ENVIRONMENT, CLIMATE AND TREE GROWTH RELATIONSHIPS AT THE WESTERN CANADIAN ARCTIC TREELINE

by

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ABSTRACT

The latitudinal forest-tundra ecotone is an area that is experiencing substantial changes with respect to tree growth and climate change. We examined the response of radial tree growth to climate in adjacent regions of northern Yukon and Northwest Territories, Canada, across environmental and spatial gradients using dendrochronological methods. Principal components analysis was used to derive the primary modes of variation in the tree-ring records, which were subsequently attributed to environmental and climatic features. We found that slope gradient (small spatial scales) and ecoregional classification (larger spatial scales) played substantial roles in determining the response of tree growth to climate. Climate correlations were found for current and previous years to growth, many of which challenge currently held assumptions regarding the dominant climatic determinants of tree growth at high latitudes. These findings indicate that Arctic forest environments are highly complex, and that expected changes in the biosphere will occur at various rates, times and places.

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DEDICATION

This thesis is dedicated to the memory of my father, Dan P. Sweeney, who taught me to love and value the forest, and to seek wisdom and solace amongst the trees.

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1. Introduction

Tremendous ecological change is occurring in the circumpolar North, particularly along the boreal forest's northern boundary, known as the forest-tundra (FT) ecotone. The northern treeline is a diverse region where the vast boreal forest and the treeless tundra converge in a delicate balance that is largely controlled by the prevailing climate. In the extreme environment of the Arctic, slight changes in the climate can significantly disrupt the FT ecotone by altering natural disturbance patterns, melting permafrost, and altering the reproductive and growth capacity of trees at the northernmost extent of the boreal forest. Currently, general observations through remote sensing and ground-based research have indicated that the FT ecotone is already responding to climatic change in the Arctic, including movement and densification of the treeline, expansion of shrubs onto formerly barren tundra, and greater frequency and severity of wildfire and outbreaks of forest insects and disease.

In an effort to provide a better understanding regarding ongoing and potential changes of the FT ecotone, this study addressed the issue of radial tree growth at the forest's edge in northwestern Canada, and how environmental variation can affect the growth response to climate. This is a key issue as it relates to the carbon cycling capacity of the boreal forest, as well as its contribution to warming temperatures via feedback mechanisms. This chapter provides a review of the current state of knowledge regarding the historical and contemporary context of climate change and tree growth in the Arctic, and identifies the climatic and environmental features most likely to have significant impacts on the FT ecotone. The following chapter (2) will explain how landscape variation can affect the observed patterns of tree growth through varying spatial scales. Chapter 3 will then show

how the environmental features identified in Chapter 2 can influence which climate parameters have the most impact on radial tree growth. Finally, the summary chapter (4) will highlight the main findings and implications of this study, and will provide an assessment of the main limitations and potential future work based on this research. As a whole, this thesis is a contribution towards the efforts of the PPS (Present processes, Past changes, and Spatiotemporal dynamics) Arctic Canada component of the International Polar Year (IPY) 2007-2008, which primarily focused on the effects and subsequent ecological and social consequences of climate change on treeline position and structure.

1.1 Climate change in the Arctic

According to the Arctic Climate Impact Assessment (2005), warming temperatures in the Arctic are expected to exert tremendous changes on vegetation, resulting in taller, denser, and more abundant plant coverage. Exotic species may begin to find their way into the Arctic via warming temperatures and increased human activities (Sala *et al.*, 2000). Thawing permafrost will pose significant adverse effects as well, by destabilising soils, increasing the paludification of northern forests, significantly altering soil moisture levels, and releasing carbon dioxide (CO_2) into the atmosphere (Lloyd *et al.*, 2003; Zimov *et al.*, 2006; Vygodskaya *et al.*, 2007). These patterns are substantiated by local knowledge from indigenous peoples in the Arctic, who frequently refer to unpredictable and changing weather patterns, warmer and shorter winters, and shifting wind patterns (Kassi, 1993; McDonald *et al.*, 1997; Krupnik & Jolly, 2002). However, the patterns of ecological change in the Arctic are and will be characterized by a great degree of spatial complexity, which will only increase the challenge of predicting and managing for future changes. A better understanding of the underlying processes behind recent and forthcoming changes, and how these processes operate at different spatial scales, is needed if sufficient measures are to be taken to adapt to and mitigate for future scenarios of circumpolar change.

1.1.1 Temperature

The multiproxy record (tree rings, lake sediment and ice cores) of the last 400 years indicates that 20th century temperatures have been the warmest during this period (Overpeck *et al.*, 1997). Much evidence exists to show the Arctic warmed substantially from 1920 to 1940, and again beginning in the 1970s (Serreze *et al.*, 2000). However, these patterns are marked by regional differences; while these patterns hold true in the western North American Arctic, eastern Canada and Greenland have experienced relatively stable, and occasionally cooling, temperatures in the past century (Hinzman *et al.*, 2005). The greatest degree of warming has generally occurred during the winter and spring months (Chapman & Walsh, 1993; Serreze *et al.*, 2000; Mbogga *et al.*, 2009), and has been most pronounced in Alaska, Siberia, and northwestern Canada (Maxwell, 1997; McBeam *et al.*, 2005). In Inuvik, Northwest Territories (NWT), average annual temperatures have increased approximately 2°C since the 1940s when instrumental measurements first began (Govt. of the NWT, 2008). Satellite data have shown that warming spring temperatures have been attended by an increase in net photosynthetic activity in some northern regions (Mynemi *et al.*, 1997). However, photosynthetic potential is also dependent upon soil moisture and nutrient availability, so warm temperatures alone may not yield increased photosynthesis in many scenarios.

Warming temperatures in the Arctic may also increase the length of the growing season by creating earlier spring snow melt dates and extending the frost free period. Along with temperature, growing season length is a major controlling factor on the stasis of the northern treeline (MacDonald *et al.*, 2008), as well for many other Arctic plants (Callaghan *et al.*, 2004b). In areas with limited nutrient availability, growing season length may also have a strong effect on the ability of Arctic plants to respond to warming temperatures (Walker *et al.*, 2006). Lengthened growing seasons typified by earlier melt dates may also impart shortages of soil moisture towards the end of the growing season, a condition that may carry over into the following year (Kirdyanov *et al.*, 2003; Barnett *et al.*, 2005).

1.1.2 Precipitation

Modeled and observed data have indicated the Arctic has generally experienced higher levels of precipitation in the last century, which will likely continue to rise into the next century (McBeam *et al.*, 2005; Mbogga *et al.*, 2009). This increase has come predominantly in the form of winter snowfall (Maxwell, 1997; Kattsov & Walsh, 2000), due to increased atmospheric vapour capacity resultant of concurrent warming air temperatures (Kattenberg *et al.*, 1996). This increasing precipitation trend is substantiated by concurrent records of increased streamflows (Groisman *et al.*, 2005; Trenberth *et al.*, 2007). However, earlier snowmelt dates and decreased snow cover have been found throughout the northern hemisphere, primarily due to increasing spring temperatures (Stone *et al.*, 2002; Barry *et al.*, 2007). Early snowmelt dates can increase spring soil temperature and affect permafrost dynamics through heightened exposure to solar radiation, which in turn can lengthen the effective growing season for many plants (Mynemi *et al.*, 1997; Hinzman *et al.*, 2005). In high mountain environments, increased springtime soil moisture availability, due to earlier snow melt dates, has been shown to be strongly positively tied to total growing season carbon uptake as well (Schimel *et al.*, 2002). Longer snow-free periods also reduce the annual surface albedo, leading to increased atmospheric heating via feedback mechanisms (Serreze *et al.*, 2000; Chapin *et al.*, 2005; Euskirchen *et al.*, 2007). Furthermore, average snow depths have decreased across Canada and some parts of Europe and western Russia (McBeam *et al.*, 2005), although some opposing examples of increased snow depths and duration have been found in much of northern Eurasia (Kitaev *et al.*, 2005; Kohler *et al.*, 2006) and some areas of Yukon (A.E. Ogden, personal communication, March 1, 2011). Decreased snow depths likely lead to lower soil temperatures that are accompanied by reduced net ecosystem respiration and CO_2 efflux in the winter (though winter efflux would be minimal even with warmer soils) (Ling & Zhang, 2007; Morgner *et al.*, 2010; Sullivan, 2010). The decreasing trends in snow cover area and depth, and earlier melt dates, appear to be counterintuitive to increased precipitation, which has been attributed to warming temperatures. However, warming temperatures are likely to melt the thinner snowpack at the margins of snow covered areas, resulting in decreased snow coverage and earlier melt dates in some places (McBeam *et al.*, 2005). As well, it is possible that more precipitation may periodically fall as a liquid during the winter, which would potentially diminish snowpack depths. Though these patterns remain relatively unclear on a global scale, decreases in snow coverage and depths are predicted for the northern hemisphere, though some areas are likely to experience opposite increases (Trenberth *et al.*, 2007).

1.1.3 Topography

Confounding the patterns and behaviour of both precipitation and temperature and their combined effect on soil moisture is the presence of mountainous topography, which can lead to more localized climate variations that may not follow the general climate trends in the Arctic (Pojar, 1996). At a local scale, soil moisture tends to be greater on the lower portion of mountainside hill slopes simply due to the effects of gravity (Carey & Woo, 2001). On a larger, regional scale in mountainous areas, orographic precipitation results as air rises and cools along windward slopes, causing the air moisture to condense and form clouds and precipitation at higher elevations (Bonan, 2008). Strong temperature inversions (a positive (e.g. reverse) adiabatic lapse rate) in northern Yukon can occur in mountainous areas in calm conditions (Wahl *et al.*, 1987; Bonan, 2008). Mountain ranges also pose as barriers to ocean-derived air masses and storms, creating continental (e.g. more extreme and variable) climates (Wahl *et al.*, 1987). Such is the case in northern Yukon, where the British-Richardson Mountains effectively block much of the Arctic Ocean air masses, which are prevalent within the adjacent Mackenzie delta region of the NWT.

1.1.4 Soil moisture balance

Soil moisture balance is highly dependent on the prevailing local temperature and precipitation patterns, as well as the topography and geology of the landscape. Changes in soil moisture availability can impart significant impacts on tree growth in cold climates (Bunn *et al.*, 2005). For example, decreased soil moisture levels have led to decreased growth and greater mortality of white spruce in interior Alaska (Juday *et al.*, 2005; McGuire *et al.*, 2010). As a result of declining soil moisture availability, drought stress has been implicated as an important factor influencing declining tree growth and increased forest disturbance in northern boreal regions (Zhang *et al.*, 2008; D'Arrigo *et al.*, 2009), although recent evidence from Alaska suggests that heightened evaporative demands may be the primary cause of drought-induced growth limitations (Beck *et al.*, 2011). Regardless of the exact mechanisms, temperature, precipitation, and topography remain the primary sources affecting the growing environment limitations of the northern treeline.

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1.2 Climate change and sub-Arctic forests

1.2.1 Treeline and the forest-tundra ecotone

There are many definitions for the northern treeline, and many ways to delineate it. The so-called treeline (or krummholz-line) is commonly cited on large-scale maps as closely following the 10°C July isotherm, but this does not well characterize tree distributions at regional and local scales (Köppen, 1936; Halliday & Brown, 1943). The forest-line is identified where the forest cover exceeds 50% of the land cover (Black & Bliss, 1978). For the purposes of this study, the area of investigation is defined as the transitional zone between continuous forest cover and open tundra (shrub or tussock), termed the forest-tundra (FT) ecotone (Hare & Ritchie, 1972; Scott *et al.*, 1997). The FT ecotone is typified by sparse individual and aggregated trees, often reflecting the underlying hydrologic, topographic, and reproductive (i.e. seed vs. vegetative layering) conditions (Arno, 1984; Scott *et al.*, 1997). Individual trees within the FT ecotone resemble those in the continuous forest, but only reach about 50% of their height (Scott *et al.*, 1993). At the furthest northern extent, trees assume krummholz stature before giving way to shrubs and open tundra.

Polar-region treelines are highly sensitive to changes in climate (Hinzman *et al.*, 2005), and are expected to exhibit some of the earliest and most pronounced visible indications of a changing climate (Payette *et al.*, 2001; Grace *et al.*, 2002; Juday *et al.*, 2005). Equally, other studies have indicated the position and density of the treeline can also affect global climate patterns (Bonan & Sirois, 1992; Foley, 1994; Crawford, 2008; MacDonald *et al.*, 2008). For instance, greater vegetative density is darker than bare tundra, and thus absorbs more solar radiation, which in turn can lead to warming of the atmosphere (Chapin *et al.*, 2005). Early responses in tree growth and recruitment, and a subsequent northward advance, densification, or species alteration of the treeline, are expected to occur in response to changes in various climate parameters (Rizzo & Wiken, 1992; Suarez *et al.*, 1999; Holtmeier & Broll, 2005), including increased temperatures and atmospheric CO_2, changing precipitation and wind patterns, and soil nitrification (Rizzo & Wiken, 1992; Lenihan & Neilson, 1995; Hartley *et al.*, 1999; Grace *et al.*, 2002; Hinzman *et al.*, 2005; Rees, 2007). In addition to climate, other factors can affect northern treeline dynamics: competition from shrubs that react positively and relatively more rapidly to warmer temperatures (Hobbie & Chapin, 1998); changes in snowpack depths and duration (Holtmeier & Broll, 2005); and changing soil temperatures and moisture levels (Black & Bliss, 1980; Wilmking *et al.*, 2004).

Treeline movement is contingent on the establishment of new seedlings in areas previously not conducive to successful tree recruitment and growth. The prevailing theory of advancing treelines suggests that increasing temperatures will lead to more favourable growing conditions for pioneer seedlings (Hobbie & Chapin, 1998). However, many other factors also contribute to the success rate of new recruits, such as fire severity (Sirois, 1993) and thinner post-fire soil organic layers (Greene *et al.*, 2007) in existing forest stands, and below-ground competition (Hobbie & Chapin, 1998) and growing degree-days thermal sum in both forested and unforested sites (Sirois, 2000; Meunier *et al.*, 2007). Current findings indicate that treeline movement has not occurred uniformly across the northern hemisphere in recent decades, though evidence of a recession of the treeline has not been prevalent (MacDonald *et al.*, 2008; Harsch *et al.*, 2009). Recent treeline advance has been observed in Quebec (Gamache & Payette, 2005; Caccianiga & Payette, 2006), northern Alaska (Suarez *et al.*, 1999), the Kluane Range of Yukon (Danby & Hik, 2007), and the Polar Urals of Siberia

(Devi *et al.*, 2008). Conversely, other studies have indicated a relatively stable treeline across Canada, with little to no advancement in recent decades (Szeicz & MacDonald, 1995b; Masek, 2001). However, the modern extent of the Arctic treeline has remained relatively stable during both warm and cold periods of the late Holocene (2000-3000 years BP) (Lavoie & Payette, 1996; Crawford, 2008).

Another component of treeline change is the densification of the FT ecotone by increased tree and shrub recruitment (Chapin *et al.*, 1995; Tape *et al.*, 2006). Shrubs have been particularly responsive to warming temperatures throughout the circumpolar region, evidenced by increased physical size, density, and expansion onto tundra (Sturm *et al.*, 2001; Tape *et al.*, 2006; Walker *et al.*, 2006; Olthof & Pouliot, 2010). Soil thaw depth is a primary control of arctic willow growth, and increasing thaw depths will likely yield more fervent willow growth in high latitude areas (Pajunen, 2009).

Additionally, forest disturbance agents, namely fire and insects and disease, have always been present in the boreal forest, and are natural components of normal forest ecosystem processes. However, climate change may predispose the boreal forest to insect outbreaks of greater scale, intensity, and frequency, due to a low diversity of host tree species and insufficient cold temperatures to control insect populations (Juday *et al.*, 2005). Instances of severe outbreaks spruce budworm and spruce bark beetle have been recently documented in Alaska (Werner, 1996; Juday *et al.*, 2005), while Yukon is experiencing the worst spruce bark beetle outbreak in Canada's history (Yukon Department of Energy, Mines, and Resources, 2009). For these cases, warming temperatures are cited as the primary cause. Severe cases of insect outbreaks reduce the carbon uptake capacity of the forest in the short term, and may eventually cause shifts in tree species compositions and distributions, as new species better adapted to warmer temperatures and heightened insect pressures migrate to the affected areas. Wildfire is also innately connected to climate change, as continuing drought will create conditions in the forest that highly are conducive to large, severe, and frequent forest fires (Rupp *et al.*, 2000). Fire intensity and frequency are highly important factors that control the range and reproductive success of black spruce at the northern treeline (Greene *et al.*, 2007; Kasischke *et al.*, 2007; Lloyd *et al.*, 2007), as well as the successional trajectory of northern spruce forests (Johnstone & Chapin, 2006).

The implications of changing patterns of tree growth in the FT ecotone will include a shifting of the timing, location, and severity of disturbance regimes; alteration of the carbon cycling capacity of the boreal forest; and a change in surface albedo and roughness, which in turn could potentially further increase a warming trend (Bonan & Sirois, 1992; Foley, 1994; Callaghan *et al.*, 2005; Chapin *et al.*, 2005; Juday *et al.*, 2005). This is in addition to many more indirect consequences, including declines in wildlife populations and altered migration routes (Post & Forchhammer, 2008), changing traditional culture and livelihoods of indigenous peoples (Ford & Smit, 2004), and loss of biodiversity. Therefore, it is crucial to understand the potential reactions of the arctic treeline to climatic regime changes (Szeicz & MacDonald, 1995b).

1.2.2 White spruce & black spruce

The most common tree species in the Canadian FT ecotone are white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) BSP), which were the subjects of this study. Tamarack (*Larix laricina* (Du Roi) K. Koch) is the only other gymnosperm present, and occurs sporadically throughout the NWT. Other prevalent species are paper birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*). White spruce occupies well-drained upland slopes and floodplains, where the permafrost is deep or non-existent (Yarie, 1983). Mature stands are associated with well-developed moss layers, which regulate rooting zone temperatures and simultaneously compete for nutrients (Nienstaedt & Zasada, 1990). In Alaska, trees growing along floodplains do not correlate well with the climate record, and thus are not suitable sites for climate-growth studies (Juday *et al.*, 2003). White spruce is the near-exclusive species in the Yukon FT ecotone, but occurs only intermittently in the NWT, as suitable sites become more infrequent in the severe climates of northern latitudes (Nienstaedt & Zasada, 1990). Black spruce typically occupies sites with poorly-drained, wet, and cold soils, and occasionally on north aspects (Johnson *et al.*, 1995). It is often present in pure dense stands on organic soils (occasionally with tamarack), and assumes stunted postures with thin crowns (Viereck & Johnston, 1990). Reproduction is either by asexual vegetative layering, or by stand-replacing wildfire which produces the heat necessary to open the serotinous cones (Black & Bliss, 1980; Viereck & Johnston, 1990). It is the most common tree in the NWT FT ecotone. In northern Yukon, it is the primary species within the continuous forest, before giving way entirely to white spruce at the onset of the FT ecotone and our study area.

1.2.3 Climate-growth relationships of spruce

1.2.3.1 Temperature

Though summer temperature is regarded as the most influential climate component that positively affects spruce growth at the northern treeline (Bonan & Sirois, 1992; Vaganov *et al.*, 1999), there is no single relationship that defines climate and tree growth (Crawford, 2008). Rather, these relationships vary accordingly to changing biophysical, genetic and climatic conditions. For example, in central Canada, black spruce at the northern and southern treelines were found to have pronounced negative correlations with summer temperatures (Brooks *et al.*, 1998), while sites at Ft. Wainwright, Alaska responded positively to winter temperatures (Juday *et al.*, 2005). Conversely, black spruce at the northern treeline in Alaska exhibited positive responses to summer temperatures, while co-occurring white spruce showed an inverse relationship (Lloyd *et al.*, 2005). These relationships are all derived from the strongest significant correlations between climate and tree ring parameters; it is possible other climate variables have some varying degrees of effect as well. Though patterns of climate-tree growth relationships vary, drought stress has been most frequently cited as a primary limitation to growth in the northern boreal forest (Jacoby & D'Arrigo, 1997; Barber *et al.*, 2000; Lloyd & Fastie, 2002; ACIA, 2005).

