FACTORS INFLUENCING THE GROWTH OF WHITE SPRUCE (*PICEA GLAUCA*) IN THE MACKENZIE DELTA, NT

by

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ABSTRACT

The growth response of white spruce in the Mackenzie Delta, NT to climatic, non-climatic and weather variables in 2006 and 2007 was investigated. Analysis of increment cores from 42 trees at the study site identified three different sub-populations of white spruce. Positive responders had significant, positive response to growing season June temperatures, while negative responders had significant, negative relations to previous June/July temperatures. Active layer depth was significantly different between positive responders and negative responders. Because of this difference, it is hypothesized that an increased availability of soil moisture to the shallow root systems late in the growing season reduced moisture stress in the positive responder sub-population. Along with high-resolution measurements of tree growth that revealed a response of a negative responder to precipitation, these factors suggest that temperature-induced moisture stress may influence individual growth response to climate.

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TABLE OF CONTENTS

CHAPTER ONE: OVERVIEW AND OBJECTIVES

CHAPTER TWO: THEORETICAL LITERATURE REVIEW

CHAPTER THREE: SITE DESCRIPTION AND METHODOLOGY

CHAPTER FOUR: SUB-POPULATION GROWTH RESPONSES TO CLIMATE AND POTENTIAL ENVIRONMENTAL CONTROLS

CHAPTER FIVE: INTRA-ANNUAL TREE GROWTH RESPONSE TO WEATHER

CHAPTER SIX: SUMMARY OF RESULTS AND CONCLUSIONS

LIST OF FIGURES

LIST OF TABLES

Chapter 1

Overview and Objectives

1.1. Introduction

This thesis investigates the response of white spruce (*Picea glauca* (Moench) Voss) in the Mackenzie Delta, NT to environmental, climatic and weather variables. White spruce are one of the most productive and widespread species within the sub-Arctic and boreal ecosystems that exist across the circumpolar north. The boreal forest covers approximately 4 million km^2 of northern Canada and has a large influence on the global climate system because of its identification as a major component of the global terrestrial carbon sink (Chapin et al. 2000; Myneni et al. 2001; Henry 2002). Year-round measurements made by the BOREAS project found that the boreal forest could have an uptake rate of 80 g (C) m^{-2} per year. However, if the boreal forest accounts for the entire sink or if it could even be a source of carbon sometimes is unknown because of its heterogenous nature, year to year climate variability and large influence of disturbance events, which prevent accurate scaling-up of site measurements (Black et al. 2005).

Northern regions of the boreal forest are expected to be the first to experience unprecedented rates of warming associated with human activities. During the 20th century, the western Arctic has experienced the most drastic surface air temperature warming within Canada, with an increase of approximately 2°C over the past 50 years (ACIA 2004). Previous research has identified summer temperature as the primary control on tree growth at northern latitudes (Garfinkel and Brubaker 1980; Cropper and Fritts 1981; D'Arrigo et al. 1992). Most studies suggest that increased temperatures due to recent warming would lead to greater tree growth (Zhou et al. 2001), and northward expansion of the treeline (Prentice et al. 1991). Increases in growth and range expansion could enhance the capacity of the boreal forest to store carbon. Increased sequestration of carbon could moderate future levels of atmospheric carbon dioxide and global temperatures. However, recent research from Alaska, and northwest Canada has found that radial growth of some white spruce trees has actually decreased over this period when air temperatures have increased rapidly (Jacoby and D'Arrigo 1995; Barber et al. 2000; Pisaric et al. 2007). In fact, recent warming has led to diverging growth responses of individual trees at many sites in the northwestern boreal forest. Some individuals have exhibited decreasing growth trends, while others have experienced increased growth in response to warmer temperatures. These sub-populations have been termed negative responders and positive responders (Wilmking et al. 2004; Wilmking et al. 2005). Currently, the mechanism(s) causing these diverging growth responses is unknown.

The discovery of an apparent non-linear response of trees in the northern boreal forest to temperature is surprising. Paleoclimatic research is predicated on the use of linear relations between natural proxies and climate data to establish estimates of past climate in order to understand the natural variability of the climate system and provide a reference for current climatic change. If there are negative growth responses to temperature across broad regions, it could limit the capacity of the boreal forest to sequester atmospheric carbon and unduly influence the outputs of carbon-cycle models.

To improve both climatic reconstructions and carbon-cycle models, detailed investigations of the factors that drive the growth of trees are necessary. These studies should approach from both top-down (influence of climate on multi-decadal scales) and bottom-up (influence of weather conditions on intra-annual scales) approaches in order to improve our understanding of tree growth.

1.2. Research Objectives

The purpose of this study is to determine the climatic and environmental factors that influence the radial growth of white spruce. Tree growth and meteorological data were collected for two growing seasons (2006 and 2007) at a single site (informally named Blueberry) near latitudinal treeline in the Mackenzie Delta, NT. The trees at this site have revealed diverging growth responses since the late 1930s (Pisaric et al. 2007). Based on the presence of these diverging growth responses, the following research objectives were proposed:

1. Determine if there are statistical differences in the microsite conditions under which the sub-populations of white spruce grow.
2. Determine the climatic variables that influence the different growth responses of white spruce.
3. Describe the phenology of growth of white spruce trees in this region.
4. Examine the short-term weather conditions that influence tree growth at treeline in the Mackenzie Delta, NT.
5. To produce a conceptual model of the climatic/environmental factors that influence tree growth within the Mackenzie Delta, NT.

1.3. Structure of Thesis

This thesis consists of six chapters. Chapter two provides a review of controls on the distribution of the boreal forest, the results of regional tree-ring studies, the physiology of tree growth and intra-annual investigations of tree growth using dendrometers. Chapter three describes the study site and the methodologies of both the field and the laboratory. Chapter four presents environmental and ecological data and investigates the response of trees to climate. Chapter five discusses the influence of weather on white spruce growth and presents a conceptual model of the important factors controlling tree growth in this region. Chapter six summarizes the research results, presents conclusions and offers suggestions for future research.

Chapter 2

Theoretical Literature Review

2.1. Introduction

A study of factors that influence tree-growth in a sub-Arctic environment requires an understanding of (1) the importance of the boreal forest and controls on its distribution, (2) the current knowledge of regional tree response to climate, and (3) the physiology of northern tree species and how this controls growth. This chapter reviews the literature on each of these areas and the methodologies used in this thesis.

2.2. The Boreal Forest

The boreal forest forms a broad geographic region that encircles the globe and spans 2000 km from north to south in Canada. It covers approximately 35 % of Canada and more than 50 % of Alaska (Fig 2.1) (Henry 2002). Characteristics of the boreal forest such as albedo, hydrological feedbacks and changes in the flux of gases such as CO_2 and CH_4, all play a role in the global atmospheric system. There is evidence that the due to its size (covering 22% of the global terrestrial surface) the boreal forest plays an essential role in maintaining the balance of the global climate system (Chapin et al. 2000). Climatic and environmental changes are already being documented in northern regions, including increases in average air temperature, changes in precipitation patterns, decreases in snow cover, permafrost degradation, and an increase in both the frequency and extent of disturbance events (Weber and Flannigan 1997; Serreze et al. 2000; Shaver et al. 2000; ACIA 2004). How changing climatic conditions such as these will influence

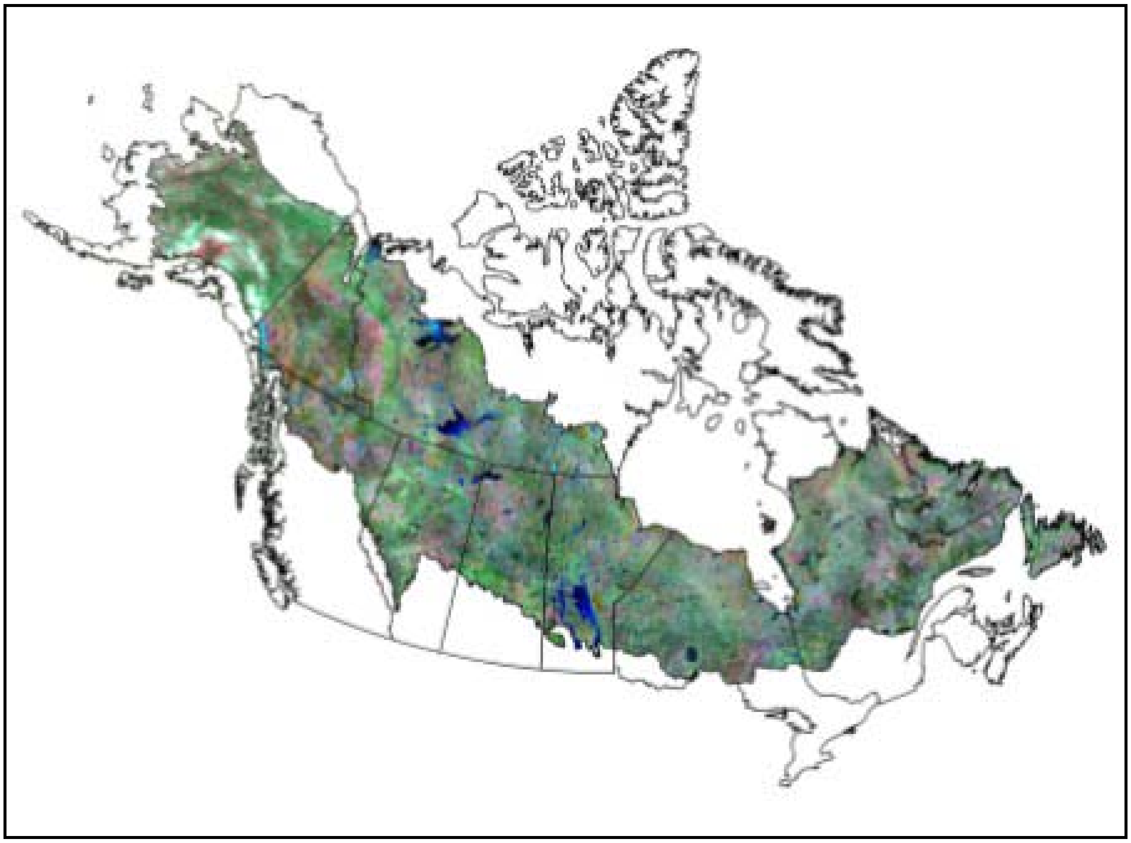

Figure 2.1. Map of the distribution of the boreal forest within North America (Natural Resources Canada, Canadian Forest Service – Pacific Forestry Centre 2005).

the functioning of the boreal forest and possibly affect the global climate system are not fully understood (Chapin et al. 2000).

The boreal forest is predominantly composed of coniferous trees with species changing across regions, each adapted to specific environmental conditions. The distribution of vegetation within the boreal forest is closely linked to climate and soil conditions (Larsen 1980a). Palynological records show species have migrated north and south of their current range many times during the Quaternary in response to the advance and retreat of ice sheets (Ritchie 1984). If favourable climatic conditions exist, species are capable of extending their range.

The forest-tundra ecotone can be studied as an example of the relation between climate and vegetation distribution. In 1936, Wladimir Köppen suggested that the position of northern treeline corresponds to the 10°C isotherm in the warmest month (July). The correlation between isotherms and the position of northern treeline was improved by Otto Nordenskjöld by also accounting for the mean temperature of the coldest months (January/February) (Henry 2002). Reed (1960) proposed that the underlying reason for this correlation with temperature was the position of three primary air masses in the region. These air masses, the Arctic, Pacific and Continental, are homogenous regions of atmospheric conditions that extend horizontally for hundreds or thousands of kilometers. By documenting the summer position of each air mass, Reed (1960) determined that the position of treeline coincides with the average summer position of the Arctic air mass. North of this, temperatures are too cold to permit tree growth or reproduction. Bryson (1966) refined Reed’s hypothesis and using a different methodology confirmed that the treeline is closely associated with the average summer position of the Arctic air mass meeting the Continental and Pacific air masses. Bryson also showed that the southern boundary of the boreal forest corresponds to the average winter positions of these three air masses. Krebs and Barry (1970) expanded this analysis by showing a strong correlation between the positions of the same air masses with the forest-tundra boundary across Eurasia. Numerous other studies also conclude that summer temperatures are the primary factor controlling the position of the northern treeline (Jarvis et al. 1989; Starfield and Chapin 1996; MacDonald et al. 1998; Grace et al. 2002).

2.3. Regional Response of Vegetation to Climate

The factors that limit the distribution of trees beyond treeline are also responsible for controlling growth within their range. Dendroclimatological studies from the boreal forest correlating tree growth with climatic variables have concluded that temperature is often the primary factor influencing tree growth. Garfinkel and Brubaker (1980) used multivariate statistical comparisons to determine climatic limitations on tree growth in the Brooks Range, Alaska. They found that radial growth of white spruce was positively influenced by warm growing season temperatures. Cropper and Fritts (1981) examined over 100 tree-ring chronologies (primarily white spruce) from the subarctic region of Alaska and northwestern Canada and found positive correlations with summer temperatures. Numerous studies conducted by Jacoby and D’Arrigo have also observed this link between summer temperatures and tree growth near the subarctic treeline (D'Arrigo et al. 1987; D'Arrigo et al. 1992; Jacoby and D'Arrigo 1995). Based on these relations Jacoby and D’Arrigo were able to confidently reconstruct summer and annual temperatures from white spruce tree-ring chronologies across northwestern Canada and Alaska (Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1993). A review article that focused on European species response to temperature found that conifer growth increased as temperatures increased (Saxe et al. 2001). In addition, an ecological model suggested that future increases in temperature during the next 200 years could lead to a shift of >1000 km in the position of the treeline across Eurasia (Prentice et al. 1991).

While the numerous dendroclimatological studies discussed above illustrate the link between tree growth and summer temperatures in the subarctic, recent data from satellite surveys provide additional support for this hypothesis. Advanced Very High Resolution Radar (AVHRR) satellite imagery reveals an increase in growth at northern latitudes (> 45°N) based on photosynthetic rates from a 10-year period (1981 to 1991), consistent with an increased growth response to temperature (Myneni et al. 1997). Most of the increased growth above treeline has been attributed, based on analysis of historic aerial photographs, to increased abundance of shrubs (Sturm et al. 2001). The increases in vegetation and growth in the northern forest-tundra ecotone are probably due to an increase in the length of the growing season (Myneni et al. 1997). However, a study using a 22-year record of AVHRR satellite observations (1982-2003) across the circumpolar north found that there were significant differences between vegetation cover types (Bunn and Goetz 2006). Tundra consistently showed a positive “greening” trend, and forested areas (regardless of forest type) were characterized by declining activity or “browning”, especially those with higher density (Bunn and Goetz 2006). Bunn and Goetz (2006) also found that there were significant seasonal trends in the data with tundra areas showing “greening” over the entire May-August period, however most forested areas showed significant “greening” during May and June and then widespread reduction in photosynthesis during July and August. This pattern was also observed in a study that concluded there was a net photosynthetic gain in the spring, which was offset by large losses of photosynthetic production in the late summer (Angert et al. 2005). This was attributed to late-summer drought conditions counteracting the effects of warmer springs.

Current understanding suggests that vegetation will respond gradually to climate change as species move into zones of climatic tolerance. However, thresholds may exist in these systems and if surpassed, could lead to a rapid shift of ecological state (Chapin et al. 2004; Smol and Douglas 2007). Alteration of these ecosystems could affect many aspects of the boreal system including changes in the landscape, regional-scale albedo and possible shifts in the flux of the three most influential greenhouse gases, carbon dioxide (CO_2), methane (CH_4) and water vapour. Each of these changes could have impacts beyond the local scale, possibly influencing global climate.

2.3.1. The Divergence Issue

Rapidly warming temperatures across northwestern North America are affecting northern ecosystems. Temperature has been identified as the primary factor influencing the growth of vegetation in these regions. This relation infers that warmer temperatures should lead to increased tree growth. However, this has not been the case across the circumpolar boreal forest. There has been an observed divergence (a negative relation) between tree growth (primarily ring widths) and summer temperatures during the last half of the 20th century (Briffa et al. 1998b; Barber et al. 2000; Lloyd and Fastie 2002; Briffa et al. 2004; D'Arrigo et al. 2004; Wilmking et al. 2004; Driscoll et al. 2005; Wilmking et al. 2005; Pisaric et al. 2007; Wilson et al. 2007; D'Arrigo et al. 2008). These studies of tree growth in northern regions have found that despite historical agreement between temperature records and ring width, during the past 60-70 years tree growth has not matched increases in air temperature and in some cases has become negatively correlated with summer temperatures.

