that create canopy gaps will likely increase diversity but will be followed by reduced diversity once the canopy cover increases. As a result, the highest diversity can be expected to decline after crown closure, which has been shown to occur within 40 years of a disturbance (Hart and Chen, 2006).

My findings that vegetation diversity was higher in stands with in low stand density support my second hypothesis. The low diversity measured in beetle-affected sites may be due to the higher crown cover, tree density and presence of *Pleurozium schreberi* (about 32% coverage, Table 5.2) in these plots. The average stand density in all plots was 813 stems per hectare while it was 1306 stems per hectare in beetle-affected plots. Similarly, the crown cover was 60% in beetle-affected stands, which was higher than the average in all other plots (41%). The relationship between stand characteristics and vegetation diversity has been recognized by various researchers. Diversity can vary by stand dynamics and vice versa (Loreau et al., 2001; Schmid, 2002), such as when the addition of a new species in a community increases species richness by one, but finally leads to decreases in local diversity due to competition (Bruno et al., 2005; Hughes et al., 2007).

Vegetation diversity also varied by stand type as higher understory diversity was found in mixed stands of aspen and white spruce. Mixed overstory stands may support higher understory diversity than pure conifer and hardwood stands because these stands are structurally more diverse due to tree species-specific growth habits; this creates a more heterogeneous light environment, higher resource heterogeneity, and allow resource-demanding vascular plants to coexist with shade-tolerant species (Hart and Chen, 2006 & Saetre et al., 1997). This finding also supports my second hypothesis that understory diversity increases with stand structural diversity. By contrast, Qian et al. (2003) found no difference in understory diversity between aspen and black spruce stands in British Columbia. They did not provide any specific reason for this finding indicating that the results may vary from one site to another. Reich et al. (2001)

reported a higher diversity in aspen stands than in spruce stands in southern boreal forest of Minnesota, USA. The aspen stands in those sites were established after a logging operation, which was the main reason for higher understory vegetation.

5.4.1.2 Disturbances vs. vegetation diversity

The highest diversity in harvested plots and the lower diversity in highly disturbed plots (fire plots) and non-disturbed or spruce bark beetle plots can be explained by the IDH (Connell, 1978), which states that higher diversity should occur at intermediate levels of disturbance and low diversity in non-disturbed or frequently disturbed areas. The thickness of the organic layer has been considered as an indicator of soil disturbance severity after fire, as found by Johnstone and Chapin (2006a) in their study in interior Alaska and central Yukon. A lower organic thickness indicates a greater effect of the disturbance. Accordingly, I infer that the recent fire plots had the highest disturbance severity (organic depth = 2.75 cm[10]) followed by salvage harvested plots (organic depth = 5.2 cm) and old fire plots (organic depth = 8.21 cm). The spruce bark beetle (organic depth = 11.29 cm) and undisturbed plots (organic depth = 8.98 cm) had the thickest organic layers. Thus, the general trends in diversity among the different disturbance types in my study support my third hypothesis. Below I discuss several caveats to this finding.

The reciprocal relationship between disturbance and diversity has been a matter of debate; namely whether disturbance determines diversity or diversity determines the severity of the effects of a disturbance (Hughes et al., 2007). The disturbance hypothesis predicts that the frequency or intensity of disturbances can affect species diversity, which in turn affects

[10] The variation in organic depths by disturbance type was significant at $p<.05$ as provided in chapter two.

ecosystem function (Loreau et al., 2002). In the long term, it may also result in the addition of disturbance-resistant species to the community (Tilman, 1996). Chapin et al. (1997) and Vitousek et al. (1997) state that land-use changes, habitat fragmentation, nutrient enrichment by decomposition or fire, and environmental stress may cause a reduction in plant diversity. Hughes et al. (2007) found that disturbances had a negative effect on diversity. Hart and Chen (2006) suggested however that fire has a positive effect by increasing understory vegetation diversity, with the highest diversity occurring within 40 years of a disturbance and gradually declining afterwards, which is consistent with the IDH (Connell, 1978).

The type of understory vegetation may be different by disturbance type as found in this study with recent fire plots having the highest number of unique species, which were not present in other type of disturbances. The disturbances also had socio-economic implications, as some of the locally used species were present or absent in a particular disturbance type. For example *Ledum groenlandicum* Oeder and *Alnus incana* (L.) Moench were present only in undisturbed or old fire plots indicating disturbances may reduce their abundance. Similarly, *Epilobium angustifolium* L.s.l. was present only in recent fire plot. *Shepherdia canadensis* (L.) Nutt. was present in all type of disturbances except in beetle-affected plots. As mentioned above, soil texture, moisture content and canopy gaps may have played role in the variation of these species among disturbance type.

5.4.1.3 Impacts of geo-climatic variation on vegetation diversity

Beside disturbances and canopy gap, variation in vegetation diversity was also related to geographical and climatic factors. The results indicated that higher diversity occurs at sites with higher mean summer maximum temperature and higher mean annual precipitation. The CCA also indicated that higher Shannon-Wiener and richness values were positively correlated with mean maximum summer temperature. Generally, nonvascular plants are more affected by limited precipitation and by the amount of available light (Busby et al., 1978). Higher temperatures support higher diversity as there is less permafrost and higher nutrient availability due to the higher decomposition rate (Van Cleve et al., 1981; Bonan & Shugart, 1989). Similarly, the higher diversity at lower elevations and on level ground can also be related to climatic factors as the lower elevation sites had higher mean temperatures and a shorter snow cover period than at higher elevations. However, Chipman and Johnson (2002) found higher species diversity on upper slopes than on lower slopes in western Canada. The higher diversity on upper slopes in their studies was related to time elapsed since occurance of last fire, as a short fire cycles increase the diversity.

5.4.2 Overall plant diversity and distribution in the study area

5.4.2.1 Diversity measurement: effectiveness and applicability

Sampling intensity is an important factor in determining diversity of any community. My species accumulation analysis indicated that 45 plots captured almost 90 % of the sampled species in the landscape. Diversity patterns are generally site-specific (Condit et al., 2002; Reyers et al., 2002; Wiersma and Urban, 2005). The minimum number of sites required to represent all species within a given area depends on the degree of species heterogeneity (beta diversity) among sites (Noss, 1996; Nekola & White, 1999; Condit et al., 2002), and within-site diversity (alpha diversity), which provides important information for biodiversity conservation and management. Similarly, I assessed variation in vegetation diversity along environmental gradients using the Shannon-Wiener Index, Simpson Index and Renyi’s alpha variation. Renyi’s profile uses many indices for species richness and diversity including modified Simpson and Shannon-Wiener indices (Kindt and Coe, 2005). I found this method to be consistent and comprehensive. The results of the Shannon-Wiener and Simpson indices were not always consistent. For example, in the elevation category the Shannon-Wiener index indicates that lower elevations had higher diversity (H = 2.07) but the Simpson index indicates both higher and lower elevation categories having higher diversity (H= 6.71). Renyi's profile was able to overcome these inconsistencies.

5.4.2.2 Overall diversity and species distribution

The overall diversity measured in this study was comparable to other studies done in the region. Douglas (1974) reported that the flora of southwestern Yukon, as with other northern floras, has fewer species than further south. He recorded 58 species of low shrub and herb stratum in his floristic study in the Alsek river region, which is close to what I recorded in this study (47 species of shrub and herb[11]). The higher abundance of herbs and shrubs in this study, with an average cover of more than 100%, indicates that they are densely distributed in most of the plots.

Pleurozium schreberi (Brid.) Mitt. and *Dicranum polysetum* Sw. were abundantly distributed in blocks B and D. Both blocks had the highest density of white spruce, had moist soils and sporadic occurrence of permafrost. The dominant presence of feather mosses can be explained by the presence of moist and shady conditions (Cody, 2000). La Roi and Stringer (1976) found that moist areas with high precipitation are generally covered by bryophytes. However, bryophytes were recorded mostly in white spruce stands in this study as deciduous stands inhibit the growth of lichens and mosses (Hart and Chen, 2006). The higher abundance of

[11] At least because four genera of herb and shrub were not identified at species level.

these mosses may be one of the reasons for the lower species richness of understory species in beetle-affected plots as species richness generally decreases with increasing total cover of bryophytes (Vellak et al., 2003). *Pleurozium schreberi* (Brid.) Mitt. was absent in fire plots where both vegetation diversity and species regeneration were higher (see Chapter 4).

The high frequency of soapberry and willows in this study is consistent with Douglas (1973), who also found high cover (mean covers of 23% and 14%, respectively) in his study in Washington and British Columbia. Douglas also observed the frequent occurrence of mountain cranberry, which is also one of the species with the highest cover in this study. Among regenerating tree species, I found the highest cover for white spruce (8.17%) and trembling aspen (4.45%). Balsam poplar had with lowest cover (0.29%), with Douglas (1974) also reporting it as one of the infrequent species within the region. Douglas and Vitt (1976) reported that white spruce and trembling aspen occur frequently with soapberry (*Shepherdia canadensis* (L.) Nutt.) and twinflower (*Linnaea borealis* L.), which is consistent with the findings of my study.

5.5 Chapter conclusions

Climate change and increasing forest disturbances have posed a great challenge and uncertainty for sustainable forest management in SWY, as there has been a poor understanding of ecosystem vulnerability in the area. I hypothesized that disturbance factors significantly affected the vegetation diversity in region, and expected plant distribution to vary with climatic factors. Results indicated that higher diversities prevailed in fire and harvested plots, which were characterized by low crown cover and low stand density, consistent with the idea that the gap dynamics are an important element for vegetation diversity. The diversity pattern of the study area could also be explained by the IDH, as the highest diversity was found at intermediate levels of disturbance. Similarly, six culturally important species were uniquely present to specific type of disturbance, implying that disturbance heterogeneity is also important factor not only for higher species but also for the availability of culturally important species.

As higher diversities were found in disturbed plots and in plots with higher mean temperature and precipitation, the predicted increase in temperature in the region (Christensen, et al., 2007) may promote overall vegetation diversity in the region in terms of its richness and abundance. However, increased frequency and severity of disturbances may negatively affect diversity, particularly if the region faces the drier summers predicted by the IPCC, which may increase the frequency of fires and bark beetles in the area.

Table 5.1 Characteristics of disturbed plots

Disturbance Type	Soil moisture (%) *p < 0.05*	Crown Cover (%) *p < .001*	Stand Density (tree/ha) *p < .001*	Organic depth (cm) *p < 0.05*	Shrub cover *p < .001*
Spruce bark beetle plots	25.96	63.93	1400	11.29	40.71
Fire plots	19.82	11.98	247	2.75	36.23
Harvested plots	18.59	29.00	591	5.19	40.08
Non disturbed	19.42	44.48	789	8.98	61.11
Old fire plots	25.14	48.21	1039	8.21	55.59
Average of all plots	21.78	39.52	813.2	7.24	46.744

[Note: The above table shows the mean values of soil moisture, organic depth, crown cover, stand density and shrub cover by disturbance types. P-values indicate significant differences among disturbance types for each variable.]

Table 5.2 Species richness and abundance in the study area

Richness		Abundance	
Total species	69	Total abundance	10125
Mean per plot	13.8	Mean	114.5
Standard Error	0.4	Standard Error	4.73
Median	14	Median	107.3
Mode	15	Mode	100.9
Standard Deviation	3.7	Standard Deviation	44.9
Range	17	Range	250.4
Minimum	4	Minimum	18.3
Maximum	21	Maximum	268.7

Table 5.3 Distribution and abundance (% of cover) of dominant vegetation by disturbance type

Species	Undisturbed	Old fire	Beetle affected	Recent fire	Harvested
Arctostaphylos uva-ursi (L.) Spreng. s.l.	11.1	9.9	12.9	3.0	4.3
***Arctostaphylos rubra* (Rehd. & Wils.) Fern**.			6.6		
***Populus tremuloides* Michx**.	6.8			6.1	7.1
Betula glandulosa Michx.				4.8	
Carex spp.					4.7
Cladina mitis (Sandst.) Hustich	4.4		3.9	6.1	5.3
Cladonia spp.		3.4	3.4		
Dicranum polysetum Sw.		3.9	7.2		
Dicranum scoparium Hedw..				24.7	
Empetrum nigrum L.	4.9	5.4			
***Epilobium angustifolium* L.s.l**.				6.2	
Equisetum arvense L.				12.5	
Festuca spp.					6.5
***Ledum groenlandicum* Oeder**	9.8	8.0			
Linnaea borealis L.			10.0		7.9
***Alnus incana* (L.) Moench**	8.7				
Peltigera canina (L.) Willd.			3.7		
Pleurozium schreberi (Brid.) Mitt.	12.8	9.5	31.9		11.0
***Shepherdia canadensis* (L.) Nutt**.	8.7	8.1		4.5	6.9
***Picea glauca* (Moench) Voss**	8.6	14.9	11.1	8.3	7.4
***Vaccinium vitis-idaea* L.**		5.5			
Salix spp.	15.7	18.3	6.1	11.4	4.6
Total coverage	**91.5**	**86.8**	**96.7**	**87.5**	**65.5**

Note: species on bold fonts are locally used species

Symbols

- (light grey) Species that uniquely occurred in a specific disturbance type (9 species)
- (medium grey) Species occurred in all types of disturbances (3 species)
- (dark grey) Species that appread in all sites except in a specific disturbance type (3 species)

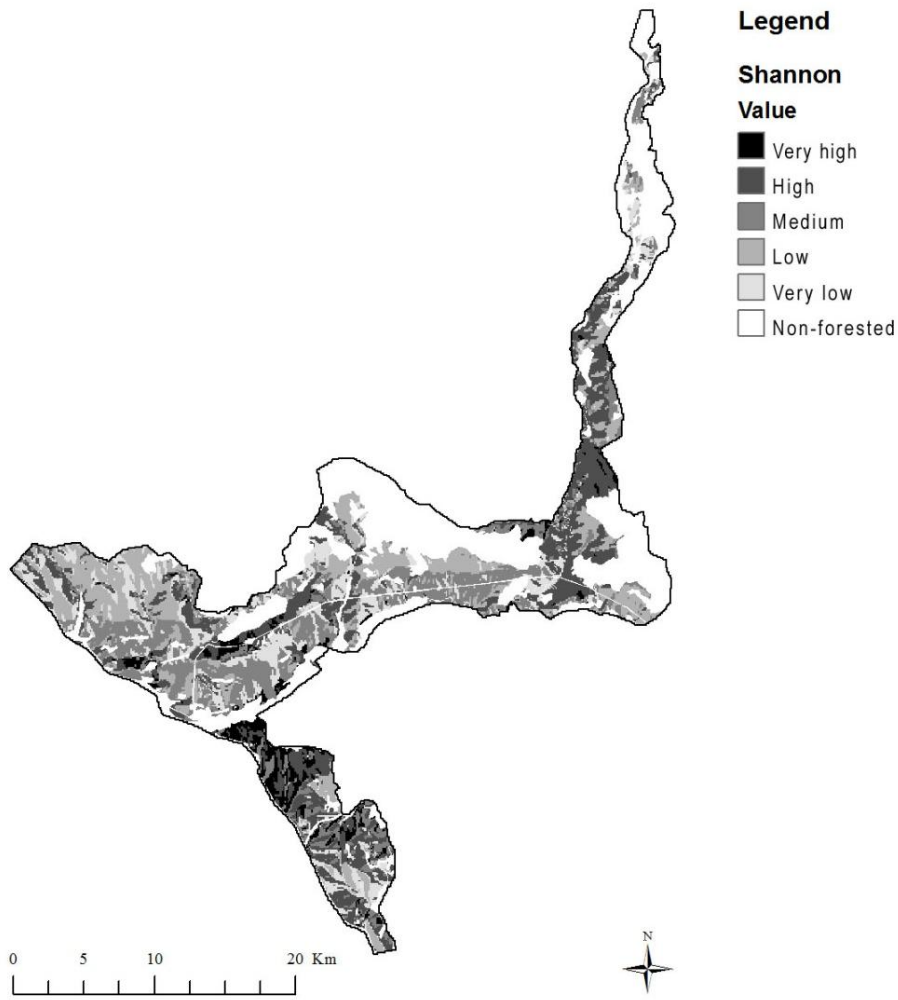

Figure 5.1 Vegetation diversity in the landscape (Shannon-Wiener index)

[Note: diversity maps indicated that higher diversity in research blocks four (fire plots), five and six (salvage harvest)]

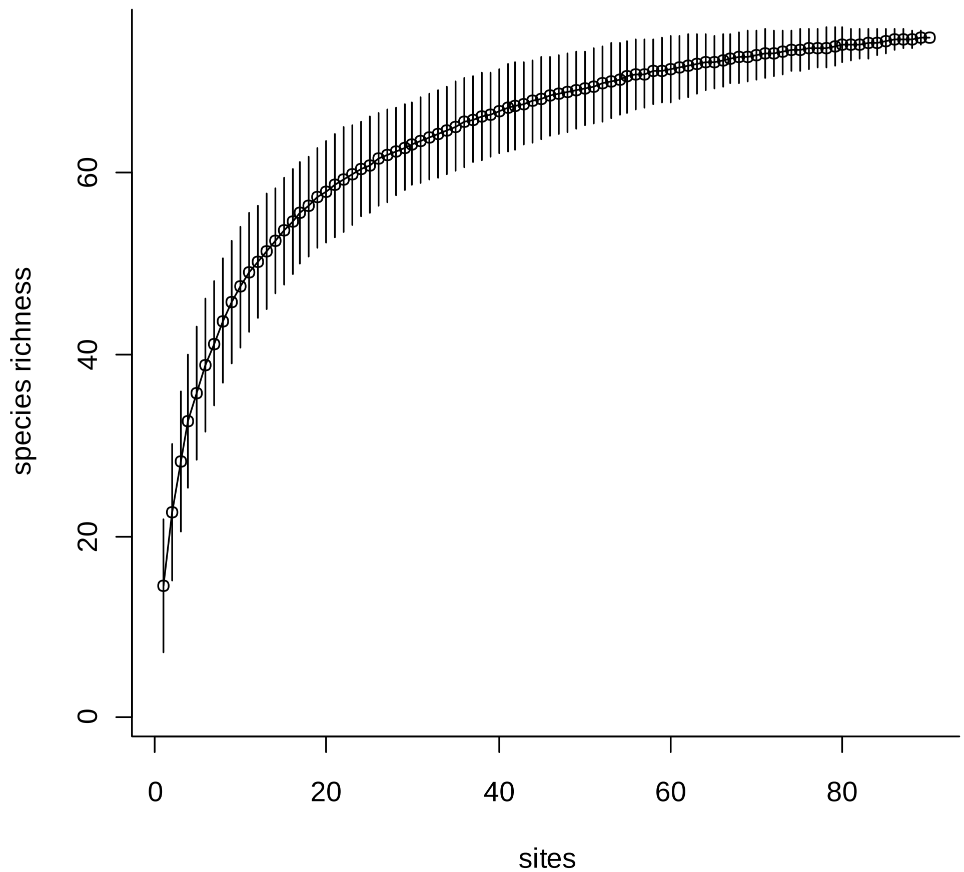

Figure 5.2 Species accumulation curve

[Note: The species accumulation curve indicates that 60 plots (sites) were sufficient to include about 90% of the species in the study area]