There is mounting evidence that some trees at the northern treeline are experiencing declining positive correlations with growing-season temperatures. Wilmking *et al.* (2004) found that approximately 40% of a large sample (n >1500) of white spruce in the Alaska and Brooks ranges of Alaska responded negatively to summer temperatures (hereafter negative responders), while less than 40% of the sample population still responded positively (hereafter positive responders) in the latter half of the 20th century. In the Mackenzie River delta, Pisaric *et al.* (2007) found that only 25% of their sample population of black spruce (n = 654) showed a positive correlation with summer temperatures, with the remaining portion beginning to lose its sensitivity in the 1930s. Similar findings have been reported for white spruce in southwest Alaska (Driscoll *et al.*, 2005), north-central Canada (D'Arrigo *et al.*, 2009), and for larch in the Taymir region of northern Siberia (Jacoby *et al.*, 2000). It appears that the trees with declining positive summer temperature associations are exceeding certain temperature thresholds beyond which they begin to alter the nature of their climatic growth response (Wilmking *et al.*, 2005). Specific threshold values are few, but estimates between 11° and 12°C (mean summer temperature) have been suggested for central Yukon and Alaska (D'Arrigo *et al.*, 2004; Wilmking *et al.*, 2004).

This trend of divergent growth responses to summer temperature has come to be known as the 'divergence problem' (Briffa *et al.*, 1998; D'Arrigo *et al.*, 2008), and has developed into a significant area of interest in northern dendroclimatic studies (Lloyd & Bunn, 2007; Wilson *et al.*, 2007; Esper & Frank, 2009; Loehle, 2009). The direct cause has largely been attributed to increasing drought stress (Barber *et al.*, 2000; Davi *et al.*, 2003; Wilmking *et al.*, 2004; Driscoll *et al.*, 2005; Pisaric *et al.*, 2007), though other local or indirect factors, such as increased plant competition (Hogg & Hurdle, 1995), insect herbivory (Fleming & Volney, 1995), or increased UV-B levels (Callaghan *et al.*, 2004a) could potentially play supporting roles. It remains unknown why particular trees respond positively or negatively to warming temperatures, and a general explanation is not likely to be construed.

1.2.3.2 Precipitation

There is a substantial lack of reliability and confidence in measured precipitation data in high latitude regions due to instrumental measurement errors and an inability to capture and record localized precipitation events. Significant correlations between precipitation and tree-ring growth are not commonly found at high latitudes, as temperature generally emerges as the dominant climatic factor. Where significant positive precipitation effects are found, summer temperatures are often simultaneously found to exert negative effects. For example, during the latter half of the 20th century in central Alaska, black spruce was found to be positively correlated with August precipitation, accompanied by negative relationships with July and August temperatures (Wilmking & Myers-Smith, 2008). Similarly, white spruce negative responders (to summer temperatures) in the Mackenzie River delta reacted positively to April precipitation (Pisaric *et al.*, 2007). However, the effect of precipitation on growth is ultimately determined by soil characteristics, topography, and rainfall distribution (Kljun *et al.*, 2007).

1.2.4 Environment of the study region in northwest Canada

Northwestern Canada, specifically northern Yukon and the northwestern corner of the Northwest Territories, was chosen as the study region due to its relative lack of treeline research, high degree of natural landscape and climate variability, and relatively easy access via the Dempster Highway. Much of the treeline research in North America has been conducted in Alaska and eastern Canada, and so our study area will also serve to bridge these distant regions and provide a more complete coverage of the North American FT ecotone. Only one limited tree growth/climate study has been conducted in this region of Yukon (Szeicz & Macdonald, 1994), and it primarily focused on reconstructing historical temperature records, without the knowledge of the now-identified ‘divergence problem’. Similarly, only a small amount of treeline research have been done in the adjacent NWT region (e.g. Black & Bliss, 1980; Szeicz & MacDonald, 1996; Pisaric *et al.*, 2007). This study attempted to build upon these past investigations and provide a more integrated and comprehensive assessment for this region of Canada.

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Few long-term climate records exist in this region as well, similar to most high-latitude regions. As such, regional climate trends are generally based on large-scale climate oscillations and a few intermittent climate monitoring stations, in addition to empirical evidence obtained from the landscape. However, this evidence exists on a large scale throughout the circumpolar region, and it has been firmly established that the Arctic is undergoing rapid climatic and environmental change, and is widely predicted to continue experiencing changes with increasing complexity, frequency and scale (ACIA, 2005; IPCC, 2007; Harsch *et al.*, 2009).

1.3 Research objectives

Climate change is continually presenting new challenges for people and landscapes in the Arctic. The Arctic is typified by a complex and varied assortment of environments that will exhibit varied responses to climate change. This is also true within the FT ecotone and along the circumpolar treeline, where variable plant and tree species, topography, permafrost dynamics and climates will create multiple scenarios of potential changes. A migration or densification of the treeline will play a large role in surface albedo feedbacks to the atmosphere, as well as changing the patterns of snow accumulation, soil temperatures and permafrost activity. Carbon cycling will also be a critical component of these changes, as the boreal forest represents one of the earth's great carbon sinks, yet stands to become a source as the landscape reacts to warming temperatures. Livelihoods of those dependent on the northern boreal forest will be affected as well, as plant and wildlife resources become more or less abundant as vegetation shifts. In response to these serious implications of a rapidly changing Arctic treeline, much research has been initiated in recent years to address the potential effects and impacts in response to climate change. Though many important and useful findings have been realized, there remain substantial gaps in our current knowledge and understanding of the dynamics of a changing northern treeline. This study aims to address some of these gaps, in an area that has yet to receive much attention on the global Arctic research front.

The primary objective of this study was to determine the varying effects of climate on tree growth at the northern latitudinal treeline, and the role that environmental variation has in shaping the climate/tree growth interrelationship. A secondary objective was to identify environmental conditions that may be contributing to disparate growth trends inherent to the 'divergence problem'.

Specific questions addressed by this study were:

1) How do climate-tree growth relationships change across an environmental gradient at the northwestern Canadian treeline? We hypothesized that tree growth would react to climate differently between and within the two study areas. For this question we assumed that the adjacent Yukon and NWT study areas were distinct environments that experience different climates, and would thus represent a viable environmental gradient. Also, we had to assume that sampling along the Dempster Highway would allow us to identify a reasonable variety of sites that would reliably represent the range of conditions throughout the study area.

2) What environmental characteristics affect the response of tree growth to climate? For this question, we tested the hypothesis that tree growth would be dependent on particular landscape characteristics unique to each study area, and relative to the spatial scale at which

the responses were observed. We assumed that by standardizing some of the site selection criteria (e.g. aspect, topography, slope position, tree species), other important environmental variables would become evident in our analysis. This required an effort to record as much pertinent environmental data as possible, given the constraints of time, available equipment and expertise, and scope of the study.

3) Which climatic variables are most influential on Arctic tree growth? We tested the hypothesis that summer temperature would not be the primary controlling climate factor over tree growth at all sites and spatial scales. For this question we assumed that climate variables could be seasonally defined to provide a more general sense of the conditions in this area. Also, we assumed that modelled data for this region would accurately reflect the general trends and variability of the prevailing climate, and would serve as a better (i.e. longer, complete, and locally representative) record than the available climate station data.

4) Does landscape variation appear to be a contributing factor to the 'divergence problem'? We hypothesized that climatic factors attributed to disparate tree growth in previous studies would be evident in our area based on landscape differences. We assumed that disparate tree growth could be delineated using principal components analysis, rather than physically categorizing individual tree-ring series. While this would have been a more thorough and robust method, this question is not the central point of this thesis, and instead we sought to provide a general assessment and starting point for further, more detailed investigations.

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Chapter 2: The effect of environmental variation on radial growth patterns of spruce at the western Canadian sub-Arctic treeline

Abstract

Tree growth responds to the combined effect of climate and environment. At the latitudinal treeline, it is frequently believed that climate exerts the greatest effect upon variable tree growth. However, emerging evidence suggests that tree growth in the North is much more complicated and variable across the landscape. We investigated the role environmental variation has in determining the annual variation of tree growth in northwestern Canada. Tree cores were sampled from across a range of sites in Yukon and Northwest Territories, and principal components analysis was used to derive the main sources of variation in the tree-ring chronologies. We found that slope gradient exerts a strong effect on tree growth at smaller spatial scales. At a larger scale, ecoregional classification seems to be the main element determining variable growth. These results highlight the importance of considering the spatial scale at which observations are made of tree growth in high latitude regions.

2.1 Introduction

The circumpolar boreal forest represents about 30% of the worlds forested area (ACIA, 2004), encompassing a wide array of environment and climatic types, from the dry, mountainous regions of western North America, to the relatively flat muskeg of Siberia. The northern extent of the boreal forest is of particular interest, as trees there exist at or near their physiological limits within an arctic environment that is currently experiencing rapid changes in climate (Hinzman *et al.*, 2005; Ballantyne *et al.*, 2010). In response to arctic climate change, it is expected that climatically sensitive northern treelines will exhibit some of the earliest and most pronounced indications of environmental change (Payette *et al.*, 2001). In order to observe emerging and ongoing changes within the circumpolar treeline, this study addresses the western Canadian arctic treeline in northern Yukon and Northwest Territories, in two adjacent but environmentally distinct regions. Specifically, the study regions encompass the transitional zone between continuous forest cover and open tundra (shrub or tussock), termed the forest-tundra (FT) ecotone (Hare & Ritchie, 1972; Scott *et al.*, 1997).

The FT ecotone is typified by sparsely spaced individual and aggregated trees, the distributions of which often reflect the underlying hydrologic, topographic, and reproductive (i.e. seed vs. vegetative layering) processes (Arno, 1984; Scott *et al.*, 1997). Trees within the FT ecotone resemble those in the adjacent continuous forest, but are only about half as tall (Scott *et al.*, 1993).Trees assume krummholz stature at the furthest northern extent of the forest's range before giving way to shrubs and open tundra.

Tree growth is a response of highly complex, integrated systems. It is a consequence of climate acting upon a specific environment supporting particular species and compositions.

In many cases in the Arctic, the physical environment may be a primary determinant of plant growth and variation (Chapin *et al.*, 1992). The effects of climate and environment are evident in the tree-ring patterns of individual trees, and these patterns have long been used to observe and study historic climate fluctuations. The dominant prevailing climatic conditions (i.e. temperature and available moisture) of each calendar year of growth, combined with the effects of microclimate resulting from environment and other biological functions, produce a chronological record of the integrated effect of the growing environment over the lifespan of each individual tree. From these records, it is presumed that we can reconstruct past climate fluctuations accurately beyond the scope of the climate station records. We can also infer particular monthly or seasonal climate factors that may be most influential on annual tree growth, an important step when using tree rings as climate proxies to model tree growth responses to future climate change.

The objective of this study was to examine tree-growth patterns across a range of sites within and between two unique environments at the western Canadian arctic treeline, in order to distinguish important environmental traits that influence tree growth at high-latitude sites. Once indentified, these traits may indicate how landscape variation can potentially create notable differences in growth limitations (and possibly adaptive traits) across small distances.

Results from climate and tree-ring studies in circumpolar regions are often extrapolated from small, widely spaced study sites to much larger geographical areas or regions, in an attempt to make broad observations about historic and potential climate conditions in an immense region (e.g. Briffa *et al.*, 2003; Lloyd & Bunn, 2007). Such a low-density sampling approach (while logistically understandable) inhibits our ability to address site-specific localized environmental conditions. Consequently, certain environmental characteristics, such as local topographic variation, soil properties, plant inter- and intra-specific competition, or genetic variability, must be generalized and, as such, are not fully considered in broadly scoped study designs and sampling procedures. In turn, a sampling approach that filters out fine-scale environmental components by necessity will potentially mask the effects of certain environmental components that could play a significant role in determining the nature of relationships between climate and tree growth in high-latitude circumpolar regions.

Furthermore, few representative sites exist in some large regions, such as Siberia and west and central northern Canada (with the exception of the Mackenzie River delta), due in large part to the general inaccessibility and high costs of conducting research in some regions of the far North. As a result, northern research areas with the easiest access to sites and facilities, such as Alaska, eastern Canada and Fennoscandia, are often favoured for northern dendroclimatic research sites. Consequently, this has led to a general disproportionate representation of these areas and subsequent biased model results based on a limited range of sites. Large unrepresented areas are also likely to harbour some of the most extreme terrestrial environments in the circumpolar north, traits that may inhibit easy access and use by researchers. This potential scenario of climatic and environmental change, combined with a general lack of ground-based research in these regions, leads to uncertain assumptions about the response of arctic tree growth to climate change, and how this response will factor into the carbon balance of the boreal forest, climate feedback mechanisms, and overall biodiversity of arctic regions (Bonan & Sirois, 1992; ACIA, 2004; Chapin *et al.*, 2005). Without a clearer understanding of these patterns the range of variability of the response and underlying mechanisms of projected changes at the Arctic treeline will remain questionable

(Vygodskaya *et al.*, 2007). Therefore, in order to improve projections of future conditions, both large- and small-scale measures of change should be integrated and assessed simultaneously.

This study addressed a significant knowledge gap in northern dendroclimatic studies by assessing the effect of environmental variation on tree growth patterns. Variable tree growth was examined in two adjacent but distinct environments in order to identify important landscape elements that may provide more thorough understanding of the effect of climate change on tree growth. Additionally, few studies of variable tree growth have been conducted in this region of northwestern Canada, and as such this study will serve to fill a gap in the coverage of circumpolar dendroclimatic studies. The primary question addressed in this study is what degree of the variation in tree growth responses to climate can be attributed to landscape variation in the Arctic? Building upon this, we ask what specific environmental features can help to define the response of tree growth to climate? And do these effects differ between tree species, or do they occur independently of species? We hypothesize that environmental variation will significantly affect the way tree growth responds to climate within the forest-tundra ecotone in northwestern Canada.

2.2 Methods and materials

2.2.1 Field sites

We selected 33 sites along the northern Dempster Highway, 14 sites in Yukon and 19 sites in the Northwest Territories (NWT). Sites were selected in the field, focusing on open-grown stands on southerly slope aspects, while avoiding concave topography that would likely provide more favourable moisture conditions and limit the climate sensitivity of trees growing in these areas. We chose sites that appeared to be the most moisture-limited in order to obtain the most complete, climatically sensitive tree ring records (Fritts, 1976), as strong limitations to growth to due to temperature are prevalent across the entire latitudinal treeline. Moisture-sensitive sites were located on predominantly dry upland slopes, generally with rocky soils, that should experience rapid soil moisture movement and runoff, as well as having limited moisture retention abilities.

2.2.1.1 Field site locations

The Yukon sites spanned the region from the Arctic Circle north to the northern extent of tree growth, just south of Wright Pass (67° 2'56.81" N, 136°12'24.73" W) in the Richardson Mountains, and were distributed along a north-south gradient, following the Dempster Highway along the western edge of the mountains (Figures 2.1, 2.2). Continuing along the Dempster corridor into the NWT, sites were distributed along an east-west gradient, from the eastern foothills of the Richardson Mountains and across the Mackenzie delta and Arctic Red River plain nearly to the town of Inuvik (Figures 2.1, 2.2). Site elevations ranged from 491 m to 758 m in Yukon, with altitudinal treeline generally observed around 700 m, comprised entirely of white spruce. Conversely, site elevations in the NWT ranged from 31 m in the delta to 400 m in the Richardson foothills, where a composition of tamarack, white and black spruce existed at the altitudinal treeline near 400 m.

2.2.2 Ecoregional classification & descriptions

2.2.2.1 Environment of Yukon

All sites in the Yukon were located in the British-Richardson Mountains ecoregion of the Taiga Cordillera ecozone (Smith *et al.*, 2004), which represents 5% of the total Yukon area, and is characterized by the largest unglaciated mountain range in Canada (Figure 2.3). Soils in this ecozone are formed on mountainside colluvium deposits and on the flat pediment surfaces of the valleys, where much of the soil development is driven by cryoturbation and physical weathering processes. On slopes, shale bedrock is often exposed or at shallow depths, and patterned ground surfaces are common. In the valleys, tussock tundra is the primary feature, with scattered populations of white spruce (*Picea glauca*) and shrubs. Near-surface permafrost is continuous in nearly all areas, the active layer depth usually near 0.5m. Vegetation in this ecozone is predominantly classified as shrub tundra, with trees generally limited to riparian zones and non-north facing slopes (Yukon Ecoregions Working Group, 2004). Climatic conditions in this region are modified by mountain topography, which contribute to orographic effects on precipitation and often channels strong winds through the valleys (Wahl *et al.*, 1987). The following estimated climate data are derived from the ClimateWNA v.4.52 model for the period 1901-2006, as no suitable representative climate station exists in this region (Wang *et al.*, 2006). Mean annual temperature for this region is about -6.4°C. January mean temperature is -24.7°C with extreme minimum temperatures approaching -40°C, whereas July mean temperatures are around 12.9°C, with extreme maximum temperatures reaching the lower 20s°C (Figure 2.4). Winter temperatures are milder at higher elevations due to inversions (Wahl *et al.*, 1987). The region receives an average annual precipitation of 437 mm, with the largest accumulations in the summer months, and falling as snow from September onward (Figure 2.5).

2.2.2.2 Environment of NWT

In the NWT, most sites were located within the Mackenzie Delta and Arctic Red Plain High Subarctic ecoregions (Level IV), which together comprise the northernmost portion of the

Taiga Plains High Subarctic ecoregion (Level III) (Ecosystem Classification Group, 2007). Three additional sites were located within the Richardson Plateau High Subarctic ecoregion (Level IV), a component of the larger Tundra Cordillera High Subarctic ecoregion (Level III) (Figure 2.3) (Ecosystem Classification Group, 2007).

Encompassing the largest river delta in Canada, the Mackenzie Delta ecoregion is characterized by level alluvial deposits surrounded by thousands of small lakes and stream channels. This region was glaciated by the Laurentide ice sheet, which led to varied soil parent materials. Soil formation is strongly affected by permafrost and the fluvial environment, exhibiting little to no horizon development and tussock formation. Vegetation is typified by dense forests of white spruce and black spruce (*Picea mariana*), with tamarack (*Larix lyallii*) and balsam poplar (*Populus balsamifera*) interspersed in some areas. Shrubs are prevalent, particularly green alder (*Alnus viridis*) and dwarf birch (*Betula glandulosa*). In higher elevations where permafrost is closer to the soil surface, forests become more open and stunted, and shrubs assume low-growing statures. The Arctic Red Plain ecoregion, also subject to Laurentide glaciations, exhibits soils similar to the Mackenzie ecoregion. Black spruce is the dominant tree species, and typically grows very slowly in open stands (Viereck & Johnston, 1990). Low shrubs such as crowberry (*Empetrum nigrum*) and cloudberry (*Rubus chamaemorus*) are common understory components, along with lichens and peat moss. Frequent fires have created large areas of pioneer dwarf birch (Ecological Classification Group, 2007).

Climate in the Taiga Plains ecoregion is largely dictated by unobstructed weather patterns originating off the adjacent Beaufort Sea. The following climate data are derived from the

ClimateWNA v.4.52 model for the period 1901-2006 (Wang *et al.*, 2006), which is approximately double the length of the permanent climate station record in Fort McPherson. Mean annual temperature in for the Fort McPherson area (representing this ecoregion) is -8.2°C. Mean January temperature is -29.4°C with extreme minimums approaching -42°C, whereas the mean July temperature is 14.4°C with extreme maximums exceeding 23°C (Figure 2.4). Mean annual precipitation is about 284mm, with the largest amounts falling in late summer to autumn (Figure 2.5).

Adjacent to the Taiga Plains ecoregion, the Tundra Cordillera/Richardson Plateau ecoregion is a transition zone from the Mackenzie Delta towards the Yukon-NWT border in the Richardson Mountains. The lower elevations of this ecoregion, where our sites were located, were also subject to glaciations, reflected in the prominence of till deposits (Duk-Rodkin *et al.*, 2004). Permafrost is nearly continuous, excepting some valley slopes and riparian areas, and consequently Cryosols are the dominant soil type. Black spruce occurs in open, wet woodlands, with shrubs – predominantly northern Labrador tea (*Ledum palustre*) and crowberry – and lichens comprising the understory. White spruce is found along narrow valley slopes and river terraces, along with abundant green alder, willow (*Salix* spp.), and dwarf birch in the understory. The climate in this ecoregion is influenced strongly by weather coming in from the Arctic Ocean, which is subsequently affected by the mountains. Mean annual temperature for this ecoregion is -7.5°C. Mean January temperature is -28.1°C, and mean July temperature is 13.6°C (Figure 2.4). Mean annual precipitation is estimated to be 378 mm, most of which falls in the summer and autumn (Figure 2.5). As there is no permanent climate station in this region, those data are derived from the ClimateWNA v.4.52 model, for the period 1901-2006 (Wang *et al.*, 2006).