2.3.1.1. Definition of Divergence

In the past 15 years, tree-ring records developed from sites that were previously considered temperature sensitive have revealed weakened relations between tree growth and temperatures during the last half of the 20th century (Jacoby and D'Arrigo 1995; Briffa et al. 1998b; Vaganov et al. 1999; Barber et al. 2000; Lloyd and Fastie 2002; Briffa et al. 2004; D'Arrigo et al. 2004; Wilmking et al. 2004; Driscoll et al. 2005; Pisaric et al. 2007; Wilson et al. 2007). Two different definitions of divergence have been proposed in the literature. The first, expresses divergence as the underestimation of the instrumental temperature record by reconstructed temperatures based on tree ring chronologies (D'Arrigo et al. 2004; Wilson et al. 2007) (Fig. 2.2). The second defines the divergence problem as the difference in growth trends between sub-populations of trees located at the same site (Wilmking et al. 2004; Wilmking et al. 2005). Three sub-populations have been defined in the literature: positive responders, negative responders and those that do not have a significant response to climate. Two distinct methodologies have been used to separate these groups. The first sorts trees from a site into two groups with a cluster analysis of correlation scores of standardized individual trees with temperatures (Wilmking et al. 2004). Positive responders were trees that had a correlation

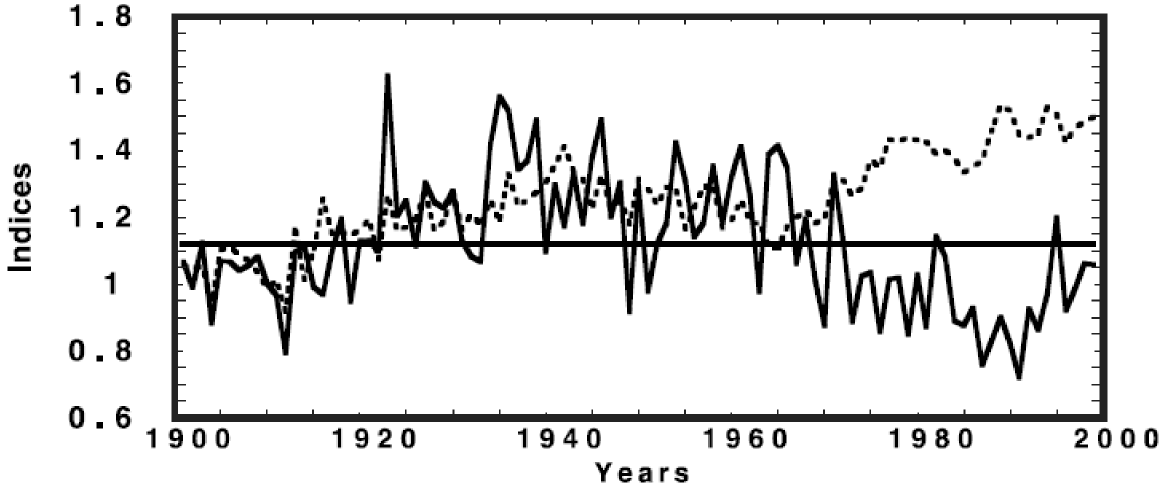

Figure 2.2. Linear relation between temperature and tree ring width. Actual (solid line) tree ring width indices from TTHH chronology. Estimated (dashed line) tree ring indices based on Dawson temperatures from 1901-1964. (From D'Arrigo et al. 2004).

score of ≥ 0.25 between ring width and spring temperatures. Negative responders were individuals that had a correlation score of ≤ -0.25 between ring width and previous July temperatures. The third group was defined as trees that had no significant correlation to either temperature variable. The second method was a visual categorization of trees that separates individuals into two groups of positive and negative responders during ARSTAN interactive detrending (Pisaric et al. 2007). Positive responders were trees that closely followed northern hemisphere temperature trends. These trees generally showed a growth increase throughout the 20th century (Fig. 2.3a). Negative responders were individuals that showed a decreasing growth trend after the late 1930s that continued until approximately the 1980s and later in some cases (Fig. 2.3b).

2.3.1.2. Development of the Divergence Issue

In the early 1990s, several authors used forest gap models to investigate possible responses to future increased climate warming (Bonan 1989; Smith and Shugart 1993). Bonan (1989) attempted to describe the ecological factors that limit growth in northern forests. Smith and Shugart (1993) used the output of two different general circulation models [Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Laboratory (GFDL)] to simulate current (1 x CO2) and future (2 x CO2) climatic conditions on vegetation. Both models found that productivity was less than expected in northern boreal forests, especially on white spruce-dominated, south-facing slopes where future temperatures were predicted to exceed the ecological range of the species. The limiting condition appeared to be increased evapotranspiration associated with warmer temperatures. The increased productivity expected in these areas was limited by apparent

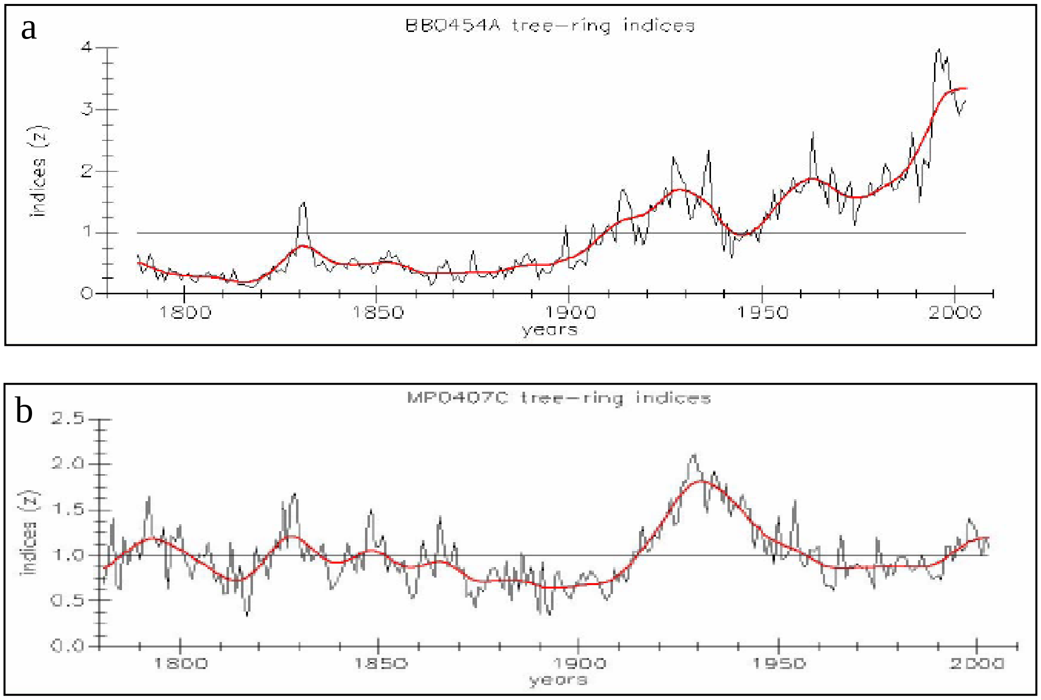

Figure 2.3. Standardized tree-ring widths from the Mackenzie Delta showing (a) positive responders and (b) negative responders (Data from Pisaric et al. 2007).

moisture stress. Both of these studies contained limitations such as using a single-step equilibrium climate model. However, despite the shortcomings of the models, both studies found that the relation between vegetation and temperature in northern ecosystems was more complex than expected.

The first dendroclimatological study to identify a possible divergence between temperatures and tree growth was Jacoby and D’Arrigo (1995). They observed that both ring width and latewood density chronologies from white spruce collected at treeline in central and northern Alaska had a weakened temperature signal in the most recent decades (from the 1970s onward). Despite higher growth rates in the 1930s and 1940s when temperatures were warm, growth did not match increasing temperature trends after the 1970s (Jacoby and D'Arrigo 1995). However, a significant increase in sensitivity of ring width to precipitation was noted after 1970.

Briffa et al. (1998a; 1998b) found a similar loss of sensitivity between tree growth and temperature from a study of over 300 different tree ring width and latewood density chronologies from conifer species collected across the circumpolar north. The goal of the study was the identification of large-scale growth signals by averaging the sites into eight regions, but the decrease in sensitivity was unexpected. Both ring width and latewood density were positively correlated with summer temperature, but the strength of the correlation changed over time. An example is the overall regional latewood density chronologies that closely followed the decadal temperature trends of the mid 20th century, but since the mid-1960s, have progressively decreased as northern temperatures have increased (Briffa et al. 1998b).

Vaganov et al. (1999) investigated the loss of sensitivity between temperature and tree growth at treeline in Siberia using correlations between pentads (periods of 5 consecutive days) of mean daily temperature and site-averaged ring width. The authors proposed that there was a short period at the start of the growing season when temperature influences cell production and controls the seasonal ring width. Higher temperatures during this early part of the season lead to increased cell production and consequently a larger annual growth ring. Vaganov et al. (1999) suggested that the reduced sensitivity found by Briffa et al. (1998b), and in their own sites, was caused by a delay in the initiation of cambial activity caused by increased winter precipitation and a delay in snowmelt. This delay means that the majority of growth is no longer during the period that had previously been the one of maximum growth sensitivity to temperature.

Ring width, latewood density and carbon-isotope records from white spruce stands in interior Alaska revealed a decrease in radial tree growth with increased temperatures in this region as well (Barber et al. 2000). Historical climate data from Fairbanks, AK was used to create a combined index of temperature and precipitation. Since 1970, increased warmth and little change in precipitation correlated with reduced ring widths. This relation was supported by a significant positive correlation between maximum latewood density and late summer temperature and a significant negative correlation between $\delta^{13}C$ discrimination and summer temperatures, which both suggested increased drought stress was leading to reduced radial growth (Barber et al. 2000).

Another study conducted in northern Alaska within the Brooks Range sampled over 1300 trees at 13 sites to examine a population-wide response to climate (Wilmking et al. 2004). This was the first study to analyze divergence by examining individual tree response to warming temperatures. The authors found a similar pattern of divergence between tree growth and summer temperatures, but more importantly, they discovered that these trends were not consistent within a site. An average of forty percent of trees were considered positive responders, 36 percent negative responders and the remaining 24 percent had no significant relation to climate (Wilmking et al. 2004). Each response was present at every site, but in different relative proportions. The authors did not document a decrease in sensitivity as others had observed (Jacoby and D'Arrigo 1995; Briffa et al. 1998b; Vaganov et al. 1999). The possible reason for this was that previous studies had not investigated individual tree response and were averaging opposite responses. Wilmking et al. (2005) applied the analysis of individual trees to a series of widely-distributed, previously published sites across the circumpolar boreal forest and found separate sub-populations of positive and negative responders at all of the sites. A comparison of positive and negative responders grouped into separate chronologies reveals that significant divergence of tree growth has taken place during the last 30-50 years (Wilmking et al. 2005).

Pisaric et al. (2007) examined white spruce ring-widths in the Mackenzie Delta, Northwest Territories and found similar patterns of diverging growth and sub-populations (75 percent negative responders and 25 percent positive responders) within nine different sites. Separate chronologies of each response type were constructed and using a wavelet coherency analysis, the authors showed that the chronologies correlated extremely well with each other over the past four centuries. However, the coherency between the two chronologies broke down rapidly following the 1930s (Pisaric et al. 2007). Divergence appeared to have taken place earlier at this location than other studies have identified. This was attributed to the higher latitude of the study sites.

The identification of tree ring records demonstrating an apparent non-stationary response to climatic influences (either as a decrease in sensitivity or as shift in the primary factor influencing growth) are not limited to northern locations. An investigation of the inter-annual climate response of European larch (*Larix decidua*) was undertaken in the Italian Alps to determine if the climate growth response was stationary over time (Carrer and Urbinati 2006). The authors found that growth is correlated with average monthly temperatures from March to July, but the most sensitive variable (June temperature) showed significant transient response within the 200-year period of analysis. Similar to previous studies, there was a shift in how trees responded to climatic variables during the period of overlap between tree growth and instrumental climate data (Carrer and Urbinati 2006). An 896-year chronology of Norway spruce (*Picea abies*) from the Swiss Alps composed of both living and dead samples revealed a similar unstable response to temperature and precipitation (Büntgen et al. 2006). The authors used moving 51-year correlations and a long instrumental dataset to conclude that this shift in response was due to late-summer drought stress. Finally, a study in the southeastern United States used daily meteorological data to simulate eight tree-ring width chronologies using the Vaganov-Shaskin mechanistic model (Anchukaitis et al. 2006). The model output was compared to 10 high quality regional conifer chronologies to determine the skill of the model. The model successfully described the primary mode of variance in the actual tree ring chronologies as well as the long-term climate response. The model also revealed that there was a significant difference in late summer growth between the period from 1976-2000 compared to 1947-1975 due to the amount of available soil moisture because of a decrease in regional precipitation. The authors conclude that shifting controls on tree growth may occur due to changes in climate (Anchukaitis et al. 2006).

2.3.1.3. Potential Causes of Divergence

There have been a number of theories proposed to explain divergence (D'Arrigo et al. 2008). These include: temperature-induced moisture stress, summer temperatures surpassing physiological thresholds, increased winter precipitation, ozone concentration in the stratosphere and decreased amounts of solar radiation due to global dimming (Briffa et al. 1998b; Barber et al. 2000; Lloyd and Fastie 2002; Barber et al. 2004; Briffa et al. 2004; Wilmking et al. 2004; Driscoll et al. 2005; Wilmking et al. 2005).

Barber et al. (2000) identified drought stress as the cause of diverging growth trends in white spruce from interior Alaska. They suggested that an increase in the length of the growing season along with warmer temperatures lead to a depletion of already limited soil moisture, reducing the mid to late-season growth of the trees. Divergence has been found in many different regions, this hypothesis implies that there has been a simultaneous loss of soil moisture across broad spatial scales. Instead of temperature leading to moisture stress, Wilmking et al. (2004) found that many trees that were classified as negative responders grew in high-density upland stands and that competition between individuals leads to the onset of drought stress. However, sites in the Mackenzie Delta with very low densities of white spruce show similar populations of trees with negative responses to warmer temperatures (Pisaric et al. 2007). In a more recent paper, Wilmking et al. (2005) suggests that individual trees are becoming more sensitive to micro-site differences meaning that some, but not all trees could experience drought stress leading to sub-populations of trees with different responses to increased growing season temperatures.

The rapid changes in climate could be another factor leading to divergence. In the Mackenzie Delta region for example, summer temperatures have increased nearly 1.6°C during the past 30 years. Such increases in climate could be outpacing the physiological adaptations of trees. Above an optimum temperature, net photosynthesis declines as rates of respiration increase, causing stress to the tree and reducing growth (D'Arrigo et al. 2004; Wilmking et al. 2004). These studies determined optimum temperatures based on previous ring-widths and then determined if temperatures since the early part of this century have been exceeding that level. Alaska sites showed a significant negative response to July air temperatures over 11-12°C since 1950 (Wilmking et al. 2004). In the north-central Yukon, an optimal July-August average air temperature of 11.3°C was calculated; this temperature has been continuously exceeded following 1965 (D'Arrigo et al. 2004). Both of these studies show that once the optimal temperature is consistently surpassed, there is a significant decrease in radial growth.

In a study of conifer tree growth across treeline in Siberia, increased winter precipitation was shown to affect annual tree growth (Vaganov et al. 1999). Much of the northern boreal forest is underlain by permafrost. At the beginning of the growing season, the frozen upper layers of soil must begin to thaw prior to radial growth commencing (Jarvis and Linder 2000). Increased winter precipitation leads to increased spring snowpack and subsequently, delayed snowmelt. Vaganov et al. (1999) suggest that late snowmelt, which prevents the seasonal thaw of permafrost from reaching a depth at which trees can access soil water, delays the commencement of cambial activity and reduces total radial growth.

Decreasing stratospheric ozone concentrations have also been suggested as a possible cause of reported divergence trends. Satellite ozone data since 1979 shows a decline in ozone over the entire land area north of 40°N (Briffa et al. 2004). Some northern regions show a correlation between residuals of latewood density measurements and ozone concentrations. The reduction in ozone has also been linked to increases in UV-B radiation at the Earth's surface. Limited research suggests that enhanced UV radiation leads to decreased photosynthesis and may lead to decreased tree productivity (Briffa et al. 1998a; Briffa et al. 2004).

The decline in the amount of solar radiation reaching the earth's surface known as "global dimming" has also been implicated as a possible factor leading to tree ring divergence (D'Arrigo et al. 2008). Global dimming is believed to be caused by increased man-made pollution, including sulphate aerosols, leading to a decline in solar radiation at the surface and a global decline in temperatures between approximately the 1940s and the 1970s. Reductions of aerosol input into the atmosphere since the 1970s have led to "global brightening" during the past decade. The implication of global dimming with respect to tree growth is that northern locations, which already receive a minimal percentage of total radiation and have a short growing season, would receive even less radiation and will experience decreased photosynthetic activity. However, it must be noted that the optimum radiation level for photosynthesis peaks well before maximum output, so light levels would need to decrease substantially to have a measurable shift on growth and climate response (D'Arrigo et al. 2008).

2.4. Physiology of Boreal Conifers

Temperature is believed to limit tree growth on macro-environmental scales. However, the understanding of the physiological influence of temperature, moisture and light on the scale of individual trees is less clear. This is due in part to the fact that most studies of physiology are almost exclusively limited to seedlings and saplings, with very few taking place in natural settings. Conclusions from these studies are often tenuously applied to mature trees. Determining the possible causes of divergence is difficult until researchers obtain a greater understanding of ecophysiology. This section will introduce the current physiological understanding of the growth of conifers and outline the process of radial growth.

2.4.1 Photosynthesis and Respiration

The basis of plant growth is photosynthesis, the process by which plants capture light energy and use it to form simple sugars from carbon dioxide and water while producing oxygen (Kozlowski et al. 1997). This reaction can be summarized in the following equation:

$$6CO_2 + 12\ H_2O \rightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O \qquad (2.1)$$

Respiration is the complementary process to photosynthesis that consumes the products of photosynthetic activity (sugars and oxygen) and produces energy that plants require for growth, maintenance of tissues and reproduction:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy} \qquad (2.2)$$

Rates of respiration have been strongly correlated to growth in conifers (Kozlowski et al. 1997). If photosynthesis is limited by environmental factors, carbohydrate resources are consumed during respiration and depleted. Prolonged limitations on photosynthesis exert stress on the tree and can lead to decreased growth and even reproductive failure (Larsen 1980a). Photosynthesis and respiration are much more complex than indicated by these equations. This thesis will focus on the primary factors that influence and limit these processes.