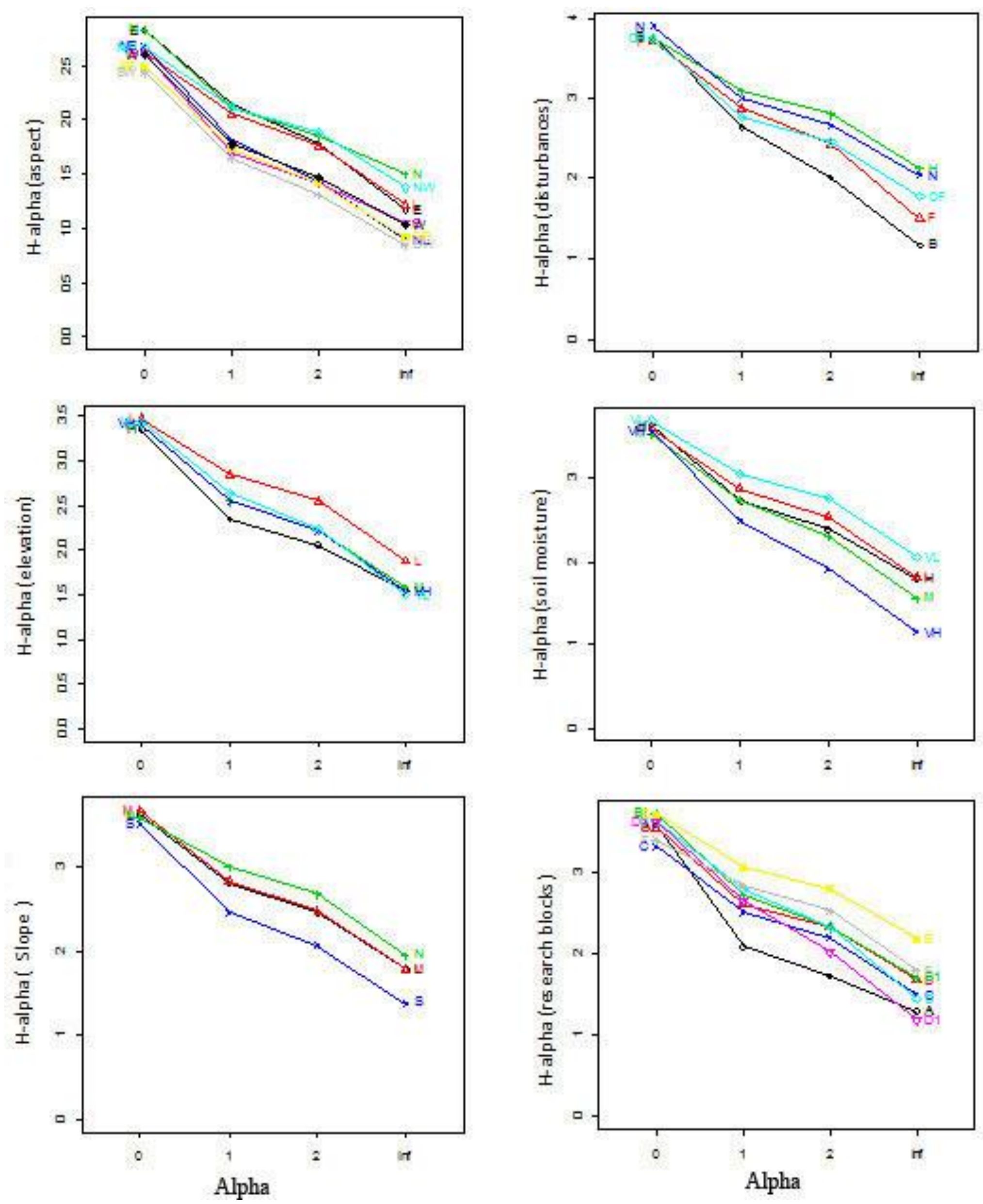

Figure 5.3 Renyi's profile showing vegetation diversity by site variables and disturbance types

[Note: The values in Y axis (H alpha) provides diversity ranking from 0 to higher level and the values X axis (Alpha) indicates different indices such as 0 = the logarithm of species richness, 1 = Shannon-Wiener diversity index, 2 = logarithm of the reciprocal of Simpson diversity Index and inf. = proportion of the most abundant species. The graph that starts and ends at higher level shows higher diversity than that of lower one. The figures indicated the higher diversity in lower elevation, lower soil moisture regime and flat sites. The variation by aspects and disturbance regime were not clear due to overlapping lines.]

[Abbreviation of names and labels: Disturbances type (B = Beetle, F = Fire, OF = Old fire, H = Harvest, N = Not disturbed), Aspect (N = North, S = South, E = East, W = West, NE = Northeast, NW = Northwest, SE = Southeast, SW = Southwest, L = Level) slope (S = steep, M = Medium, L = Low, N = No slope) moisture regime/elevation (VH = Very high, H = High, M = Medium, L = Low, VL = Very low).]

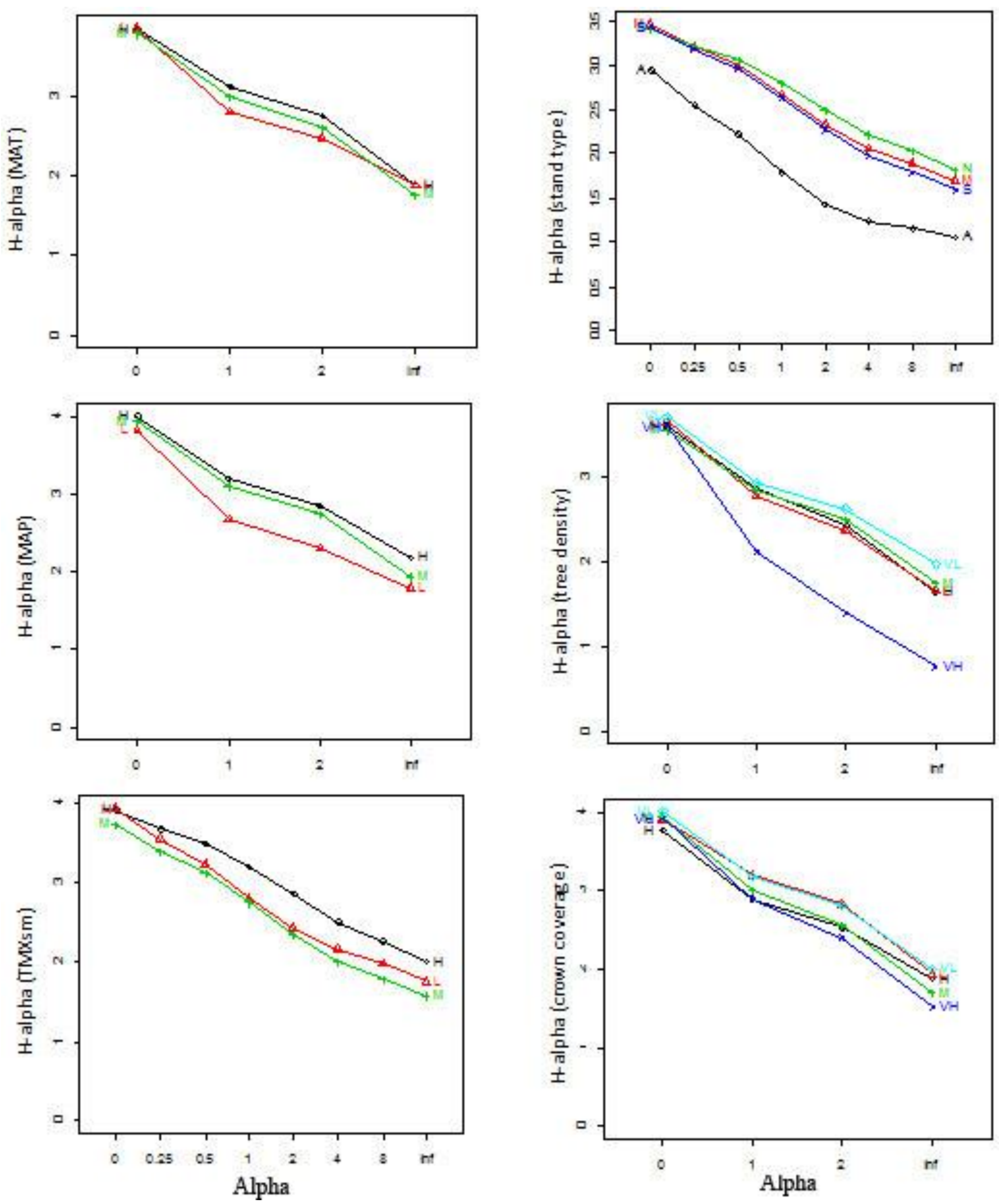

Figure 5.4 Renyi's profile showing vegetation diversity variation by climatic factors and stand types

[Note: The figures indicated higher diversity in the sites with higher precipitation and higher mean maximum summer temperature. The higher diversities were also found in sites with the lowest stand density and the lowest diversity was found in aspen stands. Abbreviation of names and labels: Mean annual temperature, precipitation and summer maximum mean temperature (H = High, M = Medium, L = Low)]Tree density; VH = Very high, H = High, M = Medium, L = Low, VL = Very low; Stand type (A = Aspen, S = white spruce, M = Mixed, N = no tree); Crown cover/tree density (VH = Very high, H = High, M = Medium, L = Low, VL = Very low).]

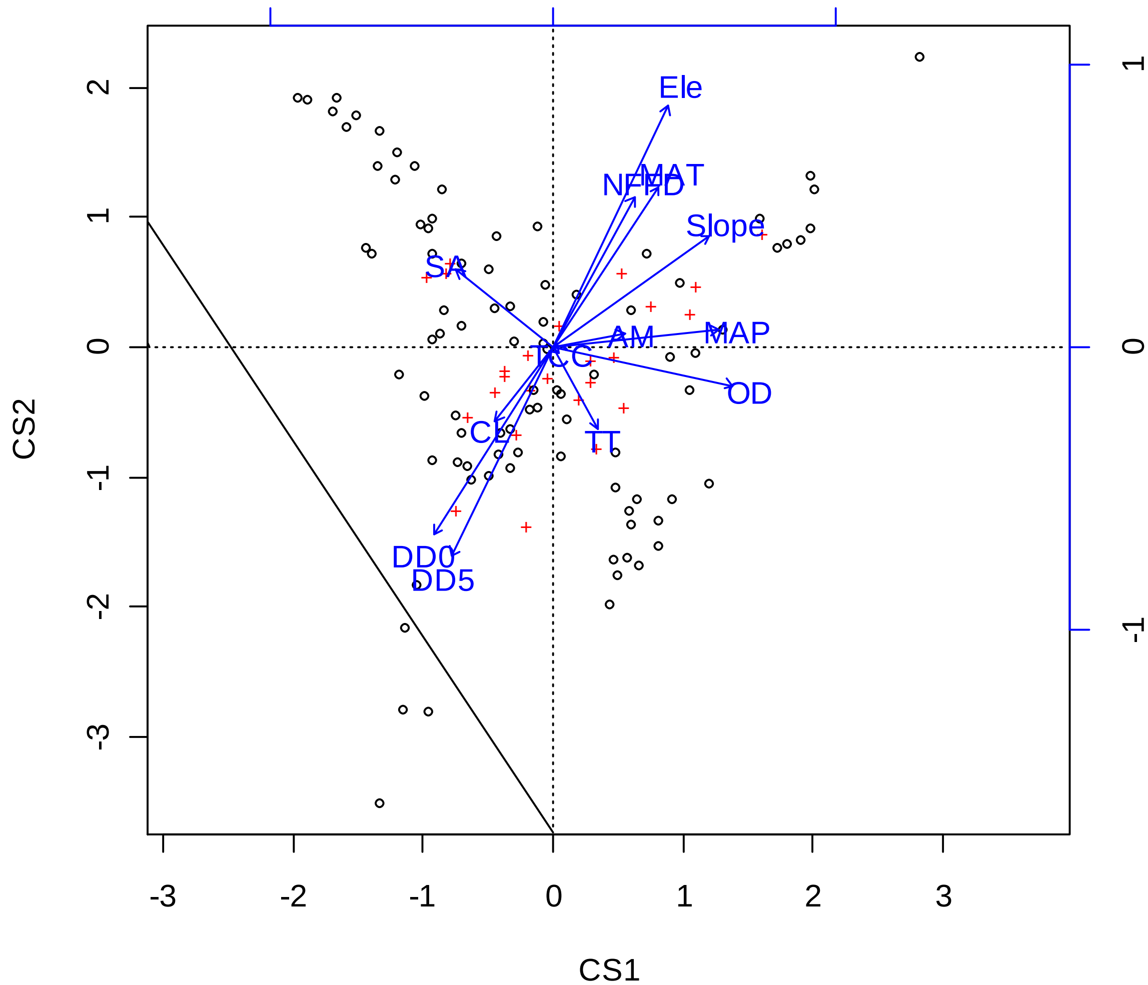

Figure 5.5 Distribution of species and environmental variables in the research sites

[Note: Figure 5.5 was the output of CCA. Round symbols indicate the 90 research plots; red + indicates species distribution. and abbreviated names are environmental variables. Abbreviation of names: DD0 = degree days below 0; DD5 = degree days above 5; CL = % soil; TT = total tree density; TCC = total crown cover; OD = Organic depth; AM = average moisture; MAP = mean annual precipitation; MAT = mean annual temperature; NFFD = number of frost free days; Ele = elevation; SA = % of sand]

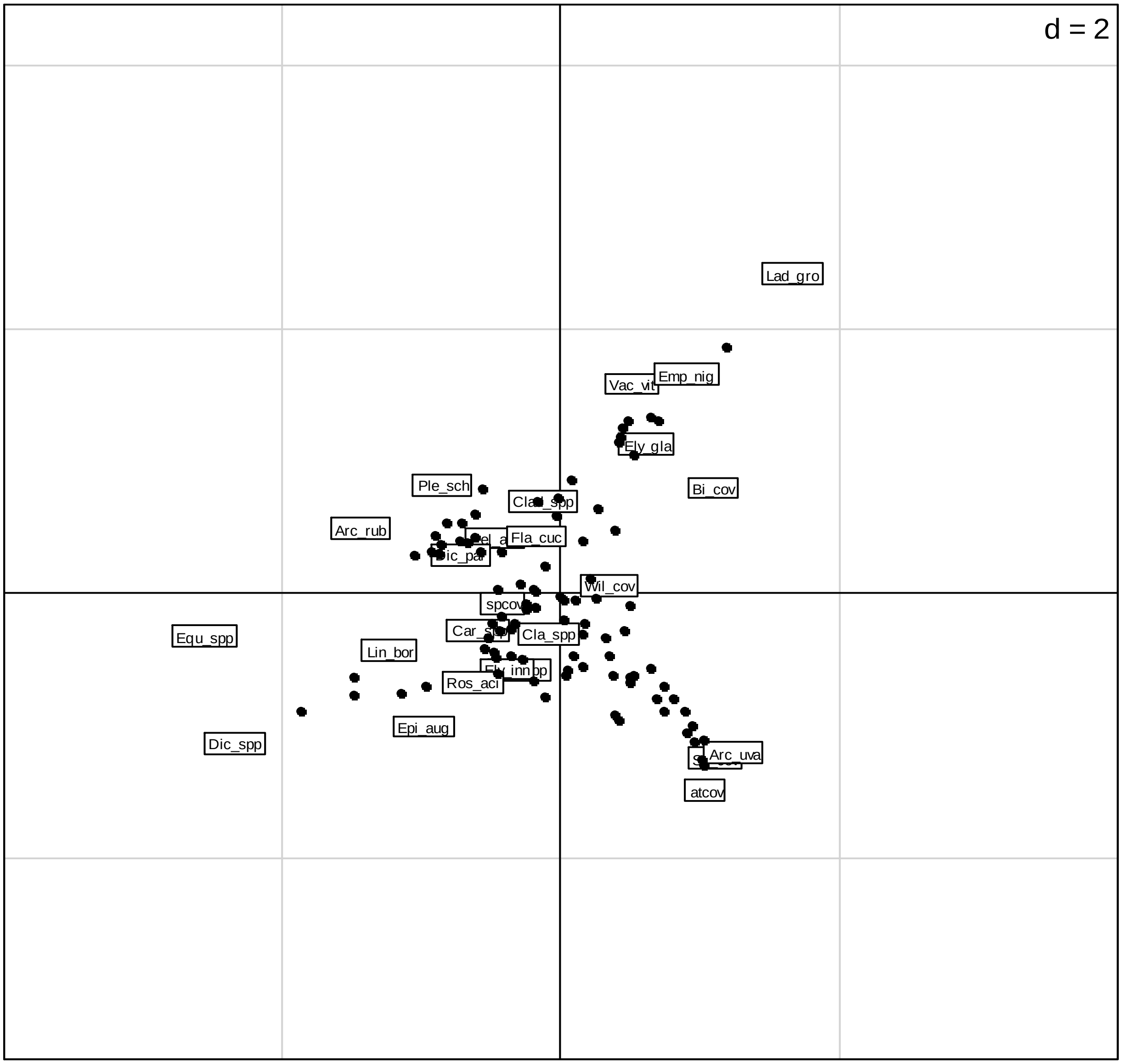

Figure 5.6 Sites position by environmental variables combinations

[Note: Figure 5.6 is another output of CCA. Black dots are research plots and abbreviated names are species names. The species clustered in one axis indicated that they required similar environmental conditions. By comparing figures 5.6 and 5.7, inferences can be made about which species prefer what kind of environmental conditions. For example *Ledum groenlandicum*, *Vaccinium caespitosum*, *Empetrum nigrum*, *Elymus glaucus* mostly prefer higher slope position, higher mean annual temperature and higher number of frost free days. Abbreviation of names as provided in Appendix A. Please also note that species distribution in the right below axis in Figure 5.7 matches with environmental variables of left upper axis in figure 5.6. and right upper axis in figure 5.7 matches with right below axis of 5.7]

6. Forest Management in response to climate variability and disturbances in the CATT

6.1 Introduction

Sustainable Forest Management (SFM) is defined as management "to maintain and enhance the long-term health of forest ecosystems, while providing ecological, economic, social, and cultural opportunities for the benefit of present and future generations" (CSA, 2002). Forest management activity did not exist in the CATT prior to the implementation of the Strategic Forest Management Plan (SFMP, 2004) with the exception of fire suppression activities, resulting in the widespread occurrence of old and disturbed forest stands. The plan provides strategic guideline to achieve the long-term goal of sustainable forest management in the region. However, in the short-term, the plan focuses on salvage harvesting due to the high intensity of spruce mortality. Although the SFMP has been in effect since 2004, there are many challenges needed for its effective implementation, which are briefly highlighted as follows;

- Uncertainty posed by climate change and forest disturbances: The growing uncertainty posed by predicted climate change, the spruce bark beetle outbreak and the increased fire hazards have created difficulties in the implementation of appropriate management interventions in the territory that could cope with the uncertainty while still meeting the social, economic and ecological goals of SFM.
- Forest area and accessibility: The majority of the forestland is presently inaccessible due to the lack of a road network.
- Lack of past experiences of forest management: The CATT did not have prior forest management experiences except for limited forestry activities. Therefore, any suggestion

about forest management and its impacts on forest ecosystem are largely dependent upon what has been learnt in other parts of boreal forests. The local communities have very small populations, and there is no history of involvement in commercial forestry.

- Uncertain market: Although a harvest plan for up to 1 million m^3 of beetle affected timber over the following ten years was approved in 2004, only 108,000 m^3 dead trees had been harvested by the end of 2012. The main reasons are lack of a market for timber in the region, lack of a timber harvest plan and lack of capacity of local industries. Moreover, the costs and benefits of forest management have yet to be analyzed.