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Dry, forested areas in this ecoregion proved much more difficult to find, as slope gradients were generally lower and soils appeared to be moister than those found in the adjoining regions in the NWT and Yukon. Thus, we identified sites that exhibited drier conditions relative to the rest of the ecoregion, though the site conditions were less dry than desired. However, we made these concessions with respect to the great variability of the landscape in this area, realizing that finding perfectly suited conditions is an unreasonable assumption.

2.2.3 Sampling strategy

Tree cores were collected from 15-18 healthy, dominant trees at each site. Inter-tree competition was not a significant factor, as nearly all the stands were open grown with relatively low stem densities (Figure 2.6, 2.7). We collected tree increment cores oriented parallel to the slope contour to minimize the influence of slope stress on ring formation (i.e. compression and tension wood). Two samples from each tree were obtained from full-diameter cores, allowing us to select the best quality core samples, as well as providing a means to visually check for missing or false rings.

White spruce was exclusively sampled in the Yukon, as it was essentially the only spruce species present within the sample site conditions. Both white and black spruce were present in the NWT on similar sites, occasionally intermixed but more often occurring separately. Tamarack and balsam poplar were also present in some stands (Figure 2.7). White spruce was favoured when possible to maximize cross-site comparisons, but in some areas black spruce was the only species present.

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Three unique hill features (hereafter termed Hill sites), approximately 15-20 m in relief of the flat surroundings, were sampled within the Arctic Red River plain between the towns of Fort McPherson and Tsiigehtchic. These small mounds featured prominent, discrete white spruce stands on the south faces, with black spruce covering every other slope as well as the surrounding flatlands (Figure 2.7). While these features are infrequent on the landscape of the plain and may not wholly represent the conditions of the entire region, finding habitat that supported white spruce in the NWT was needed in order to facilitate cross-comparisons with same species and similar habitat types found in the Yukon study area. The objective was not to extrapolate findings to entire regions, but rather to observe changes in growth patterns across a defined gradient, and sampling from the Hill sites provided the best means of doing so.

An additional chronology from the Dolomite Uplands near Inuvik, NWT was previously constructed in the mid 1990s (Szeicz & MacDonald, 1996). This data set was obtained from the International Treering Database (http://www.ncdc.noaa.gov/paleo/treering.html), and was subsequently incorporated into our analyses to increase our sample range.

Basic site and understory information was collected at each site, including slope aspect and gradient, elevation, coordinate location, slope position, and basic soil substrate types. Stand photos were taken in the four cardinal directions from a single point within each site. The relative abundance of basic vegetation types (high and low shrubs, grass, forbs, lichen/moss, litter, course and fine woody debris, litter, and bare surfaces) (Ogden, 2008) were estimated visually from a random point within each site (Appendix C).

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2.2.4 Chronology development

Tree cores were prepared according to standard dendrochronological methods (Stokes & Smiley, 1968). Samples were sanded with progressively finer grits (80-400) of sandpaper, and were visually cross-dated to assign calendar years to each ring (Cook *et al.*, 1990). Ring widths were measured using a Velmex™ measurement system, accurate to 0.001mm. Dating accuracy was checked using the standard program COFECHA (Holmes, 1983), and measurement errors were corrected where identified. Tree cores that did not crossdate well with each master chronology after visual and statistical inspection were subsequently omitted.

The R package dplR (Bunn, 2008) was used for chronology detrending. Detrending is an important step that better isolates the climate signal in the tree-ring series, by removing biological and other non-climatic growing trends, such as inter- and intra-specific competitive stresses or periodic insect or disease outbreaks. Early radial growth is often marked by greater relative ring widths in the first decade or so of a tree's existence, that gradually become smaller as limited resources are available to add to the yearly increasing surface area of the bole. Often, this leads to general J-shaped negative exponential growth patterns. However, typical negative exponential growth trends were not commonly observed in our tree ring samples. Therefore, rather than using a more traditional negative exponential or linear detrending method, each tree-ring series was detrended using a cubic smoothing spline to remove the non-climatic growth trend in each series (Cook & Peters, 1981). We used a cubic smoothing spline with a wavelength at 67% of the series length and a frequency response of 50% for all series (Cook *et al.*, 1990). A more adaptable percentage-based spline rigidity value – as opposed to a fixed number – was chosen due to the disparate length of all the series, as it could adapt similarly to short and long series. It is important to note that no detrending method can remove all biological growth trends, but a consistent method that can apply to all tree-ring series is central to creating robust chronologies. Once all series were detrended, a mean value chronology was calculated for each site by averaging each year's ring-width index value. Autocorrelation was removed from each series before averaging, which removed the cumulative growth effects from the previous year's growth within each tree, which is a standard accepted treatment to tree-ring chronologies. This is done in dplR by fitting autoregressive models to the data, and selected using Akaike's information criteria (Venables & Ripley, 2002; Bunn, 2008). The residuals from the model are then used to construct a prewhitened chronology using Tukey's biweight robust means. This ensures a relatively pure climatic signal in the chronology, with the biological and cumulative effects on growth limited in the final chronology.

2.2.5 Data analysis

2.2.5.1 Chronology analysis

Basic statistics were computed for each site chronology with COFECHA, including series length, mean sensitivity (a relative measure of ring-width variability), and intra-series correlations (a measure of the strength of the overall population signal). All chronologies (sites) were then correlated with each other in order to observe trends amongst and between regions and site types.

2.2.5.2 Multivariate analysis

Principal components analysis (PCA) is a statistical method that reorganizes a dataset so that independent groups of variables with similar patterns are identified, which can provide a basis to explore the underlying mechanisms that bring about the specific groupings. PCA was performed on the entire set of chronologies to determine the main modes of growth variation over a common time period (1929-2007) (Peters *et al.*, 1981; Driscoll *et al.*, 2005). The R package 'psych' was used to perform this analysis, including varimax rotation (Revelle, 2011). Each region was then subsequently treated separately to obtain a closer examination of each region's sources of variability. Varimax-rotated principal components (PCs) that supported the most significant modes of variation were retained for analysis (Griesbauer & Green, 2010). The PCs were Varimax-rotated to better facilitate the interpretation of the loadings, and to allow easier comparison to various environmental and climate variables (Tabachnick & Fidell, 1989). The number of retained components was determined using the scree test; the number of retained components was found at the inflection point of the scree plot of eigenvalues (Tabachnick & Fidell, 1989).

2.3 Results

2.3.1 Chronologies

In Yukon, 11 chronologies (all white spruce) were retained for analysis, ranging from 104 to 233 years in length. Intra-site correlations ranged from .523 to .627 with a mean of .584, indicating a strong population climate signal in all stands. Mean sensitivity ranged from .192 to .277 with a mean of .225 (Table 2.1). Mean sensitivity of the Yukon sites was significantly positively correlated with elevation ($r = .692$, $p = 0.018$), however intra-site correlations did not significantly correlate with any environmental factor (Table 2.2). Approximately 5% of the sample cores that did not adequately visually crossdate were omitted from the final chronologies.

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In the NWT, 17 chronologies – 9 of which were black spruce stands – were constructed, ranging from 80 to 258 years in length. Three north slope black spruce stands at the Hill sites were combined into one chronology, due to an insufficient number of quality samples in each stand. Intra-site correlations were similar to those in Yukon, ranging from .466 to .663, with a mean of .566, again indicating a relatively strong cohesive climate signal. Mean sensitivity ranged from .178 to .237 with a mean of .214 (Table 2.1). Mean sensitivity in the NWT chronologies showed only a weak, non-significant positive correlation ($r = .257$, $p = 0.32$) with elevation, but was significantly negatively correlated with longitude ($r = -.531$, $p = 0.034$). Intra-site correlation values did not significantly correlate with any other variable (Table 2.2). Approximately 12% of the sample cores were omitted from the final chronologies, as they did not adequately crossdate with the master chronology. However, most of these omitted samples came from the three aforementioned north slope Hill sites, where extremely poor growing conditions resulted in low quality tree-ring samples. Only 4% of the total cores were omitted from the rest of the sites, a comparable figure to the percentage of total cores omitted from Yukon.

2.3.2 Multivariate analysis

Principal components analysis (PCA) was conducted on the entire dataset, and the results indicated the primary source of growth variation across the entire study area was regionally divided between Yukon and the Northwest Territories (Table 2.3). Subsequently, separate PCAs were performed for each region, so that traits underlying the variation could be assessed in each region.

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2.3.2.1 Yukon principal components analysis

Principal components analysis performed on the Yukon chronologies extracted two principal components (PCs) that explained about 77% of the total chronology variance. Individually, the two PCs explained 38.9% and 38.5% respectively (Table 2.4). The first PC (YTPC1) was most strongly associated with low slope-gradient sites (between 10% and 33%). The second PC (YTPC2) was most strongly associated with high slope-gradient sites (38% to 84%) (Table 2.5). A lone exception was CaribouL, which had a recorded gradient of 10% but was correlated with the high-gradient group (YTPC2).

2.3.2.2 NWT principal components analysis

The NWT chronologies were represented by three modes of variability which explained nearly 73% of the total variance. The three PCs represented 38.9%, 17.8%, and 16.2% of the total chronology variance, respectively (Table 2.4). Occasionally two loadings were very similar for a site, and selection was then based subjectively on the most logical PC group. However, it is possible that sites with two similar loadings may represent transitional sites, exhibiting some characteristics of more than one PC group.

The first PC (NTPC1) correlated most strongly with sites located within the Mackenzie River delta, including three additional sites (slump sites) on the adjacent plateau (Table 2.6). The second PC (NTPC2) correlated most strongly with sites near the western extent of forest cover, in the foothills of the Richardson Mountains (Table 2.6). These were also the sites with the highest elevations in the NWT, and were comprised entirely of black spruce. The third PC (NTPC3) correlated most strongly with sites near the Peel River, in the Peel River plateau ecozone that serves as a transition zone between the delta and the mountains (Table 2.6).

2.4 Discussion

The overall PCA results indicated that the Yukon and NWT study regions can reasonably be characterized as distinctly different environments, which confirms our *a priori* assumption that the growing conditions were different between the two areas. Nearly all of the Yukon sites were responsible for the highest loadings in the first principal component, with the NWT sites accounting for the remaining components. These components represent distinct sources of variation that can be attributed to various environmental variables; in this case, patterns of tree growth in the Yukon study area were distinct from the patterns observed in the NWT study area. This suggests the presence of a distinct bioclimatic boundary at a small, regional scale; specifically, the narrow Richardson Mountain range that delineates the disparate adjacent regions in Yukon and the NWT. The results of the overall PCA also reflect the sampling constraints in the two regions, dictated by the course of the Dempster Highway. In Yukon, sampling sites were part of a single ecoregion, running parallel along the western flank of the Richardson Mountains across a latitudinal gradient, which subsequently led to more intensive sampling of similar site types. The NWT sites, however, ran across a longitudinal transect and encompassed multiple ecoregions and greater regional environmental diversity along the way, which resulted in a larger scale of observation with fewer sampling sites within each ecoregion. Had each ecoregion been sampled more heavily in the NWT, it is likely that more site-level characteristics would have emerged, similar to the Yukon sites.

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Additionally, the strong positive correlation between mean sensitivity and elevation in the Yukon corroborates others' findings (Fritts, 1976; D'Arrigo *et al.*, 2004) and underscores the effect of specific limiting factors commonly present at elevational treeline sites. Such a strong relationship highlights the effectiveness of sampling at elevational sites to obtain the most sensitive climate signals, even at the latitudinal tree line. Conversely, the elevational trend was not evident in the NWT even with a larger elevational range (> 350 m), likely due to separate elevational clusters in each region. This seems to suggest that elevation may not be as important in determining sensitivity when it is considered in a broader context with a higher number of other environmental factors.

2.4.1 Yukon

In Yukon, growth patterns appeared to separate based on slope angle (Table 2.5). This finding was somewhat unexpected, as slope angle is not commonly referenced as an important driver of tree-growth variation. It is a logical finding, however, as slope angle may be an important contributing factor for water runoff and retention, as well as overall site productivity (i.e. greater surface area per horizontal hectare) (Fritts, 1976; Barnes *et al.*, 1998).

Another factor affected by slope angle, particularly at high-latitude sites, is incident solar radiation (Q), which directly affects soil temperature and snow melt timing on some slope aspects (Pohl *et al.*, 2006). Solar radiation is closely related to temperature variation and moisture regimes, making it one of the most important drivers of ecological processes in nearly all ecosystems, particularly in the northern FT ecotone (Smith, 1996; Liepert, 2002). However, with increasing latitude, the overall value of Q decreases (Chapin *et al.*, 1992).

Simultaneously, the effective heating capacity of the incident solar radiation is reduced through the FT ecotone as the dark, radiation-absorbing forest transitions to a more reflective, snow-covered tundra (Hare & Ritchie, 1972). However, Hare & Ritchie note that mountains can greatly complicate these general patterns by imposing locally specific microclimates and weather (i.e. clouds) conditions. This assertion may be particularly relevant in this region since most of the Yukon sites are located proximate to the Richardson Mountains, as opposed to the NWT where many of the sites are located within the flat delta.

Solar radiation levels at high latitudes are dominated by annual cycles, with near constant irradiance during the summer and zero irradiance during the dark winter. Similarly, irradiance varies widely during the day. For example, at Barrow, Alaska (71°17'26.00" N, 156°47'19.00" W), incoming radiation levels at solar noon were 15 times greater than levels measured at solar midnight during the summer solstice (24 hours of daylight) (Tieszen, 1972). The range of radiation levels is created as the incident angle of incoming solar radiation changes with the sun's elevation in the sky. This suggests that slope angle (and to a lesser degree, slope aspect) would have an effect on total net incident radiation (Kimmins & Wein, 1986). The effect of slope angle has previously been quantified by the "equivalent latitude" concept, where for any given slope on the earth, the latitude of a corresponding horizontal surface that receives the same amount of insolation can be calculated, and thus provide an index of potential insolation (Lee, 1964). However, in at least one study, slope angle was found to have a negligible effect on soil temperature in interior Alaska (Bonan, 1991).

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In turn, solar insolation can have considerable effects upon permafrost, soil temperature and moisture, and runoff dynamics, particularly at high latitudes (Chapin *et al.*, 1992). Higher levels of solar insolation tend to warm soils and deepen active layers (Dingman & Koutz, 1974); deeper active layers were observed on steeper slopes in the study area (data not shown). Steep slopes will also facilitate rapid runoff; coupled with earlier snowmelt (due to increased solar radiation), trees growing on steeper slopes are likely to experience higher levels of drought stress than those growing on lower slope angles or flat surfaces. These factors appear to readily explain the difference of growth patterns between the high- and low-angle slopes observed in this study, where slope angle emerged as an unexpected but important factor in determining tree growth response to environment and climate. The dividing point between the two PC groups (between 33% and 38%) may be arbitrary in a broader context, but it represents an identifiable break point within the context of this study region.

2.4.2 NWT

The PC groupings in the NWT appear to indicate the presence of two distinct ecoregions as well as a transition zone between them (Tables 2.4, 2.6), which contrasts to the relatively homogenous environment in Yukon. The distinct ecoregions in the NWT, in addition to the smaller number of sampling sites in each ecoregion, likely explains why slope angle and related solar radiation were not apparent drivers of growth variation within the larger context of the NWT study area. The largest sampled environment was the Mackenzie delta (NTPC1), a unique area that harbours specific hydrologic, environmental and climatic conditions typical of large river deltas (Burn & Kokelj, 2009; Kanigan *et al.*, 2009; Cassano & Cassano, 2010). Tree growth in the delta region was strongly connected between sites regardless of tree species, underlying permafrost conditions or slope conditions, which suggests that the delta may function as a large climatic "oasis." That is, the growing conditions here may be relatively uniform throughout and less extreme from those in the surrounding areas, as indicated by its unique ecoregion classification (Ecological Classification Group, 2007). Similarly, the foothills group (NTPC2) represents a unique set of growing conditions within the NWT study range, influenced primarily by mountain-affected weather, higher elevation, and less available soil moisture (compared to the relative abundance of soil moisture in the delta). Sites located in the narrow zone between these two regions (NTPC3) represent another set of growing conditions in the area transitioning from the uplands to the delta, which is emphasized by the similar proportion of variance to the other PC groups indicated by the principal components analysis. The differentiation of this transition zone environment underscores the importance of identifying and addressing bioclimatic transition zones, as landscape variation in the Arctic is highly spatially complex within and between distinct regions.

The results from the NWT suggest that multiple climatic envelopes exist in this study area of the NWT, as the sites of each specific PC grouping can be generally be sorted by the general ecoregional classifications established by the Ecosystem Classification Group. Indeed, multiple environments may have been included in some large-scale tree-ring studies in Alaska that included sites with a large degree of spatial separation (Lloyd & Fastie, 2002; Wilmking *et al.*, 2004). It is clear that relationships between tree growth and environmental variation can be uniquely complex at multiple scales, and determining the most suitable scale for observing these relationships remains a significant, yet important challenge. There remains a substantial need for a more detailed understanding of the underlying mechanisms of environmental variation that lead to varied patterns of tree growth.

2.4.3 Conclusion

This study highlighted the importance of identifying key context-specific environmental factors that may impose limits to tree-growth relationships with climate. Arctic ecosystems are fundamentally distinct from the world's other great ecosystems, and thus require specific considerations and assumptions that extend beyond more commonly held principles of basic ecology. Identifying and addressing the key components and linkages of high-latitude bioclimatic systems is essential when considering potential scenarios of ecologic and climatic change.

This study also served to reiterate the importance of considering the context in which an area is studied and sampled. In the Yukon study area, slope gradient exerted a significant influence on determining tree growth variation on south aspects. While this is not a novel notion, slope angle regardless is not often considered in tree-ring studies at high latitudes. However, our findings indicate that it likely plays a stronger role than previously considered in determining climate/growth interactions, specifically within the context of a latitudinal gradient along the Richardson Mountain foothills. This factor may or may not have similar effects in other areas of the sub-arctic treeline, across other climatic or environmental gradients, or even during different periods of history. Similarly, environmental variation plays a significant role in the NWT, albeit reflecting different influential sources due to a much broader range of environmental conditions. Here, groups of sites that were represented by distinct growth patterns (i.e. PCA groupings) distinguished themselves based primarily on two ecoregions and an associated transition zone between them, reflecting more complex geologic, climatic, and physiographic conditions. Though viewed in a larger, more complex context than in the Yukon study area, environmental variation still appeared as a strong influence, and can be readily addressed with a basic preliminary landscape analysis.

These case studies show how varying degrees of environmental variation can play a significant role in coupled climate/tree growth interactions, and thus should be fully considered regardless of the scale or context of future dendroclimatic studies at high latitudes. Based on these initial results, future research should assess the direct effects specific components of environmental variation have on the overall and temporal effects of important climatic components upon tree growth. A broader examination of the role of slope angle throughout Yukon would also be a warranted, to determine its relative effect in a broader scope. Different latitudes, environment types (mountainous, plateau, riparian, etc.), or species compositions may affect the relative influence of slope angle, and as yet this remains relatively unknown.