2.4.2 Light

The general response of photosynthesis to irradiance is first linear and then as the amount of light increases there is a decrease in photosynthetic rate known as the light saturation point (Fig 2.4a) (Teskey et al. 1995). However, other factors such as temperature and water availability also influence the shape of this curve. Research has shown that the amount of chlorophyll in the foliage is strongly correlated to the shape of the light response curve (Leverenz 1987). A study of conifers in the northern hemisphere found that the highest amount of growth occurred around the time of maximum day length, not the time of highest temperatures (Rossi et al. 2006b). This was attributed to photoperiod influence and was considered an adaptation to ensure enough time to conclude growth prior to winter.

The process of respiration does not require light, but experiments have shown rates of respiration are different depending upon the level of irradiance. Plants with a C_3 carbon pathway (such as conifers) have much higher respiration rates in the light than in the darkness. This is known as photorespiration and as more carbohydrates are used in respiration, there are less available for use with maintenance and growth (Kozlowski et al. 1997).

2.4.3. Air and Soil Temperature

The rate of net photosynthesis in conifers varies across a range of air temperatures, generally declining both above and below an optimal value that is species specific. Generally, this is in the range of 15 to 30°C (Fig 2.4b) (Teskey et al. 1995). Northern conifers have narrower optima due to acclimatization to local temperature regimes, with one study showing optimum net photosynthesis for spruce seedlings between 15 and 23°C (Grossnickle 2000). High altitude conifers in the Alps have a thermal threshold for wood formation in the range of 6-8°C (Rossi et al. 2006a). Northern conifers have adapted to cold annual temperatures by producing tightly-packed needles that raise the ambient temperature at the surface of the needle closer to the optimum to increase their rate of photosynthesis (Smith and Carter 1988). The mechanism for reduction of photosynthesis in high or low temperatures is often the closure of stomata. These openings located on the leaves are the entrance for carbon dioxide and the exit for water vapour (Kozlowski et al. 1997). It has been reported that reductions in photosynthetic rate of conifers are related to a change in the structure or an inhibition of chloroplasts (Berry and Bjorkman 1980). Soil temperatures have also been found to limit rates of photosynthesis. This may be especially prominent in northern ecosystems underlain by permafrost, which keep soil temperatures low despite air temperatures exceeding the freezing point. Cold soil temperatures reduce water availability, gas exchange and root growth (Grossnickle 2000). A study of the effect of soil temperatures on stomatal conductance in white spruce seedlings revealed a threshold soil temperature of 5°C. Temperatures higher than this produced insignificant increases of photosynthetic activity (Landhausser et al. 2001).

The rate of maintenance respiration is strongly associated with both air and soil temperature. Between air temperatures of 10 and 25°C, respiration rates increase exponentially, whereas below 10°C the relation is linear (Fig. 2.4c) (Kozlowski et al. 1997). Rates of growth maintenance are less sensitive to changes in temperature except when they influence production of new tissues in the tree. On a seasonal basis, respiration has been found to begin much earlier in conifers (stems warmed to 3°C) than photosynthesis (Kozlowski et al. 1997).

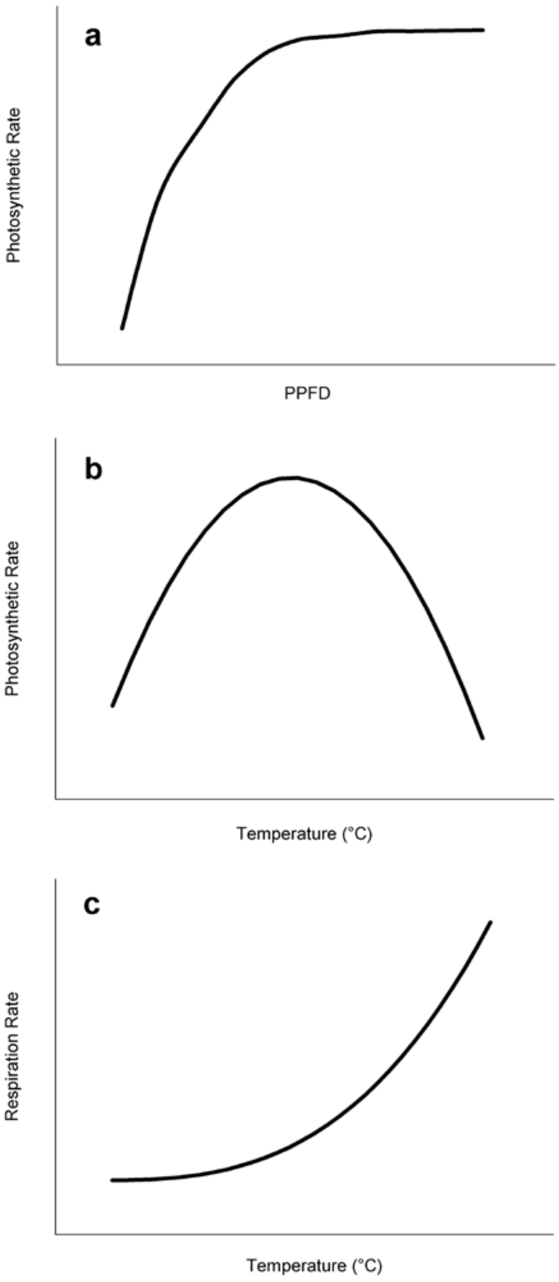

Figure 2.4. Examples of environmental effects on the photosynthesis and respiration rates of conifers. (a) Effect of light (photosynthetic photon flux density - PPFD) on photosynthetic rate (adapted from Jones 1992). (b) Effect of temperature on photosynthetic rate (adapted from Kozlowski et al. 1997). (c) Temperature influence on respiration rates (adapted from Kozlowski et al. 1997).

Landhäusser et al. (2001) showed that root respiration in white spruce increases as soil temperature increases, but above 5°C there was little difference between a growing and dormant seedling.

2.4.4. Water

Atmospheric humidity influences rates of photosynthesis by reducing stomatal conductance. As humidity falls, a stronger vapour pressure gradient and increased demand for moisture is created; this means increased water loss for a tree. To prevent this, the tree closes stomata, which limits the diffusion of CO_2 into the leaf and reduces photosynthesis (Jarvis 1976; Teskey et al. 1995). Evidence indicates that as soil moisture decreases, hormonal messengers are sent from the roots to the leaves. These hormones act to reduce conductance and conserve water, which also reduces photosynthesis (Teskey et al. 1995). The hormone that has been identified in Douglas fir (*Pseudotsuga menziesii*) and is possibly present in other conifers is abscisic acid (ABA) (Davies 1995). This hormone acts to impede growth and may be a survival mechanism for the tree (Grossnickle 2000). This is supported by the observation that evergreen conifers are a determinate growth species that will finish growing as soon as they encounter a threshold of moisture stress (Juday 2008). Excessive soil water can also limit photosynthesis due to poor aeration of the root system, which impedes water uptake (Grossnickle 2000).

Respiration is also impacted by water availability. In general, respiration is somewhat reduced by water stress, although it may increase temporarily (Kozlowski et al. 1997). More importantly, under flood conditions, excessive soil water can create anoxic conditions in the soil, which prevents respiration from occurring (Grossnickle 2000).

2.4.5. Multiple Variables

Trees are continuously exposed to a range of environmental variables. The interaction of edaphic stresses (soil water, soil temperature) with changes in the environment (air temperature, atmospheric humidity, light levels) creates different physiological responses and it is difficult to ascribe a single factor to limiting growth (Grossnickle 2000). In general, some combination of these factors plus nutrient supply limits the growth of conifers (Mooney et al. 1991).

2.4.6. Xylogenesis

Xylem is the vascular tissue that transports nutrients and water, provides structural support and acts as a storage reservoir for the tree (Kozlowski et al. 1997). Xylem along with the phloem, which transports sugars, forms the vascular system of conifers. Phloem is produced in a similar process as xylem, but proceeds outwards towards the bark. This section will focus on xylem formation because less phloem is produced annually and it has little impact on the measurement of seasonal radial growth (Kozlowski et al. 1997; Vaganov et al. 2006). Xylem cells are formed from the cambium, a single layer of cells that can undergo an unlimited number of divisions (Fig. 2.5). During the growing season, the cambium produces layers of cells capable of limited division known as xylem mother cells. Each mother cell can divide once or twice to form new xylem mother cells. Once it loses the ability to divide, the cell begins to expand and then its cell wall thickens. After completing these processes, it is considered a mature xylem cell (Vaganov et al. 2006). Ring width is a function of two factors, the number of xylem tracheid cells and the size of the cells. Seasonal dynamics, genetics and

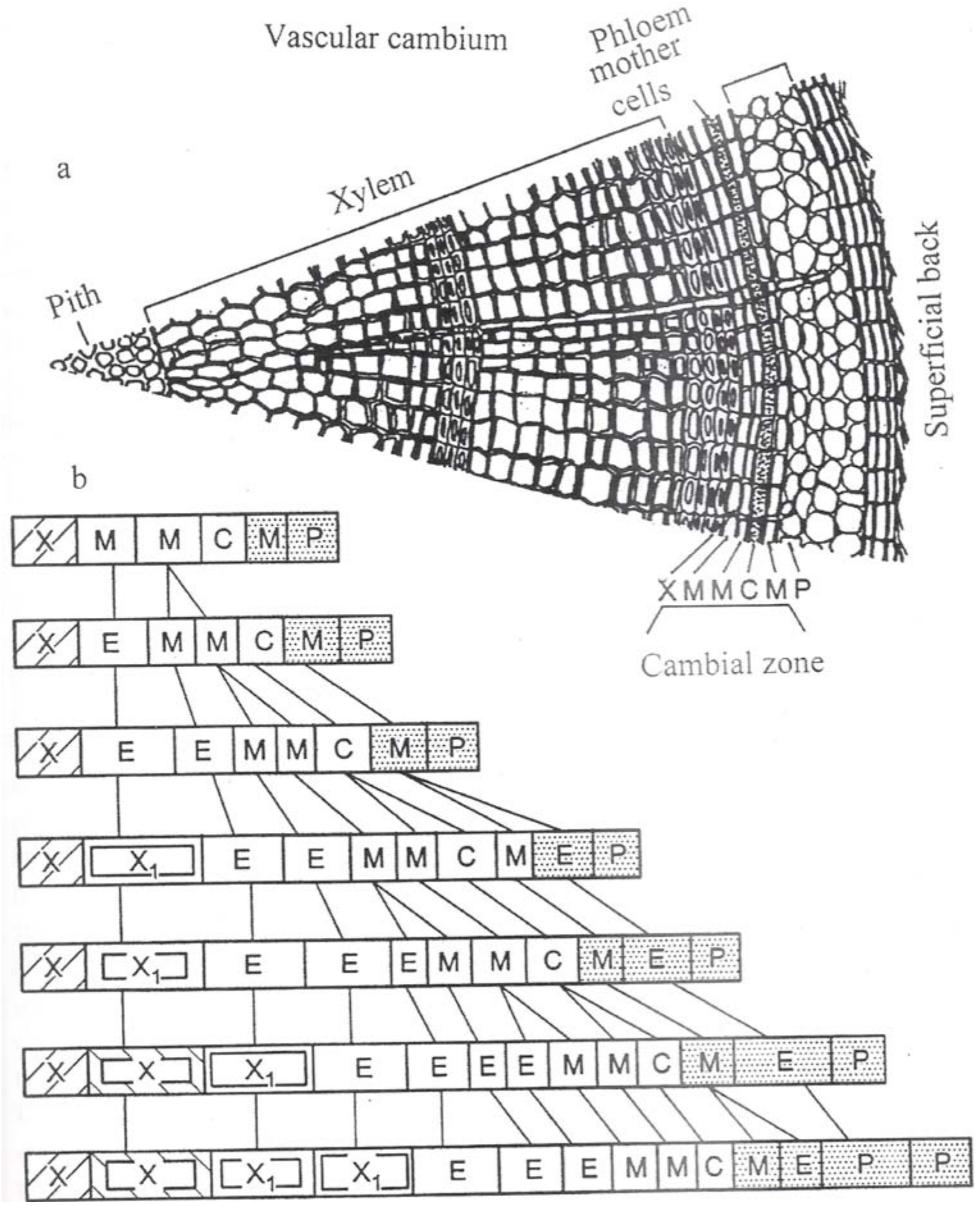

Figure 2.5. (a) Cross-section of a conifer tree wedge and (b) figure of cell production in the cambial zone: C cambial initial, M mother xylem and phloem cells, X mature xylem cells, P mature phloem cells, E cells in enlarging phase. (adapted from Vaganov et al. 2006).

environmental variables influence the rates of these processes and control the amount of radial growth (tree-ring width) of conifers. Northern conifers are considered to have an “explosive” seasonal growth rate due to the extremely short growing season in these regions (Vaganov et al. 2006). It has been reported that at the northern reaches of the Siberian taiga (~70° N), the growth season only spans 35-40 days (Vaganov et al. 2006). As distance south from the treeline increases, the growing season becomes longer, reaching a period of 150-160 days in the subtropical zone (Vaganov et al. 2006). Genetic factors allow trees to adapt to the growing season by having different phenology (the timing of bud break and initiation of growth). Environmental factors (e.g., light, temperature, precipitation) also play an important role in influencing growth. The environmental conditions at the time of cambial division influence the final size of individual cells (Vaganov et al. 2006). This means that the environmental influence of radial growth is limited to the period when cells are actively dividing from the cambium and not when they are expanding or forming secondary cell walls.

2.5. Analysis of Intra-Annual Tree Growth

An important aspect of studying change over time is comparison between the present and the past to frame the magnitude and rate of change. Trees have characteristics that make them an excellent natural archive of climate-vegetation interaction including, (1) annual resolution, (2) absolute dating, (3) longevity and (4) broad spatial distribution (Fritts 1976). These characteristics define the science of dendroclimatology, which uses tree rings to understand climatic influences on tree rings and reconstruct past climatic conditions. The reconstruction of past climates depends on knowledge of the factors that control the growth of trees under current climatic conditions. This invokes the principle of uniformitarianism, which in dendroclimatology implies that the physical and biological processes that link present environmental conditions with variations in tree growth were the same processes in operation in the past (Kaennel and Schweingruber 1995). However, the divergence trend between tree growth and climate records may be an indication of non-stationarity. If trees are not responding consistently to the environment over time (perhaps due to rapid climatic change), it becomes extremely important to investigate and quantify the variables that influence growth. Without identifying and accounting for time-dependent variables researchers could overestimate growth rates, which could affect models of treeline advance, future carbon storage and could lead to inaccurate reconstruction of past climates.

Previous studies have concentrated on using dendroclimatology to investigate past response of trees to different climatic variables. These range from temperature and precipitation to wind (Bannan and Bindra 1970; Garfinkel and Brubaker 1980; Buckley et al. 2005). However, to investigate the dynamics of seasonal growth an issue of scale arises. Generally, the finest scale that increment cores can resolve is annual and perhaps seasonal given proper conditions with notable wood signatures such as resin ducts due to frost events or physical tree damage or seasonality of past fire events as noted by fire scars (Brunstein 1996; Kipfmueller and Baker 2000). However, intra-seasonal variations and the environmental conditions that drive these variations need to be understood to gain a full understanding of the factors that influence tree growth. Indications are that daily and even hourly variations in weather conditions may affect growth even though they appear transient (Fritts 1976). This type of temporal scale requires a much different approach than is generally used in dendroclimatology.

2.5.1. Methods of Intra-Annual Growth Analysis

Several methods can be used to study (directly or indirectly) intra-annual tree growth dynamics, including internal sampling using microcores and pinning or the external but continuous records of dendrometers.

Taking microcores prior to and continually during the growing season provides “snapshots” of xylem formation (Rossi et al. 2006a; Vaganov et al. 2006; Marion et al. 2007). From these cores it is possible to measure and count cells in the cambial zone, the enlarging zone or the maturing zone to calculate a rate of division and assess the timing of each stage (Gregory and Wilson 1968; Gregory 1971). The drawback of this method is the high amount of variance in measurements due to collecting each sample from a different location on the tree and the intensive methods required to process the samples in the laboratory. A large amount of replication (close to 100 trees) may be able to overcome this limitation (Vaganov et al. 2006).

Pinning uses a small object to create periodic local damage of cambium cells (Vaganov et al. 2006; Seo et al. 2007). At the conclusion of the growing season a sample of this point is collected and it is possible to determine the amount and rate of wood formation by comparing the number of cells that are damaged with those that are un-damaged (Vaganov et al. 2006). The advantages of this technique are that the cambium is highly responsive to external impacts and this small amount of damage provides a rather simple “timer” of cambium activity (Seo et al. 2007). It is very quick and easy to perform the pinning in the field. It has been used on both coniferous and broad-leaved species of trees across both temperate and tropical climates. The limitations of this method include the high accuracy required to collect a cross-section of the damaged area, the intensive amount of laboratory work that is required for the samples and the possibility of a high amount of error at the limit of a species' range due to miscounts of tracheid cells (Vaganov et al. 2006; Seo et al. 2007).