6.1.1 Current status of forest management in the CATT

In July 2013, I contacted forestry officials in Yukon to get an update on forest management in the CATT. The following information is relevant to the management recommendations made in this chapter.

- As mentioned above, about 108,000 m^3 of wood had been salvaged by the end of 2012. It is expected that the quantity of salvage harvesting will increase due to the addition of a few small industries in the region and the growing capacity of the existing fuel wood company. Currently, a timber harvest plan is being prepared for the Burwash areas. Fuel abatement activities were carried out around Haines Junction areas in 2012.
- A forest management implementation agreement between Champagne and Aishihik First Nations and Government of Yukon represented by the Ministry of Energy, Mines and Resources was signed on 16th August 2012. According to this new agreement, the Yukon Government will carry out forest inventory in the CATT. Based on the forest inventory, both governments will collaborate to determine a new annual allowable cut in the CATT

by 2015 to ensure the continuous supply of timber and fuel wood for the next twenty years. The new annual allowable cut includes both salvage harvesting and a separate harvest rate for green trees (unaffected by beetles). Both governments also agreed to collaborate in developing and implementing community fuel abatement plans.

- The CAFN, in close collaboration with village of Haines Junction and Yukon Energy, has a plan to develop a biomass-based energy plant. This plant would require a continuous supply of biomass.

Accordding to MEMR, salvage harvesting will continue for the next two to three years with variable retentions. No decisions have been reached over the choice of the silvicultural systems that will be used after the completion of salvage harvesting. The research findings presented in this chapter are therefore of interest.

6.2 Key research findings and implications for forest management in the CATT

As social and economic studies were outside the scope of this research, the management recommendations must primarily be based on the ecological perspectives, informed by this research. Specifically, this chapter will consider (i) the current situations of ecosystems in the CATT based on the key findings of the study (synthesis of the results), (ii) predicted ecosystem scenarios with or without forest management, (iii) forest management strategies suggested by other researchers in the CATT (e.g. Waeber, 2012; Ogden 2007; and SFMP, 2004) and; (iv) suggested management activities in other boreal forests with similar ecosystems by other researchers.

6.2.1 Projected ecosystems of the CATT in the absence of forest management

The findings of this research and similar studies in the other boreal ecosystems have provided the basis for the projection of future structure and composition of forests in the CATT. As the average basal area was higher in the warmer plots, the overall forest productivity is expected to increase in the study area, as higher temperatures will generally result in a longer growing season (Johnston et al., 2006). Both understory and overstory vegetation compositions may, however, change with increased coverage of broadleaved specie and a greater abundance of some species in disturbed forests, as I found that a few species were restricted to disturbed plots. Waeber (2012)[12] also predicted a 20% reduction in white spruce forest and increase in aspen forests within a time frame of 50 to 150 years. As higher structural diversity and understory vegetation diversity were found in mixed stands, salvage harvesting and even-aged management may undermine such ecosystem benefits (Montes et al., 2005; Wimberly and Spies, 2001).

The spruce bark beetle outbreaks could continue to plague the region due to the predicted increase in temperature (Goodman and Hungate, 2006), especially in pure and mature white spruce stands as found in this study. Similarly, mortality caused by bark beetle and increased summer temperature may increase the frequency of forest fires in the CATT. Waeber (2012) predicted, however, that the risk of spruce bark beetle damage would decrease for the next 150 years due to the large amount of aspen replacing white spruce in the landscape. As more than 80% of trees in the beetle-affected plots were dead, there are significant implications for forest ecosystem management, with effects on both forest productivity and understory vegetation. My studies showed there was a lower diversity of understory vegetation in beetle-affected plots, with

[12] Waeber (2012) carried out his research in same research areas using same set of data as I have used for this research.

more than 30% cover of *Pleurozium schreberi* (red stemmed feather moss). However, beetle-affected plots had a higher abundance of white spruce regeneration, which was mostly clustered around the decaying woods. In other studies in Alaska, a lower abundance of white spruce regeneration was found in beetle-affected forests (Boucher and Mead, 2006). Due to presence of differing vegetation under beetle-affected forests, forest management should be adopted to specific stands in response to large-scale beetle infestations (Boucher and Mead, 2006). For example, if the beetle affected dead trees are not salvaged, there is a high probability that large-scale fires will occur, as has already happened in the study area. In either case (salvaged or fire), forest ecosystems would be affected as the ecosystem attributes of the salvaged and the recent fire plots were different (Figure 6.1).

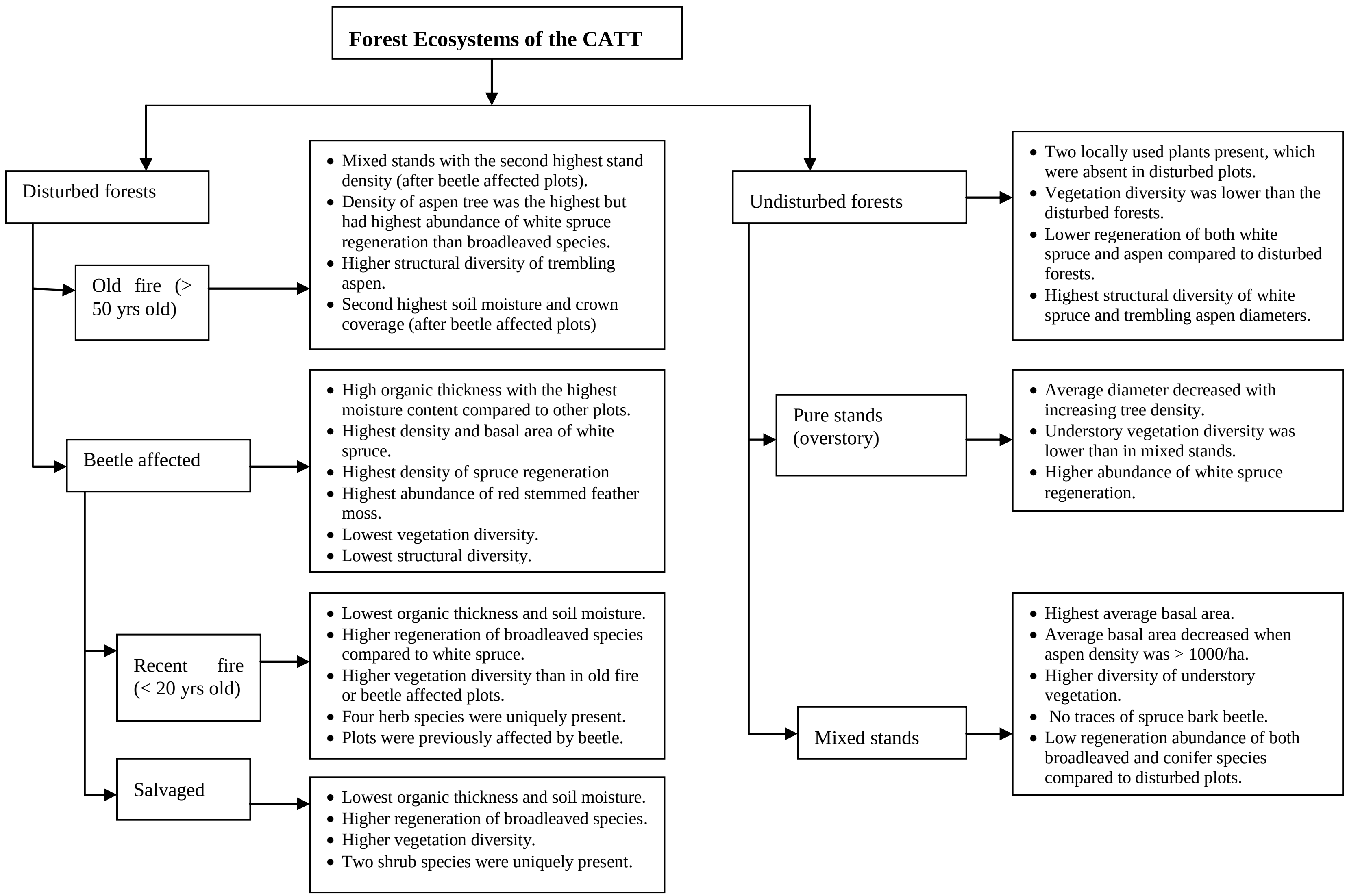

Figure 6.1 Variation of ecosystem attributes by disturbance and stand types in the CATT based on the findings of the research.
[Note: These are the current state of ecosystems in the study area. The succession trajectory of each disturbance type will largely depends upon future climate, disturbances and management interventions (suggestions are made in the next section/figure)].

6.2.2 Suggested forest management strategies in the CATT

My results indicate that mixed stands had the ecosystem attributes (Figure 6.1) that would closely meet the ecological goals of SFMP (2004), with the highest average basal area, the highest vegetation and structural diversities with no traces of spruce bark beetle; these can be considered to be the preferred state of the forest. Forest management strategies and activities should focus on achieving the desired state by applying multiple management systems within the landscape.

Reactive and proactive management approaches have been suggested by Ogden (2007) to cope with the current disturbances and to prevent drastic ecosystem changes in the CATT under possible climate change scenarios. Under reactive management, specific management activities are carried out in response to changes that have already occurred. Proactive management is suggested to minimize anticipated vulnerabilities and to avoid the undesirable situations (Ogden, 2007).

6.2.3 Management of disturbed stands: salvage harvesting as a reactive forest management

The CATT SFMP is a reactive plan (Ogden and Innes, 2007) as it identifies salvage harvesting as a short-term solution to achieve the long term management goal. However, salvage harvesting has been considered as one of the most controversial practices after clear-cutting; it is generally applied to capture economic values from dead and decaying trees and may not be an effective tool to promote ecological recovery (Lindenmayer et al., 2008). Salvage harvesting can have important implications for the forest ecosystem and biodiversity (Purdon et al., 2002). As found in this study, salvaged plots had a higher abundance of early successional species and understory vegetation with the presence of some unique species, which may compete with regenerating spruce (Goodman and Hungate, 2006). Although, higher diversity was found in salvaged plots in this study, the salvage harvesting may also create the opportunity for invasive ericaceous species (Jetté et al., 2009) and the process would also affect white spruce regeneration because of the mechanical impacts on the soil (Greene et al., 2006) and removal of decaying logs which provides an important substrate for white spruce recruitment (Lindenmayer et al., 2008). As the salvage harvesting affects overall stand structure, it would also affect overall species composition and species associated with key forest structures (Lindenmayer et al., 2008).

Salvage harvesting may be indispensable, however, when the areas and intensities of disturbances are quite large (such as in case of CATT) and can be both economically and ecologically feasible if the practice is carried out with proper planning. Retention of a minimum number of trees (even if they are dead) and decaying logs is suggested in order to maintain the structural mosaic of forest and to provide regeneration environment for the desired species and to minimize the effects on biodiversity (Fries et al., 1997; Lindenmayer et al., 2008). Prescribed burning followed by salvage harvesting would enhance white spruce regeneration and reduce competition from invasive species (Goodman and Hungate, 2006). Salvage harvesting followed by reforestation has been suggested as a way to limit the loss of forest cover, especially in response to climate change, as natural regeneration may decline due to reductions in seed germination (Le Goff et al., 2009).

Beside salvage harvesting, Boucher and Mead (2006) have recommended reforestation, wildlife habitat improvement, and removal of hazardous fuel in the post-infestation management of the beetle-killed forests of Kenai Peninsula. Such a strategy could also be applied in the forest of CATT. According to Ogden (2007), although the local forest practitioners' in SWY placed higher priority in some management activities such as fire suppression, enhancement of forest recovery by assisting tree regeneration, and minimization of habitat fragmentation and maintain connectivity, these management activities have not been implemented or realized yet.

6.2.4 Pro-active forest management to maintain forest productivity, biodiversity and species regeneration

Intensive and pro-active management activity is required to maintain healthy and productive stands, to counter the impacts of climate change and to reduce the frequency and intensity of disturbances (Stewart et al., 1998). One of the primary management activities suggested by some researchers is to divide the forest landscape into protection and intensive management zones (Le Goff et al., 2009) based on ecosystem variability, productivity and vegetation diversity. Based on the findings from Chapter 3, the stands at lower slope and elevation positions should be allocated as production zone, which has productive stands whereas stands on upper slope and elevation should be protected due to higher abundance of useful shrubs and herbs to northern communities (see Chapter 5).

As mentioned above, I suggest implementing silvicultural techniques to promote mixed stands both in currently disturbed and undisturbed stands. Bergeron and Harvey (1997) also argued that mixed stands are the most productive in terms of standing biomass. Herbaceous plant communities are more diversified in this type of forest (De Grandpre' and Bergeron, 1997),

As the canopy gaps have been found to be important for vegetation diversity and species regeneration in the study area, uneven aged management with frequent group or selection cuts could emulate the gap dynamics and maintain the mosaic of forest structures and composition

(Bouchard, 2009). Removal of mature and old-growth trees through thinning and selection harvesting would reduce or prevent further bark beetle attack in the undisturbed stands and promote regeneration and biodiversity (Jetté et al., 2009). However, as old growth forests are highly dynamics in both space and time, the treatment should be designed in such a way as to represents the spatial pattern and the associated attributes of old growth forests and to maintain the habitat of important species and the biodiversity (Grandpré et al., 2009; Gauthier et al., 2009b).

The Three-Cohort model has been suggested as a way to maintain the mosaic of forest composition and structures in the landscape; this would ensure that the various development stages of the forest have the characteristics of both mixed forest and old-growth stands (Bergeron and Harvey 1997). Under this model, the first cohort is equivalent to even-aged management with low retention canopy occupied by shade-intolerant species (such as trembling aspen) and with an understory of shade tolerant species. The second cohort has an overstory of mixed stands and the third cohort canopy is mostly dominated by the shade-tolerant species. Such a model can also be achieved by applying varying rotation length to maintain different cohorts of stands (Epp et al., 2009; Seymour and Hunter, 1999).

Prescribed burning has frequently been suggested the best approach to achieve rapid regeneration of spruce forests (Goodman and Hungate, 2006). Prescribed burning would also reduce the risk of uncontrolled fire, would enhance the fire-dependent ecosystems (Wade et al., 1989) and might control invasive species that would otherwise compete with desirable species (Le Goff et al., 2009). However, as white spruce regeneration generally depends upon an ample supply of seed trees (Timoney and Peterson, 1996) the scarcity of live seed trees in beetle-infested and salvaged-harvested plots might limit spruce regeneration. However, advanced regeneration of white spruce was abundant in the beetle-affected plots in my study area, and was mostly concentrated around decaying logs. Future salvage harvesting should maintain such decaying logs and shade trees to maintain white spruce regeneration in the study area. Shelter-wood felling might also be an option to promote regeneration especially for shade tolerant species both to provide seeds and shades (Montes et al., 2005).

As the ecosystems that were present in the CATT varied according to disturbance and stand type, as shown in Figure 6.1, specific forest management activities have been prepared for each disturbance and stand type (Figure 6.2). Similarly, forest management implications and suggestions in response to variation of stand structures, regeneration and vegetation diversity are provided in Table 6.1.

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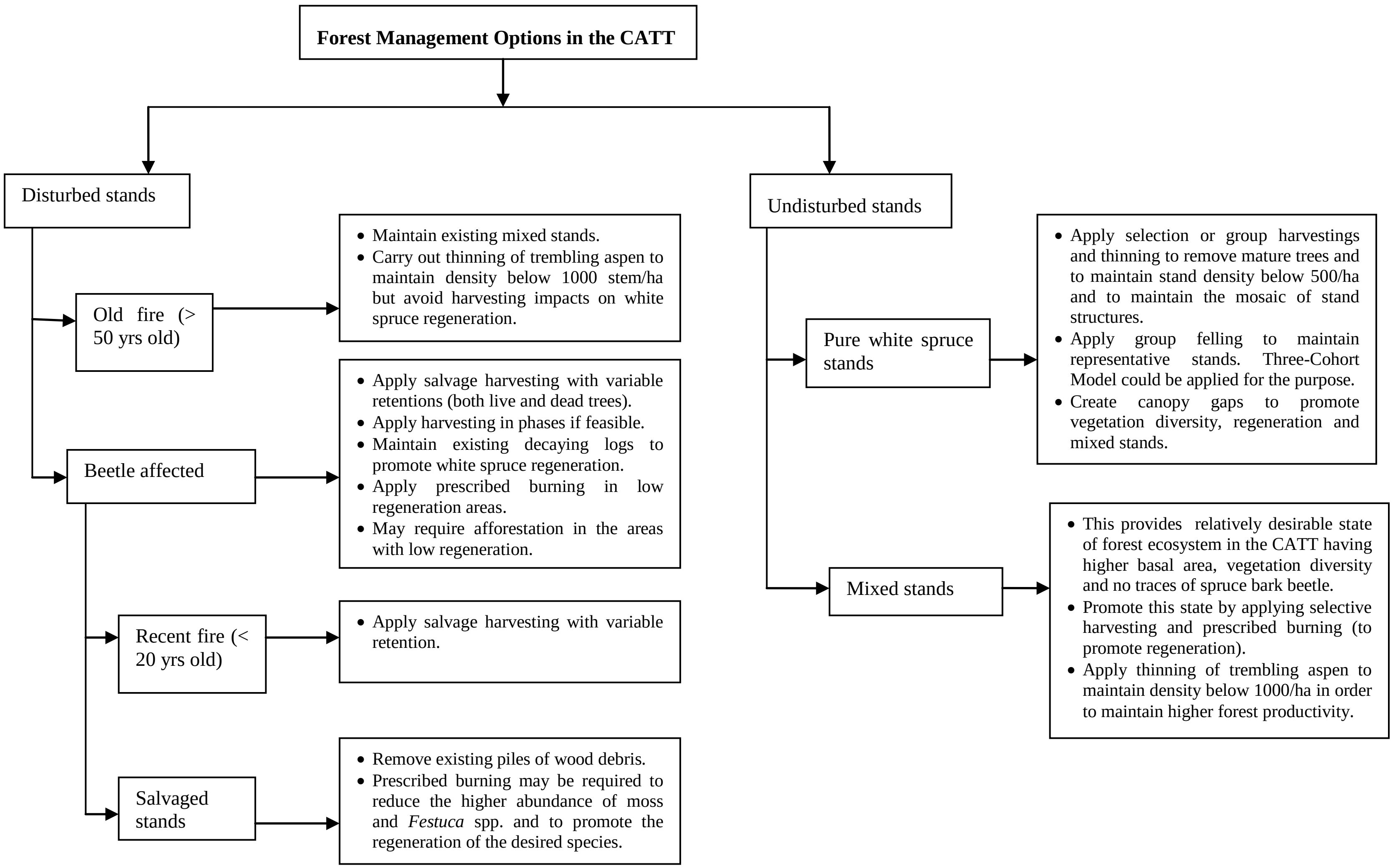

Figure 6.2 Suggested forest management strategies in response to variation of ecosystem attributes by disturbance and stand type in order to reach desired ecosystem states

Table 6.1 Key research findings and forest management implications and considerations

	Findings related to stand structure and composition (Chapter 3)		Forest management implications and considerations in the CATT
i.	Higher density and basal area were found in mixed stands than in pure stands of white spruce and aspen. However, average basal area decreased when aspen density was above 1000 stem/ha in mixed stands. These findings signify that mixed stands are important for higher stand productivity.	i.	Promote mixed stands of hard and soft wood where appropriate (Biringer, 2003; Bergeron and Harvey, 1997). Apply thinning operation to aspen stands to maintain their density below 1000 stem/ha.
ii.	The intermediate height class of white spruce had higher stand density whereas the co-dominant height class had the highest average basal area. Similarly average diameter of white spruce decreased with increasing stand density. Both findings indicate that the overall productivity of white spruce decreases with increasing stand density.	ii.	Carry out selection harvesting. Select dominant and co-dominant trees for harvesting. Carry out regular thinning operation of intermediate trees to promote their height and diameter growth of the remaining trees. Remove suppressed, diseased and poor quality individuals to increase resources availability for the remaining trees (Smith et al., 1997).
iii.	Structural diversities were found higher in undisturbed and old fire plots, which had mixed stands with higher vegetation diversity and had no traces of spruce bark beetle.	iii.	As higher structural diversity promote biodiversity and reduce the insect/pest vulnerability, maintain higher structural diversity of the forest to promote biodiversity. Maintain representative forest types along environmental gradient (Holling, 2001). Apply partial and selective harvesting to maintain the structural component of the forest (Harvey et al. 2002).
iv.	Average diameter, height, basal area and density of white spruce increased with decreasing elevations and they were higher in lower slope positions. This finding indicates that white spruce productivity varies significantly by topographic positions and could help to prioritize forest management areas.	iv.	Commercial harvesting should focus on lower elevation and lower slope position where higher basal area and density of species are available. These areas are easily accessible and would generate higher production with lower operational costs.
v.	Diameter and basal area of white spruce increased with increasing soil moisture and on northeast and southern aspects (which have longer exposure to sunlight and warmer than north aspects) which implicate both soil moisture and temperature are important factors for white spruce growth.	v.	Drought may affect growth of boreal species. Singh and Wheaton (1991) suggested prioritizing management activities giving more focus to moist areas. Introduction of modified drought resistant varieties are suggested (Gitay et al., 2001), although there is no such plan in Yukon in the immediate future.
vi.	No strong relationship was found between age and diameter growths of white spruce, although I expected higher average diameters in older trees.	vi.	White spruce age is not a good indicator of tree size in the study area. Diversification and application of silvicultural practices both for even-aged and uneven-aged stands are suggested (Harvey et al., 2002).
vii.	Disturbed plots were occupied by broadleaved species, except in forests affected by spruce bark beetle, where densities and basal areas of white spruce were significantly higher.	vii.	The productive white spruce forests were affected by bark beetles. Salvaging them may promote broadleaved species. As stated in the first point, promoting mixed stands through selective harvesting may provide a long-term solution.