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Table 2.1 Site descriptions and statistics

Site	Region	Species	Lat.	Long.	Elev. (m)	Slope (%)	Aspect	Chronology Length (years)	Intraseries Correlation	Mean Sensitivity	Site Position
Quarry	YT	W	66 75	136 33	758	46	S	125	0 523	0 277	US
CrestW	YT	W	66 82	136 36	684	17	S	173	0 582	0 216	C US MS LS
HideawayL	YT	W	66 82	136 33	662	33	S	209	0 604	0 23	LS
HideawayU	YT	W	66 82	136 33	689	22	S	162	0 585	0 249	C US
Gut	YT	W	66 65	136 34	670	38	S	183	0 563	0 246	C US MS
CaribouL	YT	W	66 72	136 38	632	10	S	233	0 611	0 205	LS T
CaribouU	YT	W	66 72	136 38	716	10	S	139	0 627	0 222	C US
Shed	YT	W	66 91	-136 36	491	72	N	104	0 596	0 192	C US
Cutbank	YT	W	66 92	136 34	504	84	S	148	0 575	0 218	C US
Bench	YT	W	66 92	136 32	541	43	S	169	0 605	0 206	C US MS
North	YT	W	66 93	136 25	677	21	S	165	0 549	0 211	US MS
Midway	NWT	B	67 22	-135 49	368	3	S	85	0 613	0 219	C US MS LS
PeelN	NWT	B	67 33	135 95	40	23	N	152	0 557	0 218	US MS
PeelG	NWT	W	67 33	-134 95	75	35	S	95	0 661	0 234	C US
PeelM	NWT	B	67 34	134 93	31	33	S	149	0 485	0 232	C US MS
HillA_G	NWT	W	67 39	134 22	78	32	S	156	0 663	0 202	C US MS
HillA_S	NWT	B	67 39	134 22	62	12	S	251	0 522	0 196	LS
Slump1	NWT	W	67 25	135 27	383	25	S	258	0 569	0 219	C US MS
Slump3	NWT	W	67 26	135 25	369	43	S	207	0 563	0 213	C US MS
Slump2	NWT	W	67 25	-135 26	369	21	S	199	0 623	0 212	US MS
HillB_G	NWT	W	67 39	134 22	85	38	S	154	0 661	0 187	C US MS
HillB_S	NWT	B	67 39	134 22	68	11	S	249	0 5	0 22	LS T
HillC_S	NWT	B	67 39	134 20	75	13	S	252	0 466	0 225	LS T
HillC G	NWT	W	67 39	134 20	90	38	S	143	0 622	0 178	C US MS
West	NWT	B	67 21	135 53	374	6	S	81	0 505	0 237	MS
Foothill	NWT	B	67 22	135 49	398	7	S	80	0 547	0 22	US
Dolomite	NWT	W	68 21	133 40	83	27	S	253	0 553	0 205	C US MS
Hill_N	NWT	B	67 39	-134 21	78	20	N	256	0 518	0 214	MS LS

W=white spruce, B=black spruce, S=south aspect, N=north aspect, C=crest, US=upper slope, MS=mid slope, LS=lower slope, T=toe of slope, Intra-series Correlation=relative strength of chronology, Mean Sensitivity=relative variance of chronology

Table 2.2 Site and chronology correlations

	YT				**NT**			
	Elevation	Latitude	Longitude	Intra. Corr.	Elevation	Latitude	Longitude	Intra. Corr
Sensitivity	.692**	-0.492	0.063	-0.599*	.257	-.277	-0.531**	-.446*
Elevation		-.606**	0.033	-.315		-.435*	-0.609**	.079
Latitude				-.034				-.056
Intra. Corr			-0.561*				0.015	

**=correlation significant at $p<0.05$; *=correlation significant at $p<0.1$; Intra. Corr. = Intra-series Correlation

Table 2.3 Principal components analysis results for entire study area

REGION	STAND	RC5	RC6	RC3	RC2	RC1	RC7	RC4
NWT	Midway	0.272	0.072	**0.659**	0.212	0.244	0.297	0.281
NWT	PeelN	0.189	0.293	**0.751**	0.188	0.146	0.027	0.118
NWT	PeelG	0.030	0.294	**0.767**	0.093	0.036	0.185	0.247
NWT	PeelM	0.252	0.360	**0.768**	0.289	0.046	0.030	0.004
NWT	HillA_G	0.253	**0.798**	0.239	0.295	0.228	0.086	0.048
NWT	HillA_S	0.331	0.326	0.239	**0.699**	0.067	0.136	0.148
NWT	Slump1	0.327	**0.491**	0.300	0.322	0.315	0.437	0.107
NWT	Slump3	0.247	**0.514**	0.246	0.347	0.126	0.400	0.303
NWT	Slump2	0.233	0.406	0.283	**0.463**	0.344	0.311	0.276
NWT	HillB_G	0.219	**0.800**	0.300	0.189	0.002	0.154	0.017
NWT	HillB_S	0.198	0.511	0.234	**0.691**	0.079	0.016	-0.083
NWT	HillC_S	0.341	**0.573**	0.326	0.430	0.008	0.064	-0.184
NWT	HillC_G	0.295	**0.780**	0.246	0.224	0.158	0.177	-0.050
NWT	West	0.147	0.041	0.238	0.055	0.038	0.081	**0.854**
NWT	Foothill	0.272	0.161	0.201	0.109	0.074	**0.799**	0.066
NWT	Dolomite	0.374	**0.647**	0.117	-0.017	0.413	-0.033	0.226
NWT	Hill_N	0.182	**0.548**	0.272	0.528	0.217	0.026	0.209
YT	SheepN	0.216	0.104	0.482	0.008	**0.583**	0.242	-0.268
YT	SheepS	0.378	0.272	0.290	**0.525**	0.429	0.228	-0.120
YT	Quarry	**0.814**	0.180	0.169	0.065	-0.038	0.325	0.115
YT	CrestW	**0.801**	0.244	0.268	0.188	0.270	0.124	0.099
YT	HideawayL	**0.601**	0.258	-0.047	0.308	0.519	0.088	0.108
YT	HideawayU	**0.720**	0.221	0.006	0.318	0.266	0.158	0.232
YT	Gut	**0.737**	0.237	0.170	0.334	0.161	-0.052	-0.034
YT	CaribouL	**0.685**	0.230	0.396	0.250	0.270	0.208	-0.093
YT	CaribouU	**0.795**	0.255	0.185	0.183	0.251	0.132	0.099
YT	GlacierCr	**0.611**	0.275	0.008	0.254	0.570	-0.102	-0.033
YT	Shed	**0.696**	0.285	0.409	0.000	0.145	0.198	0.069
YT	Cutbank	**0.465**	0.268	0.335	0.444	0.294	0.211	-0.031
YT	Bench	0.472	0.217	**0.580**	0.291	0.372	0.106	0.038
YT	RockRiver1	**0.464**	0.073	0.162	0.462	0.407	0.175	0.197
YT	RockRiver2	**0.511**	0.171	0.189	0.501	0.419	0.130	0.168
YT	North	0.389	0.177	0.239	0.166	**0.667**	0.053	0.191

	RC5	RC6	RC3	RC2	RC1	RC7	RC4
Loadings	7.071	5.113	4.392	3.787	3.088	1.786	1.536
Proportion of Variance	0.214	0.155	0.133	0.115	0.094	0.054	0.047
Cumulative Variance	0.214	0.369	0.502	0.617	0.711	0.765	0.811

Table 2.4 Summary of regional principal components analysis

	Yukon		NWT			
Component	1	2		1	2	3
Eigenvalues	4.27	4.23		6.62	2.75	3.02
Variance (%)	38.9	38.5		38.9	16.2	17.8
CumulativeVariance (%)	38.9	77.3		38.9	55.1	72.9
Loadings:						
Quarry	.565	**.595**	Midway	.224	**.591**	.607
CrestW	**.736**	.593	PeelN	.350	.227	**.792**
HideawayL	**.889**	.271	PeelG	.234	.367	**.732**
HideawayU	**.851**	.360	PeelM	.462	.170	**.795**
Gut	.562	**.597**	HillA_G	**.870**	.175	.270
CaribouL	.527	**.722**	HillA_S	**.684**	.330	.237
CaribouU	**.690**	.601	Slump1	**.695**	.504	.253
Shed	.237	**.851**	Slump3	**.650**	.583	.157
Cutbank	.375	**.765**	Slump2	**.641**	.571	.221
Bench	.362	**.810**	HillB_G	**.773**	.110	.344
North	**.709**	.343	HillB_S	**.805**	.057	.287
			HillC_S	**.773**	-.023	.398
			HillC_G	**.841**	.116	.299
			West	-.039	**.766**	.191
			Foothill	.292	**.555**	.199
			Dolomite	**.658**	.322	.079
			Hill_N	**.752**	.309	.246

Numbers in **bold** indicate highest loading

Table 2.5 Yukon PCA loadings and site characteristics

SITE	PC1	PC2	SLOPE (%)	ASPECT	ELEVATION
HideawayL	**0.889**	0.271	33	135	662
HideawayU	**0.851**	0.360	22	135	689
CrestW	**0.736**	0.593	17	120	684
North	**0.709**	0.343	21	180	677
CaribouU	**0.690**	0.601	10	84	716
Shed	0.237	**0.851**	72	20	491
Bench	0.363	**0.810**	43	158	541
Cutbank	0.375	**0.765**	84	142	504
CaribouL	0.527	**0.722**	10	84	632
Gut	0.562	**0.597**	38	112	670
Quarry	0.566	**0.595**	46	166	758

Table 2.6 PCA groups and ecological characteristics

Region	ID	Ecological Classifcation (Level III/IV)	Ecological Description
Yukon	YTPC1	Taiga Cordillera Ecozone / British-Richardson Mountains Ecoregion	Sites with slope gradients between 10% and 33%
	YTPC2	See above	Sites with slope gradients between 38% and 84%
NWT	NTPC1	Taiga Plains High Subarctic / Mackenzie Delta & Arctic Red River High Subarctic	Sites within the Mackenzie River delta region.
	NTPC2	Tundra Cordillera High Subarctic / Richardson Plateau High Subarctic	Westernmost sites in foothills of Richardson Mountains.
	NTPC3	Borderline of two regions above	Sites located between delta and foothills near Peel River

Figure 2.1 Location of study area in northwest Canada

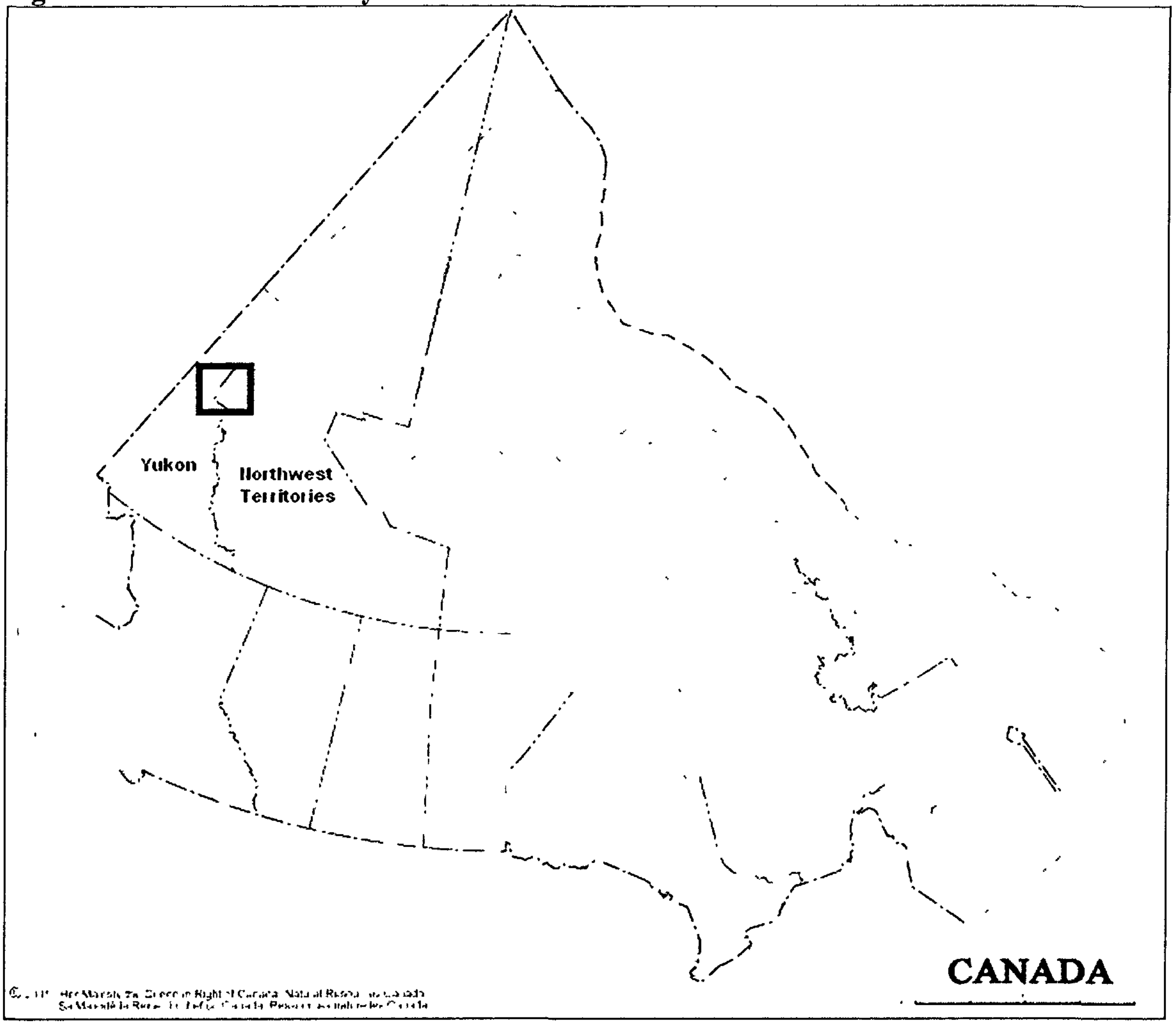
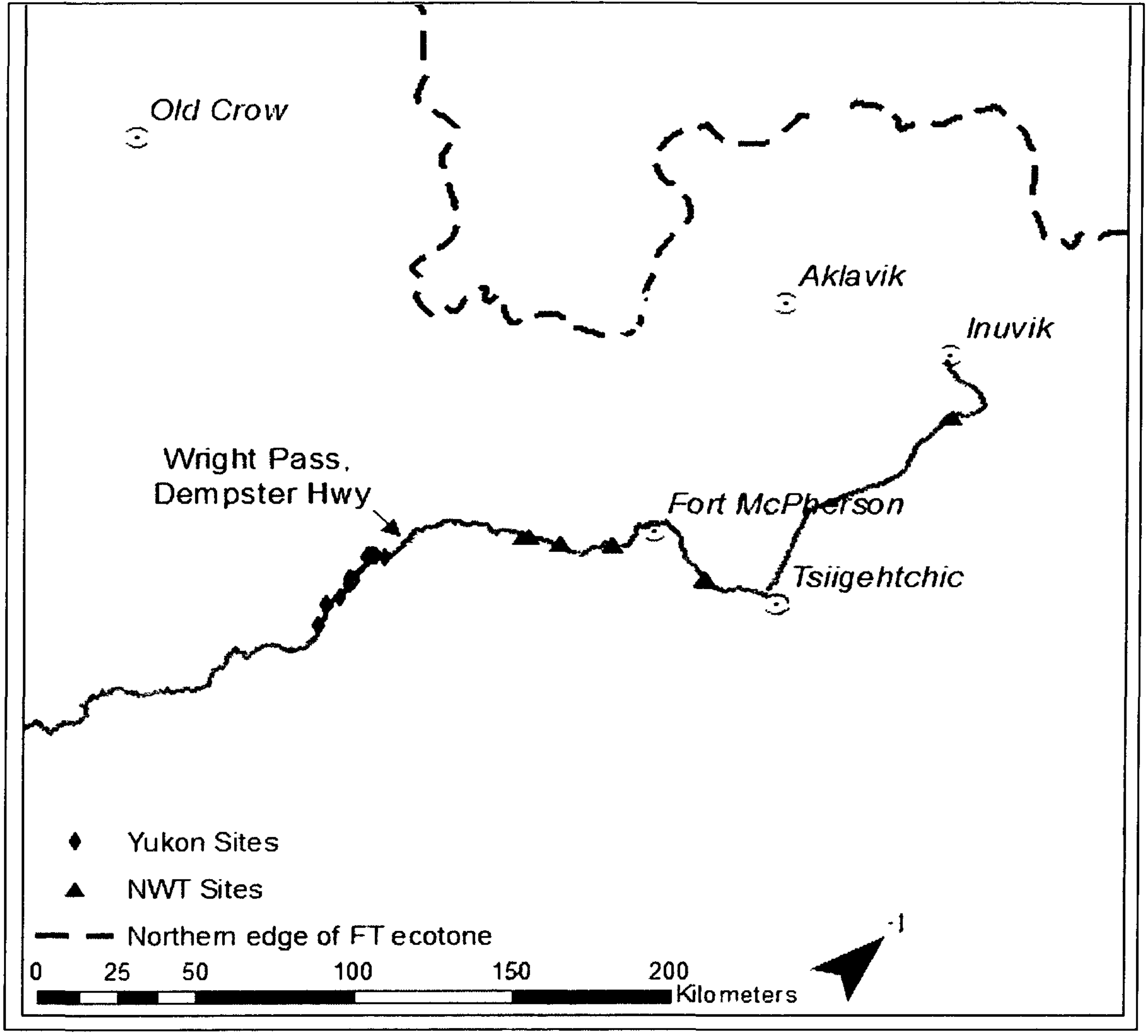


Figure 2.2 Site locations in Yukon and Northwest Territories



Forest-tundra (FT) ecotone data courtesy of the Alaska Geobotany Center, Institute of Arctic Biology, University of Alaska-Fairbanks.