The current study employs the use of automatic point dendrometers, which are sensors that record slight variations in radial expansion of a tree over short time periods. Dendrometers were first developed by Harold Fritts and his father (Fritts and Fritts 1955). There are two common types of dendrometers, band dendrometers and point dendrometers. Band dendrometers measure changes in the circumference of the stem by means of a metal band that extends around the tree and a visual or automatic vernier scale. Point dendrometers have a single sensor that measures changes in a single radius of the stem (Bormann and Kozlowski 1962; Fritts 1976). Measurements can be taken at intervals ranging from 15 minutes to a single measurement each day. Automatic point dendrometers are an excellent tool to study intra-annual tree growth because they can record measurements at a high temporal resolution continuously during the growing season and they cause no damage to the tree. One of the major limitations to using dendrometers is that they are measuring the change in size of the stem of the tree, which includes both absolute growth (tracheid cell production) and reversible trends (water movement up and down the stem). These reversible hydration trends must be removed from the data to assess true growth (Vaganov et al. 2006).

2.5.2. Development of Intra-Annual Growth Analysis with Dendrometers

Despite the excellent temporal resolution that can be gained with dendrometers, few published studies have made use of them (compared to more common dendroclimatological methods). Primarily, the literature is based on the development of the instrumentation and most of that dates from the 1940s to the mid 1960s (Reineke 1932; Hall 1944; Fritts and Fritts 1955; Liming 1957; Bormann and Kozlowski 1962; Kozlowski and Winget 1964; Impens and Schalck 1965). However, in the past decade a number of studies have prominently used automatic dendrometers, sometimes in combination with other methods. In Australia, automatic point dendrometers were used to measure daily stem growth patterns of *Eucalyptus globules* and *Eucalyptus nitens* trees (Downes et al. 1999). The authors were able to resolve the daily growth into three phases within a single diurnal cycle: shrinkage, recovery and the daily growth increment. They correlated climate variables with stem growth through a single growing year. Downes et al. (1999) found a change in limiting factors during the growing season, with temperature being important in the spring and precipitation during the summer. This study also noted a large difference between the two species in growth rates when comparing the diurnal and monthly growth trends and that the weather conditions during the increment phase did not explain significantly more variance than average daily conditions (Downes et al. 1999).

In the eastern boreal region of Quebec automatic point dendrometers were used to record the daily stem growth of balsam fir (*Abies balsamea*) trees over a three year period between 1998 and 2001 (Deslauriers et al. 2003b). Deslauriers et al. (2003b) divided their records into four phases, the same three as Downes et al. (1999) (contraction, expansion and stem radius increment) and an additional phase, the entire circadian cycle. The authors used an *in-situ* weather station to determine the mean weather conditions of each phase of growth that was compared to the daily stem radial increment using correlation and response function analysis. The authors found that weather conditions between 1600/1700 - 0800/0900 hours had the greatest impact on stem radial increment (Deslauriers et al. 2003b). They also found that daily water balance in the form of rainfall was the most important factor for the growth of the trees and that night temperatures were more important than daytime temperatures (Deslauriers et al. 2003b). Combined, the response functions explained up to 95% of the variance of the stem radial increment.

A third study was conducted with automatic point and band dendrometers in the highlands of Mexico on Mexican mountain pine trees (*Pinus hartwegii* Lindl.) (Biondi et al. 2005). The study also made use of an automated weather station and qualitative comparisons were made to gain an understanding of when the growing season began and how trees responded to various environmental changes. The most intriguing result from Biondi et al. (2005) was the observation of the radial growth response to a beetle infestation at the site over two years.

More recently, studies have taken place in the Italian Alps that have successfully used a combination of automatic dendrometers and microcoring to obtain a greater understanding of the seasonal dynamics of tree growth (Rossi et al. 2006b; Deslauriers et al. 2007a; Deslauriers et al. 2007b; Giovannelli et al. 2007). Rossi et al. (2006b) conducted a study of the timing of maximum growth rates of European and North American conifers between 1996 and 2003. Using both cambial activity (microcores) and stem variation (automatic dendrometers) to assess growth, the authors found that maximum growth occurred during periods of maximum day length, not periods of maximum temperature. Deslauriers et al. (2007a) investigated the time-scales that could be investigated with dendrometers and the growth information that can be inferred. The authors found the stem radius variability was larger than actual growth during latewood production and prevents growth and climate analysis for that period. Deslauriers et al. (2007b) used a dendrometer growth record split into the daily stem cycle phases to assess the causal effects of precipitation and temperature flucuations on stem growth and shrinkage. They found that the effect of temperature on stem radial variation was due to temperature influencing the length of the growth phase and not altering metabolic activities. However, precipitation was found to have both an effect on phase length as well as a direct effect on stem radius increment. Finally, Giovannelli et al. (2007) used dendrometers to assess the tolerance of two different poplar (*Populus spp.*) clones to artificial drought stress by monitoring their mean daily stem radial increment and mean daily shrinkage.

All of these studies reveal that trees are influenced by local environmental conditions. It is clear that dendrometers are incredibly useful and can produce excellent high-resolution data that could provide information to improve mechanistic models of tree growth.

Chapter 3

Site Description and Methodology

3.1 Introduction

This study investigates the factors that influence the growth of white spruce trees within the Mackenzie Delta. Tree radial expansion and environmental conditions were monitored over two growing seasons at a single site located on East Channel (informally named Blueberry), just north of Inuvik, NT. This chapter describes the location and physical characteristics of the study site as well as the methods used to collect and analyze the data.

3.2 The Mackenzie Delta

3.2.1 Location

The Mackenzie Delta is located near the western border of the Northwest and Yukon Territories. It occupies the flat plain between 67-70°N and 134-136°W (Fig. 3.1) and formed following the last glacial maximum over the last 14,000 years (Burn 2002). With an area of approximately 13,000 km^2 the Mackenzie Delta is Canada’s largest delta, the second largest arctic delta and the second largest delta in North America (Burn 2002). The delta is composed of a network of channels and numerous lakes across an alluvial plain that ranges between elevations of 0 and 10 m above sea level (a.s.l.) depending on the patterns of sediment deposition and erosion as well as the influence of ground ice (Pearce et al. 1988).

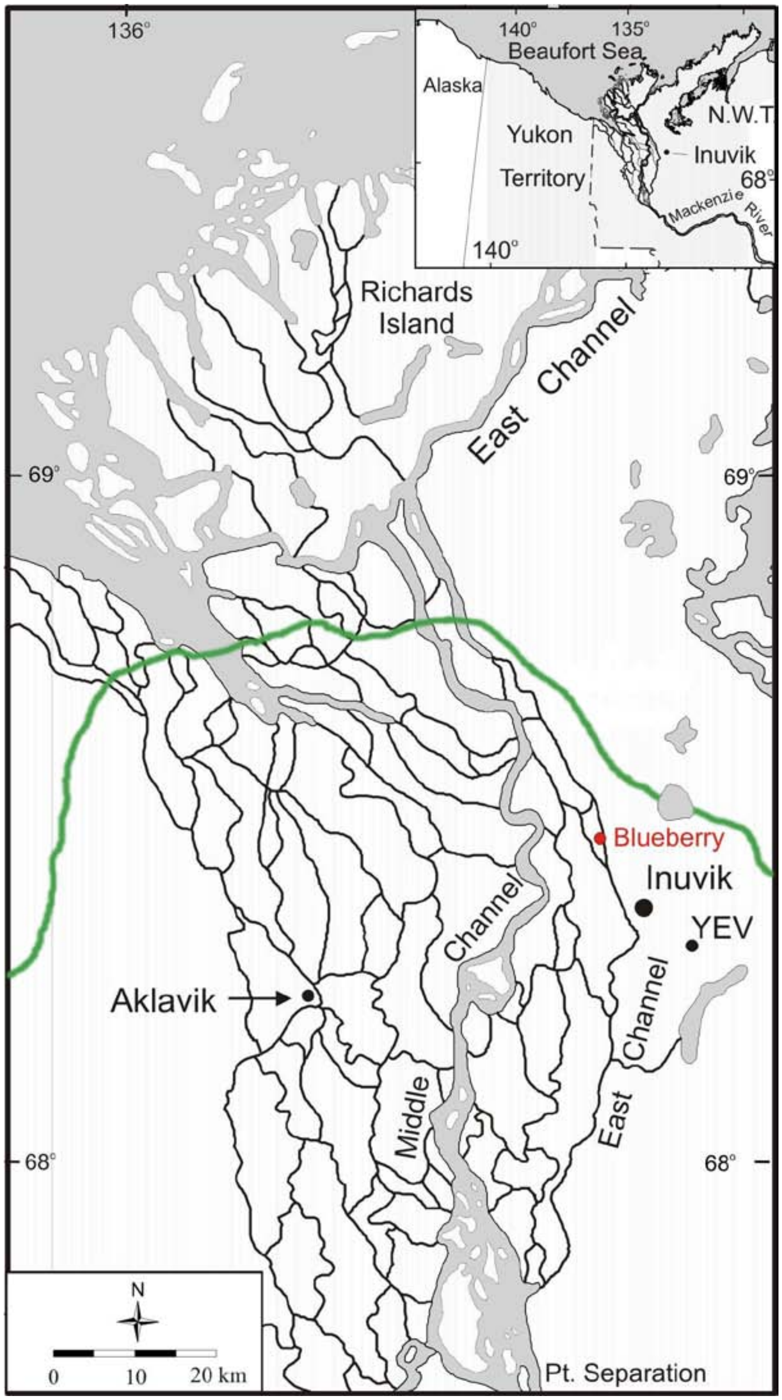

Figure 3.1. Map of the Mackenzie Delta. YEV represents the Mike Zubko International airport. The study site (Blueberry) is marked by the red circle. The green line is the approximate location of treeline.

3.2.2 Climate

The Mackenzie Delta lies within the high sub-arctic and low arctic climatic zones, experiencing long, cold winters and short summers. The region experiences large ranges in temperature both daily and annually. Precipitation is generally low due to the dry polar air which dominates the weather patterns and because of its location in the rain shadow of the Cordilleran mountains (Dyke 2000; Burn 2002). At Inuvik, the 30 year climate normal (1971-2000) shows that the average annual temperature is -8.8°C and total annual precipitation is 248.4 mm (Fig. 3.2) (Environment Canada 2004). The mean wind speed at Inuvik is 9.7 km/h with the winds predominantly coming from the east because of the clockwise circulation around the arctic high (Dyke 2000).

During the winter, the region is influenced by cold, dry air moving south from the high Arctic. The coldest month is January with an average temperature of -27.3°C and with an average of 18 days with a minimum temperature below -30°C (Fig. 3.2). Half of the precipitation measured at Inuvik falls as snow during the fall and winter months, with the most coming in October (34.9 cm) and November (23.7 cm) before artic high pressure develops and blocks humid maritime air from the west (Dyke 2000; Environment Canada 2004).

Summers are relatively warm, as arctic high pressure moves north and the daylight hours become longer (Dyke 2000). The warmest month is July with an average monthly temperature of 14.2°C (Fig. 3.2). The daily maximum temperature rarely exceeds 30°C during the summer. Approximately a third of the total annual precipitation falls as rain during the summer with the most coming in August (37.5 mm).

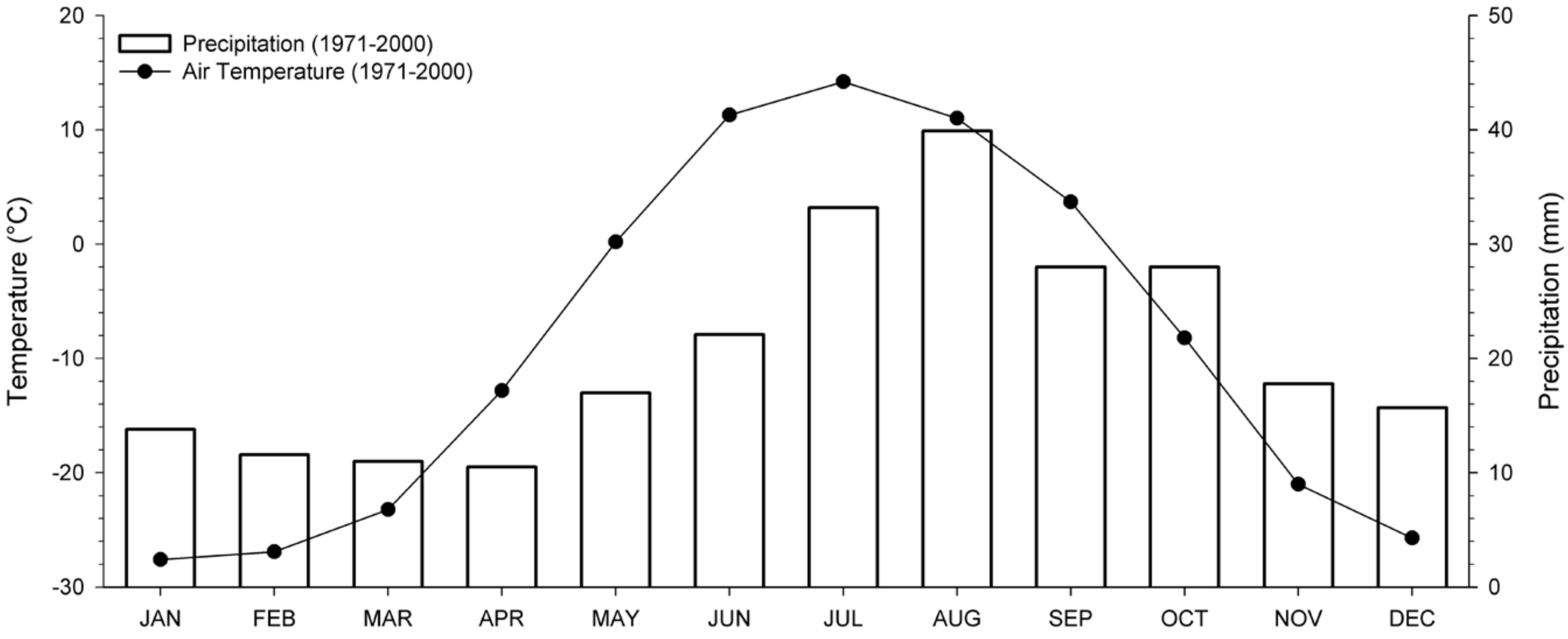

Figure 3.2. Mean monthly air temperature and precipitation (1971-2000), Inuvik A meteorological station (Environment Canada 2004).

Most precipitation is light with only ~7 days per year exceeding 5 mm of total rainfall (Environment Canada 2004). Within the Delta, evaporation exceeds precipitation in most summers and sometimes exceeds annual precipitation (Marsh and Bigras 1988).

3.2.3 Hydrology

The Mackenzie Delta is formed by the division of the Mackenzie River into East Channel, Middle Channel and numerous smaller tributaries at Point Separation as well as the Peel and Rat Rivers, which enter the delta to the west (Pearce et al. 1988). With a total annual discharge of 2.86 x 1011 m^3 per year, the Mackenzie River is the principal contribution to the hydrologic regime within the delta (Burn 2002). Water levels in the delta reflect inputs from the Mackenzie River, fluctuation in Beaufort sea level, and ice jamming during spring break-up. The highest flows are during snowmelt with peak discharge occurring June 3 with a standard deviation of 4 days (Marsh and Hay 1989). The discharge drops as the summer progresses and continues to decline until the drainage basin begins to freeze (Burn 1995). Tides influence water levels in the outer third of the delta, but are generally limited to late in the season when water levels are lower. However, storms from the northwest can raise water levels by up to one meter in the middle of the delta and are detectable at Point Separation gauging stations after approximately 21 hours (Marsh and Schmidt 1993). Initial freezing in November and December can increase river levels by concentrating water flow into fewer channels. In the spring, ice jams during peak flow, along with rapid runoff from further south in the drainage, can dramatically increase the water levels and create flooding through many of the lower surfaces in the delta (Marsh and Hay 1989). Annual flooding maintains the productivity of the Mackenzie Delta by depositing nutrient-rich sediments on the delta surfaces. The floodwaters melt snow (reducing albedo) and begin to thaw the ground leading to deeper active layers within the delta than in the surrounding uplands (Gill 1973).

There are approximately 25,000 lakes within the Mackenzie Delta. In the middle of the delta, over half of the surface area is water. The biological regime of lakes in the delta is dominated by deposition of sediment from spring and summer floods. This deposition is controlled by the elevation of the lakes and the channels that connect them. About 67% of lakes flood annually in the spring while the remaining lakes have a flood frequency of two to four years (Marsh and Hay 1989).

3.2.4 Soils and Permafrost

The delta is composed of alluvial sediment, deposited primarily during the spring due to ice break-up and ice-jam flooding. Deposition on the delta plain occurs when the river exceeds its banks. Sediment deposition rates are generally a few millimeters to a few centimeters of sandy or silty alluvium depending on the level of the flood and the variability of topography (Pearce et al. 1988). At most elevated sites there is organic material that accumulates above these alluvial sediments. However, its depth depends on the elevation of each site, its vegetation composition and the frequency of flood events. A core of a complete section of deltaic deposits showed about 180 feet of stratified silts, fine sand and organic material overlay 50 feet of dense, silty clay (Johnston and Brown 1965).

Permafrost is ground that remains at or below 0°C for two or more years. The Mackenzie Delta is considered a zone of discontinuous permafrost, with less than 80% of its surface underlain by frozen ground. This is anomalous within the Western Arctic which is underlain by continuous permafrost up to 300 m thick (Burn 2002). The presence of permafrost in the delta is dependent upon the depth of lakes and the organization of channels. Surfaces farther away from channels have thicker permafrost than newly formed point bars (Smith 1975). Depending on the site, some of the near surface permafrost in the Mackenzie Delta contains large amounts of aggradational ice (Kokelj and Burn 2005). Point-bar willow and alder communities have ice-poor permafrost (less than 20% excess ice content) compared to spruce forests that are above the level of annual flooding that are underlain by ice-rich permafrost with excess ice accounting for up to 60% of the soil volume down to 100 cm below the permafrost table. This percentage decreases the deeper you move into permafrost which suggests the current spruce forests began as point bars and as they aggraded, ground ice began accumulating (Kokelj and Burn 2005). The presence of this ice-rich permafrost can alter the flooding frequency of sites and influence the ecological succession at these sites.