Findings related to tree regeneration (Chapter 4)	Forest management implications and considerations in the CATT
i. The regeneration abundances of all three species were higher in fire plots, signifying fire as an important disturbance factor promoting regeneration in the study area. Regeneration of trembling aspen was significantly higher than white spruce in fire plots.	i. Selection or group harvesting with regeneration protection have been suggested as disturbances that have minimum effects on regeneration; clear cutting over small to large areas followed by seeding or planting has been suggested for severely disturbed forest (Bergeron et al., 1999). A selection system with variable retention is recommended for spruce bark beetle affected areas to maintain some shade that will promote white spruce regeneration (Goodman and Hungate, 2006).
ii. White spruce regeneration was positively correlated with lower slope, elevation, presence of fire, higher mean annual temperatures and higher crown coverage. A higher density of white spruce regeneration was found in pure aspen stands. This species seems to benefit from disturbances that expose mineral soils, raise the soil temperature and have less impact on the forest canopy.	ii. Apply prescribed burning after selection harvesting to promote natural regeneration of both white spruce and trembling aspen.
iii. Both trembling aspen and balsam poplar regeneration were strongly affected by the presence of parent trees. Their regeneration was also higher in harvesting plots indicating their preference for open habitat.	iii. Promote natural regeneration (Kellomaki et al. 2005; Ogden and Innes, 2008). Regeneration models (Chapter 4) would help to assess the possibility of natural regeneration of white spruce, trembling aspen and balsam poplar.
iv. Regeneration of trembling aspen and balsam poplar exceeded the ratio compared to their parent trees compared to white spruce suggesting that broadleaved forest may dominate and prevail for long time periods if disturbance occurs persistently .	iv. In areas where natural regeneration may be limited, the planting of alternative tree species or ecotypes may be an option (Singh and Wheaton, 1991). Spittlehouse and Stewart (2003) suggested identifying and planting more suitable genotypes through provenance trials, although this option did not receive high priority from local forestry practitioners (Ogden, 2007).

Findings related to vegetation diversity (Chapter 5)	Forest management implications and considerations in the CATT
i. *Populus tremuloides* Michx., *Shepherdia canadensis* (L.) Nutt. and *Arctostaphylos uva-ursi* (Rehd. & Wils) Fern. were highly centered in one cluster in the analysis, indicating that they prefer similar environmental conditions. Similarly, *Ledum groenlandicum* Oeder, *Vaccinium caespitosum* Michx., *Empetrum nigrum* L., and *Elymus glaucus* Buckl. were on the same axis indicating their similar environmental requirements.	i. Species that require a similar environment can be managed by maintaining similar habitat and providing similar growth environment. Silvicultural practices should focus on maintaining species site relationships (Spittlehouse, 1997; Spittlehouse and Stewart, 2003) by creating favourable environments as required by the species such as creating gaps to maintain light-demanding species.
ii. Vegetation diversity was higher in open areas, implying that gaps are important for promoting vegetation diversity. Understory diversity was also higher in mixed stands than in pure stands.	ii. Patches of canopy gaps and higher structural diversity should be maintained to enhance higher biodiversity. As biodiversity was higher in mixed stands, I recommend maintaining mixed stands by selective and partial harvesting and promoting other species (Harvey et al. 2002).
iii. Vegetation diversity was higher in moderately disturbed plots (in terms of severity which was assessed by measuring thickness of the organic layer), supporting the hypothesis that moderately disturbed stands have higher diversity than less or severely disturbed stands.	iii. Apply ecosystem-based management by emulating natural disturbances (Gauthier et al., 2009a) to promote vegetation diversity.
iv. Diversity was higher in plots with higher mean summer temperature. Predicted higher mean temperature in the region may promote both richness and abundance of the vegetation diversity.	iv. To facilitate forest ecosystem to adapt to climate change, apply aggressive selection logging in uneven-aged stands, reforestation with multiple species with the retention of climax stands in harvesting areas (Harding and McCullum, 1997)
v. Of the 21 species that are used locally, eleven species had below 1% cover (Annex J). Some of the locally important berry plants such as *Rubus arcticus* L. spp. had covers of less than 0.1% and had limited distribution (relative to total coverage by all 69 species).	v. Focus should be given to conserving and managing locally important species listed in Annex J. Based on management objectives and important of particular species, the habitat of rare species should be protected or managed to avoid their extinction. Control undesired invasive species to reduce competition with the desirable species. If necessary, develop gene management and create artificial reserve to preserve these rare species (Noss, 2001).
vi. Research blocks A and B had the highest percentage cover with 70%, and 96%, respectively. The highest herb cover (109%) was found in highest elevation in the research areas (1005 to 1158 meters above msl). These blocks also have the highest cover of *Ledum groenlandicum* (which is widely used as tea) with an average of 31% in each plot.	vi. Higher elevation areas have a higher abundance of important locally used species; allocate and prioritize these areas for biodiversity conservation.

6.3 Chapter conclusions

The findings indicated that mixed stands are the most desirable situation to meet the ecological objectives of SFMP (2004). However, the ecological attributes of stands varied significantly by disturbance and stand types. Multiple management activities should be implemented specifically designed for each type of disturbance and stand type to reach the most desirable ecosystem states. For example, salvage harvesting with variable retention followed by prescribed burning is suggested for beetled-affected plots, which had lower vegetation diversity and higher stand productivity. Similarly, selective to group harvesting with thinning of mature stands is suggested in less perturbed plots to maintain the mosaic of stand structures and to emulate the gap dynamics to promote mixed stand in the long term.

7. Conclusions and recommendations

7.1 Major findings

The forests of the southwest Yukon are facing the impacts of climate change, particularly through increases in the occurrence and severity of disturbances. A Strategic Forest Management Plan (SFMP, 2004) for the Champagne and Aishihik Traditional Territory (CATT) was implemented in 2004 in response to forest disturbances in the region with the objectives to maintain, restore or enhance forest succession, species and ecosystem diversity. To support the implementation of the recommendations in the 2004 SFMP, a study on the impacts of disturbances on the forest ecosystems of the Champagne and Aishihik Traditional Territory (CATT) was suggested by Ministry of Energy, Mines and Resources (MEMR), Government of Yukon.

I assessed the impacts of bio-geoclimatic and disturbance factors on three attributes of the forest ecosystems in the CATT, namely (i) impacts on stand structure and composition, (ii) impacts on distribution and abundance of tree species regeneration and (iii) impacts on vegetation diversity. Five disturbance types and more than 30 bio-geoclimatic variables were considered as independent variables for assessing the ecosystem responses. I found that all the geographical variables (slope, elevation and aspect) were significant in explaining the variation in stand structure, regeneration and vegetation diversity in the region. Edaphic variables (soil texture and moisture) had impacts on tree species regeneration and structural variability (average height, diameter and basal area). However, soil texture did not have a significant impact on vegetation diversity. While the majority of climatic variables were significant in explaining species regeneration, mean annual temperature (MAT), mean annual precipitation (MAP) and mean summer maximum temperature (TMXsm) were important for the variation stand structures and vegetation diversity.

Recent fires have had significant positive impacts on the regeneration of all three dominant tree species; white spruce, trembling aspen and balsam poplar. In addition to fire plots, aspen and balsam poplar regeneration was also higher in harvested plots. White spruce regeneration was more prolific in beetle-affected plots. Disturbances had significant impacts on stand composition as higher densities of broadleaved trees were found in fire and harvested plots. The study did not find any direct impact of the spruce bark beetle on species regeneration or stand structure. However, stand densities and basal areas of white spruce, which were mostly dead, were significantly higher on spruce bark beetle plots, indicating that beetle-affected areas were more productive compared to other plots. According to the original plan of the Government of Yukon, the majority of these beetle-affected forests will probably be salvaged. This may significantly change the forest composition in the future, either with or without salvage harvesting, towards broadleaved stands, as found in the salvaged plots. The key findings and the summary of responses of stand structure variables, regeneration and vegetation diversity to bio-geoclimatic and disturbance factors are highlighted in the bullet points below and are synthesized in Table 7.1.

Ecosystem variations in response to disturbances

- Disturbed plots varied significantly by organic depth, soil moisture, crown coverage and shrub coverage. Beetled-affected and undisturbed plots had the highest soil moisture, organic thickness and crown cover. In contrast, the recent fire and salvaged-plots had the lowest organic thickness and soil moisture.

- Although white spruce dominates the study area with the highest stand composition index, its regeneration was proportionately less than that of trembling aspen, especially in disturbed plots. Similarly, the regeneration abundances for broadleaved species was higher in exposed and disturbed sites especially in fire and harvesting plots indicating their strong preference for disturbed sites.
- Plots affected by the spruce bark beetle generally had high densities and basal areas of white spruce. Trembling aspen stand density was higher than average in old fire plots with more co-dominant and intermediate height class trees.
- The diversity pattern in the study area could also be explained by the intermediate disturbance hypothesis (IDH) as the highest diversity was found at intermediate levels of disturbance. The depth of organic matter was considered as a criterion to classify the disturbance severity.
- The distribution and abundance of understory vegetation were affected by disturbance type, as nine understory vegetation species were uniquely present in specific types of disturbance.

<u>Ecosystem variations in response to climate variability</u>

- Higher stand basal area and vegetation diversity were found in warmer plots signifying that the projected increase in temperature (2 ^{o}C by 2040) may favour these two variables.
- The regeneration of white spruce was strongly influenced by climatic factors, especially temperature variables, which varied significantly by geographical positions with more regeneration abundance at lower elevation and slope positions. Spruce regeneration was favoured by higher mean annual temperatures, higher growing degree-days and higher

summer temperatures. However, regeneration of broadleaved species was negatively correlated higher temperatures.

Ecosystem variation in response to other environmental variables

- Stand density and basal area varied significantly with geographical positions, temperature and soil texture. Productivity of white spruce was higher at lower elevation and slope position. Intermediate height class white spruce dominated the landscape, with 24.3% of the total cover, followed by co-dominant (20.6%) and dominant trees (18.3%).
- The average DBH was not related with environmental variation although variations in diameter among soil texture, elevation and aspect were statistically significant.
- The mixed stands of aspen and white spruce had higher basal area per plot than the pure white spruce stands. However, average basal area decreased when aspen density was above 1000 stem/ha in mixed stands. The average stand diameter was positively correlated with tree density up to 500 per hectare, but beyond that, the average diameter decreased signifying that density more than 500 per hectare will have negative impact on total aspen productivity.
- White spruce regeneration was more abundant with increasing crown coverage and soil moisture signifying that regeneration of this species will be affected by increasing temperature if drought condition prevails in the study area.
- Vegetation diversity was significantly greater in plots that were characterized by low crown cover and low stand density (in open areas), at lower elevations and on flat sites. The results indicated the importance of gap dynamics in determining the vegetation diversity of the area. Diversity in mixed stands was higher than in pure stands.

- Of the 21 species with documented local use (Johnson et al., 1995; Holloway and Alexander, 1990), 11 species had just less than 1% cover (Annex J). Some of the important berry plants such as arctic raspberry *(Rubus arcticus* L.) had covers of less than 0.1% and had limited distribution.

Table 7-1: Summary table: responses of stand structure variables, regeneration and vegetation diversity to bio-geoclimatic and disturbance factors

Variables	**Species regeneration**			**White spruce structure**				**Trembling Aspen structure**				**Balsam poplar Density**	**Vegetation diversity**
	White Spruce	*Aspen*	*Balsam Poplar*	*DBH*	*Height*	*Density*	*Basal Area*	*DBH*	*Height*	*Density*	*Basal Area*		
Geographical variables													
Slope	-	-	-	-	-	-	-	-	-	x	x	x	-
Elevation	-	-	-	-	-	x	-	-	-	x	x	x	-
Aspect	+L/NE	+E/SE	+L/SE	+NE/S	-N/+NE	+S/NE	+S/NE	+E	+E	+NE/SW	+SW	+S	+NW
Disturbance regime													
Fire	+	+	+	x	x	-	-	x	x	+	x	-	+
Harvesting	-	+	+	x	x	-	-	x	x	x	x	+	+
Old fire	-	-	-	+	x	+	-	x	x	+	x	x	-
Spruce bark beetle	+	-	-	+	+	+	+	x	x	-	x	-	-
No disturbances	-	-	-	x	x	+	-	x	x	+	x	x	-
Climatic variables													
MAT	+	-	-	x	x	+	X	-	-	-	x	x	+
MAP	-	-	x	+	-	x	-	-	-	-	x	x	+
TMXsm	+	-	-	x	+	x	x	x	+	x	x	x	+
TMNwt	-	x	x	x	x	x	x	x	X	x	x	x	x
DD>5	+	-	x	x	+	+	+	+	+	x	x	x	x
NFFD	x	x	x	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
Ecological variables													
Soil texture	L/SL	+SL/L	S/SiC	x	x	X	x	LS	LS/SiL	S/LS	S	S	x
Organic soil depth	-	-	x	x	x	+	x	-	-	x	x	-	x
Soil moisture	-	-	x	+	+	+	+	x	x	x	x	x	-
Total crown coverage	+	-	-	n/a	n/a	n/a	n/a	n/a	n/a	n/a	x	x	-
Total density	n/a	-	x	x	x	x	x	x	x	x	x	x	-
Species density	n/a	+	+	-	x	n/a	+	+	x	x	+	x	x
Species basal area	-	x	+	+	x	+	n/a	+	x	+	n/a	n/a	n/a

[Note: + = positive response; - = negative responses; x = no responses; N/A = not applicable or not assessed. Abbreviation of labels: L= level; NE = northeast; E = East; S = south; SW = southwest; NW = Northwest]

7.2 Socio-economic implications

Although a detailed forest socio-economic implication of the results is outside the scope of this research, some brief highlights are provided here, especially results related to vegetation diversity, as there is the potential for some useful follow-up research. The information on distribution and abundance of locally used plants in the CATT is useful both for CATT community and forest managers to prioritize management activity in the future to conserve and maintain these plants.

The study found 21 species have traditionally been used for food, medicines, fuel or timber in Yukon Territory and as such have socio-economic value in the region (Annex J). These 21 locally used species cover about 45% of the total ground cover, of which about 30% is shrubs and herbs. Eleven species had less than 1% cover. Research blocks A and B had the highest percentage of cover with 70%, 83% and 109%, respectively. The shrub coverage was the highest (109%) in the higher elevation plots (1005 to 1158 meters above MSL) of block B. The block also has the highest cover of *Ledum groenlandicum* Oeder with an average of 31% in each plot (within the Block B) and covers 4% of total herbs abundance in the study area. *Shepherdia canadensis,* (L.) had the highest percent cover in the shrub category (8%) and was also widely distributed in the research areas. However, more than 50% of locally used species had less than 1% cover in the study area (Annex J).

The disturbances also had socio-economic implications, as some of the locally used species were present or absent in a particular disturbance type. For example, *Ledum groenlandicum* Oeder and *Alnus incana* (L.) Moench were present only in undisturbed or old fire plots indicating disturbances may reduce their abundance. Similarly, *Epilobium angustifolium* L.s.l. was present only in recent fire plots. *Shepherdia canadensis* (L.) Nutt. was present in all type of disturbances except in beetle affected plots. These findings indicated that the abundance and distribution of some locally used species would be significantly affected by change in the magnitude and frequency of disturbances. Forest management may require emulating natural disturbance to promote or reduce the abundance of species of interests.

7.3 Forest management implications

Forest management involves balancing ecological, economic and social values and objectives associated with forest resources (Hickey, 2008). The health and vitality of the forest ecosystem are important in achieving the goal of sustainable forest management. However, climate change and natural disturbances pose major uncertainty for future forest condition, growth, and uses, and an understanding of such uncertainties is important in making forest management decisions (Juday et al., 2005; CCFM, 2006).

Although forest managers are already dealing with fire and insects outbreaks within the available institutional and financial capacity, new challenges and surprises are expected that will require adaptive forest management planning (Stewart et al., 1998). Intensive and proactive management activities may be required to counter the impacts of climate change and to reduce the frequency and intensity of disturbances. Ecosystem-based adaptive management approaches may help to cope with the uncertainty posed by climate change and disturbances (Spittlehouse and Stewart, 2003; Schlaepfer, 1997). Ecosystem-based management (EBM) aims to maintain an ecosystem within its range of natural variability and to fulfill societal needs by reducing the differences between natural and managed forest landscapes (Gauthier et al., 2009; Schlaepfer, 1997). EBM acknowledges the disturbance dynamic as a part of an ecosystem, and therefore, considers mimicking natural disturbance as an important approach for sustainable forestry (Noss and Cooperrider, 1994). Similarly, an adaptive approach has been considered an important tool for tackling challenges and uncertainties posed by climate change and disturbances that emphasizes adapting the forest management practices based on feedback provided by regular forest monitoring (Spittlehouse and Stewart, 2003; Ogden and Innes, 2008).