Figure 2.3 Ecoregions and PC groups

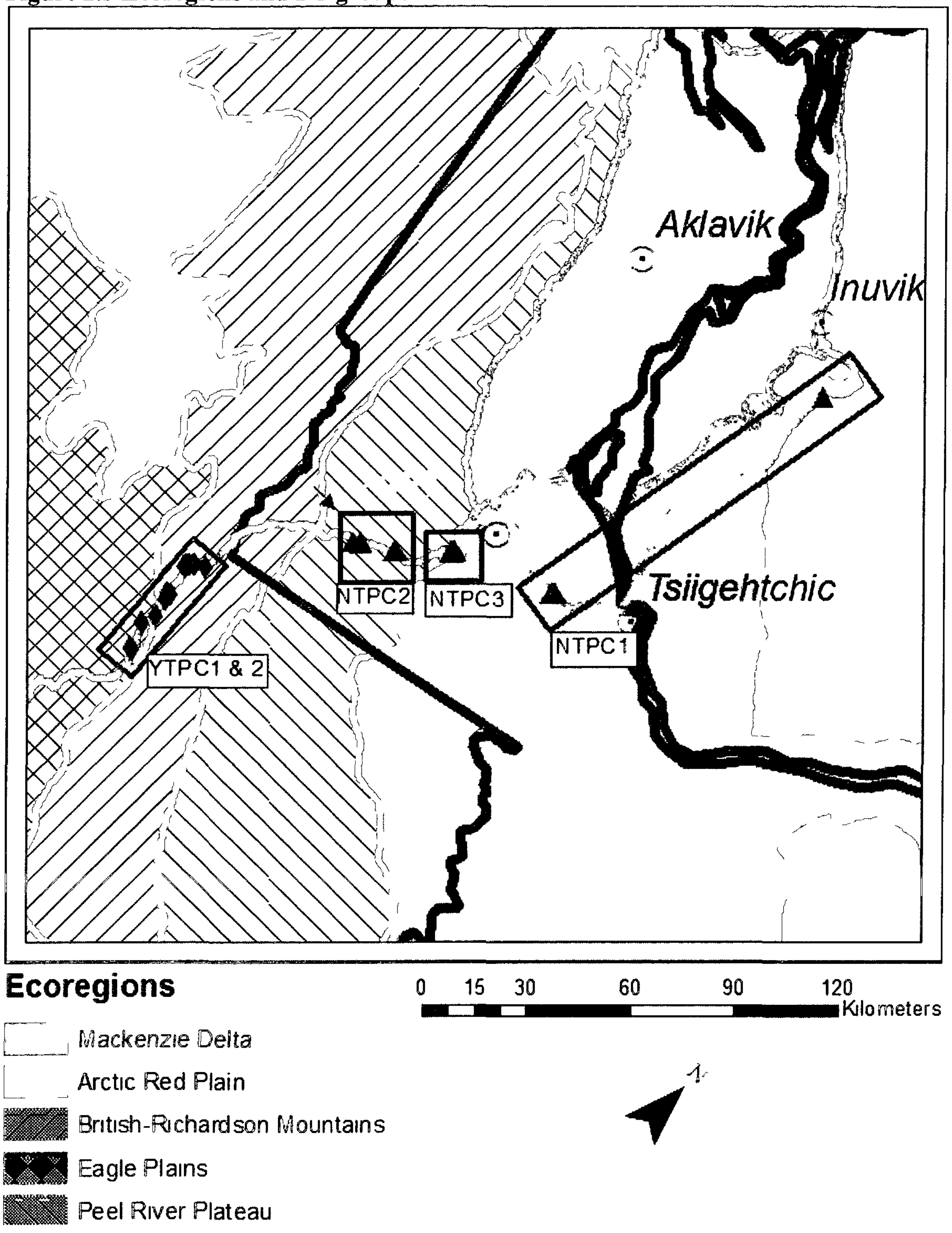


Figure 2.4 Mean regional temperatures

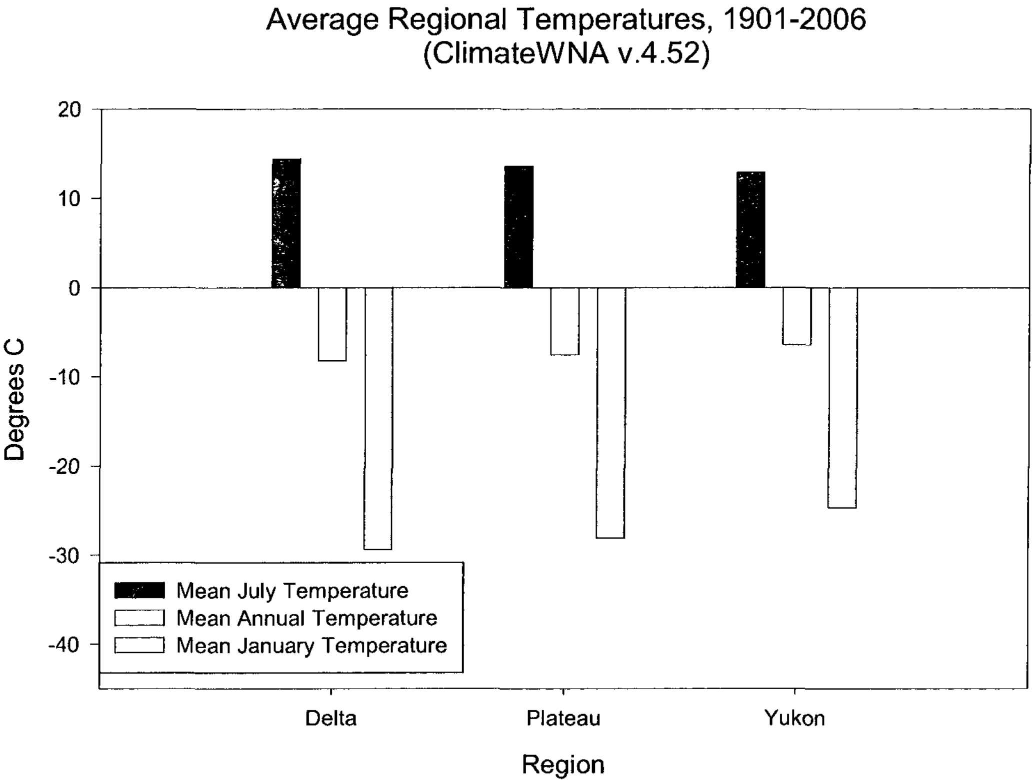


Figure 2.5 Regional mean annual precipitation

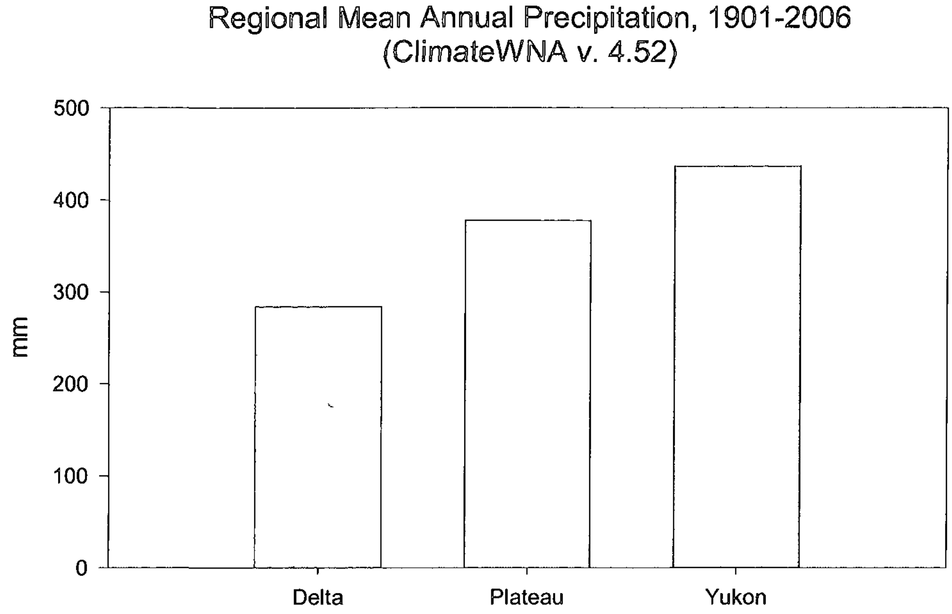
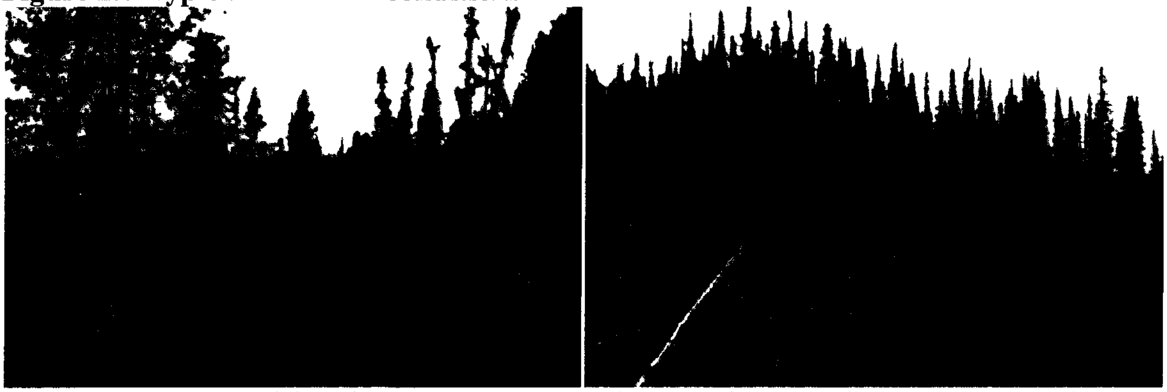


Figure 2.6 Typical Yukon white spruce stands

(L) Photo depicts typical open-grown stand with low understory cover in Yukon. (R) White spruce stand on a south-facing slope in the Yukon.

Figure 2.7 Typical NWT site conditions



(L) Common stand conditions in the NWT, with black spruce interspersed with tamarack and poplar. Understories typically more dense than those found in Yukon. (R) Example of a Hill site, NWT. Stand of tall white spruce growing on south face of small hill, surrounded by black spruce and tamarack. Near Tsiigehtchic, within the Arctic Red River plain.

Appendix A.Yukon site data

All coordinates in UTM zone 08 west. W = white spruce; F = flat; C = slope crest; US = upper slope; MS = middle slope; LS = lower slope; T = toe of slope; R = riparian

Name	Year	Species	Slope (%)	Aspect	Elevation (m)	Latitude (UTM)	Longitude (UTM)	Slope Position
Quarry	2009	W	46	166	758	7404656	441584	US
CrestW	2009	W	17	120	684	7412117	440362	C US MS LS
HideawayL	2009	W	33	135	662	7412362	441569	LS
HideawayU	2009	W	22	135	689	7412362	441569	C US
Gut	2009	W	38	112	670	7392516	440867	C US MS
CaribouL	2009	W	10	84	632	7400513	439117	LS T
CaribouU	2009	W	10	84	716	7400513	439117	C US
GlacierCr	2009	W	0	F	660	7392525	441333	R
Shed	2009	W	72	20	491	7421843	440368	C US
Cutbank	2009	W	84	142	504	7422812	441308	C US
Bench	2009	W	43	158	541	7423430	442221	C US MS
RockRiver1	2009	W	0	F	482	7421423	440379	R
RockRiver2	2009	W	0	F	482	7421423	440379	R
North	2009	W	21	180	677	7424335	445477	US MS

Appendix B. Northwest Territories site data

Name	Year	Species	Slope (%)	Aspect	Elevation (m)	Latitude (UTM)	Longitude (UTM)	Slope Position
Midway	2008	B	3	S	368	7455907	478865	C US MS LS
PeelN	2008	B	23	N	40	7468846	459343	US MS
PeelG	2008 2009	W	35	S	75	7468399	502318	C US
PeelM	2009	B	33	S	31	7468886	502981	C US MS
HillA_G	2009	W	32	S	78	7474778	533582	C US MS
HillA_S	2009	B	12	S	62	7474714	533624	LS
Slump1	2009	W	25	S	383	7459399	488360	C US MS
Slump3	2009	W	43	S	369	7459988	489016	C US MS
Slump2	2009	W	21	S	369	7459568	488803	US MS
HillB_G	2009	W	38	S	85	7474574	533570	C US MS
HillB_S	2009	B	11	S	68	7474564	533525	LS T
HillC_S	2009	B	13	S	75	7475033	534331	LS T
HillC_G	2009	W	38	S	90	7475065	534390	C US MS
West	2009	B	6	S	374	7454846	477002	MS
Foothill	2009	B	7	S	398	7456316	479037	US
Dolomite	2009	W	27	S	83	7566640	566190	C US MS
Hill_N	2009	B	20	N	78	7474822	N/A	MS LS

All coordinates in UTM zone 08 west. W = white spruce; B = black spruce; C = slope crest; US = upper slope; MS = middle slope; LS = lower slope; T = toe of slope

Appendix C. Soil, vegetation, and groundcover data

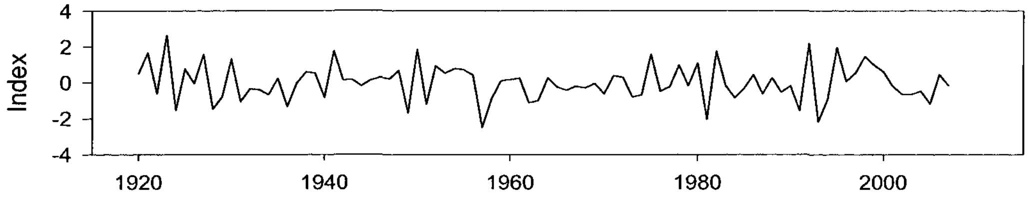
Name	Mean Active Layer Depth (m)	Tall Shrub	Low Shrub	Grass	Herb	Moss/ Lichen	Litter	CWD	FWD	Burn	Bare Soil	Rock
Yukon												
Quarry	0.54	0	10	5	1	5	0	0	0	0	0	70
CrestW		5	25	1	0	35	5	5	0	0	0	30
HideawayL		5	35	10	5	60	0	0	0	0	0	0
HideawayU		5	40	0	1	15	0	0	5	0	0	25
Gut		10	35	0	0	20	5	0	5	0	0	50
CaribouL		70	20	5	0	20	5	0	10	0	5	0
CaribouU		5	20	0	0	30	5	0	0	0	0	70
GlacierCr												
Shed		5	30	0	1	80	5	0	0	0	0	5
Cutbank		40	60	0	5	30	10	5	10	0	0	0
Bench		80	50	1	0	15	5	0	0	0	0	1
RockRiver1												
RockRiver2												
North		90	40	1	15	60	0	1	5	0	0	0
NWT												
Midway	0.51											
PeelN												
PeelG	0.67	80	40	10	5	5	60	5	10	0	0	0
PeelM		15	40	5	1	20	15	1	5	0	5	0
HillA_G	0.97	15	20	0	10	40	30	5	10	0	0	0
HillA_S	0.72	30	40	0	0	80	10	5	5	0	0	0
Slump1		80	25	5	15	30	1	5	5	0	0	0
Slump3		90	80	5	0	75	15	10	10	0	0	0
Slump2		65	50	1	1	75	5	1	5	0	0	0
HillB_G	1.12	5	60	1	5	15	20	5	10	0	5	0
HillB_S	0.7	20	30	1	0	80	1	0	15	0	0	0
HillC_S	0.73	5	70	0	0	70	5	1	5	0	0	0
HillC_G	1.08	10	40	1	5	25	15	5	15	0	5	0
West		5	30	5	20	40	1	0	5	0	1	0
Foothill		35	60	10	5	20	1	0	5	0	0	0
Dolomite		30	50	5	5	25	10	1	5	0	0	0
Hill_N	0.75	15	40	0	0	75	5	5	10	0	0	0

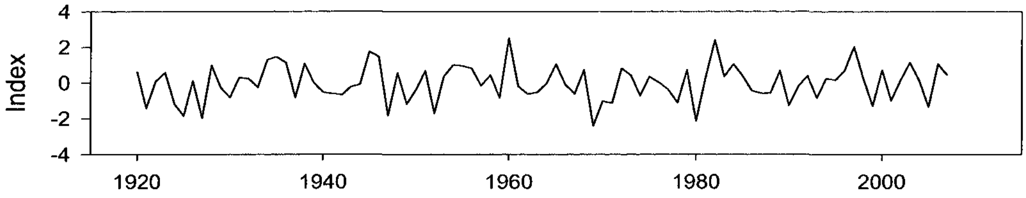
Mean active layer depths were computed from measurements taken 1.5 m upslope of every sampled tree within each site during mid-August, 2009. Accurate depth probe measurements in the Yukon were not possible due to extremely rocky soils. Percentage coverage of vegetation and ground cover was estimated visually from a random point within each site. Class specifications were defined by the Field Manual and Monitoring Protocols, Yukon Forestry Monitoring Program (Ogden, 2008). Data were not collected from riparian sites or sites sampled in 2008, which were not included into the analyses of this project.

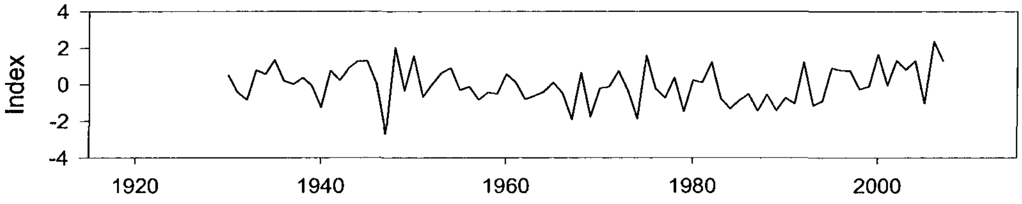
Appendix D. Chronology summary data

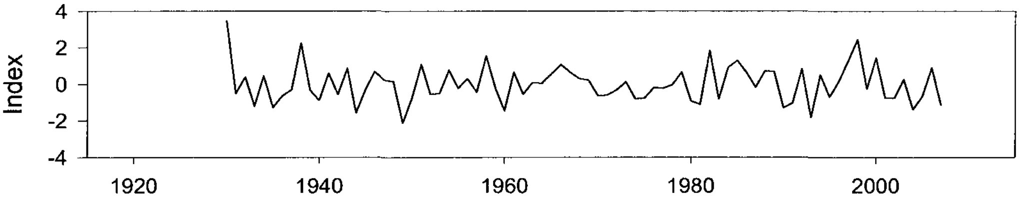
Name	Region	Trees (n)	Chronology (years)	Interseries Correlation	Mean Sensitivity
Quarry	YT	12	125	0.523	0.277
CrestW	YT	29	173	0.582	0.216
HideawayL	YT	17	209	0.604	0.230
HideawayU	YT	15	162	0.585	0.249
Gut	YT	12	183	0.563	0.246
CaribouL	YT	30	233	0.611	0.205
CaribouU	YT	27	139	0.627	0.222
GlacierCr	YT	19	191	0.592	0.208
Shed	YT	29	104	0.596	0.192
Cutbank	YT	16	148	0.575	0.218
Bench	YT	16	169	0.605	0.206
RockRiver1	YT	13	187	0.583	0.199
RockRiver2	YT	19	284	0.581	0.191
North	YT	27	165	0.549	0.211
Midway	NWT	15	85	0.613	0.219
PeelN	NWT	15	152	0.557	0.218
PeelG	NWT	34	95	0.661	0.234
PeelM	NWT	14	149	0.485	0.232
HillA_G	NWT	28	156	0.663	0.202
HillA_S	NWT	13	251	0.522	0.196
Slump1	NWT	18	258	0.569	0.219
Slump3	NWT	16	207	0.563	0.213
Slump2	NWT	17	199	0.623	0.212
HillB_G	NWT	15	154	0.661	0.187
HillB_S	NWT	14	249	0.500	0.220
HillC_S	NWT	12	252	0.466	0.225
HillC_G	NWT	16	143	0.622	0.178
West	NWT	15	81	0.505	0.237
Foothill	NWT	16	80	0.547	0.220
Dolomite	NWT	18	253	0.553	0.205
Hill_N	NWT	21	256	0.518	0.214

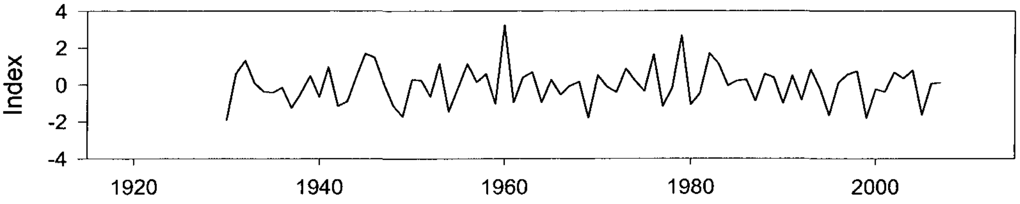
Appendix E. Tree growth indices derived from PCA


YTPC1 (shallow)


YTPC2 (steep)


NTPC1 (delta)


NTPC2 (uplands)


NTPC3 (transition)

Chapter 3: Scale-dependent climate and tree growth relationships at the western Canadian subarctic treeline

Abstract

Summer temperature has frequently been assumed to be the dominant climate component controlling tree growth at the latitudinal treeline. However, recent findings have indicated more complex patterns of tree growth and climate interrelationships. We investigated how these relationships change through variations in environment and spatial scales in northern Yukon and Northwest Territories. Climate data were correlated to annual growth series derived from a principal components analysis performed on a large set of tree-ring chronologies. We found that climate effects on tree growth significantly changed based on high and low slope gradients at smaller, local scales. Differences were also found at a larger, regional scale, where significant climate effects were differentiated by ecoregional classifications. These results show that climate and tree growth associations are not static across the landscape or through different spatial scales, and future studies of potential changes of the circumpolar treeline should acknowledge the inherent complexity of this region.

3.1 Introduction

The location, density, and species composition of circumpolar latitudinal treelines are widely expected to experience significant responses to emerging climatic changes in Arctic regions (Holtmeier & Broll, 2005). In order to understand the effects of climate change on circumpolar treeline structure and processes, it is necessary to identify and assess the most important climatic parameters that affect tree growth. Effects of climate on tree growth can be inferred from tree-ring patterns by identifying the climate signal apart from the effects of non-climatic factors, such as topography, stand density, or disturbance. To obtain a clear climate signal within the tree-ring record, specific site selection criteria, such as identifying moisture-limited sites with low inter-tree competition, are employed to identify areas with the most climatically sensitive tree populations (Fritts, 1976). However, environmental characteristics not directly accounted for in site selection, such as soil and permafrost characteristics, variable solar insolation, or slope steepness, can often be overlooked, but may yet impart a significant influence on the true nature of climate and tree growth interactions. Regional responses of tree growth may be influenced by specific combinations of climate, environment, and forest characteristics. The combined effects of these regional responses will determine the overall trajectory of future changes to the entire circumpolar treeline. Therefore it is important to identify distinct areas with unique relationships between climate and tree growth, and the specific environmental characteristics that determine the nature of these relationships and the boundaries that separate them. The objective of this study was to identify important climate variables as they occurred across an environmental gradient in northwestern sub-arctic Canada. A secondary objective was to assess the viability of using interpolated climate data for high-latitude sites, in lieu of using climate station data from far away, unrepresentative sites, which may also have short or incomplete historical records.