3.2.5 Vegetation

Nutrient-rich flood waters, warmer air temperatures and a deeper active layer are several of the reasons why there is more abundant vegetation within the delta than on the adjacent uplands (Gill 1973; Jones 2002). All six tree species located in the western Arctic are found within the delta. These include the coniferous white spruce (*Picea gluaca*) and black spruce (*Picea mariana*), the deciduous white birch (*Betula papyrifera* var. *papyrifera*), trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balamifera*) and the deciduous conifer tamarack (*Larix laricina*). The most common tree located within the Mackenzie Delta is white spruce, which maintains one of the most northerly extensions of the boreal forest in North America.

The vegetation of the delta is a mixture of boreal and arctic species and the climate, along with flooding frequency and sediment deposition patterns interact to determine plant distribution and the ecological succession in the delta (Gill 1973; Pearce et al. 1988). Previous work has identified common vegetation assemblages (based upon the relative abundance of different species at sample sites) across the Delta. There is evidence that each of these assemblages is a point on a successional gradient and that each influences microclimate and permafrost conditions (Gill 1975; Smith 1975; Pearce et al. 1988; Kokelj et al. 2007). As delta surfaces are deposited and aggrade, point bars are colonized by several species of willow (*Salix* spp.) and balsam poplar even though flooding occurs regularly (Gill 1972; 1973). As time passes and the surfaces continue to rise, green alder (*Alnus crispa*) and white spruce seedlings begin to establish on these sites. As more sediment is deposited and the delta surfaces rise above the level of annual flooding, white spruce becomes more abundant and the first stage of forest succession in the delta, the white spruce/alder-bearberry (SAB) association is established. In these environments, floods occur every 5-10 years, the organic layer is thin (<5 cm) and the active layer is thick (90-120 cm) (Kokelj et al. 2007). As the surface continues to aggrade and flooding frequency decreases (to >10 years) the SAB forests transition to white spruce/feathermoss (SF) forests where the organic layer deepens (10-25 cm) and the active layer thins (50-80 cm) due to the presence of a thick moss cover (Kokelj et al.

2007). The permafrost in SF sites contains a higher percentage of ice and as this ice forms it heaves the ground upwards (Kokelj and Burn 2005). The third forest type in the successional trajectory, the white spruce/lichen-crowberry (SCL) assemblage is present on these surfaces. The flooding frequency of these communities is high (50-100 years) with very little sediment deposition, allowing a deep organic layer (20-40 cm) to develop and reducing the depth of the active layer (40-70 cm) (Kokelj and Burn 2005; Kokelj et al. 2007). Tree ages at these SCL sites are up to 500 years old, indicating that this successional pathway takes place over hundreds of years. An alternate final assemblage that may form on poorly drained sites is the white spruce/tamarack-sphagnum (STS) which has a very deep organic layer and a shallow active layer (20-40 cm) (Pearce et al. 1988).

3.2.6 Study Period

Fieldwork and data collection for the project took place during the summers of 2006 and 2007. The first season of fieldwork took place from June 20 to September 4, 2006. The second field season in 2007 took place from May 14 to September 10, 2007. Tree growth varies intra-annually due to the influence of the climate in the region. To understand how representative the study period was, the mean monthly temperature and precipitation for the duration of the study (January 2006 - December 2007) were compared to the 30 year climate normals (1971-2000) from Inuvik (Fig. 3.3 and 3.4).

The mean annual air temperature for 2006 and 2007 were the same (-6.2°C) and were 2.6°C warmer than the climatic normal. In 2006, this was influenced by a warm February, September, October and December while in 2007 it was influenced more by

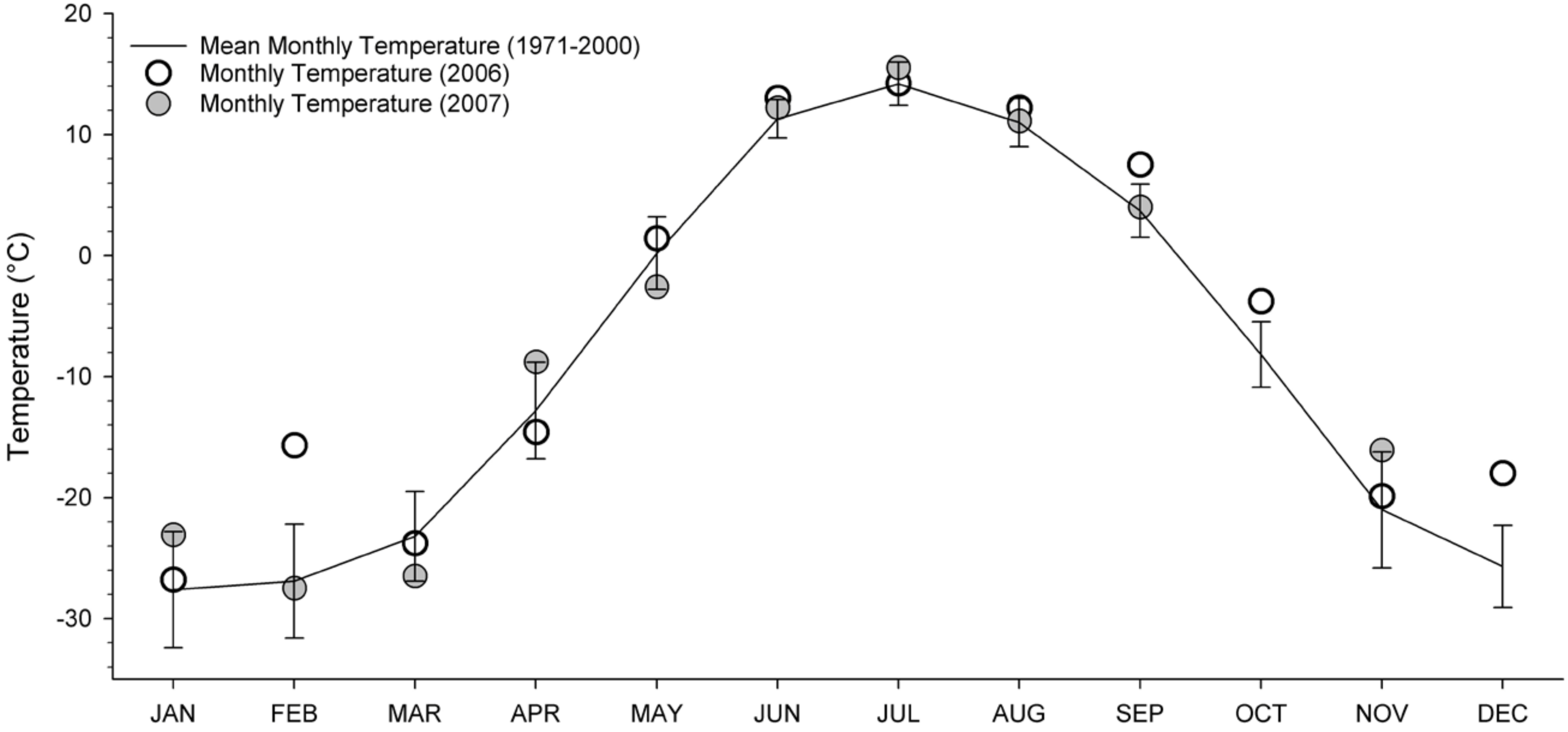

Figure 3.3. Mean monthly air temperature with one standard deviation (1971-2000) from the Inuvik A meteorological station (Environment Canada 2004), compared to the mean monthly air temperatures from the Inuvik Climate station during the study period (Environment Canada 2008).

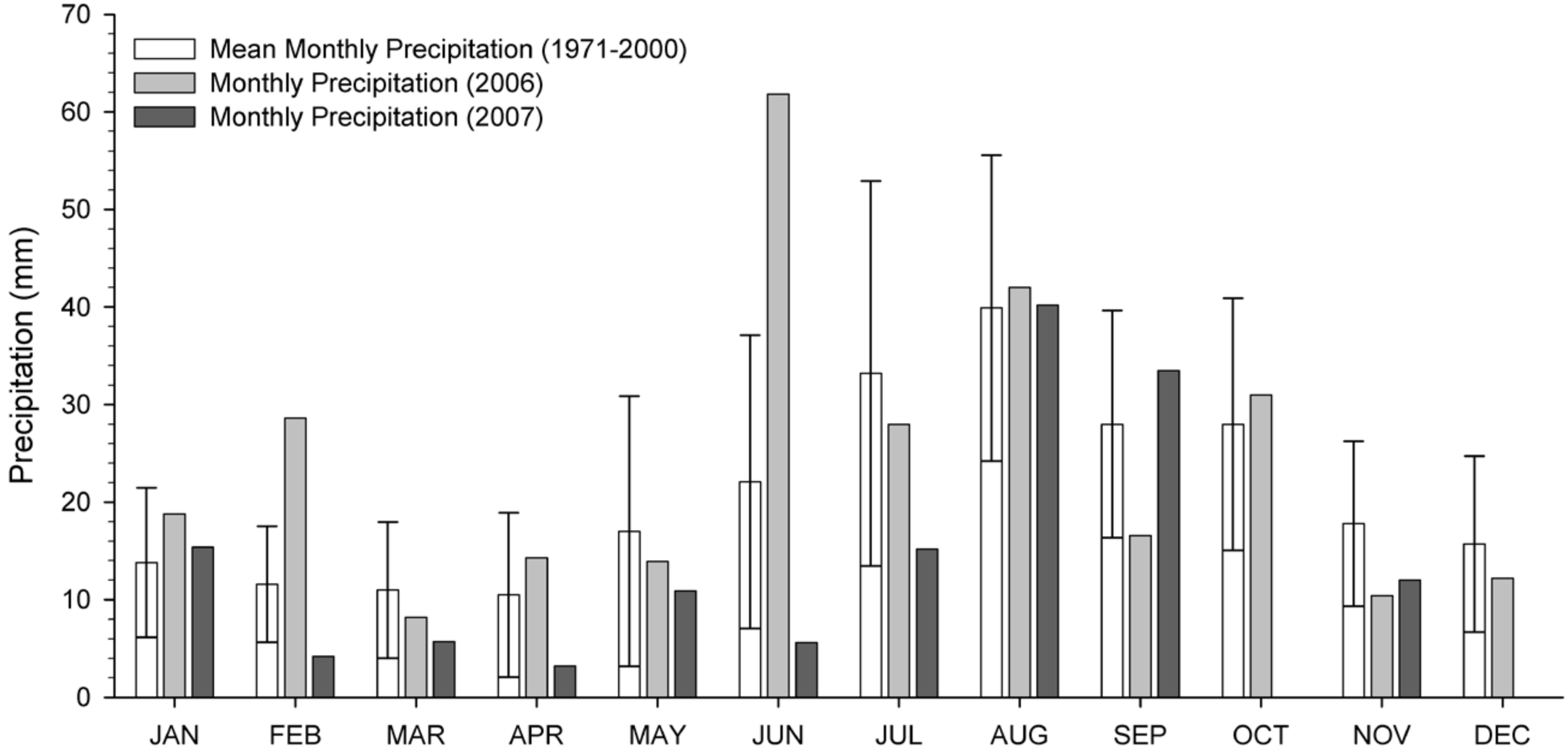

Figure 3.4. Mean monthly precipitation totals with one standard deviation (1971-2000) from the Inuvik A meteorological station (Environment Canada 2004), compared to the mean monthly total precipitation amounts from the Inuvik Climate station during the study period (Environment Canada 2008).

warmer temperatures in January, April and November (Fig. 3.3). The total precipitation was 285.8 for 2006 which was 37.4 mm more than average and 145.9 for 2007 (no data for October and December) which is 102.5 mm less than average (Fig. 3.4). The difference in 2006 can be attributed to the large amount of precipitation received in June. The difference in 2007 is due to unusually low amounts of precipitation from February through to July.

3.3 Field Methodologies

3.3.1 Site Description and Selection

Blueberry is located in the Mackenzie River Delta, between East Channel and Bombardier Channel, approximately 13 km north of the town of Inuvik (Fig. 3.1 and 3.5). Blueberry has an elevation of approximately 7.5 m a.s.l., which is above the level of the annual flood (average peak level over period of record (1985-1990; 2002-2007) is 5.05 m a.s.l.) (Fig. 3.6) (Water Survey of Canada, Yellowknife, NT 2007). These sites have been elevated by a combination of sediment and organic deposition and cryostatic uplift from high amounts of ground ice (Pearce et al. 1988; Kokelj and Burn 2005).

The vegetation assemblage consists of an open canopy that leads to a diverse understory and groundcover of shrubs, herbs, mosses and lichens (Table 3.1 and 3.2) (Fig. 3.7 and 3.8). The percentage canopy cover at Blueberry is approximately 7% and consists mostly of white spruce, but several tamarack are present in wetter areas of the site. Most white spruce trees at Blueberry had patches of yellowing needles and of the 42 white spruce trees sampled, 48% had forks associated with dead tops. These characteristics were ubiquitous among both positive and negative responders. Dead tops

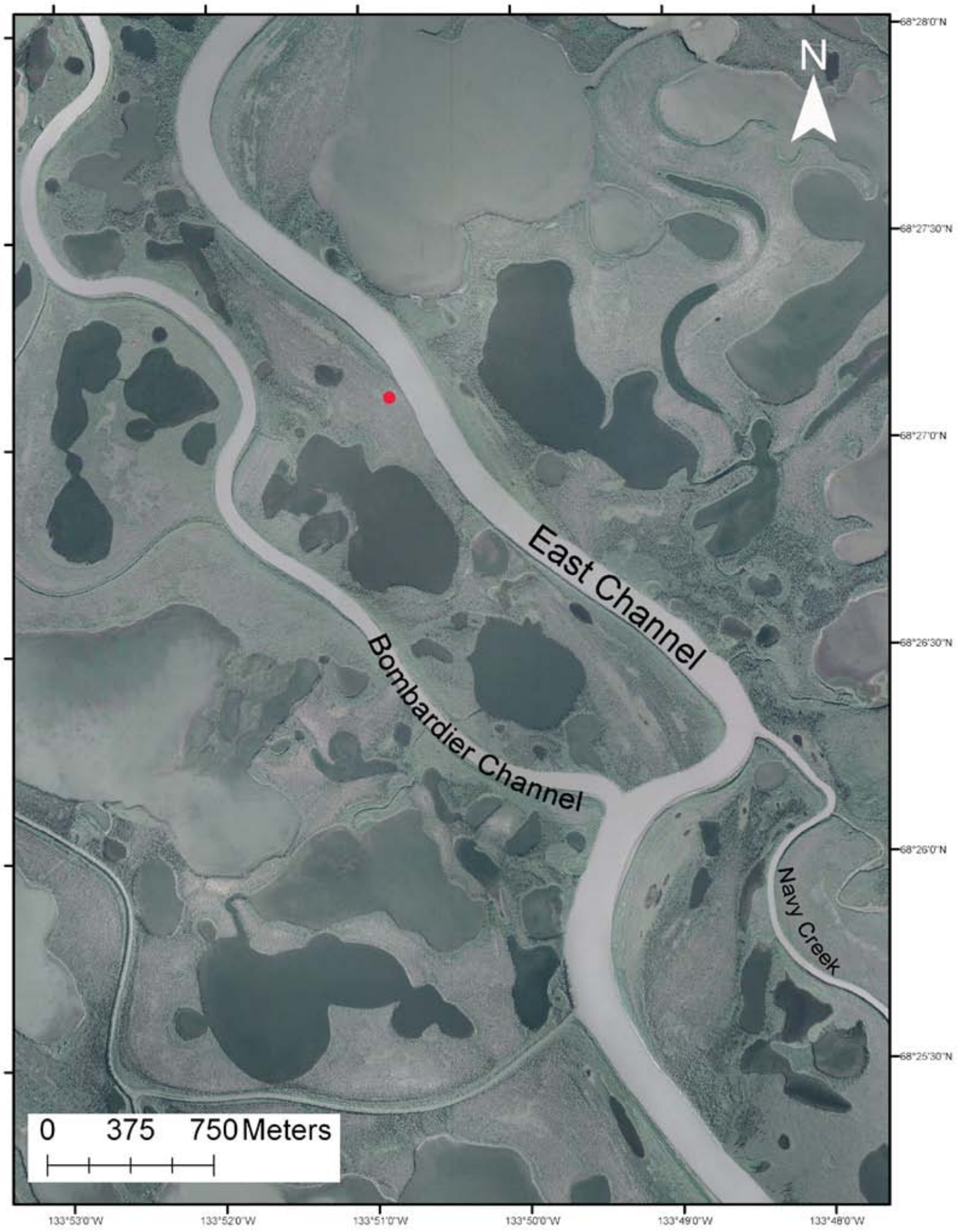

Figure 3.5. Aerial photograph of the study site (marked by the red circle) and surrounding area. Parts of aerial photograph A-31865 197. © 2005 Government of Canada with permission from Indian and Northern Affairs Canada.