The scope of this study was to assess our understanding of some important ecosystem elements of the CATT and their responses to bio-geoclimatic and disturbances factors, which would provide forest managers with a basic understanding of local ecosystems that they could use in management planning (Kimmins, 1996). The results shed some light on the implications of climate variability and disturbances on regional ecosystems. Although, the variability of mean annual temperature and precipitation of the study area were only 1.3 ^{o}C (-1.1 ^{o}C to -2.4 ^{o}C) and 80 mm (270 mm to 390 mm), respectively, stand structure, regeneration and vegetation diversity varied significantly within this temperature range. Overall forest productivity was higher in the warmer plots. Similarly, the abundance of white spruce regeneration was greater in warmer plots but the regenerations of broadleaved species were significantly lower. Vegetation diversity was higher in plots with higher mean summer temperature and mean annual precipitation. As stated in section 1.3.1, under predicted climate change scenario, the mean annual temperature in the region is projected to increase by 2 ºC by 2040 and 7 ºC by 2100 (ACIA, 2004), which is considerably higher than the variability of mean annual temperature in the study area (1.3 ^{o}C). As a result, climate change may significantly affect the forest ecosystems in the region. Higher temperature may also be associated with higher precipitation in the region (Christensen et al., 2007), which would affect the regeneration of white spruce by increasing soil moisture (see Chapter 4).

Although increasing mean temperature may benefit some attributes of the CATT ecosystem, it may negatively impact forest ecosystems by increasing forest disturbances. For example, regeneration of white spruce was proportionately less than that of trembling aspen in disturbed plots suggesting broadleaved species may prevail if disturbance persists in the region in the future. As projected by other researchers, the findings also indicated that there is a possibility of a shift in the general pattern of forest vegetation to warm and dry climate areas (Hebda, 1998), leading to more open stands at lower elevation that may be converted into dense shrubs (Hebda, 1997). Climate change may also result in the loss or reduction of alpine and subalpine ecosystems, affecting the unique species of plants and animals found there (Krannitz and Kesting, 1997).

One of the goals of the SFMP (2004) is to maintain the ecosystem functioning. The findings indicated that undisturbed mixed stands are the most desirable situation to meet the ecological objectives of SFMP (2004). However, the ecological attributes of stands varied significantly by disturbance and stand types. Multiple management activities should be implemented specifically tailored to each stand and disturbance type. The findings on stand structure variations (Chapter 3) would help forest managers to plan management activities such as delineating the locations for thinning, prioritizing possible harvest locations or changing stand structure to make the forest less vulnerable to fires (Lindenmayer and Franklin, 1997). The information and knowledge on regeneration distribution and its abundance in the landscape in response to bio-geoclimatic and disturbance factors (Chapter 4) would help forest managers to understand regeneration potential with or without disturbances and climate change scenarios and select appropriate management activities. For example, as the open areas created by disturbances are being occupied by light-demanding early successional species such as trembling aspen, selective harvesting with prescribed burning could be one possible management intervention in such areas to facilitate white spruce regeneration (Goodman and Hungate, 2006). Similarly, knowledge of the distribution and abundance of useful plants (Chapter 5) is important for forest managers when prioritizing areas for special consideration for management and conservation for useful and/or rare species. This will provide information on the existing habitat condition of these species, which would help to guide managers to improve their habitat condition. Establishing biodiversity priority areas, applying multiple conservation strategies and adopting an adaptive management approach are some of the strategies suggested for biodiversity conservation by Lindenmayer et al. (2000).

7.4 Applicability of the research to other boreal regions

Boreal forests vary significantly in terms of species composition, stand structure and biodiversity in North America and Eurasia. For example the species that occur in succession sequences are different in North America and Eurasia (Kuusela, 1990). Moreover, disturbance regimes and ecosystem resiliency to disturbances also differ from one region to another. For example natural disturbances are considered as major issues in North American boreal forests while forestry has been considered as an important issue in European boreal forests (Niemela, 1999).

This research was undertaken in the context of disturbances and climate variability in the forest landscape of the Champagne and Aishihik Traditional Territory (CATT) of the southwest Yukon of Canada. As explained in Chapter 1, the research need was identified by Ministry of Energy, Mines and Resources Government to support a management goal and objectives of the Strategic Forest Management Plan (2004) of CATT. The research results were based on the local ecosystems in the study area with respect to bio-geoclimatic and disturbance factors and the results may not apply to boreal forests in other regions or countries. Specifically, the results related to stand structure and biodiversity are generally site specific. However, the research results have been compared to similar research in eastern Canada, Alaska and Europe, with detailed literature citations in the discussion sections of each chapter and results were generally found to be consistent with studies done in other regions.

7.5 Research limitations

Although I have tried my best to include as many variables as possible and used various complementary methods to assess the impacts of bio-geoclimatic disturbance factors on forest ecosystems in the region, there are still some limitations and gaps in the research.

One of the limitations of the research was that due to time and limited research scope, I was able to assess only three elements of the ecosystems (stand structure, regeneration and vegetation diversity). Ecosystems are complex phenomena and have numerous variables that could be assessed, including impacts on soil nutrients, their cycles and effects, microorganisms, wildlife habitat and populations, etc. However, the three elements that I included here are also important factors. Knowledge and information about these factors could directly affect management decisions. Similarly, I was unable to include socio-economic aspects of the ecosystem changes in the region. This would be of interest to local government and policy makers, especially how changes in the ecosystems due to climate change and disturbances will or could affect the socio-economic and cultural dynamics of the local residents. However, no research was undertaken in this area as the community had recently been the subject of detailed consultative research (Ogden, 2007) and I was advised that community members were beginning to show signs of having been exposed to too many surveys and questionnaires.

7.6 Recommendations and future research

As indicated in the previous section, ecosystem impacts have been analysed using current climatic scenarios. It would be interesting to see how future predicted climate would affect the ecosystems in the region. One of the recommendations for future research would be to include both current and future climate scenarios to see their impacts and implications for forest management.

Similarly, impacts on the socio-economic system is lacking in this research. Potential follow-up research would be to examine how the ecosystem variations caused by climate variability and disturbances would affect the socio-economic and cultural systems of local residents. This would be the interest to local forest managers in making appropriate forest management decisions. In addition, based on the findings in this thesis, it would be interesting to develop forest management scenarios to minimize the possible ecosystem effects of disturbances in the region.

Postscript

This research began with a broad scope of integrating social and ecological variables to develop an adaptive forest management tool in response to climate change and forest disturbances in the CATT. However, the social component of the research had to be dropped as we were informed that local people had been exhausted by the numerous surveys undertaken in the area in recent years. As a consequence, the research scope was narrowed to the ecological component in order to understand existing ecosystem attributes in the region with respect to forest disturbances and environmental gradients.

The research had to cover a relatively large forest landscape (approximately 53,000 ha) in a short period of time (3 months) and involved collecting information on more than 30 ecological variables. This was achieved by a team of researchers from the Sustainable Forest Management Laboratory of the Faculty of Forestry at UBC. The advantages of conducting joint and collaborative research is one of the important lessons learned from this research, as it made possible for us to collect a large data set from 90 plots, 270 sub-plots and 270 mini plots. The team approach also made it possible to understand different ecological dynamics within the CATT forests, as different researchers focused their research on different aspects using the same set of data. Besides collecting ecological data, the research team also installed two weather stations in the region in order to collect long-term weather data. Due to time limitations, we were able to collect data on spatial variability but not on temporal variability. Temporal variability for indices such as soil moisture would provide important extra information, and this therefore reflects one of the limitations of the study.

Based on the ecological findings about current climate variability and disturbance regimes, I have recommended several silvicultural options, which would contribute to closely meeting the ecological goals of the region. However, these recommendations were largely based on ecological perspectives and learning from other boreal regions faced with similar situations. Therefore, the proposed silvicultural options should be considered only as preliminary recommendations; local people were not involved in developing these, and have not agreed with the suggested options. I believe that forest management has to be based on local perspectives and wishes and should consider local knowledge of forest management. It should also consider how people would like to see their forests in the future. Although, I did not conduct formal interviews with local community members, I did receive some informal suggestions that the majority of local people are not in the favour of large-scale salvage harvesting, which may significantly alter the landscape in terms of vegetation composition and the visual aspects of the forest. The experiences from the salvage harvested areas of pine beetle affected forests in British Columbia have revealed that such practices may not actually result in desirable forest condition. Previous work in the area has also suggested that local are not in favour in introducing new tree species to the area, and would like to see the landscape returned to the condition that it was in prior to the bark beetle outbreak. Given the extent of climate change in the area, this may not be possible.

Based on my experience, I suggest that there is a need for an action research approach involving local communities during the whole research process, from the development of research questions to the finalization of research results. Such an approach would provide an opportunity for local communities to understand their ecosystems, the changes occurring in them and the factors responsible for the changes. In addition, they would also be able to share their local knowledge and experience in coping with forest disturbances and could suggest management tools that would be acceptable for them. Similarly, action research would also motivate local communities to take ownership of research findings and to implement them locally. For example, we established weather stations without the involvement of local people, which resulted lack of ownership and management of these stations, which have remained idle for the past three years.

Some of the findings of this research have direct value to local communities, such as the spatial variation of forest productivity, and the spatial distribution and abundance of locally important non-timber forest products. Action research would have provided opportunities for local people to learn the status of these locally important species, and to take decisions accordingly on management and utilization options for these resources. Similarly, I would consider the research finding regarding the factors associated with vegetation distribution and abundance in the study area as a significant scientific contribution, as these findings could form the basis for a vegetation classification that is still lacking in the region.

Personally I learned a lot from this research. The subject matter, context and study areas were completely new for me, as I came from another part of the world (Nepal) with completely different types of forests, forestry and people. My former experience mainly included working for community forest management. However, my PhD mainly focused on ecological science using a variety of multivariate tools. Although, I went through a very difficult path during my research, it also provided me with a great learning opportunity, expanded my thinking process and built my confidence in forest ecology and management.

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Appendix A: Scientific and common names of vegetation, their code names and type[13]

Scientific name	Code	Type[14]	Common name
Achillea millefolium L.s.l.	Ach_mil	H	Common yarrow
Aconitum delphinifolium DC.	Aco_del	H	Monkshood
Alnus incana (L.) Moench	Aln_inc	S	Grey alder
Aquilegia formosa Fisch. Ex DC.	Aqu_for	H	Red Columbine
Arctostaphylos rubra (Rehd. & Wils.) Fern.	Arc_rub	H	Red Berry
Arctostaphylos uva-ursi (L.) Spreng. s.l.	Arc_uva	H	Kinnikinnick (bearberry)
Arnica cordifolia Hook.	Arn_cor	H	Heart-leaved arnica
Aster alpines L.ssp.	Ast_alp	H	Aster
Aulacomnium palustre (Hedw.) Schwagr.	Aul_pal	B	Big moss or glow moss
Betula glandulosa Michx.	Bet_gla	S	Ground birch
Carex spp.	Car_spp	H	Sedge
Castilleja spp.	Cas_spp	H	Indian paint-brush
Cetraria pinastri (Scop.) A. Gray	Cet_pin	L	Moonshine cetraria
Cladina mitis (Sandst.) Hustich	Clad_mit	L	Green reindeer lichen
Cladonia spp.	Cla_spp	L	Pixie cup lichen
Dichodontium pellucidum (Hedw.) Schimp.	Dic_pel	B	Wet rock moss
Dicranum polysetum Sw.	Dic_pal	B	Electric eels moss
Dicranum scoparium Hedw..	Dic_sco	B	Broom moss
Elymus glaucus Buckl.	Ely_gla	H	Blue wild rye
*Elymus innovates (*Beal) Pilg.	Ely_inn	H	Fuzzy spike wild rye
Empetrum nigrum L.	Emp_nig	H	Black crow berry
Epilobium angustifolium L.s.l.	Epi_aug	H	Fireweed
Equisetum arvense L.	Equ_arv	H	Common horsetail
Erigeron peregrines (Pursh)	Eri_per	H	Subalpine daisy
Festuca spp.	Fes_spp	H	Fescue
Flavocetraria cucullata (Bellardi) Karnefelt & A. Thell	Fla_cuc	L	Curled snow lichen
Geocaulon lividum (Richards.)	Geo_liv	H	Bastard toad flax
Hedysarum mackenzii (Richards)	Hed_mac	H	Wild sweet pea

[13] Species were identified and verified using local flora books (Cody, 2000; Johnson et al., 1995) and online USDA database (plants.usda.gov). However some species could not be identified at species level due to lack of flowering during data collection.

[14] Note: T= Trees; H = Herbs; S = Shrubs; L = Lichen; B = Bryophytes

Scientific name	Code	Type*	English name
Hookeria lucens (Hedw.) Sm.	Hoo_luc	B	Clear moss
Hordeum brachyantherum Nevski	Hor_bra	H	Meadow barley
Hyacinthoides non-scripta (L.) Chouard ex Rothm.	Hya_non	H	English blue bell
Hypogymnia physodes (L.) Nyl.	Hyp_phy	L	Hooded tube lichen
Juniperus communis L.s.l.	Jun_com	S	Common Juniper
Ledum groenlandicum Oeder	Led_gro	S	Labrador tea
Linnaea borealis, L.	Lin_bor	H	Twin flower
Lupinus arcticus Wats.	Lup_arc	H	Arctic lupin
Mimulus guttatus DC.	Mim_gut	H	Monkey flower
Oxycoccus microcarpus Turcz.	Oxy_mic	S	Small bog cranberry
Oxytropis campestris (L.) DC.	Oxy_can	H	Field locoweed
Peltigera aphthosa (L.) Willd.	Pel_aph	L	Freckled lichen
Peltigera canina (L.) Willd.	pel_can	L	Dog lichen
Petastites frigidus (L.) Fries	Pet_fri	H	Palmate leaved Coltsfoot
Picea glauca (Moench) Voss	Pic_gla	T	White spruce
Pleurozium schreberi (Brid.) Mitt.	Ple_sch	B	Red stemmed feather moss
Polytrichum commune (Hedw.)	Pol_com	B	Common hair cap moss
Populus balsamifera L.	Pop_bal	T	Balsam poplar
Populus tremuloides Michx.	Pop_tre	T	Trembling aspen
Potentilla anserine L.s.l.	Pot_ans	S	Silverweed
Potentilla fruiticosa L.	Pot_fru	H	Shrubby Cinquefoil
Pulsatilla patens (L.) Mill.	Pul_pat	H	Pasque flower
Pyrola asarifolia Michx.	Pyr_asa	H	Pink wintergreen
Pyrola picta Sm.	Pyr_pic	H	Whiteveined wintergreen
Rhytidiopsis robusta (Hook.) Broth.	Rhy_rob	B	Pipe cleaner moss
Rosa acicularis Lindl. s.l.	Ros_aci	H	Prickly rose
Rubus arcticus L. ssp.	Rub_arc	H	Dwarf nagoonberry
Salix spp.	Sal_spp	T	Willow
Sanicula marilandica L.	San_mar	H	Black snakeroot
Saxifraga tricuspidata Rottb.	Sax_tri	H	Three toothed saxifrage
Sedum lanceolatum Torr.	Sed_lan	H	Stonecrop
Shepherdia canadensis (L.) Nutt.	She_can	H	Soapberry, Soopolallie
Solidago multiradiata Ait.	Sol_mul	H	Northern goldenrod
Sphagnum papillosum Lindb.	Sph_pap	B	Fat bog moss
Taraxacum officinale Weber ex	Tar_off	H	Common dandelion
Tortula ruralis (Hedw.) G. Gaertn.	Tor_rur	B	Sidewalk moss
Trillium grandiflorum (Michx.) Salisb.	Tri_gra	H	Trillium
Usnea hirta (L.) F.H. Wigg.	Usn_hir	L	Sugary beard
Vaccinium caespitosum Michx.	Vac_cae	S	Dwarf blueberry
Vaccinium vitis-idaea L.	Vac_vit	S	Lingonberry
Viola adunca J.E. Smith	Vio_adu	S	Hook-spur violet

Appendix B: Descriptive analysis of collected variables

Table B-1: Descriptive statistics of environmental variables

	Elevation (m)	Slope (%)	Total soil depth (cm)	Organic depth (cm)	Average soil moisture (%)
Mean	817.72	12.32	48.53	7.62	21.19
Standard Error	13.48	1.50	2.26	0.80	1.10
Median	781	8.75	44.5	4.75	19.66
Mode	781	0	23	6	19.66
Standard Deviation	127.90	14.24	21.46	7.58	10.44
Skewness	0.58	2.17	0.88	1.58	0.98
Range	507	74.75	95	30	47.47
Minimum	651	0	15	0	4.29
Maximum	1158	74.75	110	30	51.76
Sum	73595	1108.52	4368	685.5	1907.39
Count	90	90	90	90	90

Table B-2: Descriptive statistics of climate variables

	MAT (^{O}C)	MAP (mm)	TMXwt (^{O}C)	TMXsm (^{O}C)	PPTwt (mm)	PPTsm (mm)	DD0 (^{O}C)	DD5 (^{O}C)	NFFD (no)
Mean	-1.7	319.6	-9.7	18.0	60.5	129.9	2098.5	743.3	117.0
Standard Error	0.0	2.0	0.2	0.1	1.4	1.8	17.3	4.0	0.5
Median	-1.9	316.5	-10.89	18.235	69.15	122.6	2214	747.5	115
Mode	-2	346	-10.94	17.3	44.4	111.5	1894	790	114
Standard Deviation	0.42	19.12	1.51	0.66	13.55	17.52	164.13	38.29	4.54
Skewness	-0.09	0.30	0.21	-0.42	-0.03	0.52	-0.11	-0.40	-0.20
Range	1.3	80	3.96	2.34	34.5	64.3	424	161	15
Minimum	-2.4	290	-11.44	16.5	44	109.4	1892	632	108
Maximum	-1.1	370	-7.48	18.84	78.5	173.7	2316	793	123
Sum	- 148.5	28761	-874.7	1618.96	5440.6	11687.7	188868	66895	10530
Count	90	90	90	90	90	90	90	90	90

[Note: MAT = mean annual temperature; MAP = Mean annual precipitation; TMXsm = Mean summer maximum temperature; TMXwt = Mean winter maximum temperature; PPTsm = summer precipitation; PPTwt = Winter precipitation; DD0 = degree days below 0 C; DD5 = degree days above 5 C; NFFD = Number of frost free days]

Table B-3: Descriptive statistics of stand structure variables

	Spavht (m)	Spavdia (cm)	Atavht (m)	Atavdia (cm)	Poavht (m)	Poavdia (cm)	AtBA (m^2)	PoBA (m^2)	SpBA (m^2)	ToBA (m^2)
Mean	9.01	13.37	4.68	7.24	2.35	3.98	3.90	0.59	16.07	17.26
Standard Error	0.46	0.60	0.39	0.64	1.05	1.98	0.97	0.46	1.49	1.48
Median	9.33	14.36	4.55	7.21	1.54	2.11	2.06	0.14	12.76	15.04
Standard Deviation	4.07	5.28	2.20	3.65	2.11	3.95	5.47	0.92	13.19	13.24
Skewness	-0.18	-0.58	0.34	0.39	1.69	1.99	3.72	2.00	1.08	0.91
Range	16.06	22	7.98	13.65	4.525	8.125	29.84	1.87	52.19	52.19
Minimum	0.56	0.63	1.33	2	0.9	1.775	0.13	0.10	0.01	0.01
Maximum	16.61	22.63	9.3	15.65	5.425	9.9	29.96	1.96	52.20	52.20
Sum	702.53	1043.23	149.68	231.58	9.4	15.9	124.74	2.34	1253.44	1380.52
Count	78	78	32	32	4	4	32	4	78	80

[Note: Spavht = white sprue average height; Spavdia = White spruce average diameter; Atavht = aspen average height; Poavht = balsam poplar average height; Poavdia = balsam poplar average diameter; AtBA = aspen basal area; PoBA = balsam poplar basal area; SpBA = white spruce basal area; ToBA = total basal area]

Appendix C: Multiple Co-inertia analysis outputs[15]

pseudoeig: 20 pseudo eigenvalues

9.923, 2.795, 1.382, 1.13 0.9023 ...

call: mcoa(X = KTABLAS, option = "uniform")

	data.frame	nrow	ncol	content
1	$SynVar	90	2	synthetic scores
2	$axis	24	2	co-inertia axis
3	$Tli	360	2	co-inertia coordinates
4	$Tl1	360	2	co-inertia normed scores
5	$Tax	16	2	inertia axes onto co-inertia axis
6	$Tco	24	2	columns onto synthetic scores
7	$TL	360	2	factors for Tli Tl1
8	$TC	24	2	factors for Tco
9	$T4	16	2	factors for Tax
10	$lambda	4	2	eigen values (separate analysis)
11	$cov2	4	2	pseudo eigen values (synthetic analysis)

[1] 9.922991e+00 2.795277e+00 1.382351e+00 1.129755e+00 9.022824e-01 6.741350e-01 4.529459e-01 4.277802e-01

3.246419e-01 5.597977e-02 2.220464e-02

[12] 5.840040e-03 2.665416e-03 1.176611e-03 3.327083e-04 3.347987e-05 2.058054e-05 1.336260e-05 1.163953e-27

1.651378e-31

Array number 1 Enviro Rows 90 Cols 18

	Iner	Iner+	Var	Var+	cos2	cov2
1	9.824	9.824	9.824	9.824	0.997	9.799
2	2.794	12.618	2.794	12.618	1	2.794

Array number 2 Sw Rows 90 Cols 2

	Iner	Iner+	Var	Var+	cos2	cov2
1	1.891	1.891	1.207	1.207	0.035	0.042
2	0.109	2	0.793	2	0	0

[15] The fonts in the appendixes are same as the software outputs.