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The historic and projected ecological processes and climatic response of the northern treeline is often inferred from tree-ring proxy records sampled from distant sites across broad and diverse regions (Luckman & Wilson, 2005; Wilson *et al.*, 2007; MacDonald *et al.*, 2008). However, this coarse approach to observing northern treeline dynamics may not adequately consider important relationships between the forest, climate, and environment that are inherent at different scales, which may skew our assumptions and interpretations of climatically induced changes at the northern treeline. Broad regional assessments are important, and for now provide some of the best information available for addressing circumpolar issues of climatic and environmental change. However, a more detailed understanding regarding the environmental limits to tree growth and the scale at which these limits are evident is needed to address future scenarios of climate change and associated forest responses at high latitudes.

In this study, we attempted to understand the role of environmental variation and scale of observation when determining treeline growth responses to climate at the western Canadian forest-tundra (FT) ecotone. To what degree do variable landscape features determine the dominant climatic factors on tree growth? Can these factors help explain disparate tree growth trends in the Arctic? We hypothesize that the environmental features identified in Chapter 2 will support distinct climatic influences upon tree growth at the sub-Arctic treeline.

3.1.1 Climate-growth relationships of spruce

3.1.1.1 Temperature

Summer temperature most often correlates (positively) with tree growth at the northern treeline (Bonan & Sirois, 1992; Vaganov *et al.*, 1999; Kirdyanov *et al.*, 2003). For example, black spruce at the northern treeline in Alaska exhibited positive responses to summer temperatures (Lloyd *et al.*, 2005), as did white spruce at the northern treeline in central Canada (D'Arrigo *et al.*, 2009). Late summer temperature was also identified as having a significant positive effect on growth of both white and black spruce at the treeline in Nunavut (MacDonald *et al.*, 1998). Similar observations were made of black spruce in northern Quebec (Wang *et al.*, 2002) as well as larch in the Siberian subarctic (Kirdyanov *et al.*, 2003). Additionally, white spruce has been shown to lose its summer temperature sensitivity with advancing age in the Yukon sub-arctic (Szeicz & MacDonald, 1995a). Occasionally winter temperatures also affect black spruce growth, evidenced by positive correlations with prior October (e.g. early winter) temperatures in Nunavut (MacDonald *et al.*, 1998), and prior winter seasonal temperatures at Ft. Wainwright near Fairbanks, Alaska (Juday *et al.*, 2005). These types of varied growth responses are likely the result of different regional climates and environments, indicating that no one climatic variable can best explain tree growth across the entire circumpolar region.

The relationship between summer temperature and tree growth holds true for most latitudinal treeline sites, but is not evident south of the treeline within the continuous forest. At multiple sites across Canada from Yukon to Quebec, these trends tend to reverse, as the strong positive effect of summer temperature diminishes in lieu of stronger effects of spring and summer precipitation (positive) and early summer temperatures (negative) (Brooks *et al.*, 1998; Tardif & Bergeron, 2001; Miyamoto *et al.*, 2010). This reversing trend indicates that the forest-tundra ecotone is a distinct bioclimatic zone apart from the boreal forest.

There is mounting evidence that some trees at the northern treeline are losing their positive association with growing-season temperatures. Wilmking *et al.* (2004) found that approximately 40% of a large sample (n >1500) of white spruce in the Alaska and Brooks Ranges of Alaska responded negatively to summer temperatures (hereafter negative responders), while less than 40% of the sample population still responded positively (hereafter positive responders) in the latter half of the 20th century. In the Mackenzie River delta, Pisaric *et al.* (2007) found that only 25% of their sample population of black spruce (n = 654) showed a positive correlation with summer temperatures, with the remaining portion beginning to lose its sensitivity in the 1930s. Similar findings have been reported for white spruce in southwest Alaska (Driscoll *et al.*, 2005), north-central Canada (D'Arrigo *et al.*, 2009), and for larch in the Taymir region of northern Siberia (Jacoby *et al.*, 2000). It appears that the trees with declining positive summer temperature associations are exceeding a certain temperature threshold at which they become unduly stressed in response to increasing Arctic temperatures. Specific threshold values are few, but estimates between 11° and 12°C (mean summer temperature) have been suggested for central Yukon and Alaska (D'Arrigo *et al.*, 2004; Wilmking *et al.*, 2004).

These emerging patterns of contrasting growth responses to summer temperature has come to be known as the 'divergence problem' (Briffa *et al.*, 1998; D'Arrigo *et al.*, 2008), and currently represents a central focus in northern dendroclimatic studies (Lloyd & Bunn, 2007; Wilson *et al.*, 2007; Esper & Frank, 2009; Loehle, 2009). Drought stress has been the most frequently suggested cause (Barber *et al.*, 2000; Davi *et al.*, 2003; Wilmking *et al.*, 2004; Driscoll *et al.*, 2005; Pisaric *et al.*, 2007; D'Arrigo *et al.*, 2009; Beck *et al.*, 2011), though other confounding factors, such as increased plant competition (Hogg & Hurdle, 1995), insect herbivory (Fleming & Volney, 1995), or increased UV-B levels (Callaghan *et al.*, 2004a) potentially contribute to these patterns as well. Currently, it is not certain why particular trees respond positively or negatively to warming temperatures, but it is likely that a combination of environmental, biotic and abiotic factors contribute to this issue.

3.1.1.2 Precipitation

It is important to note that precipitation data are often less reliable than temperature data, and in the circumpolar region, coverage is sparse and intermittent, measured time spans are short, and datasets are often replete with missing values. As a result, the closest long-term climate data is often collected at stations located a significant distance from most study sites (e.g. Szeicz & MacDonald, 1995a; Wilmking & Juday, 2005). Alternately, interpolated data can be derived from climate normals and general circulation models to approximate local conditions and predict future scenarios (Mbogga *et al.*, 2009). Recognizing that all forms of available precipitation data have inherent limitations, general observations can still be made that are relevant to current issues of climatic and environmental change in the north.

As evidenced by the aforementioned studies implicating temperature as the prime control over tree growth in the Arctic, precipitation appears to have less of a controlling effect on tree growth than temperature, though it may be increasingly important in future (drier) situations. Precipitation may affect overall soil moisture deficits that can contribute to drought limitations, but it is equally, if not more likely that increased evaporative demands may be the leading cause (Beck *et al.*, 2011). Significant correlations between precipitation and tree-ring growth are not commonly found at high latitudes, as temperature is the dominant climatic limitation. Where significant positive precipitation effects are found, summer temperatures are often simultaneously found to exert negative effects. For example, during the latter half of the 20th century in central Alaska, black spruce was found to be positively correlated with August precipitation, accompanied by negative relationships with July and August temperatures (Wilmking & Myers-Smith, 2008). Similarly, white spruce negative responders (to summer temperatures) in the Mackenzie River delta reacted positively to April precipitation (Pisaric *et al.*, 2007).

Although there are some general notions of the relationship between tree growth and growing season temperatures and precipitation, a review of current findings clearly shows a more complex situation than previously assumed. Tree growth response to climate across the northern treeline is not static or similar at all sites and for all species, yet large-scale inferences of past climates and projected changes are regularly produced. The fact that so much irregularity exists in circumpolar tree growth/climate relationships necessitates more detailed studies to fully understand the nature and implications of these relationships.

3.2 Methods and materials

3.2.1 Field sites

We selected 33 sites along the northern Dempster Highway, 14 sites in Yukon and 19 sites in the Northwest Territories (NWT). Specific site selection strategies and criteria are outlined in Chapter 2, Section 2.2.1.

3.2.1.1 Site locations

The Yukon sites spanned the region from the Arctic Circle north to the northern extent of tree growth, just south of Wright Pass (67° 2'56.81" N, 136°12'24.73" W) in the Richardson Mountains (Figures 2.1, 2.2), and were distributed along a north-south gradient, following the Dempster Highway along the western edge of the mountains. Continuing along the Dempster corridor into the NWT, sites were distributed along an east-west gradient, from the eastern foothills of the Richardson Mountains and across the Mackenzie delta and Arctic Red River plain nearly to the town of Inuvik (Figure 2.2). Site elevations ranged from 491 m to 758 m in Yukon, with altitudinal treeline generally observed around 700 m, comprised entirely of white spruce. Conversely, site elevations in the NWT ranged from 31 m in the delta to 400 m in the Richardson foothills, where a composition of tamarack, white and black spruce existed at the altitudinal treeline near 400 m.

3.2.2 Ecoregional classification & descriptions

Detailed descriptions of the British-Richardson Mountains ecoregion in Yukon, as well as the Richardson Plateau and Arctic Red River Plain ecoregions in the NWT, are given in Chapter 2, Section 2.2.2.

3.2.3 Sampling strategy

Our sampling strategy is described in detail in Chapter 2, Section 2.2.3.

3.2.4 Chronology development

Tree cores were prepared according to standard dendrochronological methods (Stokes & Smiley, 1968). Specific details of sample preparation, measurement, and detrending are described in Chapter 2, Section 2.2.4.

3.2.5 Data analysis

A detailed description of the methods employed for the analysis of the chronologies is located in Chapter 2, Section 2.2.5. This same section also describes the application of principal components analysis on the set of chronologies.

3.2.5.1 Climate data

Climate stations in the far north of Canada are sparsely located, and often do not have adequately long and/or complete records. The station with the longest record (approximately 100 years) in the area is in Dawson City, Yukon, which is located over 300 km from the nearest study site. In addition, the Dawson precipitation record is fraught with missing values. Other stations, such as the ones near Old Crow, Inuvik, and Fort McPherson, are closer to the study area, but do not have long enough records to be effectively utilized in this study.

To address this situation, we used climate data derived from the ClimateWNA v.4.52 model, which is an expanded version of the ClimateBC model (Wang *et al.*, 2006). ClimateBC has been used in prior studies conducted in British Columbia, Canada, with satisfactory results (O'Neill *et al.*, 2008; Stoehr *et al.*, 2009; Griesbauer & Green, 2010b), supporting the use of this data in applied situations. ClimateWNA extracts and downscales monthly PRISM data

(Daly *et al.*, 2002) using years 1961-1990 as the reference period. It then calculates monthly and annual climate data based on latitude, longitude and elevation. Representative locations were determined for both Yukon (Quarry site) and NWT (Fort McPherson), based on their average location and elevation amongst the sites of each region. Using all the output from the model would be prohibitive for interpretation and analysis, so seasonal variables were used in the analyses. Each variable was checked for normality using the Shapiro-Wilkes test, and log transforms were applied to those not passing the initial test. The relationship between modeled and measured data was tested by correlating the station data with modeled data using the exact coordinates of the particular climate station. However, the output from ClimateWNA would be expected to correlate highly with station data of the same location, as the model was partially built using observed data from the entire regional coverage. It is beyond the scope of this study to fully assess the precision of the ClimateWNA output, and thus we assumed that the data is a realistic representation of the conditions in our study area.

3.2.5.2 Climate-growth analysis

Chronological scores from the regional PCs were correlated with corresponding ClimateWNA output using Pearson's simple correlation coefficient. Climate indices representing general circulation patterns were also correlated to the PC chronologies, including the Arctic Oscillation, El Niño-Southern Oscillation, Pacific Decadal Oscillation, and the Pacific North American Oscillation.

3.3 Results

The results of the chronology analyses and subsequent principal components analysis are found in Chapter 2, Sections 2.3.1 and 2.3.2.

3.3.1 Climate data

Monthly temperature values from ClimateWNA correlated extremely well with the station data; in Dawson (1901-2006), mean monthly temperature correlation coefficients ranged 0.95 to 0.99, and values from Inuvik (1957-2006) ranged 0.94 to 0.99. The Rock River climate station (1995-2006), nearest to the Yukon sites, had lower but still strong correlations, likely a reflection of the very short time period. This is not surprising nor entirely helpful, as ClimateWNA output is largely based on measured station data. Precipitation records are prone to more uncertainty, due to changing methods of measurement, frequent missing data, and variable forms of precipitation. In Dawson, correlation coefficients for precipitation ranged 0.46 to 0.88, while in Inuvik the coefficients range 0.53 to 0.95. The two lowest values in Dawson correspond to the months of May and October, when precipitation is most likely changing from snow to rain, increasing the likelihood of measurement errors as well as confounding the extrapolation ability of the climate model. Similar observations are true for Inuvik, except the "shoulder" months occur farther apart (February/March and November).

High correlations between the station and modelled data would be expected, however, as the modelled data is derived mainly from the station data (Wang *et al.*, 2006). Corrected temperature data (to account for measurement equipment upgrades and/or station relocation) from available stations in the study area (Dawson City, Old Crow, Rock River, Inuvik) were correlated against each other using the longest possible common time periods, to assess the relative regional cohesiveness of the climate variability (Table 3.1). Strong positive correlations suggest that climate conditions fluctuate similarly across the study area, though the absolute values may differ between the stations. This lends credibility towards using the modelled data, as it likely portrays the common climate variation reflected by the area's climate station records. The modelled data also allow for more accurate absolute temperature (and to a lesser extent precipitation) values based on the coordinates and elevation that represent the Yukon and NWT study areas. Temperature appears to be more accurately predicted by the model, which allowed us to use temperature parameters with a greater degree of confidence than those based on precipitation. Precipitation values, though more variable and generally less correlated with station data than temperature, are still useful due to uncertainties in both station and modelled data. The modeled data from ClimateWNA provided a localized approximation of the conditions at the sites, and were thus presumed to represent meaningful values.

3.3.2 Climate-growth relationships

3.3.2.1 Yukon

Spruce growth on low-gradient slopes (represented by YTPC1) correlated negatively ($p < 0.05$) with the previous season's winter, current summer and annual precipitation. Strong positive correlations ($p < 0.01$) were found with previous autumn temperatures and the associated previous season's frost-free period. Continentality, a measure of the difference between the warmest and coldest monthly temperatures, also had a positive effect on tree growth at these sites. A weak but significant positive correlation with the current season's mean warmest month temperature (MWMT, usually July) was also present (Table 3.2, Figure 3.1). No climate index (e.g., PDO) was significantly correlated with this PC.

Spruce growth on high-gradient slopes, represented by YTPC2, was negatively affected most strongly by the previous summer's temperatures, with the maximum and mean temperatures highly significant ($p < 0.01$). A weaker positive correlation is associated with the current spring precipitation, likely falling as snow, although no individual chronology represented by this PC showed a significant correlation to this variable (Table 3.2, Figure 3.1). No climate index was significantly correlated with this PC.

3.3.2.2 NWT

Tree growth within the Mackenzie River delta (NTPC1) was primarily affected by previous summer temperatures, particularly the MWMT. This pattern was evident in negative correlations to the previous summer heat-moisture index and continentality (difference between warmest and coldest monthly mean temperatures, often inferred as a measure of winter severity), as well as the beginning Julian date of the frost-free period. Positive correlations were weakly attributed to previous autumn and winter temperatures. No climate index was significantly correlated to this PC (Table 3.2, Figure 3.1).

Tree growth in the foothills of the Richardson Mountains (NTPC2) was positively correlated to current summer temperatures, including the number of frost-free days and continentality; all of these variables were highly significant ($p < 0.01$). Previous summer frost-free period also had a positive effect. Weaker negative correlations were attributed to previous MWMT and MCMT variables, and previous season continentality. No climate index was significantly correlated (Table 3.2, Figure 3.1).

Tree growth on the Peel River plateau (NTPC3) had the fewest significant correlations. Previous summer temperatures were negatively correlated to growth, while previous winter temperatures had an opposite positive effect. No climate index was significantly correlated (Table 3.2, Figure 3.1).

3.4 Discussion

3.4.1 Climate and tree growth in Yukon

In general, YTPC1 variation (representing low slope gradients) appeared to be temperature limited, while the high gradient group (YTPC2) appeared to be more limited by moisture, supporting the finding in Chapter 2 that tree growth patterns do indeed appear to be differentially affected by slope gradient. The strongest climate-growth associations for YTPC1 appeared to favour warm temperatures in late summer in the prior season. Warmer temperatures in the autumn would intrinsically be associated with a longer frost-free period by delaying the onset of freezing temperatures late in the growing season. In turn, trees can accumulate additional carbohydrate resources into the fall before shutting down for the winter season, and utilize these resources the following year for more productive growth (Kozlowski *et al.*, 1991). This is important on low gradient slopes, where slower runoff rates and decreased solar insolation levels favour the retention of soil moisture, in which case potentially heightened photosynthetic activity would allow excess resources to be allocated partially towards radial growth (Waring & Pitman, 1985; Barnes *et al.*, 1998). Also for this group (YTPC1), weaker positive correlations were observed for the mean temperature of the warmest month (in this region, always July) and continentality (a measure of the disparity between the warmest and coldest monthly mean temperatures). The association with continentality was likely a reflection of the correlation to warmer summer temperatures; however, winter temperatures are warming at a greater rate than summer temperatures throughout Yukon, leading to a decreased continental effect (Figure 3.2). Thus, the positive correlation to continentality was likely to be increasingly weakening in light of the decreasing continentality trend.

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Mean annual and summer precipitation also had a weak but negative effect on tree growth on low gradients. Significant positive correlations to precipitation are occasionally found at other circumpolar sites, but negative responses are extremely rare in the literature. In areas of continuous permafrost, it is possible higher precipitation levels could accumulate in the shallower active layers and temporarily waterlog sites on low gradients. This would be particularly detrimental to white spruce, such as those in this region, which are not well-suited to growing in hydric soil conditions. Low gradient slopes are also subject to lower intensities of solar radiation due to the extremely obtuse angle of incoming radiation at high latitudes, particularly on southerly aspects; wetter soils on these slope types are generally colder during the growing season and require greater heating loads to warm, and will thus conceivably be less prone to evaporative drying (Lee, 1964). Combined with low runoff capability, these conditions promote greater moisture retention in the soil.

Forest growth on lower gradient slopes will potentially respond positively to predicted warming temperatures in the Arctic. Conditions favourable to soil moisture holding capacity may prevent drought-like conditions to prevail, and thus facilitate increased radial growth in response to increasing growing season temperatures. However, it is possible that some trees may not possess the adaptive capacity to positively respond to warming temperatures (Callaghan *et al.*, 2004b). Heightened temperatures may also impose evaporative demands that overcome the available soil moisture (Beck *et al.*, 2011), creating drought-like conditions for individual trees. Though low gradient sites may support positive tree growth, it is likely that future growth responses will vary according to the capabilities of individual trees to respond.

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Fewer significantly correlated climate variables were associated with YTPC2 (high gradients). The strongest relationship was a negative correlation to summer temperatures in the previous season. A weaker positive association with current year spring precipitation was also evident, though this variable did not correlate significantly with any individual chronology represented by this PC. Negative associations with temperature coupled with positive precipitation correlations have also been reported in central Alaska and within the eastern Mackenzie delta, though black spruce was the species under consideration in both instances (Pisaric *et al.*, 2007; Wilmking & Myers-Smith, 2008).

Steeper slopes are prone to increased rates of drainage due to gravity, and consequently are likely to be moisture limited during the growing season (Bonan, 2008). They are also subject to higher levels of solar radiation-induced evaporation, particularly at such high latitudes, leading to increased moisture deficiencies as well (Barnes *et al.*, 1998). High summer temperatures are frequently correlated to overall drier conditions, meaning that trees at these site types will have a reduced capacity to store adequate reserve carbohydrates to be used for new growth in the following early growing season. Thus, the following season's growth will be limited from the very beginning. However, greater precipitation in the spring (falling predominantly as snow in this region) will normally extend the date of snowmelt, thus effectively shortening the growing season on the early end. In this case, a shortened growing season may diminish the period of water loss by extending the time of snow cover, which in turn would negate some of the effects of diminished resource stores caused by prior growing season temperature extremes. Increased duration and amount of snow cover will also create a water reservoir for moderating early season soil moisture. However, with increasing temperatures in the future, forest stands on steeper slopes may experience reduced growth as the growing season becomes longer in response to earlier snow melt. Longer growing seasons may ultimately exacerbate the already strong negative effect of prior season temperatures.

The potential effects of solar radiation and seasonally continuous sunlight are suggested here, however little research has gone into quantifying the precise nature of its effect on tree growth at high-latitude areas. A specific band of solar radiation, UV-B, has been proposed as a contributing factor to the 'divergence issue,' but only as a function of decreasing ozone levels (Hansell *et al.*, 1998; Callaghan *et al.*, 2004a). There are many other factors that lead to variable solar radiation levels, with incidence angle only one contributing factor. The nature of incoming radiation, direct or diffuse, is largely affected by cloud cover and prevailing atmospheric conditions; indeed, Young *et al* (1997) showed in the high arctic that cloudy conditions diminished the effect of slope angle on overall solar input. However, cloud cover is difficult to monitor and quantify over large areas in the field, with satellite measures of outgoing long-wave radiation regarded as the only acceptable proxy measure for cloudiness (Wheeler & Kiladis, 1999). Cloudiness could also be anecdotally inferred from temperature trends, as cooler seasons would likely be characterized by increased cloud cover and precipitation (e.g. Figure 3.4). Pohl *et al* (2006) indicated that fine-scale spatial variability was highly important when considering solar radiation effects on the landscape, supporting the notion that many factors, likely difficult to quantify, contribute to actual received solar insolation at specific sites. However, the evidence from this study and in the literature still seems to suggest that incidence angle and solar insolation play a significant role in the multi-faceted system of tree growth and climate interactions.