Figure 3.6. Photograph of the cut-bank of the study site from East Channel on July 9, 2006. The water level measured that day at station 10LC002 (Mackenzie River (East Channel) at Inuvik) was 2.2 m a.s.l.

Table 3.1. Percent cover, count and frequencies for trees, shrubs and herbs at Blueberry.

SCIENTIFIC NAME	COMMON NAME	COVERAGE % [a]	COUNT [b]	FREQUENCY [c]	RELATIVE FREQUENCY [d]
Trees					
Picea glauca	white spruce	0.3	5	23.8	2.2
Shrubs					
Alnus spp.	alder	2.4	4	19.0	3
Salix spp.	willow	3.3	13	61.9	3
Betula glandulosa	bog birch	0.2	1	4.8	1
Vaccinium uliginosum	bog blueberry	11.0	21	100.0	9.3
Vaccinium vitis-idaea	lingonberry	8.0	19	90.5	8.4
Ledum palustre	northern labrador tea	8.6	20	95.2	8.8
Arctostaphylos rubra	red fruit bearberry	7.5	17	81.0	7.5
Empetrum nigrum	black crowberry	7.7	19	90.5	8.4
Herbs					
Pyrola grandiflora	largeflowered wintergreen	0.2	3	14.3	1.3
Equisetum scirpoides	dwarf scouringrush	13.4	21	100	9.3
Equisetum arvense	field horsetail	0.8	3	14.3	1.3
Boschniakia rossica	northern groundcone	0.1	3	14.3	1.3
Carex aquatilis	water sedge	0.6	4	19.0	1.8
Eriophorum angustifolium	tall cottongrass	0.3	3	14.3	1.3

a - % cover for 1 m x 1 m study plots
b - number of plots where species was identified
c - % of plots where species was found (n = 21)
d - % of species present compared to all other species

Table 3.2. Percent cover, count and frequencies for mosses and lichens at Blueberry.

SCIENTIFIC NAME	COMMON NAME	COVERAGE % [a]	COUNT [b]	FREQUENCY [c]	RELATIVE FREQUENCY [d]
Mosses					
Aulacomnium palustre	tufted moss	9.9	16	76.2	7.0
Schistidium apocarpum	schistidium moss	2.9	3	14.3	1.3
Lichens					
Cladina mitis	green reindeer lichen	27.4	17	81.0	7.5
Cladonia bellidiflora	british soldiers	0.1	2	9.5	0.9
Cladonia unicialis	prickle cladonia	0.4	2	9.5	0.9
Cladonia deformis	deformed cup	0.4	11	52.4	4.8
Cladonia gracilis	smooth cladonia	0.1	1	4.8	0.4
Cetraria nivalis	flattened snow lichen	0.7	4	19.0	1.8
Cetraria cucullata	curled cetraria	0.3	3	14.3	1.3
Peltigera apthosa	freckle pelt	0.4	5	23.8	2.2
Peltigera neopolydactyla	frog's pelt	0.5	3	14.3	1.3
Cladonia cornuta	pioneer cladonia	0.2	4	19.0	1.8

a - % cover for 1 m x 1 m study plots
b - number of plots where species was identified
c - % of plots where species was found (n = 21)
d- % of species present compared to all other species

Figure 3.7. A panorama photograph of the study site showing the sparse canopy of trees and the shrub understory.

Figure 3.8. Photograph of representative ground cover showing representative ground cover at Blueberry.

(death of apical meristem) may be the result of previous floods or periods of high moisture stress. During a flood all available oxygen in the water and soil are consumed which can adversely influence growth, especially if the flood is of a longer duration or takes place at the beginning of the growing season (Kozlowski 1984). Extreme soil moisture stress could also result in a reduction in growth and possibly localized meristem death (Grossnickle 2000). There were also no visible signs of spruce budworm at the study site.

Six types of shrub are found at the site (alder and willow species were not classified to the species level). The most extensive shrub cover consists of shorter shrubs, especially bog blueberry, northern Labrador tea, and black crowberry. There are six species of herb found at the site, with dwarf scouringrush being the most common.

There is no mineral soil visible at the site. The ground cover is dominated by reindeer lichen, but there are areas within the site where tufted moss is more prominent. These two species generally occur in different environmental conditions, with moss found in the mesic areas on hummock sides and in hollows, whereas lichen dominates in large mats on drier areas of the hummock tops. A large diversity of lichen species occurs at the study site.

Pearce et al. (1988) had previously identified four white spruce assemblages in the Mackenzie Delta. Based on vegetation data, Blueberry was determined to be most similar to white spruce/crowberry-lichen sites with 18 of 27 species identified at Blueberry being in common with those identified by Pearce et al. (1988).

Blueberry was selected as our study site for several reasons. First, the site is easily accessible and similar to other treeline sites in the region where environmental conditions are a primary influence over tree growth. There is also little competition between individuals, maximizing the climate signal in the tree ring records. Third, permafrost features have been studied for the past five years at this site and a dendrochronological study previously identified diverging growth response at this site (Kokelj and Burn 2004; Kokelj and Burn 2005; Kokelj et al. 2007; Pisaric et al. 2007). Finally, meteorological data has been collected for close to 80 years at the Aklavik and Inuvik airports, which provides long-term climate data for comparison to tree ring records.

3.3.2 Increment Cores

Trees were sampled for dendroecological analysis at random within a 40 m radius of the site data logger. The samples were collected to categorize individuals as positive responders or negative responders based upon their past growth (ring width) response to climate. Tree cores were collected from living white spruce trees using a 14-inch Haglof increment borer with an inside diameter of 4.3 mm. Cores were sampled at about 1 m above the ground, perpendicular to the stem and then placed in plastic straws for storage and transportation to the laboratory. Two to three cores were extracted from each tree in order to assess intra-tree variability with respect to ring width. In 2006, 16 trees were cored on 24 June. In 2007, an additional 26 trees were sampled on 20 May. Each tree was tagged with an identification number that is matched to the increment core and the instrumentation on the tree. As well, a handheld GPS was used to record the position of each tree and the location of the meteorological station and the central POD (data logger for the dendrometers) (Fig. 3.9).

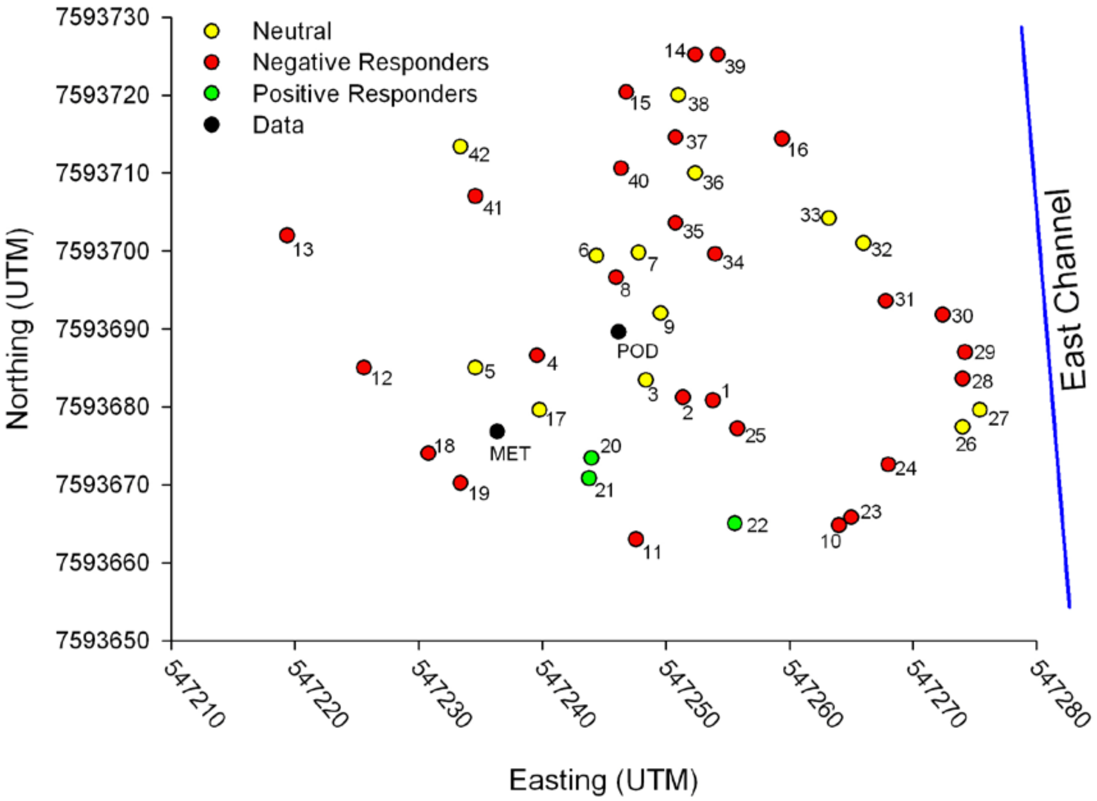

Figure 3.9. Coordinates (UTM) of sampled trees and data loggers at the study site. The relative position of the East Channel is included for reference.

3.3.3 Vegetation

3.3.3.1 Trees

In 2007 diameter at breast height (DBH), tree height and distance to nearest neighbour were measured for each individual tree that had been tagged and cored. Diameter measurements were made 1.5 m from the ground using a diameter tape. Tree height was measured using a clinometer to sight the top of the tree and then trigonometric functions to convert the angle and distance from the tree to height. The distance from each tree to its nearest neighbour was measured to assess any possible influence of competition between individuals for resources.

Cone counts and seed collection were carried out to assess any reproductive differences amongst individuals at the site. Cone counts were conducted using a pair of binoculars and counting all unopened cones (darker in colour, still sealed with resin) from the current year (2007) and counting the number of opened cones that remained on the trees from the previous years (*cf.* Peters et al. 2003; Lamontagne et al. 2005). A pair of extendable tree shears was used to collect a sample of cones from 9 different trees at the site. The remainder of the trees had few to no cones to collect, whereas others had cones that were out of reach of the shears.

3.3.3.2 Understory and Ground Cover

Previous literature had identified four unique spruce assemblages that existed within the delta (Pearce et al. 1988). In 2007, a 1x1 m quadrat was constructed out of copper pipe to compare study site vegetation to the results from surveys of Mackenzie Delta spruce forest assemblages conducted in the literature. Twenty-one plots were randomly located by throwing a marker pin and establishing that location as the lower right corner of the quadrat. For each plot, each species present was identified and their percent cover recorded. Count, frequency and relative frequency were also calculated.

3.3.4 Thaw Depth

During both field seasons, weekly measurements of thaw layer depth were made by probing the ground with a graduated steel rod (*cf.* Mackay 1977). In 2006, 15 random measurements were made during each visit to determine an overall site average. In 2007, 30 random measurements were made during weekly visits for a site average. At the end of the growing season in 2007, five measurements of active layer thickness were taken within 2 meters of the base of each of the 42-cored trees to determine if the active layer depth around each individual had an influence on tree growth.

3.3.5 Tree Growth

Automatic point dendrometers manufactured by Agricultural Electronics Corporation in Tucson, Arizona are high resolution sensors that were used to continuously monitor the variations of the radial stem size of trees at the site (Fig. 3.10). Installation involved mounting the dendrometers on metal rods anchored into the xylem of the tree. The dendrometers measure the linear displacement of a sensing rod that is held against the outside of the trunk by a counter-weight. As the radius of the tree changes, the position of the sensing rod is altered. A linear variable differential transformer (LDVT) moves simultaneously with the sensing rod converting the displacement measurements into an electric voltage. This signal is sent to a central

Figure 3.10. Picture of automatic point dendrometer (#13) installed on tree 32 at Blueberry: (a) sensing rod, (b) constant force cantilever, (c) steel mounting rod, (d) LVDT cable connector.

enclosure (POD) where data is stored and downloaded. The resolution of the dendrometer is 2 μm over an unadjusted range of 15,000 μm. The sensing rod is made of 304 stainless steel with a thermal coefficient of linear expansion of 17 μm/m/°C (Deslauriers et al. 2003b).

On June 23, 2006, three randomly selected white spruce trees at the study site were instrumented with automatic point dendrometers (Tree 1, Tree 5 and Tree 7). The radial stem increment was measured and recorded every 30 minutes and hourly averages were calculated afterwards. The automatic dendrometers were removed from the trees on September 2, 2006. During the second field season in 2007, two separate installations took place due to equipment and supplier problems. The first took place on June 20, when the original three dendrometers from the previous season were re-installed on the same trees (Tree 1, Tree 5 and Tree 7). The second installation took place on July 22 when an additional 11 automatic dendrometers were installed on white spruce trees at the site (Tree 9, Tree 11, Tree 12, Tree 15, Tree 20, Tree 21, Tree 22, Tree 26, Tree 32, Tree 36 and Tree 40). The newly instrumented trees were selected to represent an equal number of tree responses across all age classes. All of the dendrometers were installed at a height of approximately 1.5 m and on the east/south-east (93°) side of the trunk. The selection of trees was limited to within 40 m of the POD due to cable length. In 2007, the radial stem increment of all trees was measured and recorded every 15 minutes, with hourly averages calculated afterward. All of the automatic dendrometers were removed from the trees on September 9, 2007. During the 2007 growing season, only two dendrometers (Tree 1 and Tree 5) captured the main period of stem growth (which finished 25 July). Analysis of dendrometer data in 2007 was limited to these two individuals.

3.3.6 Meteorological Data

A Campbell Scientific meteorological station (with a CR-10X datalogger) was installed at the site on 27 August 2006. The meteorological station monitored and recorded weather data *in situ* to ensure the data was similar to what the trees actually experienced (Fig. 3.11).

The meteorological station was originally instrumented to measure air temperature (T_{mean}, T_{max} *and* T_{min} (°C) with a Campbell Scientific model T107 probe), precipitation (P (mm) with a Campbell Scientific model TE525 tipping bucket rain gauge), photosynthetically active radiation (PAR - 400 to 700 nm (kW/m^2) using a LICOR model LI200S pyranometer), and snow depth (cm) (Campbell Scientific model SR50 Sonic Ranger). In June 2007, the air temperature sensor was replaced by a sensor used to measure both air temperature and relative humidity (RH (%) using a Campbell Scientific model HMP45C212 probe) and eight sensors to measure volumetric soil moisture (VWC (m^3/m^3) using Hoskin Scientific ECH$_2$O E5 probes) were added. These variables were selected for their influence on tree growth as identified in the literature. The air temperature, relative humidity, PAR and precipitation were measured every minute and the data was stored in a Campbell Scientific SM4M Storage Module as 15-minute average values. Snow depth was measured every two hours. Maximums, minimums, averages and standard deviations were calculated for all of the variables.

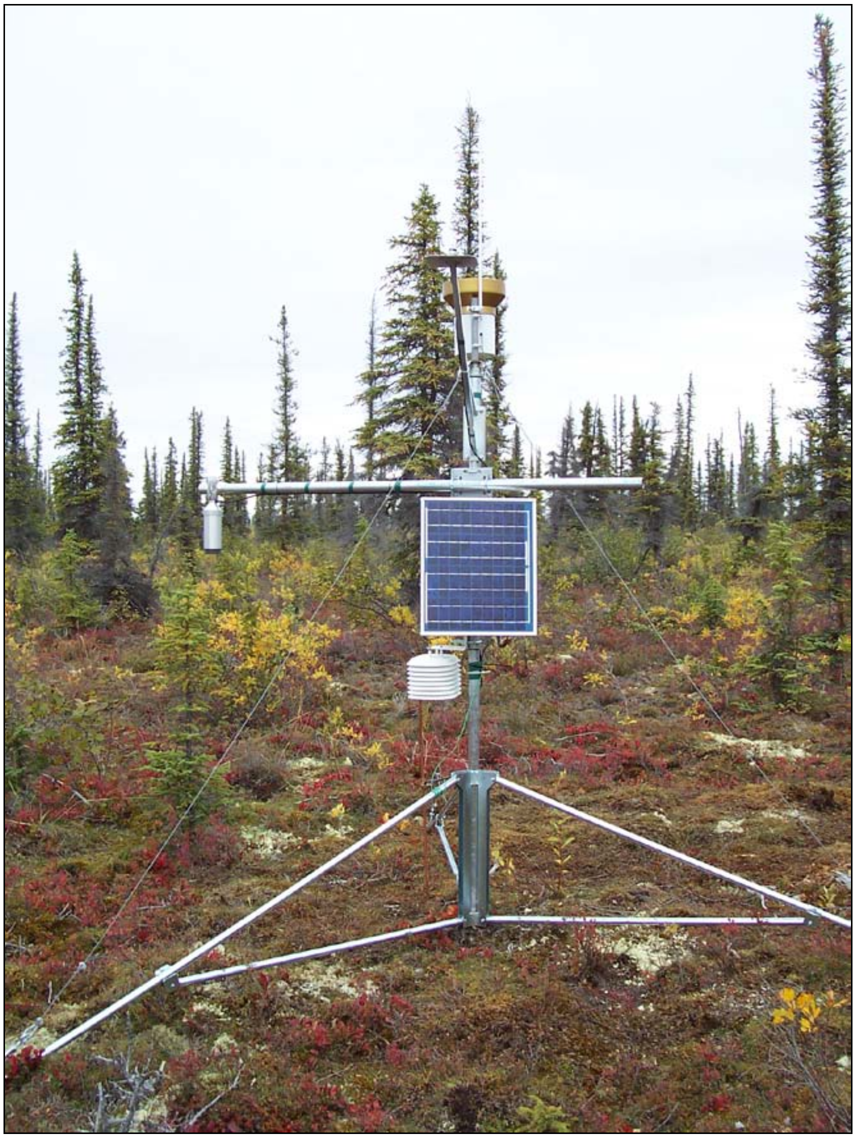

Figure 3.11. Picture of the Campbell Scientific meteorological station that was installed at the study site on 27 August, 2006.