Array number 3 At Rows 90 Cols 2

	Iner	Iner+	Var	Var+	cos2	cov2
1	1.976	1.976	1.969	1.969	0.024	0.048
2	0.024	2	0.031	2	0.033	0.001

Array number 4 Ab Rows 90 Cols 2

	Iner	Iner+	Var	Var+	cos2	cov2
1	1.961	1.961	1.956	1.956	0.017	0.034
2	0.039	2	0.044	2	0.002	0

MCOA and Axis

	Axis1	Axis2
ele	-0.27201273	-0.233031651
slope	-0.16339181	-0.224227584
Cosasp	0.06937639	-0.371011447
Sinasp	0.18241733	0.072623398
mat	-0.30332398	0.138265752
TMXwt	-0.31811243	-0.008857122
TMXsm	0.29497003	0.165895527
TMNwt	-0.31757522	0.031986812
TMNsm	-0.29325288	0.199443093
PPTwt	0.29119171	-0.205323731
PPTsm	-0.29989281	-0.144754754
DD0	0.31745294	-0.034924514
DD5	0.16882948	0.391733215
NFFD	-0.28979661	0.199601497
Soil_D	0.01681583	0.359387913
Org_D	-0.04475665	-0.145826098
SoilMoist	-0.04699352	0.028980809
SwHt	0.99309842	0.117283967
SwDBH	0.11728397	-0.993098420
AtHt	0.66402320	0.747711968
AtDBH	0.74771197	-0.664023202
AbHt	-0.74113007	-0.671361470
AbDBH	-0.67136147	0.741130068

Appendix D: Canonical correlation outputs

Table D-1: Relationship among site characteristics and tree regeneration in Southwest Yukon

The CANCORR Procedure

Canonical Correlation Analysis

	Canonical Correlation	Adjusted Canonical Correlation	Approximate Standard Error	Squared Canonical Correlation
1	0.997833	0.996933	0.000478	0.995671
2	0.827347	0.735080	0.034841	0.684503
3	0.753143	0.594060	0.047792	0.567225
4	0.727287	.	0.052019	0.528946
5	0.687891	.	0.058176	0.473195
6	0.614102	0.517309	0.068785	0.377121

- Test of H0: The canonical correlations in the current row and all that follow are zero
- Eigenvalues of Inv(E)* = CanRsq/(1-CanRsq)

	Eigenvalue	Difference	Proportion	Cumulative	Likelihood Ratio	Approximate F Value	Num DF	Den DF	Pr > F
1	230.0264	227.8568	0.9741	0.9741	0.00009135	5.77	186	280.03	<**.0001**
2	2.1696	0.8589	0.0092	0.9833	0.02110485	1.87	150	237.53	<**.0001**
3	1.3107	0.1878	0.0056	0.9889	0.06689397	1.63	116	193.33	0**.0014**
4	1.1229	0.2247	0.0048	0.9936	0.15456970	1.52	84	147.47	0**.0133**
5	0.8982	0.2928	0.0038	0.9974	0.32813575	1.38	54	100	0.0823
6	0.6054		0.0026	1.0000	0.62287859	1.19	26	51	0.2937

Table D-2: Multivariate statistics and F approximations

S=6 M=12 N=22

Statistic	Value	F Value	Num DF	Den DF	Pr > F
Wilks' Lambda	0.00009135	5.77	186	280.03	<.0001
Pillai's Trace	3.62666098	2.51	186	306	<.0001
Hotelling-Lawley Trace	236.13325553	56.44	186	195.03	<.0001
Roy's Greatest Root	230.02640465	378.43	31	51	<.0001

Table D-3: Correlations between the tree regeneration and their canonical variables

	reg1	reg2	reg3	reg4	reg5	reg6
Spsed	0.0419	0.2362	0.4730	0.5134	-0.6663	-0.1059
AtSed	-0.0363	0.9022	0.2253	-0.0253	0.3121	0.1895
Popsed	0.8767	0.0609	0.3153	-0.1612	-0.1006	-0.3037
Atsap	-0.0291	0.3333	-0.2644	0.5072	0.4259	-0.6161
Spsap	-0.0208	-0.4968	0.5042	0.4950	0.4242	0.2712
Popsap	0.9997	-0.0001	-0.0165	-0.0011	-0.0070	0.0158

Table D-4: Correlations between the site characteristics and their canonical variables

	site1	site2	site3	site4	site5	site6
lat	-0.1514	-0.1311	-0.1865	-0.0902	0.2108	-0.1359
long	-0.1228	-0.1836	-0.3133	-0.2356	0.2286	0.0469
ele	-0.0424	-0.0281	-0.4580	-0.3307	0.1746	0.0277
slope	-0.0886	-0.1028	-0.3031	-0.3895	0.1588	-0.1017
aspcon	-0.0492	-0.1146	-0.0733	-0.1197	-0.0540	-0.1168
mat	-0.1395	-0.2103	-0.1650	-0.1318	0.1476	0.0619
map	0.1372	0.0488	-0.1557	-0.2280	-0.1722	0.2453
TMXwt	-0.1073	-0.1700	-0.2972	-0.2309	0.1835	0.0346
TMXsm	0.0711	0.1063	0.4073	0.2968	-0.1788	-0.0223
DD0	0.1142	0.1987	0.2571	0.2105	-0.1773	-0.0568
DD5	0.0159	0.0117	0.4812	0.3213	-0.1059	0.0163
NFFD	-0.1206	-0.1919	-0.1457	-0.1235	0.2005	0.0777
BT	-0.0592	-0.2810	0.1855	0.2810	-0.1207	0.3076
FR	-0.0097	0.4852	0.5213	-0.1893	-0.1978	-0.2882
OLDFR	-0.0523	-0.0789	-0.0476	0.1359	0.3656	-0.0052
SALV	0.2310	0.0204	-0.1751	0.1323	0.1372	-0.1197
TD	-0.0794	0.2300	0.1348	0.0303	0.2725	-0.2550
OD	-0.0820	-0.3870	0.0115	0.1924	-0.0314	0.2279
T1M	-0.0951	-0.3748	0.1941	-0.1305	0.1132	-0.1001
AM	-0.0757	-0.4142	0.0724	-0.1229	0.0954	-0.0086
CL	-0.0596	-0.1310	0.3632	-0.1462	0.0046	-0.1091
SA	0.1347	0.2030	-0.1773	0.1223	0.2253	-0.1417
STT	-0.0747	-0.4883	0.1873	0.1165	0.1085	0.4819
ATT	-0.0452	0.0300	-0.2425	-0.0386	0.2119	-0.1484
PTT	0.9156	-0.0056	-0.0385	0.0317	-0.1224	0.0406
TCC	-0.0871	-0.3114	0.1672	0.1641	0.3244	0.4388
TshrubC	0.1262	0.1475	-0.1427	0.1066	0.3551	0.0884
TherbC	-0.0399	-0.0846	0.1690	-0.0613	-0.1435	0.1683
PoBA	0.9923	-0.0069	-0.0247	0.0156	-0.0441	0.0291
SpBA	-0.0184	-0.2797	0.1050	-0.0101	0.0345	0.5542
AtBA	-0.0416	-0.0331	-0.1798	-0.0886	0.1092	-0.0537
ToBA	-0.0141	-0.2848	0.0538	-0.0340	0.0633	0.5320

Table D-5: Correlations between the site characteristics and the canonical variables of the tree regeneration

	reg1	reg2	reg3	reg4	reg5	reg6
lat	-0.1510	-0.1085	-0.1404	-0.0656	0.1450	-0.0835
long	-0.1225	-0.1519	-0.2360	-0.1713	0.1572	0.0288
ele	-0.0423	-0.0232	-0.3449	-0.2405	0.1201	0.0170
slope	-0.0884	-0.0850	-0.2283	-0.2833	0.1093	-0.0624
aspcon	-0.0491	-0.0948	-0.0552	-0.0871	-0.0372	-0.0717
mat	-0.1392	-0.1740	-0.1242	-0.0959	0.1015	0.0380
map	0.1369	0.0404	-0.1173	-0.1658	-0.1185	0.1506
TMXwt	-0.1071	-0.1406	-0.2239	-0.1679	0.1262	0.0213
TMXsm	0.0709	0.0880	0.3068	0.2159	-0.1230	-0.0137
DD0	0.1140	0.1644	0.1936	0.1531	-0.1220	-0.0349
DD5	0.0158	0.0097	0.3624	0.2336	-0.0729	0.0100
NFFD	-0.1203	-0.1588	-0.1098	-0.0898	0.1379	0.0477
BT	-0.0591	-0.2325	0.1397	0.2043	-0.0830	0.1889
FR	-0.0097	0.4014	0.3926	-0.1377	-0.1360	-0.1770
OLDFR	-0.0521	-0.0653	-0.0358	0.0989	0.2515	-0.0032
SALV	0.2305	0.0169	-0.1319	0.0962	0.0944	-0.0735
TD	-0.0792	0.1903	0.1015	0.0221	0.1875	-0.1566
OD	-0.0818	-0.3202	0.0086	0.1399	-0.0216	0.1400
T1M	-0.0949	-0.3101	0.1462	-0.0949	0.0779	-0.0615
AM	-0.0755	-0.3427	0.0545	-0.0894	0.0656	-0.0053
CL	-0.0595	-0.1084	0.2735	-0.1063	0.0032	-0.0670
SA	0.1344	0.1680	-0.1335	0.0889	0.1550	-0.0870
STT	-0.0745	-0.4040	0.1411	0.0847	0.0746	0.2959
ATT	-0.0451	0.0248	-0.1827	-0.0281	0.1458	-0.0911
PTT	0.9136	-0.0046	-0.0290	0.0230	-0.0842	0.0250
TCC	-0.0869	-0.2576	0.1259	0.1194	0.2232	0.2695
TshrubC	0.1259	0.1221	-0.1075	0.0775	0.2443	0.0543
TherbC	-0.0398	-0.0700	0.1273	-0.0446	-0.0987	0.1034
PoBA	0.9902	-0.0057	-0.0186	0.0113	-0.0303	0.0179
SpBA	-0.0184	-0.2314	0.0791	-0.0073	0.0237	0.3404
AtBA	-0.0415	-0.0274	-0.1354	-0.0644	0.0751	-0.0330
ToBA	-0.0141	-0.2357	0.0405	-0.0247	0.0435	0.3267

Appendix E: Full imputed and observed values

	SpsedTot	AtsedTot	PosedTot	SpsedTot.o	AtsedTot.o	PosedTot.o
1	933	0	0	21733	0	0
2	40133	15867	0	14000	13467	0
3	106667	0	0	6800	166267	0
4	248400	113200	0	84000	260133	0
5	6933	13600	0	17200	24933	0
6	13333	147733	0	40133	15867	0
7	0	0	0	533	82267	0
8	20400	120000	0	10000	0	0
9	79600	56933	0	190800	13333	23333
10	30133	10133	0	36933	0	0
11	0	0	0	70000	0	3333
12	6933	0	0	80267	73600	0
13	248400	113200	0	90267	400000	0
14	8800	0	0	16800	0	0
15	91467	0	0	60133	0	0
16	53867	117733	0	103200	0	0
17	137467	0	0	126000	0	0
18	6800	166267	0	106667	0	0
19	251200	0	0	263867	0	0
20	30133	10133	0	3333	0	0
21	92400	50133	0	6667	0	0
22	70800	23333	0	13333	0	0
23	23333	0	0	3467	0	0
24	250267	13333	0	417733	33333	0
25	23333	0	0	72800	0	0
26	107200	0	0	44933	0	0
27	80267	73600	0	6933	0	0
28	3467	0	0	133	0	0
29	21733	0	0	933	0	0
30	30133	10133	0	133	0	0
31	10000	0	0	0	0	0
32	3467	0	0	23333	0	0
33	8800	0	0	3333	0	0
34	113333	13333	0	171067	0	0
35	6933	13600	0	45200	0	0
36	0	0	0	92400	50133	0
37	52133	6667	0	57333	0	0
38	60133	0	0	91467	0	0
39	13333	0	0	70800	23333	0
40	57333	0	0	52133	6667	0
41	13333	0	0	533	0	0
42	10000	0	0	20400	120000	0
43	133	0	0	30133	10133	0

	SpsedTot	AtsedTot	PosedTot	SpsedTot.o	AtsedTot.o	PosedTot.o
44	350000	83333	0	660000	110400	3333
46	126667	103733	30000	406667	96667	63333
47	133733	0	0	84533	0	0
48	190800	13333	23333	80000	53600	0
49	83333	0	3333	50000	43867	3333
50	50000	43867	3333	83333	0	3333
51	3333	0	0	70400	0	0
52	83333	0	3333	273333	136133	26667
53	80000	53600	0	100000	123600	13467
54	197333	0	0	201867	10000	0
55	251200	0	0	135333	0	3333
56	53867	117733	0	62000	129067	0
57	190800	13333	23333	79600	56933	0
58	106667	0	0	56667	46800	0
59	133733	0	0	250267	13333	0
60	113333	13333	0	168267	3333	0
61	16800	0	0	8800	0	0
62	107200	0	0	131067	0	0
63	106667	0	0	308133	0	0
64	126000	0	0	137467	0	0
65	8800	0	0	16800	0	0
66	113333	13333	0	133733	0	0
67	126000	0	0	197333	0	0
68	135333	0	3333	251200	0	0
69	533	0	0	0	0	0
70	168267	3333	0	120400	171733	0
71	248400	113200	0	125733	33333	0
72	90267	400000	0	46667	816667	0
73	131067	0	0	107200	0	0
74	933	0	0	36667	23333	6667
75	171067	0	0	113333	13333	0
76	406667	96667	63333	130667	0	138400
77	168267	3333	0	350000	83333	0
78	533	0	0	0	0	0
79	92400	50133	0	0	0	0
80	103200	0	0	53867	117733	0
81	84000	260133	0	248400	113200	0
82	60133	16667	0	6800	10000	0
83	0	0	0	43733	23333	0
84	10000	0	0	33600	107067	0
85	17200	24933	0	10667	23600	0
86	17200	24933	0	6933	13600	0
87	133	0	0	20000	13333	0
88	6800	10000	0	60133	16667	0
89	40133	15867	0	13333	147733	0
90	3333	0	0	13333	36667	0

Appendix F: Species richness and abundance (%) by sites

sites	richness	abundance	sites	richness	abundance	sites	richness	abundance
101	7	62.3	218	14	142.1	418	11	140.4
102	5	83.3	219	15	80.6	419	21	125
103	10	61.8	220	17	268.7	420	16	159.6
104	7	101.5	301	13	61.1	421	11	113.7
105	16	100.9	302	13	73.5	422	9	105.5
106	10	146.3	303	12	89.4	423	13	168.1
107	12	172.3	304	9	85.7	424	14	159.2
108	10	95.6	305	15	57.5	425	16	144.3
109	16	122	306	12	67.9	501	9	113.2
110	13	128.1	307	13	70.7	502	16	180.4
111	14	101.6	308	11	55.2	503	20	161.7
112	15	117.9	309	12	100.9	504	17	209.4
113	17	93.8	310	9	57.1	505	15	90
201	11	100.6	401	10	72.8	506	16	18.3
202	16	95	402	16	90	507	14	94.3
203	11	117.4	403	19	125.2	508	18	116.6
204	11	143.4	404	21	106.5	509	19	173.1
205	13	109.8	405	12	102.9	510	7	101.6
206	15	157.7	406	13	99.5	511	4	86.7
207	11	107	407	14	117.1	512	21	139.7
208	10	170.4	408	11	133.7	513	20	155.9
209	14	162.3	409	11	139.8	601	19	74
210	13	50.3	410	15	106.1	602	15	39.4
211	15	77.5	411	15	142.2	603	21	153.2
212	17	153.3	412	13	107.6	604	17	112.3
213	15	176.7	413	14	99.8	605	15	75.5
214	13	110.3	414	11	49.7	606	18	90.4
215	15	119.9	415	16	116.8	607	19	84
216	11	201	416	21	153.2	608	19	63.1
217	14	263.5	417	14	128.4	609	11	75.7

Appendix G: Abundance rank and spatial distribution of species in the study area

Rank	Scientific name	Type	Block A	Block B	Block C	Block D	Block E	Block F	Total	% of total	no of sites
	Trees										
1	*Salix* spp.	T	208.4	410.1	88.2	230.1	87.4	22.8	1047	9.86	8
2	*Picea glauca* (Moench) Voss	T	74.6	221	161.2	259.2	89.8	61	866.7	8.17	8
3	*Populus tremuloides* Michx.	T	218.2	1.9	19.4	106.8	85.1	41.1	472.6	4.45	7
4	*Populus balsamifera* L.	T	2.3			5.2	23.6		31.2	0.29	3
	su total		**503.5**	**633**	**268.8**	**601.3**	**285.9**	**124.9**	**2417.5**	**22.77**	
	Average per plot		**38.73**	**31.65**	**26.88**	**24.05**	**21.90**	**13.88**	**26.86**		