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In reported instances of the 'divergence effect,' slope gradient has not yet appeared as a potential causal factor, though no definitive influence has been determined. However, drought stress appears to be the leading hypothesis, and sites on steep gradients would logically be more susceptible to moisture deficits. Though this proposition requires further investigation, slope gradient appears to be a valid contributing factor towards the 'divergence effect' through its potential ability to encourage drought-like conditions (see Results in Chapter 2).

3.4.2 Climate and tree growth in the NWT

The climate-growth associations in the Northwest Territories were much more varied, as the PC groups were more broadly defined by ecoregions identified in Chapter 2, rather than finer-scale attributes such as slope gradient, artifacts of the more limited sample range in the Yukon study area. Ecoregions encompass many distinct ecological characteristics, including climate, physiography, soils, etc. (Ecological Classification Group, 2007). It is beyond the scope of this study to link individual climate parameters to specific environmental characteristics inherent to each ecoregion. However, it is clear that unique relationships between climate and tree growth exist within distinct ecoregions.

NTPC1 (delta sites) correlated exclusively to prior season climate variables, a possible indication that current year tree growth is heavily influenced by the conditioning of growth traits in the prior growing season. The strongest, most significant of these was a negative correlation with the mean warmest month temperature (again, July in this region) of the previous year, coupled with slightly weaker negative correlations with other measures related to growing season temperature. Ground temperatures in and around the delta are higher than adjacent uplands due to the moderating effect of the abundant water bodies (Burn & Kokelj, 2009), which was likely a primary trait distinguishing NTPC1 from the other groups. Tree root growth would be vigorous in a warm growing season coupled with the warmer soil temperatures of this region, which may in turn prohibit the sensitive roots from achieving full cold-hardiness during abrupt transitions into winter (Raghavendra, 1991). This would manifest in the following growing season as the trees reallocate resources towards regrowing or repairing damaged root shoots from the previous autumn, thus limiting overall radial growth. Warmer summer temperatures also tend to result in lower streamflows in the following season, which may indicate decreases in precipitation and snowpack reservoirs in years of low streamflows. This was particularly evident in the NWT, where temperature data from Inuvik was negatively correlated to the 30-year streamflow record of the adjacent east channel of the Mackenzie River; similar patterns occur in the between the Fort McPherson temperature record and streamflow records of the upper Peel River and the Arctic Red River mouth (Figure 3.3).

Another possible contributing factor towards these significant climate relationships is the desiccating effect of strong winter winds (Baig & Tranquillini, 1980). Winter winds blow across the frozen Beaufort Sea ice, creating very cold and dry air conditions that can move unimpeded onto the flat expanse of the Mackenzie delta region and exert a considerable effect on tree growth and survival (Ecological Classification Group, 2007). Slow diffusion of water vapour can occur through the closed stomates and cuticle of the trees' needles, and the moisture cannot be replenished from the frozen ground until the active layer thaws in the following growing season (Marchand, 1996). This may enhance the negative effect of warmer and potentially more drought-prone conditions of previous growing seasons, and contribute to a cumulative, prolonged water deficit that becomes apparent in the following season's growth. However, winter desiccation damage is dependent on many interrelated factors (Kozlowski *et al.*, 1991), and likely plays a complementary role to other related processes. Regardless, it would appear likely that wind plays some role in the climate and tree growth relationships in this region. This hypothesis was not tested in this study, however could potentially be a worthwhile avenue of further research on limits to tree growth at high latitudes.

The climate associations here generally agree with the findings of Pisaric *et al.* (2007), where a majority (75%) of their tree samples in the Mackenzie delta did not positively associate with current summer temperatures. This group of "non responders" appeared to lose their positive association with summer temperature in the 1930s, the same decade when our analyses begin. The study area of Pisaric *et al.* was focused on the eastern side of the Mackenzie delta, whereas our range encompassed much of the southern delta and Arctic Red River plain. Though this study did not focus on individual tree responses, our similar results still implicate the delta as a broad region where tree growth does not often respond positively to summer temperatures, which may lead to continued growth decreases and increased mortality in response to further warming in the delta region. The aforementioned possible mechanisms behind this trend suggest that similar results would be found in other large river deltas throughout the circumpolar region, although supporting evidence is not currently available.

Sites in the Richardson foothills (NTPC2) exhibit strong and highly significant positive correlations with current growing season temperatures, implicating these sites as being cold limited. Sites in this area are much more prone to extreme weather affected by the mountains, including high winds, colder temperatures, and increased precipitation due to orographic effects (Figure 3.4). Likewise, ground temperatures are generally lower than the adjacent lowlands in the delta, and soil active layer depths are likely more shallow (Burn & Kokelj, 2009). To compensate for such unfavourable growing conditions, carbohydrate reserves in spruce are allocated primarily to belowground root systems, at the expense of radial stem growth (Bonan, 2008; Crawford, 2008). This allows the trees to tolerate and survive particularly cold years when normal photosynthesis would be diminished (Philipson, 1988). Warmer years more conducive to growth would then likely lead to increased resource allocations to less critical parts of the tree, such as radial growth. The conditions here are affirmed by a different class II ecoregion delineation than the rest of the NWT sites, based on significant changes in climate and physiography (Ecological Classification Group, 2007). The highly significant correlations to summer temperature variables reflect the limited growing conditions here, and is a classic example of temperature-sensitive sites frequently cited in dendroclimatic studies.

The response of this group was similar to the results found of black spruce in Alaska and Quebec (Wang *et al.*, 2002; Lloyd *et al.*, 2005). This suggests that black spruce growing within the FT ecotone, exclusive of river deltas, may exhibit similar positive responses to warming temperatures across North America, though this limited sample size precludes any definitive conclusion. Sites like these may represent areas where expanded growth and treeline advancement will occur.

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The third PC group (NTPC3) represents the transition zone between the delta and adjacent uplands. This PC did not significantly correlate with many climate parameters, creating a somewhat ambiguous description of the conditions inherent to transitory areas such as this. However, this PC group shows a somewhat similar pattern to the delta sites, primarily with negative associations with previous summer temperatures. This suggests that drought-inducing higher summer temperatures stress trees in this area to a point where they cannot store enough reserves to facilitate early, vigorous growth in the following summer season. Higher summer and annual mean temperatures in the Fort McPherson area also correspond to lower June streamflows in the Peel River during the following season, which could feasibly create moisture limited growing conditions during the subsequent early growing season. The sites represented by this PC, though distinct, resemble those of the delta (NTPC1) more so than the upland sites (NTPC2), being farther removed from the effects of the mountains, and closer to the large water network (e.g. Peel River) of the Mackenzie delta. Though direct measures were not taken, it would be likely that soil temperatures are warmer here than in the uplands, implicating similar mechanisms of climate/tree growth interactions inherent to NTPC1. The relative lack of significant climate correlations highlights the transitory nature of this PC, where two distinct environments converge and create a small but complex forest-climate system.

3.4.3 Conclusion

The results of this study show how climate can affect tree growth in different ways when considered in varying contexts. Particular seasonal or monthly climate variables impart effects on tree growth that may only be observed at specific scales. As the scale of observation increases, some important climate variables evident at smaller scales may become obscured by the increasing complexity of the climate and environmental system. This has serious implications when attempting to reconstruct historical (and project future) climate records using tree ring records, as a single climatic variable must be attributed as the main source of ring width variation. The correct variable must be chosen based upon the scale of the sample region, taking into consideration the level of environmental variation within and between distinct ecoregions.

In Yukon, a single ecoregion (Taiga cordillera) was studied. Slope gradient appeared to be the primary environmental trait affecting the response of tree growth to climate within this specific area. Tree growth on steeper slopes appears to be more affected by moisture, as steep gradients do not favour moisture retention through various aforementioned mechanisms. Conversely, low gradient slopes were more prone to temperature sensitivity. Therefore, future studies should identify sample sites with slope gradient in mind, and determine if varying climate sensitivities are important to the goals of the research. If temperature reconstruction is the primary goal, then it may be prudent to choose sites from lower gradient slopes within a specific ecoregion. Slope gradient may or may not be the most important landscape attribute contributing to tree growth variation, and thus a comprehensive assessment of the entire landscape would be a reasonable follow up from this baseline study. However, similar areas to the Taiga cordillera of northern Yukon across the circumpolar treeline could similarly be affected by slope gradient and its effect upon the extreme solar patterns inherent to high latitude regions.

Slope gradient may also prove to be a contributing factor in the ‘divergence effect’ evident throughout the FT ecotone. Though the effects of gradient were not explicitly investigated in this study, the findings suggest a possible mechanism that may partially explain disparate growth responses to climate. Based on our conclusions, low-gradient slopes are likely to be less prone to issues of divergence, and would thus be better suited sites for tree-ring based historical temperature reconstructions. The findings of this study show a high degree of variability of responses across the landscape, which would suggest a similar, wide range of variability of responses to future climate changes.

Once the scale of observation includes multiple ecoregions with greater degrees of environmental and climatic variation, such as in the NWT component of this study, small-scale landscape traits such as slope gradient become less important considerations. Although this is likely due to more limited sampling power with each region (as compared to the Yukon study area), we did find variable growth responses regardless of the spatial scale, which underscores the highly complex nature of Arctic landscapes the associated growth responses. The response of tree growth to climate within a broader context is the result of a complex system of multiple environmental and climatic traits acting upon tree growth. At this scale in the NWT, functional ecoregions become a primary factor determining distinct tree growth patterns. Specifically, the distinct PCA grouping of all sites in the Mackenzie delta suggest that river deltas throughout the circumpolar region are likely to harbour disparate growing conditions apart from all other sub-arctic landscapes. Sites here are strongly affected by warmer soil temperatures, deeper active layers, and greater moisture availability due to the ubiquitous presence of water. It is not likely that these conditions would be found anywhere outside of a river delta. Therefore, it may not be practical to equally compare climatically influenced tree growth against that found in other non-delta environments. Furthermore, river deltas are not practical locations for obtaining reliable climate reconstructions, as tree growth largely appears to not respond positively to current summer temperatures.

Tree growth responses seem to become more ambiguous and difficult to define where ecoregions transition from one major type to the next. These transition zones may represent areas of abrupt or gradual shifts between adjacent regions. This depends largely on the nature of the criteria used to define ecoregions, such as topography, parent soil types, and hydrological characteristics. Unless these zones are well documented and delineated, it is best to avoid sampling trees near these zones, and focus on sites that are categorically representative of the specific ecoregional traits.

Identifying the specific environment or landscape feature that strengthens the signal of a specific, desired climate parameter is a necessary step for future dendroclimatic studies conducted along the sub-arctic treeline. Taking these precautions to ensure a highly robust and reliable climate record from tree rings will enhance our perception of current and future changes within the FT ecotone and throughout the circumpolar region. Specific examples have been shown for Yukon and the Northwest Territories, Canada, but it remains unclear if the patterns observed here can be attributed to similar high-latitude areas. However, the evidence suggests that addressing scale-dependent environmental variation can and should be readily addressed in future studies of tree growth and climate change.

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Table 3.1 Climate station monthly mean temperature correlations

	Old Crow		Rock River		Inuvik	
	Jan	*Jul*	*Jan*	*Jul*	*Jan*	*Jul*
Dawson City	.633**	.556**	.607*	.945**	.449**	.590**
Old Crow			.599	.887**	.860**	.809**
Rock River					.825**	.934**

** = $p < 0.01$ * = $p < 0.05$

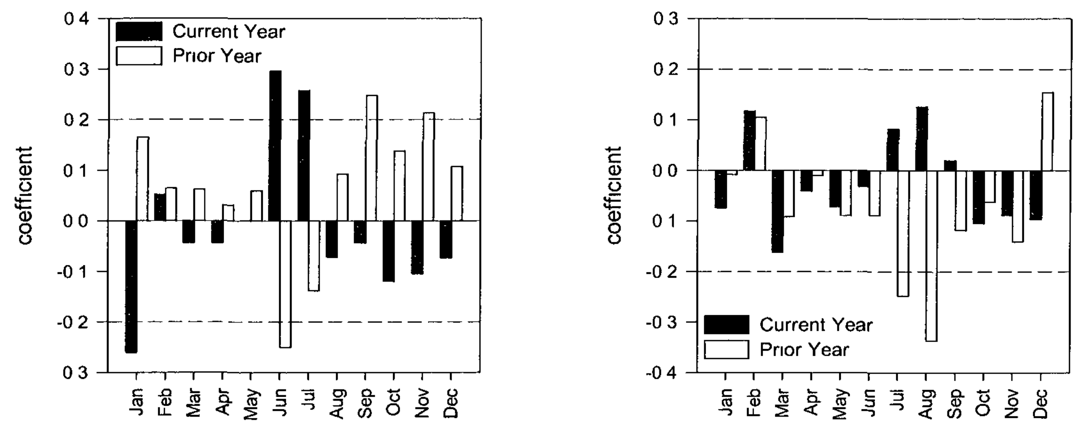
Table 3.2 Seasonal climate & PCA correlations

	Yukon		**Northwest Territories**		
	YTPC1	YTPC2	NTPC1	NTPC2	NTPC3
Annual					
Mean precipitation	-.228*				
ENSOf	-.260*				
Continentality	.263*			.360 **	
Previous Annual					
Continentality			-.266*	-.248*	
Spring					
Precipitation		.220*			
Summer					
MSP	-.211*				
Precipitation	-.244*				
Max temperature				.307**	
Mean temperature				.340**	
Min temperature				.341**	
MWMT	.231*			.381**	
NFFD				.293**	
Previous Summer					
Max temperature		-.330**			-.281*
Mean temperature		-.317**			-.267*
Min temperature		-.249*			
MWMT		-.244*	-.298**	-.251*	
HM index			-.278*		
FFP	.283**			.246*	
bFFP			-.264*		
eFFP				.307**	
Previous Autumn					
Max temperature	.259*				
Mean temperature	.284**				
Min temperature	.296**		.233*		
Winter					
MCMT				-.225*	
Previous Winter					
Max temperature					.236*
Mean temperature			.228*		.245*
Min temperature			.233*		.248*
Precipitation	-.227*				

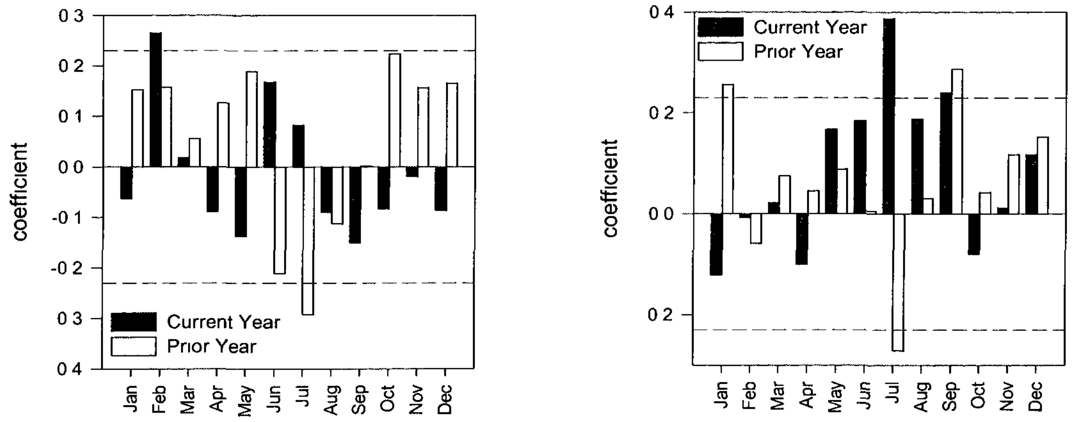
** = $p < 0.01$; * = $p < 0.05$; MSP = mean summer precipitation (May – Sept); MWMT = mean warmest monthly temperature; MCMT = mean coldest monthly temperature; HM index = heat-moisture index, a measure of drought; NFFD = number of frost free days; FFP = frost free period (continuous); bFFP = first Julian day of frost free period; eFFP = last Julian day of frost free period

Figure 3.1 Current and prior year monthly climate correlations

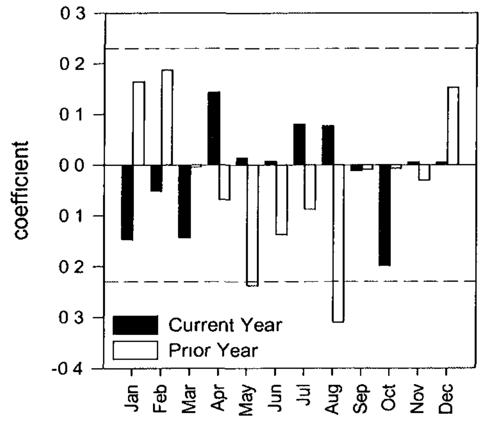
YTPC1 Monthly Mean Temperature Correlations **YTPC2 Monthly Mean Temperature Correlations**



NTPC1 Monthly Mean Temperature Correlations **NTPC2 Monthly Mean Temperature Correlations**

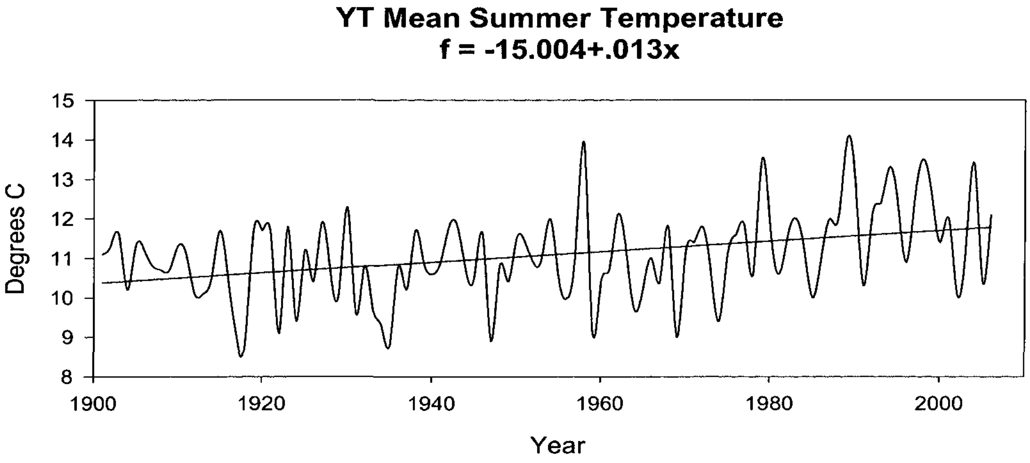


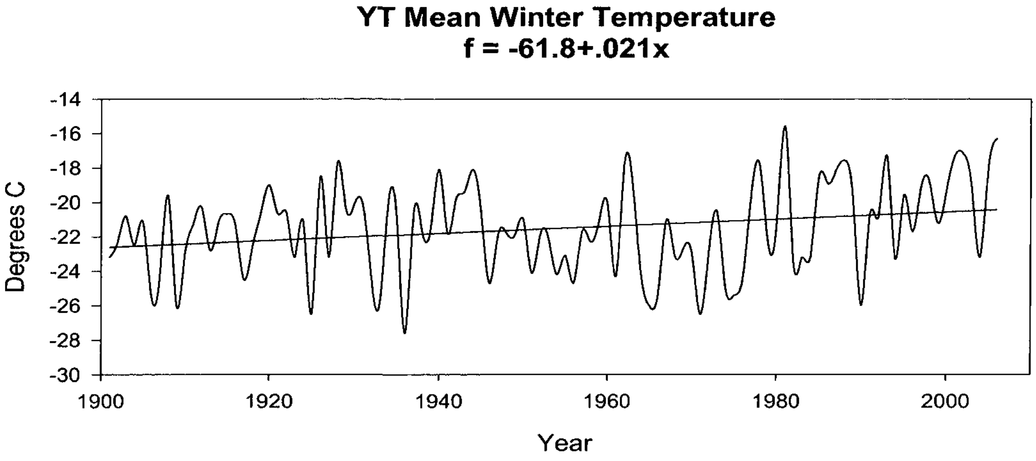
NTPC3 Monthly Mean Temperature Correlations