3.4 Laboratory Methodologies

3.4.1 Increment Cores

The increment cores collected from each of the trees were air-dried, vertically aligned, glued to wooden mounts and progressively sanded (up to 600 grit sandpaper) until cell walls were visible (Stokes and Smiley 1968). The cores were then counted using a Nikon SMZ-800 binocular microscope. A list of characteristic marker rings (exceptionally narrow or wide rings, those with extensive resin ducts indicative of damage and low density latewood) was developed and used to visually cross-date the trees (Yamaguchi 1991). Cross-dating is the procedure of matching diagnostic patterns in ring characteristics among several individual trees in order to confirm the dated year (Fritts 1976). The ring-widths for each core were measured to the nearest micron (0.001 mm) using a Velmex measuring system and the software program J2X. The measured ring-widths were then used to verify the visual cross-dating using the statistical program, COFECHA (Holmes 1983; Grissino-Mayer 2001). COFECHA uses correlations between the ring-widths of tree-ring series within a chronology to assign dates to individual rings. After all of the tree-ring series were cross-dated, ring width series from the same tree were averaged. Each tree was then standardized using conservative methodologies (to retain low frequency climate signals), using a combination of negative exponential and linear functions (Cook 1985). Standardization creates a dimensionless index of tree growth with a mean of one and a stable variance (Fritts 1976). It maintains climatic information in the tree-ring record, while removing age-related trends in the tree-ring series (Cook 1985). The majority of trees did not show an age-related trend and linear functions were used to conserve the climate signal. Standardization is performed using the computer software program ARSTAN (Cook 1985).

Following Wilmking et al. (2004) and Pisaric et al. (2007), the averaged ring widths of each tree were analyzed individually to assess their response to climate. The interactive detrending option was used in ARSTAN to plot both the raw ring widths and the standardized ring width index for all of the 42 trees cored at the site. The standardized chronologies were used for all further analysis to ensure low-frequency long term climate signals were retained. This was instead of using the residual chronologies which retain more high-frequency signals. Using a visual categorization (*sensu* Pisaric et al. 2007), each tree was assigned to a group as a positive responder, a negative responder or to a third category (neutral) where the ring widths show no visual trend during the period of analysis (1927-2006)(Fig. 3.9).

Once each individual was assigned to a population, the averaged ring width chronologies were developed for each group. The software program DENDROCLIM2002 was used to determine if there was temporal change in the relation between tree growth and climate over time (Biondi and Waikul 2004). The program computed bootstrapped confidence intervals by generating 1000 repetitions (selected at random with replacement) and then running numerical computations on each sample to assess the significance of response functions. Computations involve linear correlation, Jacobean rotations for eigenvalues, singular-value decomposition and solutions of linear systems accompanied by principal component regression (Biondi and Waikul 2004). This study used mean monthly temperature values (previous March to current Oct) from 1927 to 2006 and total monthly precipitation values (current January to current Oct) from

1957-2006 to calculate both moving response intervals and evolutionary response intervals (forward and backward). To ensure enough intervals are calculated and that sufficient degrees of freedom are maintained, the minimum base length of the evolutionary and moving interval analysis must be less than 80% of all available years and at least twice the number of predictors (Biondi and Waikul 2004). Moving intervals slide a common period forward through time after beginning with the oldest year in common among the variables. Evolutionary intervals start with an interval and then progressively increase the period of years with either a fixed beginning year (forward evolutionary) or a fixed ending year (backwards evolutionary) (Fig. 3.12) (Biondi 1997; Biondi and Waikul 2004). Comparison between these three different methods gives an assessment of the stability of climate relations over the period of the climate record.

3.4.2. Ecological Data

Once the trees were averaged into their sub-populations, a Mann-Whitney U test and a Kruskal-Wallis test were used to determine if there are significant differences between sub-populations considering the tree characteristics and microsite data (age, DBH, tree height, nearest neighbour, active layer depth, reproductive ecology).

Cones collected from the trees were stored at -3°C in individual paper bags prior to analysis. The seeds were extracted by soaking each cone in hot water (60°C) for 6 hours and then drying them at 80°C for 8 hours. Once dried, the cones were placed in metal tins and shaken for 30 minutes to remove seeds (*cf.* Black and Bliss 1980). Each cone underwent this process twice. Once seeds from each tree had been collected, they were counted and stored in a fridge below 4°C. Seeds were dewinged and dissected bi-

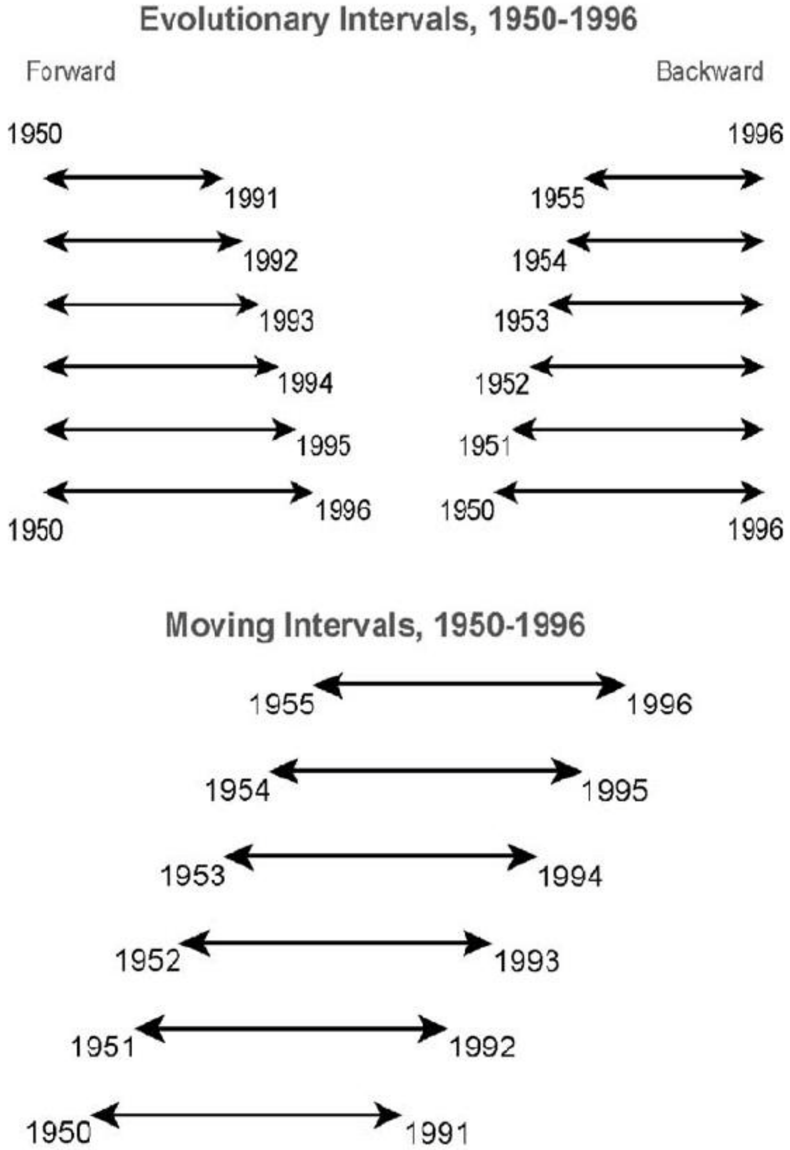

Figure 3.12. Graphical representation of the type of intervals used in DENDRCLIM2002 for analysis of the stability of growth response to climate (from Biondi and Waikul 2004).

laterally using a scalpel. Seeds were counted as viable if the endosperm and embryo were complete. However, this offers only a maximum viability estimate because many seeds that contain complete embryos may actually be non-viable (Baskin and Baskin 1998).

3.4.3. Dendrometer and Meteorological Data

Automatic point dendrometers record both reversible and irreversible stem variations. The reversible stem variations, shrinking (day) and swelling (night), occur due to water movement in the xylem. These trends were removed to reveal an estimate of true radial growth using a modified SAS program provided by Deslauriers et al. (2003). The program creates hourly means of the raw dendrometer measurements (from every 30 minutes in 2006 and every 15 minutes in 2007). The program then uses an autoregressive integrated moving average (ARIMA) model (p,d,q) x (P,D,Q)_s with the variables (2,1,0) x (1,1,0)_24 in order to fill any gaps in the data. However, few gaps required filling as the record was quite robust. The data was then smoothed and each point was assigned as expansion or contraction by comparing it to the previous hour. The data for each tree was graphed and examined individually to correct any errors produced in this step. The corrected data from each tree were combined and a separate third phase was defined. Each daily cycle was divided into three phases: (i) a contraction phase - the period between the morning maximum and daily minimum, (ii) the expansion phase - the total period from the daily minimum to the following morning maximum (iii) the stem radius increment (SRI) phase - part of the expansion phase from the time the stem radius exceeds the morning maximum until the next maximum. The entire circadian cycle defined by the three phases is considered a fourth phase (Deslauriers et al. 2003b;

Deslauriers et al. 2007b). The estimate of SRI is the difference between the maximum of expansion and the end of the third phase and is represented by $\Delta R+$ (μm), where R represents the radius. When the previous cycle maximum was not reached, a stem radius decrease (SRD) is calculated, represented by $\Delta R-$ (μm), but no 3rd phase is defined (Fig. 3.13). The beginning of each of these phases from each tree during each season was calculated and an average time was determined.

Once the phases were defined, the entire record of each tree was graphed. These graphs were examined to establish the main period of stem growth (cell division and expansion) from the remainder of the record (primarily cell wall thickening). Based on the literature, this occurs when the slope of the plotted raw dendrometer data noticeably decreases (Deslauriers et al. 2003). The main period was considered period (a) and the remaining data was considered period (b). To support these divisions the frequency of $\Delta R+$ and $\Delta R-$ cycles in each period was calculated. A chi-square (χ^2) test was performed to determine if there was a significant difference between the two periods.

For comparison with tree growth, only the common period (June 25-Sept 2, 2006; June 21-Sept 10, 2007) of meteorological measurements was used. Hourly averages of each meteorological variable were calculated. For 2006, hourly relative humidity (RH) data and daily precipitation (P) data from the Environment Canada (EC) weather station at the Inuvik airport were used. Vapour pressure deficit (VPD, kPa) was calculated from the hourly values of T_{mean} and RH following (Jones 1992):

$$\text{VPD} = a \exp \{ bT / c + T\} (1-\text{RH}/100) \qquad (3.1)$$

Where T is temperature (°C), RH is relative humidity (%), VPD is in kPa and the empirical coefficients are a = 6.1078, b = 17.269 and c = 237.3.

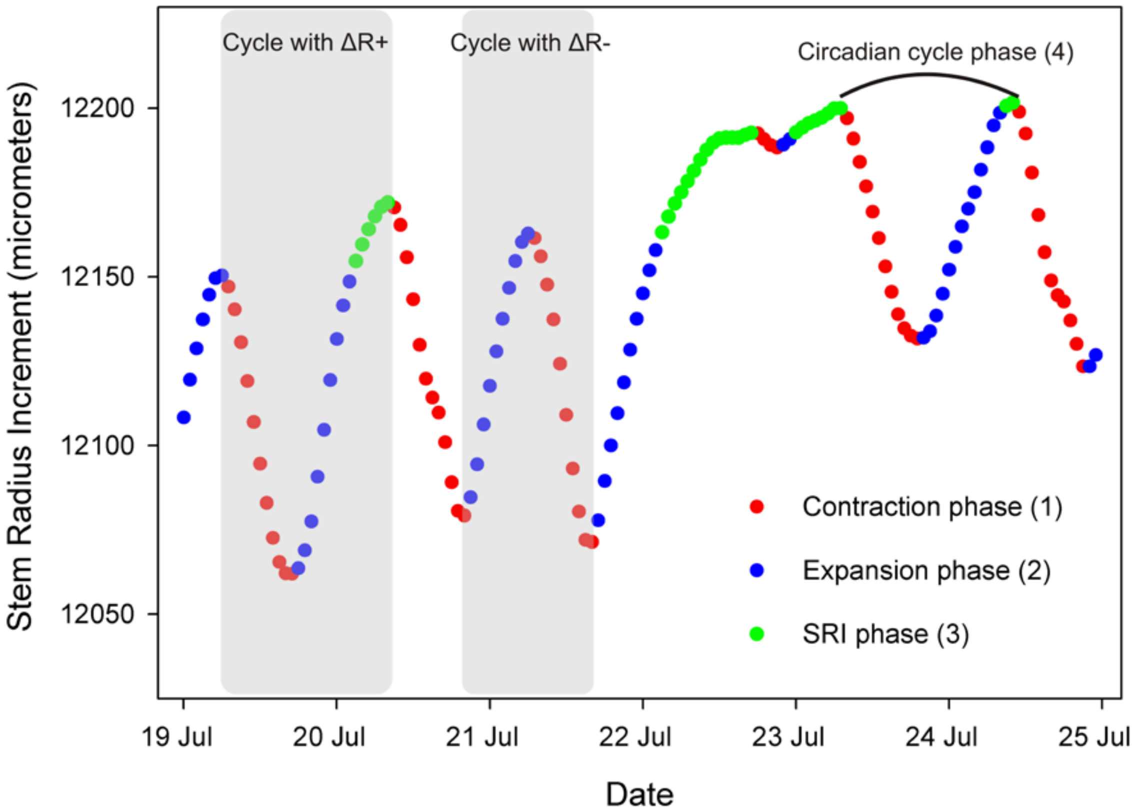

Figure 3.13. Stem circadian cycle divided into three distinct phases and examples of cycles that include ΔR+ and ΔR- for *Picea glauca* from the study site for the period from July 19 -July 25, 2006.

For 2007, daily precipitation (P) from the Inuvik Climate station was used and VPD was calculated from the measured RH values. In both years, each of the meteorological variables was processed following the stem phase divisions (based on the time of day). This means that for each day, there are four T_{max} values (T_{max1}, T_{max2}, T_{max3}, T_{max4}), each corresponding to the phases on that day. All variables (both growth and weather) were graphed to ensure they satisfied the assumptions of normalcy. Several transformations were required for both years of data. The logarithm ($\log_{10}$) of VPD and of the contraction data was taken and used in all analysis. The logarithm ($\log_{10}$) of the stem radius increment (SRI) was taken (150 μm were added to the SRI measurements so there were no negative values). These transformed and processed meteorological and growth variables were then correlated with the SRI phase (ΔR+) from the main period of growth using simple Pearson correlation analysis (*sensu* Deslauriers et al. 2003b).

Defining the average beginning of each phase required the use of circular statistics (Batschelet 1981; Tran 2007). Each time was converted to an angle and the sine and cosine of each angle was calculated. The mean angle was calculated by:

$$\bar{\phi} = \arctan\left(\bar{y} / \bar{x}\right) \tag{3.2}$$

Where $\bar{\phi}$ is the mean angle, $\bar{y}$ is the sum of the sine values divided by the total number of observations and $\bar{x}$ is the sum of cosine values divided by the total number of observations. The length of the mean vector was calculated by:

$$r = \frac{1}{n}\left[\left(\sum \cos\phi\right)^2 + \left(\sum \sin\phi\right)^2\right] \tag{3.3}$$

The standard deviation was calculated from the length of the mean vector by:

$$\sigma = \left\{-2 \cdot \log r\right\}^{0.5} \tag{3.4}$$

3.4.4. Conceptual Model of Tree Growth

Tree ring analysis commonly assumes that tree growth can be reasonably approximated by a linear function with temporal invariance and local inputs of temperature and precipitation. However, tree growth is often controlled by multivariate, nonlinear biological and physiological processes (Vaganov et al. 2006). The use of a mechanistic forward model that can resolve critical processes linking climate variables to tree-ring formation and can lead to a better understanding and the development of more accurate estimates of past climate (Anchukaitis et al. 2006). A working mechanistic model was not created in this study. However, a conceptual model that includes the most important environmental influences on the growth of both the positive responder and negative responder sub-populations is presented at the end of chapter five.

Chapter 4
Sub-Population Growth Responses to Climate and Potential Environmental Controls

4.1. Introduction

The investigation of the factors that influence tree growth requires a full understanding of the environment in which they grow. This chapter presents and discusses the climate growth relations that define the sub-populations of white spruce (positive responder, negative responder, neutral) that were identified at Blueberry. Based on these sub-populations, an investigation of environmental conditions on tree growth was conducted to determine if specific controls exist for the identified growth responses of white spruce on the landscape. The specific objectives addressed by this chapter are:

1. Determine the climatic variables that influence the different growth responses of white spruce.
2. Determine if there are statistical differences in the microsite conditions under which the sub-populations of white spruce grow.

4.2. Tree Response to Climate

Previous literature has identified different sub-populations of white spruce based on annual growth patterns during the 20th century (*cf.* Wilmking et al. 2005; Pisaric et al. 2007). Based on this, each tree at Blueberry was grouped into three sub-populations (positive responders, negative responders and neutral) according to their previous growth. This was determined by visually examining the raw and standardized ring width records from each tree. Of the 42 trees studied at the site, 3 were considered positive responders, 13 neutral and 26 negative responders (Table 4.1). The tree ring records for each sub-

Table 4.1. Individual trees assigned to each of the three sub-populations identified at Blueberry.