Rank	Scientific name	Type	Block A	Block B	Block C	Block D	Block E	Block F	Total	% of total	no of sites
	Herbs and Shrubs										
1	*Arctostaphylos uva-ursi* (L.) Spreng. s.l.	H	366.6	26.5	57	172.9	132.2	20.2	775.3	7.3	8
2	*Shepherdia canadensis* (L.) Nutt.	H	356	53.6	37.5	115.5	36.4	95.5	694.6	6.54	8
3	*Ledum groenlandicum* Oeder	S		419.1		0.3	6.7		426.1	4.01	4
4	*Linnaea borealis* L.	H		11.3		170.1	28.6	127.3	337.3	3.18	6
5	*Alnus incana* (L.) Moench	S		299			3.6	0.3	302.9	2.85	4
6	*Elymus glaucus* Buckl.	H				296.7			296.7	2.8	2
7	*Epilobium angustifolium* L.s.l	H	6.7	224.4		14.9	3.3		249.3	2.35	5
8	*Betula glandulosa* Michx.	S		92.2			140		232.2	2.19	3
9	*Vaccinium vitis-idaea* L.	S		183.4	23.6	17.5			224.5	2.11	5
10	*Arctostaphylos rubra* (Rehd. & Wils)	H		50	12.6	125.6			188.2	1.77	5
11	*Elymus innovates* (Beal) Pilg.	H		107.8	1.6	15.5	53.6		178.5	1.68	6
12	*Empetrum nigrum* L.	H	7.5		28.3	22.2	97.2	22.1	177.3	1.67	6
13	*Equisetum arvense* L.	H	7.9	0.9	2.9	87	31.1	27.4	157.2	1.48	7
14	*Rosa acicularis* Lindl. s.l.	H	6.2	16.5	8.4	45.7	10.5	69.2	156.5	1.47	8
15	*Castilleja* spp.	H	2.6	3.8	0.9	18	95.3	1.9	122.5	1.15	8
16	*Erigeron peregrines* (Pursh)	H		0.6		106			106.6	1	3
17	*Pulsatilla patens* (L.) Mill.	H	1.7	42.2		38.6	20		102.5	0.97	6
18	*Carex* spp.	H	0.3	27.5	40	30.8	0.6		99.2	0.93	7
19	*Aquilega formosa* Fisch. Ex DC.	H	23.6	1.2		10.9	28.8	1.2	65.6	0.62	5
20	*Geocaulon lividum* (Richards.)	H	1.6			39	6.7	17.1	64.4	0.61	5
21	*Pyrola picta* Sm.	H	0.3	46.5		8.1		7.8	62.7	0.59	5
22	*Saxifraga tricuspidata* Rottb.	H		40.3					40.3	0.38	2
23	*Hedysarum mackenzii* (Richards.)	H	2.3	7.1	0.9	21.1	6.9		38.4	0.36	6
24	*Solidago multiradiata* (Ait.)	H	0.3		0.3	5.1	30.3		36	0.34	5
25	*Potentilla anserine* L.s.l.	S		6.7		26.7			33.3	0.31	2
26	*Petastites frigidus* (L.) Fries	H		27.3		3.3			30.6	0.29	3
27	*Achillea millefolium* L.s.l.	H	1.2			2.4	22	3.3	28.9	0.27	5

28	*Arnica cordifolia* Hook.	H	5.4	1.2	3.2	16.5	1.6		27.9	0.26	7
29	*Hordeum brachyantherum Nevski*	H				25			25	0.24	1
30	*Aconitum delphinifolium* DC.	H					11.3	10.8	22.1	0.21	2
31	*Lupinus arcticus* Wats.	H	0.3	21.7					22	0.21	2
32	*Aster alpines* L.ssp.	H					14.1	2.6	16.7	0.16	2
33	*Vaccinium caespitosum* Michx.	S	10	2					11.9	0.11	3
34	*Festuca* spp.	H					11.7		11.7	0.11	1
35	*Hyacinthoides non-scripta* (L.)	H	0.3	0.6	0.6	9.9			11.5	0.11	5
36	*Potentilla fruticosa* L.	H	1.9	8.6					10.5	0.1	3
37	*Rubus arcticus* L. ssp.	H		10		0.3			10.3	0.1	2
38	*Sedum lanceolatum* Torr.	H	0.3	8.3					8.6	0.08	3
39	*Trillium grandiflorum* (Michx.) Salisb.	H	1.9		5.6				7.5	0.07	2
40	*Oxytropis campestris* L. (DC.)	H	2.8	0.6	1.9	0.9	0.6		6.9	0.06	5
41	*Oxycoccus microcarpus* Turcz.	S	5.3						5.3	0.05	1
42	*Taraxacum officinale* Weber ex	H		1.7		0.3	1.7		3.6	0.03	3
43	*Juniperus communis* L.s.l.	S					1.7	1.7	3.3	0.03	2
44	*Viola adunca* J.E. Smith	S					1.7		1.7	0.02	1
45	*Pyrola asarifolia* Michx.	H	0.6						0.6	0.01	1
46	*Mimulus guttatus* DC.	H				0.3			0.3	0	2
47	*Sanicula marilandica* L.	H				0.3			0.3	0	2
	su total		**813.6**	**1742.6**	**225.3**	**1447.4**	**798.2**	**408.4**	**5435.3**	**51.18**	
	Average per plot		**62.58**	**87.13**	**22.53**	**57.90**	**61.40**	**45.38**	**60.39**		

	Brayophytes										
1	*Pleurozium schreberi* (Brid.) Mitt.	B	8.9	484.2	98.9	598.3	86.5	80.2	1357.1	12.79	8
2	*Dicranum polysetum* Sw.	B		54.2	60.3	73.6	65	18.8	271.9	2.56	7
3	*Dichodontium pellucidum (Hedw.) Schimp.*	B			0.6	39.5	7.8		47.9	0.45	3
4	*Rhytidiopsis robusta* (Hook.) Broth.	B	0.3	8.9		24.9	1.6		35.7	0.34	6
5	*Tortula ruralis* (Hedw.) G. Gaertn.	B					28.6		28.6	0.27	1
6	*Sphagnum papillosum* Lindb.	B	0.3	2.2	5.5	16.6		1.7	26.4	0.25	6
7	*Hookeria lucens* (Hedw.) Sm.	B					21.6		21.6	0.2	1
8	*Polytrichum commune* (Hedw.)	B	0.3	3.3			5		8.6	0.08	3
9	*Dicranum scoparium* Hedw.	B		3.6					3.6	0.03	1
10	*Aulacomnium palustre* (Hedw.) Schwagr	B		0.6					0.6	0.01	1
	subtotal		**9.8**	**557**	**165.3**	**752.9**	**216.1**	**100.7**	**1802**	**16.98**	
	Average per plot		**0.75**	**27.85**	**16.53**	**30.12**	**16.62**	**11.19**	**20.02**		

	Lichens										
1	*Cladonia* spp.	L	17.6	79.2	24.8	73.9	179.9	25.5	400.9	3.78	8
2	*Flavocetraria cucullata* (Bellardi) K.&A. Thell	L	8.6	0.6	0	51.5	165.6	21.5	247.8	2.33	8
3	*Peltigera aphthosa* (L.) Willd.	L	2.5	84.9	26.1	39.5	3.3	29.9	186.3	1.75	8
4	*Peltigera canina* (L.) Wildd.	L	0.3			40.3	6.6	3.3	50.5	0.48	4
5	*Cladina mittis* (Sandst.) Hustich	L	20.4		8.6				29	0.27	2
6	*Cetraria pinastry* (Scop.) A. Gray	L					11.6	11.6	23.2	0.22	2
7	*Hypogymnia physodes* (L.) Nyl.	L	7	2	0.3				9.2	0.09	3
8	*Usnea hirta* (L.) F.H. Wigg.	L		0.9				0.9	1.8	0.02	2
	sub total		**56.4**	**167.6**	**59.8**	**205.2**	**367**	**92.7**	**948.7**	**8.94**	
	Average per plot		**4.34**	**16.76**	**2.99**	**20.52**	**14.68**	**7.13**	**105.41**		
	Total abundance per plot		**106.7**	**155**	**71.9**	**120**	**128.5**	**80.4**	**117.8**	**100**	

Appendix H: Species richness, abundance, Shannon and 1/Simpson indices by environmental gradient

Table H-1: Variation by research sites

Blocks	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	Mean 1/Simpson	Mean Shannon
A	13	41	12	1387	107	3.5	1.51
B	10	35	13	1214	121	5.4	1.88
B1	10	42	15	1594	159	5.28	1.92
C	10	27	12	719	72	4.27	1.70
D	11	39	14	1236	112	5.51	1.96
D1	14	41	14	1771	127	4.6	1.85
E	13	43	15	1667	129	7.14	2.14
F	9	28	17	768	85	8.43	2.39

Table H-2: Indices by elevation category

Elevation	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	Mean 1/Simpson	Mean Shannon
Very high	4	29	15	542	135	4.41	1.78
High	14	46	12	1844	132	6.71	1.62
Medium	15	43	13	1810	121	5.34	1.85
Low	32	53	15	3154	99	6.71	2.07
Very low	25	46	14	3007	120	5	1.9

Table H-3: Indices by slope category

Slope	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	Mean 1/Simpson	Mean Shannon
Low	47	62	14	5285	112	5.23	1.88
Medium	21	58	14	2210	105	5.55	1.92
Level	16	46	14	1854	116	6.31	2.02
Steep	6	32	14	1006	168	4.27	1.76

Table H-4: Indices by aspects

Aspect	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
Eest	9	44	17	956	106	6.22	2.16
Level	20	53	15	2392	120	6.36	2.04
North	1	17	17	269	269	6.39	2.12
Northeast	5	39	15	757	151	4.89	1.85
Northwest	18	51	14	2203	122	6.45	2.03
South	3	27	14	334	111	4.43	1.75
Southeast	13	41	13	1273	98	4.38	1.71
Southwest	12	38	12	1212	101	3.9	1.64
West	9	42	13	960	107	4.64	1.79

Table H-5 Indices by disturbance types

Disturbance	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
Beetle	14	46	15	1877	134	4.67	1.84
Fire	11	40	15	1237	112	5.5	1.96
Harvested	20	47	15	1949	98	7.19	2.16
Undisturbed	31	63	13	3822	123	4.85	1.79
Oldfire	14	43	13	1470	105	4.91	1.81

Table H-6: Indices by tree density variation

Tree density	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	Mean 1/Simpson	Shannon
Very high	6	36	13	578	96	3.18	1.45
High	11	42	14	1205	110	6.30	2.06
Medium	14	42	14	1662	119	5.83	1.98
Low	24	56	14	2394	100	5.79	1.99
Very low	35	68	14	4517	129	5.24	1.85

Table H-7: Indices by crown cover variation

Crown cover	No of sites	Cumulative richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
Very high	16	52	14	1857	116	4.68	1.73
High	19	47	14	1905	100	5.49	1.91
Medium	16	54	14	1889	118	5.42	1.94
Low	13	47	16	1365	105	6.79	2.17
Very low	26	66	13	3339	128	5.19	1.86

Table H-8: Indices by stand types

Stand	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
Aspen	4	19	10	438	109	3.42	1.49
Mixed	28	60	15	2653	95	6.22	2.04
No trees	13	51	13	1553	119	5.83	1.92
Spruce	45	65	14	5712	127	5.01	1.86

Table H-9: Indices by soil moisture variation

Soil moisture	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
Very high	5	34	13	685	137	4.43	1.66
High	16	51	15	1930	121	5.44	1.89
Medium	14	47	13	1552	111	4.66	1.8
Low	46	68	14	4809	105	5.67	1.95
Very low	9	68	14	1379	153	5.97	2.01

Table H-10: Indices by Degree days below 0^0C

DD0	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
Very high	9	28	17	768	85.3	8.43	2.39
High	38	57	15	4674	123	5.73	1.98
Low	23	46	12	2106	91.6	3.85	1.59
Very low	20	47	14	2807	140.4	5.34	1.9

Table H-10: Indices by degree days above 5^0C (DD>5 ^{o}C)

DD5	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
Very high	36	50	13	3813	106	1.82	4.7
High	14	47	15	1824	130	2.14	6.98
Medium	32	60	14	3482	109	1.93	5.8
Low	5	27	13	767	153	1.76	4.36
Very low	3	29	16	469	156	1.9	4.78

Table H-11: Indices by number of frost free days

NFFD	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
High	6	34	14	1076	179.3	4.35	1.77
Low	31	55	14	3925	126.6	6.01	2.02
Medium	7	31	12	749	107	4.52	1.79
Very high	37	56	12	3838	103.7	4.57	1.73
Very low	9	28	17	768	85.3	8.43	2.39

Table H-12: Indices by variation of mean annual temperature

MAT	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
High	32	53	16	3736	117	6.7	2.12
Medium	15	44	14	1705	114	5.29	1.94
Low	43	60	13	4914	114	4.54	1.74

H-13: Indices by variation in mean annual precipitation

MAP	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
High	19	55	15	2743	144	6.26	2.02
Medium	42	61	15	4675	111	6.02	2.03
Low	29	51	12	2938	101	4.05	1.65

H-14: Indices by variation in mean annual TMXsm

MAP	No of sites	Richness	Mean richness	Total abundance	Mean abundance %	1/Simpson	Shannon
High	48	59	15	5531	115	6.25	2.06
Medium	18	42	11.6	1579	88	4.41	1.68
Low	24	54	13.4	3245	135	4.56	1.76