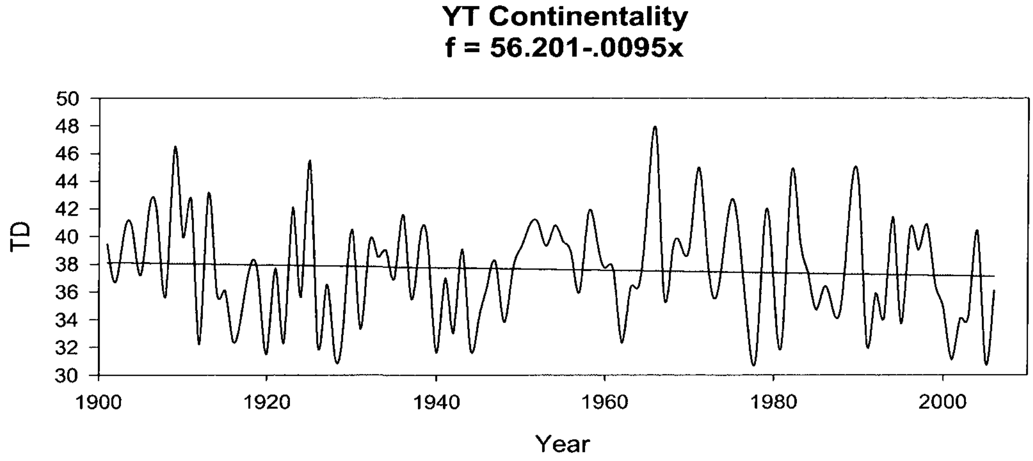


Dashed lines indicate 95% significance level Climate data was derived from ClimateWNA v 4 521

Figure 3.2 Temperature and continentality trends in Yukon study area

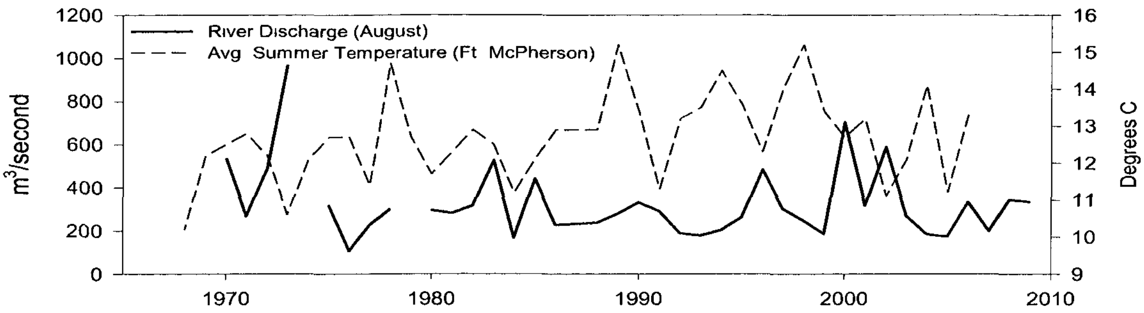


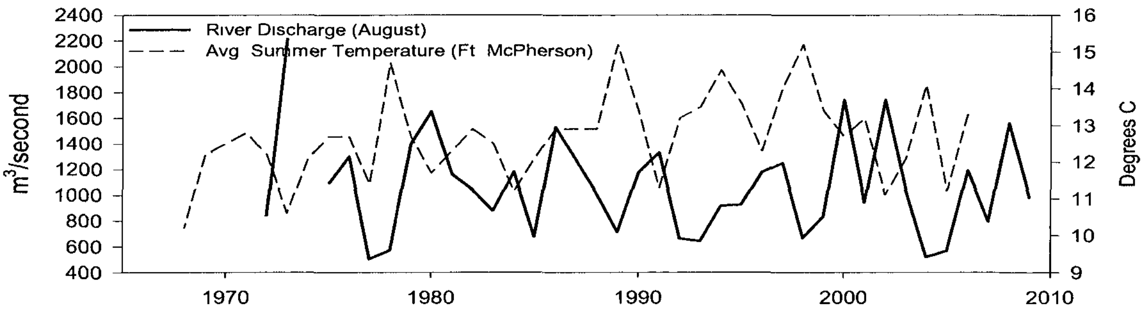


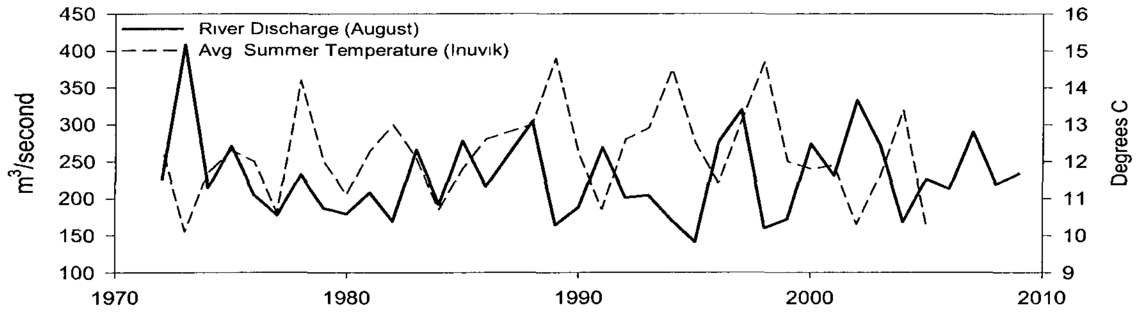


Both summer and winter mean temperatures are increasing in northern Yukon near our study sites, though winter temperatures are accelerating more rapidly This results in a decreasing continentality trend, as the difference between extreme seasonal temperatures grows less (Data obtained from ClimateWNA v 4 52)

Figure 3.3 Concurrent river flows and temperature trends in the NWT

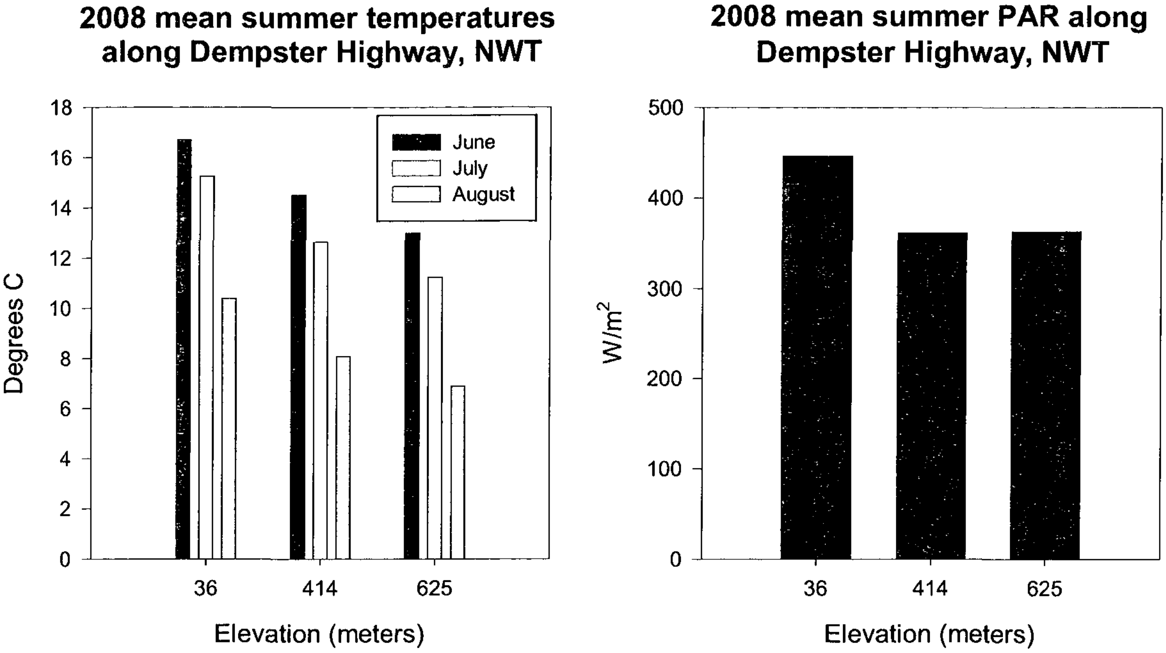

Arctic Red River Discharge (mouth)
r = -.430 (p = 0.01)


Peel River Discharge (above Ft. McPherson)
r = -.472 (p = 0.005)


Mackenzie River Discharge (east channel)
r = -.433 (p = 0.012)

River flows frequently negatively reflect the concurrent mean summer temperatures. Warm summers will often be accompanied by lower moisture levels, indicated by decreased river flows, as a result of decreased precipitation, earlier and faster snowmelt, and/or increased evaporation. (Hydrologic data obtained from the Water Survey of Canada (Environment Canada), http://www.wsc.ec.gc.ca/applications/H2O/index-eng.cfm?stype=station)

Figure 3.4 Climate trends along the Dempster Highway, NWT



Data derived from mobile HOBO climate stations during the summer of 2008, showing decreasing temperatures and PAR (photosynthetically active radiation) with increasing elevation. The low elevation (36 m) station was located at the Fort McPherson airport; the mid-elevation station was located near the sites represented by NTPC2; and the high elevation station is located within the Richardson Mountains near Wright Pass. The decreasing PAR is likely indicative of increased cloudiness near the mountains due to orographic effects.

Chapter 4: Summary

4.1 Introduction

This study aimed to partially fill knowledge gaps concerning radial tree growth and climate at the latitudinal treeline in northern Yukon and Northwest Territories. Tree ring chronologies were sampled in two adjacent, environmentally distinct regions within the forest-tundra ecotone in order to explore the importance environmental variation has on the climatic growth responses of spruce. Specifically, we sought to a) examine radial tree growth patterns across an environmental gradient in northern Canada; b) identify key environmental features that affect how tree growth responds to climate within the forest-tundra ecotone (Chapter 2); and c) identify important climatic drivers of tree growth as they relate to the environmental features established in the previous step (Chapter 3). Additionally, we assessed the feasibility of using modelled climate data in lieu of climate station data, in order to address issues related to short record time spans, missing values, and long distances between stations and study sites.

4.2 Key results and implications

Our first research question regarded how climate and tree growth relationships change across an environmental gradient at the northern treeline in northwestern Canada. We tested the hypothesis that tree growth would react to climate differently between and within the two study areas, and found that environmental variation can affect the way trees respond to climate at the latitudinal treeline. Following this, we asked what particular environmental characteristics determine the way tree growth responds to climate, hypothesizing that growth response would be dependent on landscape features and spatial scales unique to each study area and sampling outcome. We found that growth patterns were indeed affected by the spatial scale at which they were observed, while ecoregional delineations, including boundary zones, appear to be an important determinant of climate and tree growth relationships.

In the NWT study area, growth variation was distinctly divided between two adjacent ecoregions and a third transition area along the boundary between the two regions, which suggests that the bioclimatic, topographic, and hydrologic conditions unique to any given northern ecoregion, combine to create distinctive tree-ring records of climate. This is clearly evident in the study area, as the Mackenzie River delta environment and climate differs greatly from the surrounding ecoregions.

In the Yukon study area, one ecoregion was sampled much more thoroughly than those in the NWT study area. Here, the underlying environmental characteristics of this ecoregion were theoretically similar at all sites, thus enabling the effect of other sub-ecoregional environmental traits to become apparent in the tree-ring records. Specifically, slope gradient was found to be a primary determinant of tree growth response to climate, an important effect that is apparent at a local spatial scale, but is likely obscured – possibly by differences in sampling intensity in this study – at larger, regional scales, such as the NWT study area. Steeper slopes likely exacerbate moisture deficiencies, as they receive more direct solar insolation that in turn warms (and dries) soils. Consequently, trees growing on steeper slopes in high latitude regions will tend to reflect moisture limitations in their tree-ring patterns. Conversely, lower gradient slopes tend to have deeper soil active layers, more soil moisture, and less solar heating, and trees on these sites are more likely to respond to temperature limitations.

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Thirdly, we aimed to illuminate the most influential climate components to tree growth within the context of the environmental variability identified in the previous steps. We hypothesized that summer temperature is not the only climate parameter to have a significant effect on growth, as the general paradigm of the climatic control of the northern treeline suggests. We found that while summer temperature does impart a substantial influence on tree growth, other variables such as prior season autumn temperatures and frost free period (i.e. growing season length) often exacted more significant impacts based on certain environmental settings. Tree growth on high gradient slopes appeared to be more sensitive to moisture deficits, the steeper slope angles seemed to hold less soil moisture, while simultaneously being prone to more direct (i.e. increased) solar heating and drying. Traditional summer temperature limitations were found in the mountain foothills in the NWT study area, but the effect was lessened within the Mackenzie River delta valley, where slightly more favourable growing conditions tended to promote negative, lagged relationships with summer temperatures. This finding underscores the importance of recognizing the variability of climate and tree growth relationships, and challenges the notion that summer temperature is the primary control throughout the entire circumpolar region.

Last, we asked how variable landscapes may contribute to cases of disparate tree growth, where the commonly-held assumption of dominant summer temperature controls was not evident. We hypothesized that previously indentified climatic influences, namely drought, could be attributed to variable landscapes. We found evidence suggesting that environmental variation may in fact be a contributing cause to previously reported instances of disparate growth. The results from the Yukon study area suggest that slope gradient is an important consideration when choosing sites for polar-region climate reconstructions. Even within a single ecoregion, choosing sites from a wide range of slope gradients will lead to a variety of climate signals amongst the tree-ring records, which may potentially create spurious and undesirable results, either with weak, washed-out climate signals or altogether false representations of the actual conditions. This could prove to be an underlying cause of the reported 'divergence problem' at many northern sites. Many tree-ring studies have reported disparate growth responses to summer temperatures, but no definitive cause has yet been found, though it is likely a result of many confounding factors. Thus far, the solution has been to identify individual trees with positive summer temperature correlations to be used for climate reconstructions and predictions. We suggest that by restricting the sampling strategy to low gradient slopes, as well as avoiding climatic "oases" such as large river deltas and their immediate surrounding landscapes, more positively responding (to summer temperature) trees will be present. This likely will not fully alleviate the problem of encountering disparate growth trends; however, it is a feasible, better informed approach that is less likely to produce inaccurate observations of paleoclimates. Factoring in slope gradient along with already-established standard site selections criteria, such as maintaining similar aspects, species, and stem densities, while keeping in mind the suitability and potential problems of sampling within a given ecoregion, is an essential step for future dendrochronology studies conducted in high-latitude environments.

In addition to the specific research questions, our findings also indicate a high degree of spatial complexity within and between high latitude environments. Variable tree growth was reflected by the degree of biophysical and climatic variability inherent to various spatial scales. This is a critical notion when considering the response of the northern treeline to climate change, as it is likely to exhibit a range of responses of radial growth, densification, and recruitment across the entire circumpolar region. Future studies that aim to reconstruct paleoclimates and make projections about future treeline conditions need to consider to spatial scale from which they draw their conclusions. If the goal is to make general assessments and predictions for broad regions, countries or continents, then using the ecoregion as a unit of observation would be most useful and informative. However, for local mitigation planning and management purposes, smaller scale monitoring would be more appropriate. This would require a more thorough understanding of the environment of a specific ecoregion, and acknowledge that forests will still exhibit variable responses to climate. For instance, slope gradient was found to be a primary environmental trait affecting tree growth, although it is unclear if this remains true for other regions in the North. However, because solar incidence angles are extreme at high latitudes, it is likely that slope gradient would be an important consideration in most if not all northern sites.

Finally, this study demonstrates the potential utility of modelled climate data in areas without long-term, representative climate station data. Uncertainties do exist regarding the accuracy of the modelled data, but it appeared to be an adequate representation of local conditions. For this study, absolute values were not as important as was capturing trends in the climate data that could be reflected in the tree-ring chronologies.

4.3 Limitations and future research

This study was conducted in an area that has received relatively little attention from the scientific community, particularly researchers observing the latitudinal treeline. Much of the supporting research used in support of our study was conducted in Alaska or eastern Canada.

Though similar in regards to general characteristics of sub-Arctic North America, they are still relatively distinct from our study area. As such, little precedence has been established for dendroclimatological studies in northern Yukon and NWT. Therefore our investigation was relatively exploratory in nature, lacking substantial prior knowledge or experience in this specific region of Canada. As a result, our observations and conclusions are relatively broad, but will hopefully serve as a viable platform from which future investigations will originate.

Our sampling strategy was also hampered by being mostly confined to the course of the Dempster Highway. As a result, we were required to sample more intensively within a single ecoregion in Yukon, allowing us to observe patterns at a smaller, localized scale. In the NWT however, the highway spanned a greater variety of ecoregions, thus allowing us to capture a larger range of conditions, at the expense of intensive sampling similar to that in the Yukon study area. This sampling strategy provided both opportunities and limitations for our analyses and subsequent interpretations, allowing us to find significant evidence of the role of environmental variation within different spatial scales, but leaving us unable to compare the two study areas on an equal basis. Our findings would be greatly substantiated by applying the sampling strategy from each region to the other; that is, look for and compare environmental attributes that operate at similar scales across both regions. This would enable us to better observe spatial transitions of environment and tree growth in this area. However, doing this would require much more time, effort and funding, as areas beyond the highway are much more difficult and time consuming to access.

Also, this study was limited by a lack of sufficient, reliable and representative climate data. The nearest long-term (e.g. longer than 80 years, about the length of our tree ring chronologies) climate station was located over 400 km away in Dawson City, Yukon, which we determined would not accurately reflect the conditions in the forest-tundra interface in northern Yukon, let alone across the mountains in the Mackenzie delta region. Other stations closer by were either relatively short time spans, replete with missing values, located in environments much different that the study areas (e.g. Old Crow flats), were not accurately adjusted for changes in measurement devices or techniques, or more often a combination of most of these factors. Therefore we used modelled climate data from ClimateWNA v.4.52, a model that was developed in British Columbia and recently updated to include the entire western North America. It may be likely that the authors of the model did or could not account for the extreme and variable nature of climate in the Arctic, but we believe that it could still provide a relatively accurate representation of local conditions. However, as with any climate study in the far North, there is a large degree of uncertainty regarding the exact values and precise behaviour of climate, and thus conclusions based on any source of Arctic climate data should be regarded with a degree of reservation.

This study could be further enhanced by utilizing the absolute ring width measurements and converting them into basal area measurements, as opposed to converting widths to unit-less indices as was done in this study. Measurements were standardized in order to better observe and analyze relative growth trends between sites. Using basal area measurements would provide a means to assess the actual physical growth gains and declines, which in turn could facilitate discussions and conclusions regarding the carbon cycling capacity of the boreal forest. As well, a tangible measure of growth trends would be more useful for forest managers and users, as it would more accurately represent the physical changes occurring on the landscape.

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Much opportunity exists to expand upon this research. Aside from increasing the scope and sampling power of this initial study, one relevant topic would be to quantify the effect of various aspects of environmental variation on divergent growth responses. This would entail categorizing individual trees based on their response to summer temperatures, and then looking for group differences based on slope gradient or ecoregion. This would lend credible evidence towards a determination of the driving mechanisms of divergent tree growth. Another useful future endeavour would be observing the climate and tree growth trends through time, and assessing the relative stability of these relationships. These temporal trends could be linked to larger scale climatic patterns, including general circulation patterns such as the Arctic Oscillation or the El Niño-Southern Oscillation indices. This would enable better predictive modelling and projections of future conditions by incorporating a greater degree of variables in the Arctic biosphere.

4.4 Conclusions

This study illustrated the complex nature of climate and tree growth relationships as they occur amongst varying environments and spatial scales in the Arctic. Our results support an improved understanding of the northern treeline, and will contribute to the fast expanding knowledge of latitudinal treeline dynamics. Arctic ecosystems are expected to continue changing at a rapid pace in response to concurrent climatic change, which will necessitate prompt, informed, and versatile planning and management efforts to ensure successful adaptation and mitigation strategies. The Arctic treeline remains a relatively underdeveloped area of research, yet it will serve as a sentinel of coming environmental change. Thus, it will prove sensible to invest further efforts into understanding the complex ecology of this critical component of the Arctic biome.