Appendix I: Canonical Correspondence Analysis outputs

```
Partitioning of mean squared contingency coefficient:
              Inertia Proportion
Total           5.766     1.0000
Constrained     1.808     0.3136
Unconstrained   3.958     0.6864

Eigenvalues, and their contribution to the mean squared contingency coefficient

Importance of components:
                        CCA1    CCA2    CCA3    CCA4    CCA5   CCA6    CCA7
Eigenvalue            0.4371 0.33820 0.22238 0.17688 0.11250 0.1050 0.09551
Proportion Explained  0.0758 0.05865 0.03857 0.03068 0.01951 0.0182 0.01656
Cumulative Proportion 0.0758 0.13445 0.17302 0.20370 0.22321 0.2414 0.25798
                         CCA8    CCA9   CCA10   CCA11   CCA12   CCA13   CCA14
Eigenvalue            0.07159 0.06545 0.05270 0.04302 0.03727 0.03368 0.01705
Proportion Explained  0.01241 0.01135 0.00914 0.00746 0.00646 0.00584 0.00296
Cumulative Proportion 0.27039 0.28174 0.29088 0.29834 0.30481 0.31065 0.31360
                          CA1     CA2     CA3     CA4     CA5     CA6     CA7
Eigenvalue            0.43221 0.31869 0.28003 0.22996 0.20666 0.19005 0.15515
Proportion Explained  0.07496 0.05527 0.04856 0.03988 0.03584 0.03296 0.02691
Cumulative Proportion 0.38856 0.44383 0.49240 0.53228 0.56812 0.60108 0.62798
                          CA8    CA9    CA10    CA11    CA12    CA13    CA14
Eigenvalue            0.14564 0.1395 0.12665 0.12311 0.12028 0.11271 0.09959
Proportion Explained  0.02526 0.0242 0.02196 0.02135 0.02086 0.01955 0.01727
Cumulative Proportion 0.65324 0.6774 0.69941 0.72076 0.74161 0.76116 0.77843
                         CA15    CA16    CA17    CA18    CA19    CA20    CA21
Eigenvalue            0.08932 0.08161 0.07909 0.07213 0.06782 0.06159 0.06081
Proportion Explained  0.01549 0.01415 0.01372 0.01251 0.01176 0.01068 0.01055
Cumulative Proportion 0.79392 0.80808 0.82179 0.83430 0.84607 0.85675 0.86729
                         CA22    CA23    CA24    CA25    CA26    CA27    CA28
Eigenvalue            0.05625 0.05120 0.04882 0.04463 0.04249 0.03811 0.03641
Proportion Explained  0.00976 0.00888 0.00847 0.00774 0.00737 0.00661 0.00631
Cumulative Proportion 0.87705 0.88593 0.89440 0.90214 0.90950 0.91611 0.92243
                         CA29    CA30    CA31    CA32    CA33    CA34    CA35
Eigenvalue            0.03538 0.03380 0.03174 0.02700 0.02518 0.02392 0.02294
Proportion Explained  0.00614 0.00586 0.00550 0.00468 0.00437 0.00415 0.00398
Cumulative Proportion 0.92856 0.93442 0.93993 0.94461 0.94898 0.95313 0.95710
                         CA36    CA37    CA38    CA39    CA40    CA41    CA42
Eigenvalue            0.02221 0.01988 0.01892 0.01738 0.01666 0.01502 0.01417
Proportion Explained  0.00385 0.00345 0.00328 0.00301 0.00289 0.00261 0.00246
Cumulative Proportion 0.96096 0.96440 0.96769 0.97070 0.97359 0.97620 0.97865
                         CA43    CA44    CA45     CA46     CA47     CA48
Eigenvalue            0.01371 0.01228 0.01094 0.009794 0.008358 0.007403
Proportion Explained  0.00238 0.00213 0.00190 0.001700 0.001450 0.001280
Cumulative Proportion 0.98103 0.98316 0.98506 0.986760 0.988210 0.989490
                          CA49     CA50     CA51     CA52     CA53     CA54
Eigenvalue            0.006916 0.006548 0.006211 0.005444 0.004938 0.004291
Proportion Explained  0.001200 0.001140 0.001080 0.000940 0.000860 0.000740
Cumulative Proportion 0.990690 0.991820 0.992900 0.993850 0.994700 0.995450
                          CA55     CA56     CA57     CA58     CA59     CA60
Eigenvalue            0.003882 0.003208 0.002983 0.002697 0.002543 0.002153
Proportion Explained  0.000670 0.000560 0.000520 0.000470 0.000440 0.000370
Cumulative Proportion 0.996120 0.996680 0.997190 0.997660 0.998100 0.998480
                          CA61     CA62     CA63     CA64      CA65      CA66
Eigenvalue            0.001801 0.001446 0.001276 0.001010 0.0008993 0.0005748
Proportion Explained  0.000310 0.000250 0.000220 0.000180 0.0001600 0.0001000
Cumulative Proportion 0.998790 0.999040 0.999260 0.999440 0.9995900 0.9996900
                          CA67      CA68      CA69      CA70      CA71
Eigenvalue            0.000525 0.0004096 0.0002893 0.0001915 0.0001589
Proportion Explained  0.000090 0.0000700 0.0000500 0.0000300 0.0000300
Cumulative Proportion 0.999780 0.9998500 0.9999000 0.9999400 0.9999600
                           CA72      CA73      CA74      CA75
Eigenvalue            0.0001022 5.086e-05 3.629e-05 1.766e-05
Proportion Explained  0.0000200 1.000e-05 1.000e-05 0.000e+00
Cumulative Proportion 0.9999800 1.000e+00 1.000e+00 1.000e+00

Accumulated constrained eigenvalues
Importance of components:
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                       CCA1   CCA2   CCA3    CCA4    CCA5    CCA6    CCA7
Eigenvalue            0.4371 0.3382 0.2224 0.17688 0.11250 0.10497 0.09551
Proportion Explained  0.2417 0.1870 0.1230 0.09782 0.06221 0.05805 0.05282
Cumulative Proportion 0.2417 0.4287 0.5517 0.64953 0.71175 0.76980 0.82262
                        CCA8    CCA9   CCA10   CCA11   CCA12   CCA13   CCA14
Eigenvalue            0.07159 0.06545 0.05270 0.04302 0.03727 0.03368 0.01705
Proportion Explained  0.03959 0.03619 0.02915 0.02379 0.02061 0.01862 0.00943
Cumulative Proportion 0.86220 0.89840 0.92754 0.95134 0.97195 0.99057 1.00000

Scaling 2 for species and site scores
* Species are scaled proportional to eigenvalues
* Sites are unscaled: weighted dispersion equal on all dimensions
Species scores

              CCA1      CCA2      CCA3     CCA4      CCA5      CCA6
STT      -0.004614 -0.814222  0.027358 -0.22589  0.041493 -0.045213
ATT       0.431965 -0.402952  0.961227 -0.26304  0.481020  0.346846
PTT       0.502891  0.793442  0.007846 -0.50741 -0.415324 -0.635293
spsap     0.044695 -0.586156 -0.200193  0.13300  0.136240 -0.166468
atsap     0.726728  0.593519  0.811439  0.28266  0.160341  0.201202
spsed     0.397170  1.031961 -0.917202 -0.96652 -0.116312  0.076696
spsed1    0.376649  0.117924 -0.293695  0.26146  0.116475 -0.141355
atsed     0.573977  0.674147  0.240252 -0.17967  0.011537  0.127179
posed     0.476036  0.797480 -0.811485  0.20769  0.178852  0.058837
Wil_cov  -0.286559  0.202185  0.264844  0.43125 -0.271542 -0.363299
So_cov    0.511751  0.113305  0.934134  0.15429 -0.423159 -0.109783
Ma_cov   -2.193401  0.810660  0.509416  0.48692 -0.155888  0.303306
Bi_cov   -0.708995  1.218729 -0.429631 -1.35180  0.511582  0.100375
Pr_cov    0.047981  0.051839  0.091372  0.14844 -0.613289  1.571930
Ju_cov    0.345079  0.490701 -0.083384 -0.88814 -1.343729  1.086863
Cr_cov    0.292593  0.728931  2.554662  0.58679  0.006104  0.309300
Cf_cov   -0.369726 -0.540319  0.758129  0.12275 -0.996165 -1.106395
Rc_cov   -1.528442  0.930650  1.185210 -0.02920  0.523632  0.843384
Cet_pin   0.654844 -1.130291  1.541046 -1.02874  1.737026 -0.003829
Oxy_can   0.520234 -0.509171  0.865905 -0.48714  1.004906 -0.040066
Pel_aph  -0.239484 -0.651464 -0.051646 -0.23028  0.076643  0.126256
Sol_mul   0.556731  1.246970 -0.889012 -0.97016 -0.310076 -0.575706
Tor_rur   0.542959 -0.462129  0.915140 -0.12593  0.942071  0.027451
Car_spp   0.388309  1.075530 -1.105226 -0.77965 -0.315427 -0.598149
Hed_mac   0.293600 -0.118380 -0.355589  0.17933  0.061790 -0.092990
Hyp_phy   0.392333 -0.097335  1.440271  0.43865 -0.256802 -0.925974
Dic_pal  -0.019360 -0.459936 -0.393705 -0.48410  0.340262  0.072458
Fes_spp   0.497567  0.912610 -0.730997 -0.71498 -0.247812 -0.140044
Pyr_pic  -0.254238 -1.407806 -0.040659  0.02665 -0.447458  0.805262
Pyr_asa   0.638472  0.602292  1.320666 -0.02237 -1.342978 -2.036503
Usn_spp  -0.135392 -1.300251  0.037704 -0.66108 -0.846812  0.661597
Clad_spp -0.488554  0.161877 -0.435434 -0.35751  0.729457  0.103286
Rhy_rob  -0.514492 -0.398464 -0.720017  0.69690 -0.313682 -0.202909
Arc_uva   0.524902  0.273238  0.853961 -0.04230  0.141796 -0.144990
Vac_cae   0.341470 -1.086216  1.775151 -1.67783  2.376412  0.266009
She_can   0.511148 -0.078507  1.535966 -0.09930  0.410694 -0.844481
Ely_gla  -1.195688  1.117092 -0.165314 -0.09979 -0.047212 -0.084657
Equ_spp   0.269576  0.149740 -0.837681  1.23309  0.294939  0.406577
Ple_sch  -0.477598 -0.587606 -0.323824  0.03996 -0.144629  0.061676
Pet_spp  -0.657452  0.280908 -0.054244  0.47227 -1.318584 -1.844063
Aul_spp  -2.089818  0.600094  0.603545 -0.04772  0.651589  1.063222
Sed_spp  -2.401677  0.832688  0.659584 -0.29074  0.849915  1.374136
Sax_spp  -1.008974 -0.405803  0.525847  0.38380 -0.524923 -0.963391
Dic_pel  -2.115774  1.031247  1.455621  2.32337 -0.988475 -0.240796
Dic_spp   0.729415  0.822568 -0.715508  1.34760  0.778950  0.447269
San_spp   0.506092  0.410399 -1.591414  1.47640  0.959019  0.119508
Hor_bra   1.176981  1.012647 -0.187908  1.19101  0.475160  0.369803
Epi_aug   0.638096  0.390133 -0.362593  0.26026 -0.146062  0.473120
Mim_spp   1.176981  1.012647 -0.187908  1.19101  0.475160  0.369803
Sph_pap  -0.890509  1.249926 -0.275665 -1.31397  1.412831  0.644005
Ely_gla1  0.382221 -0.562520 -0.749428  0.68409  0.157819  0.315870
Pot_spp  -0.096336 -0.410336 -0.796551  1.03630 -0.486156 -0.333251
Hoo_spp   0.462287  1.486113 -1.212597 -1.22559 -0.687318 -0.966530
Aqu_for   0.422337  0.633297  0.411920 -0.35794 -0.096566 -0.079189
Ast_spp   0.490884  1.162871 -0.761139 -1.21012 -0.722723 -0.259865
Aco_del   0.501379  0.491237 -0.472531 -0.90489 -1.305169  0.584188
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Pol_spp	-0.801215	1.268133	-0.272326	-1.31527	1.011950	0.645706
Eri_per	0.502207	0.902510	-0.651207	-1.60941	-0.551964	-0.471607
Cas_spp	0.632879	0.178449	0.069714	-1.17381	-1.126684	1.111812
Pyr_spp	-1.598747	0.337675	0.390746	-0.52537	0.007611	0.772102
Vio_adu	0.614229	1.436370	-0.901506	-1.32668	-0.456793	-0.757793
Ach_mil	0.431529	0.907575	-0.636182	-0.99965	-0.620787	-0.171203
Rub_arc	-2.485164	1.571198	0.134819	-1.21863	2.805217	1.588117
Lin_bor	0.317969	-0.386572	-0.221526	-0.02159	-0.770776	0.984332
Cla_spp	0.230810	0.407863	-0.280529	-0.48442	-0.128449	-0.109832
Dic_spp1	0.687132	0.746409	-0.808102	1.42737	0.574433	0.379115
Arc_rub	-0.125444	-0.713951	-0.455681	0.42267	-0.090542	-0.188457
Ely_inn	0.474334	0.605233	-0.459258	-0.68306	-0.245819	-0.053581
Geo_liv	0.493579	-0.389876	-0.083904	-0.18113	-0.144267	0.951918
Vac_vit	-1.282782	0.052848	0.022495	0.19156	0.074747	-0.265936
Emp_nig	-1.253147	-0.032620	0.016244	-0.22082	0.190477	-0.494772
Arn_cor	0.432821	-0.222015	-0.144138	0.44106	-0.230890	-0.332894
Hya_non	0.820922	0.745086	-0.155558	1.11925	0.532946	0.403718
Pel_can	0.646291	0.142588	-0.589920	0.48397	0.153587	0.393273
Ros_aci	0.613124	0.041883	0.264534	-0.37252	-0.496474	0.781960
Spa	0.089278	-0.664123	-0.139090	0.24579	0.096640	0.432005
Fla_cuc	-0.348798	0.005604	-0.255249	-0.01968	1.369542	0.412063
Cro_spp	0.245634	-0.717035	-0.848125	0.10191	0.315231	0.285554
Tar_off	0.496569	1.395483	-1.159409	-1.31002	-0.691541	-0.967881
Lad_gro	-2.176354	0.654318	0.219314	0.05543	0.082674	0.205222
Pot_nan	0.753166	-1.492972	2.033768	-1.61974	2.605104	0.264608
Lup_arc	0.049439	-0.247893	0.213009	-0.25145	-1.783506	0.649235
Tri_gra	0.227644	0.047205	-0.585279	-0.49339	-1.837313	1.099197

Site scores (weighted averages of species scores)

	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
X101	0.28224	-1.3228	0.96455	-0.417186	0.351738	-1.01165
X102	0.40594	-0.6902	2.50927	-0.022206	0.437962	-2.81663
X103	1.26666	1.1947	2.45927	-0.301913	1.018023	0.98868
X104	1.03054	0.6509	2.08359	-0.092054	-0.299673	-0.05381
X105	0.66752	-1.2948	2.75451	-1.661889	3.655019	0.71937
X106	1.19129	0.6562	3.09491	-0.011967	1.561929	0.39317
X107	1.05059	1.0086	3.02822	0.012085	-0.021805	-0.37723
X108	0.74177	-0.1712	2.57555	-0.056318	-0.587758	-0.99784
X109	0.78893	0.4095	1.36319	0.720901	-0.162561	-1.30022
X110	0.32085	0.2368	2.08437	1.305523	-2.311269	-2.02310
X111	0.52482	0.3108	1.90453	1.085963	-1.622305	-1.74843
X112	0.72204	0.3000	1.60220	0.256986	-1.012646	-1.31715
X113	1.01309	1.4125	1.28020	-0.288331	0.360103	0.40882
X201	-0.50525	-1.9548	-0.41890	-0.763778	-0.004967	-0.12841
X202	-0.13312	-1.7304	-0.39962	-0.469718	0.295489	-0.51403
X203	-0.71794	-1.0619	-0.34989	-0.155385	0.499891	-1.15651
X204	-0.57296	-1.1404	-0.53181	-0.287751	0.911995	-1.40092
X205	-1.18124	-0.7231	-0.08308	-0.042220	0.384197	-1.40328
X206	-0.34582	0.1291	-0.10969	0.700232	-2.485267	-2.89856
X207	-1.61313	-0.3957	0.08207	0.474064	-0.361147	-0.37918
X208	-2.84804	0.6993	0.48601	0.977851	-0.515944	-0.01792
X209	-2.59882	0.5125	0.23438	0.538204	-0.233757	-0.87509
X210	-2.88241	1.4768	0.92247	0.448476	-0.406952	2.34989
X211	0.56490	-0.1286	-0.34140	0.551362	0.220292	-1.09337
X212	-0.18067	-0.9376	-0.14025	0.230145	-1.035076	-1.94537
X213	-0.83460	-0.8258	-0.09262	0.183788	-0.206400	-1.22395
X214	-0.27697	-0.5109	0.95072	-0.052600	-0.329461	-0.82756
X215	-2.22826	0.9229	1.53373	1.546214	-1.272557	0.02509
X216	-2.80948	0.6064	0.53300	0.913946	-0.472101	-0.03514
X217	-2.31136	0.6590	0.37824	0.431278	-0.372845	0.01753
X218	-4.24979	1.8021	1.41821	0.565252	-0.339567	3.43477
X219	-1.86603	0.2896	-0.30352	-1.714541	2.622094	-1.84330
X220	-2.24559	1.0348	-0.83472	-2.214441	3.522095	1.70943
X301	0.39676	-0.5138	-0.77777	0.549380	0.755183	-1.29738
X302	-0.09988	-1.3040	-0.62567	-0.739606	2.292532	0.11648
X303	0.29312	-0.3295	-0.12789	-0.234579	1.788472	0.02914
X304	-0.15621	-1.8432	-0.49220	-0.847820	0.554655	-0.17836
X305	0.24315	-1.3064	0.39880	-0.424322	1.263980	-0.70847
X306	0.55837	-0.7950	0.62077	-0.279397	1.154125	-0.16401
X307	0.02097	-0.9785	-0.22253	0.443911	0.130122	-1.16301

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X308 -0.35006 -1.9887 -0.30917 -0.607032 -0.096538 -0.26698
X309  0.19663  0.1156  1.59141  0.040103  0.263006 -0.52388
X310  1.03519 -0.2251  2.65489 -1.065495  1.337049  1.47903
X401  0.84708  0.6896 -0.86877  1.243482  0.649354 -0.81286
X402  0.92355  1.1198 -0.76459  0.109655 -0.992240  1.62616
X403  0.89248  0.9310 -1.66558  2.528295  1.424586  0.25629
X404  0.32943 -0.2240 -0.55626  1.721109  0.122763 -0.47734
X405  1.02031  1.3121 -1.71894  3.493436  2.069116  1.41126
X406  0.70101  0.6688  0.56551  2.039836 -0.973613  0.28254
X407  1.44957  1.6220 -2.12214  5.241437  2.904215  2.43758
X408 -0.18752 -1.0980 -1.30398  1.258141 -0.348826 -0.33215
X409  0.96690  1.2200 -0.99872  2.404212  1.714016  0.73356
X410  0.90948  0.9971 -0.90883  2.009675  0.373138  2.36008
X411  0.16166 -0.4669 -0.04443 -0.314099  2.281392 -0.19232
X412  0.29433 -0.8103  0.14691 -0.151508  0.241708  0.48005
X413  1.04525  1.1665  1.44384  0.827315  0.547465  1.54111
X414  0.75479  0.2129 -0.53205  0.694341  0.260726  0.36064
X415 -0.04791 -1.2312 -0.67585 -0.314186 -0.075759  1.13727
X416  0.68698  0.2923  0.23947 -0.009725  0.696557 -0.08799
X417  0.63183 -0.2334  0.69922  0.736586  0.138123 -0.53116
X418 -0.40242 -1.8851 -0.69345 -0.347472 -0.814591  0.89195
X419  0.41101 -0.7177 -1.08009 -0.295237  0.497354 -0.30463
X420  0.05860 -1.1417 -1.05504  0.430561  0.183718 -0.25613
X421 -0.09719 -0.9446 -0.82930  0.571524 -0.736884 -0.23731
X422 -0.22525 -1.5858 -0.90832  0.217227 -0.487409  0.34210
X423 -0.18810 -1.0813 -1.49657  1.308965 -1.612823  0.23981
X424  0.02483 -1.2017 -1.02241  0.512844 -0.687635  0.16141
X425  0.08657 -1.1440 -0.93136  0.259465 -0.497768  0.44069
X501  0.45432  3.1009 -3.09102 -4.362047 -3.378264 -4.32658
X502  0.74347  1.4604 -0.09914 -1.574153 -0.408121 -0.34460
X503 -0.05183 -0.1705 -0.88063 -1.559712  1.043809  0.21861
X504  0.77224  1.8307  0.07799 -2.201158  0.439967  0.36553
X505  0.45036 -0.1468 -0.98961 -0.035320 -0.396070  0.23593
X506  0.51377 -0.4111  0.35600 -0.422826  0.369415  0.52219
X507  0.14308 -0.3056 -0.16942 -0.409051 -1.325327 -0.13382
X508  0.81624  1.0028 -0.79740 -0.208576 -0.139975 -0.60257
X509  0.46406  1.1950 -1.21275 -1.018165 -0.230117 -1.19197
X510  0.20513  2.7052 -2.82623 -3.431674 -2.293798 -2.14929
X511  0.58337  3.1972 -4.36492 -4.134339 -2.684365 -4.84289
X512  0.60118  1.8485 -0.71023 -2.644156 -0.617208  0.27876
X513  0.82319  0.7686 -0.03248 -0.403221  0.021095  0.26098
X601  0.41786 -0.5242  0.16021 -1.297318 -1.856202  2.71206
X602  0.30996 -0.8950  0.23695 -0.428498 -0.659197  0.64439
X603  0.61926 -0.1445  0.93051 -0.432468 -2.069540  2.18539
X604  0.26878 -0.5179 -0.04602 -0.456604 -2.731442  2.28151
X605  0.15595 -1.3548  0.17018 -0.824673 -1.326003  1.67226
X606  0.43960 -0.7018  0.09320 -1.095841 -2.938624  2.98291
X607  0.50245 -0.5983 -0.02388 -0.422636 -2.073485  2.91854
X608  0.70364  0.2094  0.44954 -0.975046 -1.244170  2.04804
X609  0.73261 -0.6723  1.06146 -0.570076 -2.605540  5.05148

Model: cca(formula = CommunityDataset ~ lat + Ele + Slope + MAT + MAP + DD0 + DD5 + NFFD + OD +
AM + CL + SA + TT + TCC, data = EnvironmentalDataset)
Df  Chisq      F N.Perm Pr(>F)
lat       1 0.1994 3.7785     99   0.01 **
Ele       1 0.2680 5.0786     99   0.01 **
Slope     1 0.1700 3.2222     99   0.01 **
MAT       1 0.1373 2.6026     99   0.01 **
MAP       1 0.1486 2.8164     99   0.01 **
DD0       1 0.1423 2.6961     99   0.01 **
DD5       1 0.0697 1.3209     99   0.09 .
NFFD      1 0.1279 2.4234     99   0.01 **
OD        1 0.0964 1.8262     99   0.01 **
AM        1 0.0589 1.1157     99   0.25
CL        1 0.0543 1.0285     99   0.46
SA        1 0.0571 1.0820     99   0.40
TT        1 0.1931 3.6591     99   0.01 **
TCC       1 0.0853 1.6164     99   0.02 *
Residual 75 3.9578
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Signif.codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
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Appendix J: List of vegetation locally used in Yukon (sources: Johnson et al., 1995; and Holloway and Alexander, 1990)

SN	**Scientific name**	**Total cover %**	**Proportion ate Cover %**	**Available blocks**	**Local uses**
1	*Salix* spp.	1047.0	9.86	A,B,C,D,E & F	Pain soothe
2	*Picea glauca* (Moench) Voss	866.7	8.17	A,B,C,D,E & F	Timber, medicine
3	*Shepherdia Canadensis* (L.) Nutt.	694.6	6.54	A,B,C,D,E & F	Food, dessert
4	*Populus tremuloides* Michx.	472.6	4.45	A,B,C,D,E & F	Fuel, mosquito repellent
5	*Ledum groenlandicum* Oeder	426.1	4.01	B,C & D	Tea
6	*Alnus incana* L. (Moench)	302.9	2.85	B,E & F	As dye and medicines
7	*Epilobium augustifolium* L.s.l.	249.3	2.35	A,B,D & E	Food, Jam
8	*Vaccinium vitis-idaea* L.	224.5	2.11	B,C & D	Food
9	*Arctostaphylos rubra* (Rehd.&Wils.) Fern.	188.2	1.77	B,C & D	Food flavour
10	*Aquilegia Formosa* Fisch. Ex. DC.	65.6	0.62	A,B,D,E & F	Medicine
11	*Hedysarum mackenzii* (Richards.)	38.4	0.36	A,B,C,D & E	Food, Fodder, Medicine
12	*Potentilla anserine* L.s.l.	33.3	0.31	B & D	Food, medicine
13	*Populus balsamifera* L.	31.2	0.29	A,D & E	Fuel, tea, medicine
14	*Petastites frigidus* (L.) Fries	30.6	0.29	B & D	Used as seasoning
15	*Achillea millefolium* L.s.l.	28.9	0.27	A,D,E&F	Medicine; tobacco
16	*Arnica cordifolia* Hook.	27.9	0.26	A,B,C,D &E	Medicine
17	*Aconitum delphinifolium* DC.	22.1	0.21	E & F	Pest control agent
18	*Rubus arcticus* L. ssp.	10.3	0.10	B & D	Food
19	*Vaccinium oxycoccus*	5.3	0.05	A & B	Food
20	*Juniperus communis* L.s.l.	3.3	0.03	E & F	Medicine
21	*Pyrola asarifolia* Michx.	0.6	0.01	A	Medicine
	Total	**4778.2**	**45.02**		