	Growth Response	
Positive responders (POS)	**Negative responders (NEG)**	**Neutral (NEUT)**
BB20	BB01	BB03
BB21	BB02	BB05
BB22	BB04	BB06
	BB08	BB07
	BB10	BB09
	BB11	BB17
	BB12	BB26
	BB13	BB27
	BB14	BB32
	BB15	BB33
	BB16	BB36
	BB18	BB38
	BB19	BB42
	BB23	
	BB24	
	BB25	
	BB28	
	BB29	
	BB30	
	BB31	
	BB34	
	BB35	
	BB37	
	BB39	
	BB40	
	BB41	

population were combined and average chronologies (POS, NEG and NEUT) were developed (Fig. 4.1a-c). While three sub-populations have been identified in previous studies, it is unclear if all three are present at Blueberry. Principal components analysis suggests that the NEUT and NEG chronologies are similar and may in fact not be statistically distinct from one another (Fig. 4.1d). Given these similarities, much of the subsequent analyses will focus on the differences between the positive responder and negative responder sub-populations.

To examine the climate-growth response of the three sub-populations, Pearson correlations were calculated for each chronology and monthly climate data from Inuvik. Based on the correlation analysis (Table 4.2), it is clear that the three sub-populations respond to climate differently. The POS chronology is the only one that has a positive relation with June temperature during the growing season. The NEUT and NEG chronologies are negatively correlated with temperatures during the growing season, especially the latter part of the summer. The NEG chronology also has significant negative relations with temperature during the previous June, July and September. These relations are also noted for the NEUT and to a lesser extent, POS chronologies (Table 4.2).

Previous years' growth has been identified as being important for conifer growth at northern treeline. Conifers in northern climates are able to use previously stored photoassimilate for current years' growth, thus integrating the influences of previous growing seasons into current growth (Jacoby and D'Arrigo 1995; Kagawa et al. 2006). In this study, warm temperatures during June and July of the previous growing season appear to have a negative impact on growth the following year. Warm temperatures can

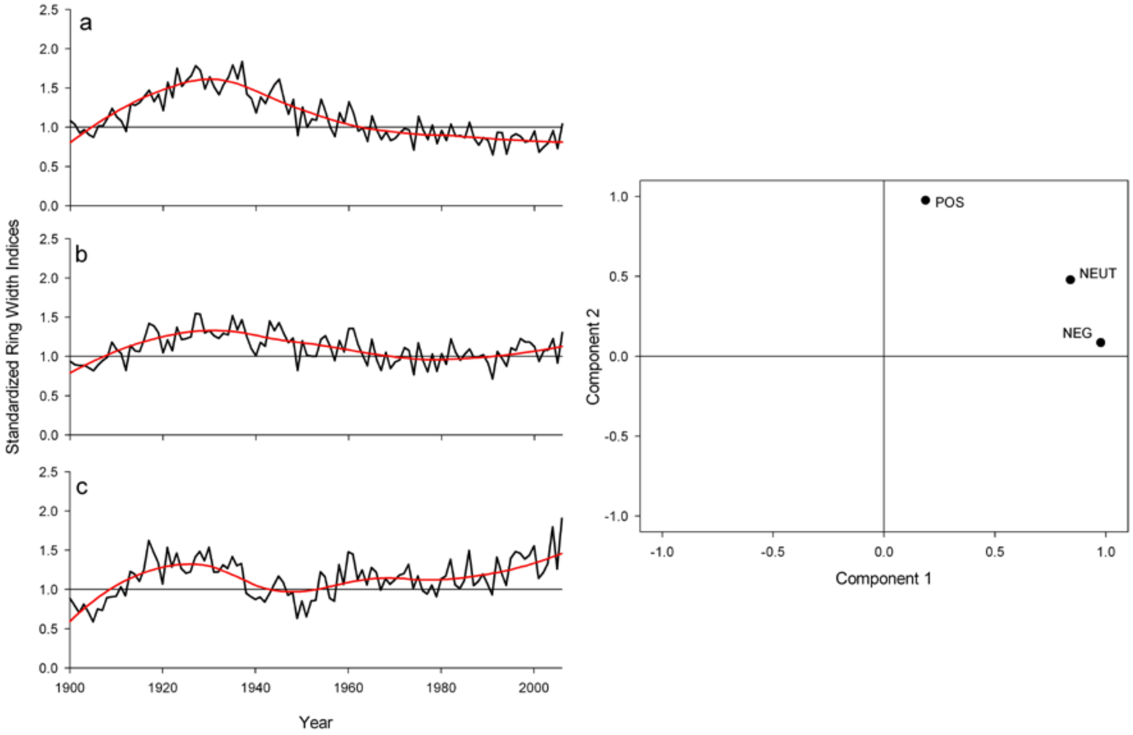

Figure 4.1. Standardized ring widths since 1900 for the three sub-populations of trees identified at Blueberry: (a) negative responders (NEG), (b) neutral (NEUT) and (c) positive responders (POS). (d) Principal components analysis (Varimax rotation) of averaged sub-population chronologies from 1900 to 2006. The first component explains 72% of the variance in the data set.

Table 4.2. Pearson correlations between the averaged sub-population chronologies and temperature and precipitation records from the Inuvik climate station. The period of record for temperature is 1927-2006 (N=80) and for precipitation, 1959-1994 (N=36). Only significant correlations (p≤0.05) are reported.

	Growth Response		
Climate variable	Positive responders (POS)	Neutral (NEUT)	Negative Responders (NEG)
Temperature			
pJune		$-.245^{*}$	$-.415^{**}$
pJuly	$-.352^{**}$	$-.420^{**}$	$-.419^{**}$
pSeptember		$-.224^{*}$	$-.295^{**}$
June	$.435^{**}$		
August			$-.271^{*}$
September			$-.287^{**}$
Precipitation			
April	$.364^{*}$	$.508^{**}$	$.394^{*}$

Significance levels: $^{*}p < .05$ $^{**}p < .01$

deplete soil moisture, which can lead to a reduction in photosynthesis and increases in leaf senescence (Kozlowski et al. 1997). As a result, trees would produce less photoassimilate that can be used at the beginning of the following growing season. These findings are consistent with previous studies that have cited temperature-induced drought stress as a possible mechanism for recent growth declines at some treeline sites in North America (Szeicz and MacDonald 1996; Barber et al. 2000; Wilmking et al. 2004). Although the POS chronology has a negative relation with previous July temperature, more prominent is a positive response to current June temperatures. Early growing season temperatures have been identified as being important in cell development and ultimately annual growth (Antonova et al. 1995; Kozlowski et al. 1997; Vaganov et al. 2006). This is because warmer June temperatures often coincide with the highest rate of cambial division, which leads to increased ring width during these years.

Relations between precipitation and the three sub-population chronologies are more limited than with temperature. Both the POS and NEG chronologies have a positive correlation with April precipitation during the period of overlap (1959-1994) (Table 4.2). Szeicz and MacDonald (1996) found similar growth responses from the nearby Campbell-Dolomite Upland. However, Wilmking (2004) did not find any significant correlation with precipitation variables in northern Alaska.

Szeicz and MacDonald (1996) suggest late-winter precipitation (which falls as snow at the study site) may help to protect the shallow root systems of white spruce in this region to damaging cold temperatures during the transition from winter to spring. April precipitation might also have a strong correlation with growth because it contributes to increased soil moisture availability during the early growing season once the ground thaws (Vaganov et al. 1999; Jarvis and Linder 2000).

Based on the correlation analysis, it is clear that temperature and precipitation during the growth year and the year prior play an important role in tree growth at Blueberry. However, this does not indicate if the responses of the three sub-populations are time-stable. Several recent studies have indicated that climate growth relations have changed during the later half of the 20th century (Jacoby and D'Arrigo 1995; Barber et al. 2000; D'Arrigo et al. 2004; Wilmking et al. 2004; Wilmking et al. 2005; Pisaric et al. 2007). To investigate the stability of the climate-growth relations (mean monthly temperature and total monthly precipitation) for each sub-population, the ring widths of each averaged chronology were assessed and compared using DENDROCLIM2002 (Biondi and Waikul 2004) (Fig. 4.2 to 4.4).

The NEG chronology shows a stable response to previous July temperatures over the entire period of record (Fig. 4.2). The backward evolutionary response function (BERF) shows a similar stable response to previous June temperatures, while the forward evolutionary response function (FERF) and moving response function (MRF) indicate that previous June temperatures have only become significant since the mid 1940s. The FERF also shows a stable response to April precipitation over the entire record, while the BERF and MRF only reveal this response when the period from 1958 to 1961 is included. After this, no significant response with precipitation is observed (Fig. 4.2). The POS chronology is correlated with current June temperatures over the entire period of analysis (Fig. 4.4), suggesting this response is time stable. The POS chronology also shows a negative response to previous July temperatures. However, considering that moving

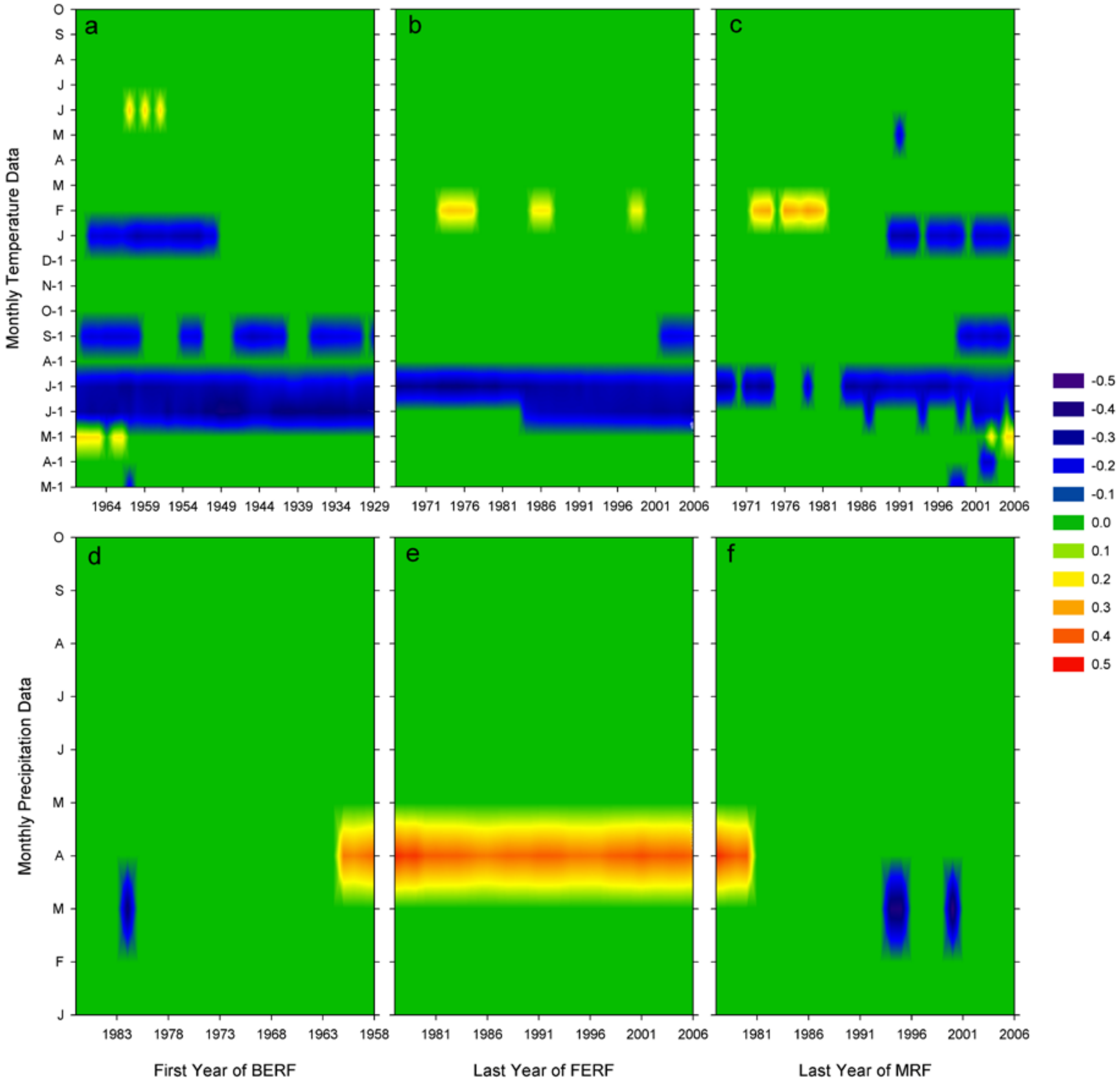

Figure 4.2. Climatic response of the NEG chronology. (a) Backward and (b) forward evolutionary response functions (BERF and FERF), and (c) moving response functions (MRF) for mean monthly temperatures (previous March to current October; 1927-2006). (d) Backward and (e) forward evolutionary response functions, and (f) moving response functions for total monthly precipitation (current January to October; 1958-2006). Only significant response functions at the 95% confidence interval were graphed. BERF are plotted against the beginning calibration year; FERF and MRF are plotted against the last year of the period. MRF baselength for analysis was 40 years for temperature and 20 years for precipitation.

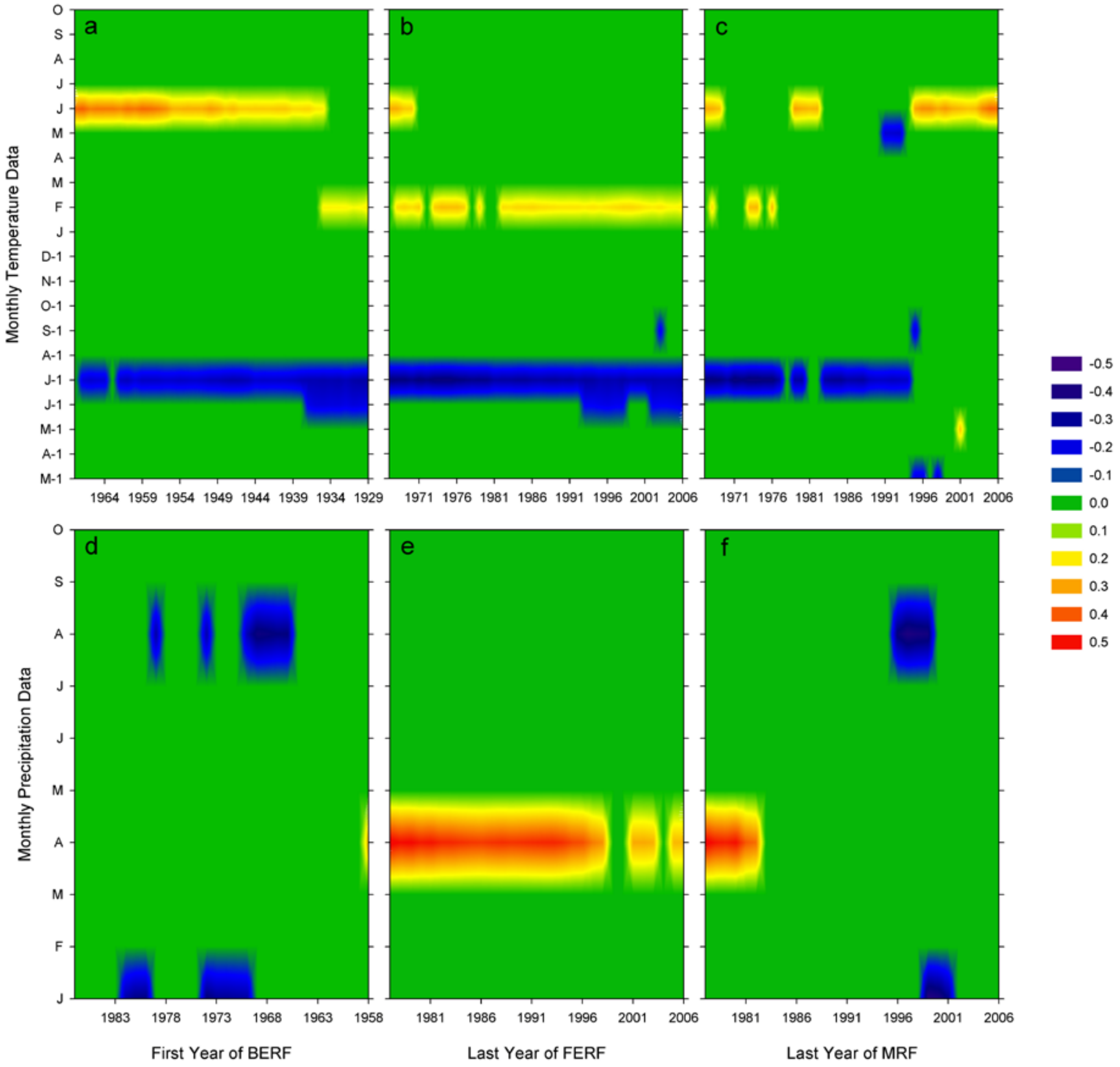

Figure 4.3. Climatic response of the NEUT chronology. (a) Backward and (b) forward evolutionary response functions (BERF and FERF), and (c) moving response functions (MRF) for mean monthly temperatures (previous March to current October; 1927-2006). (d) Backward and (e) forward evolutionary response functions, and (f) moving response functions for total monthly precipitation (current January to October; 1958-2006). Only significant response functions at the 95% confidence interval were graphed. BERF are plotted against the beginning calibration year; FERF and MRF are plotted against the last year of the period. MRF baselength for analysis was 40 years for temperature and 20 years for precipitation.

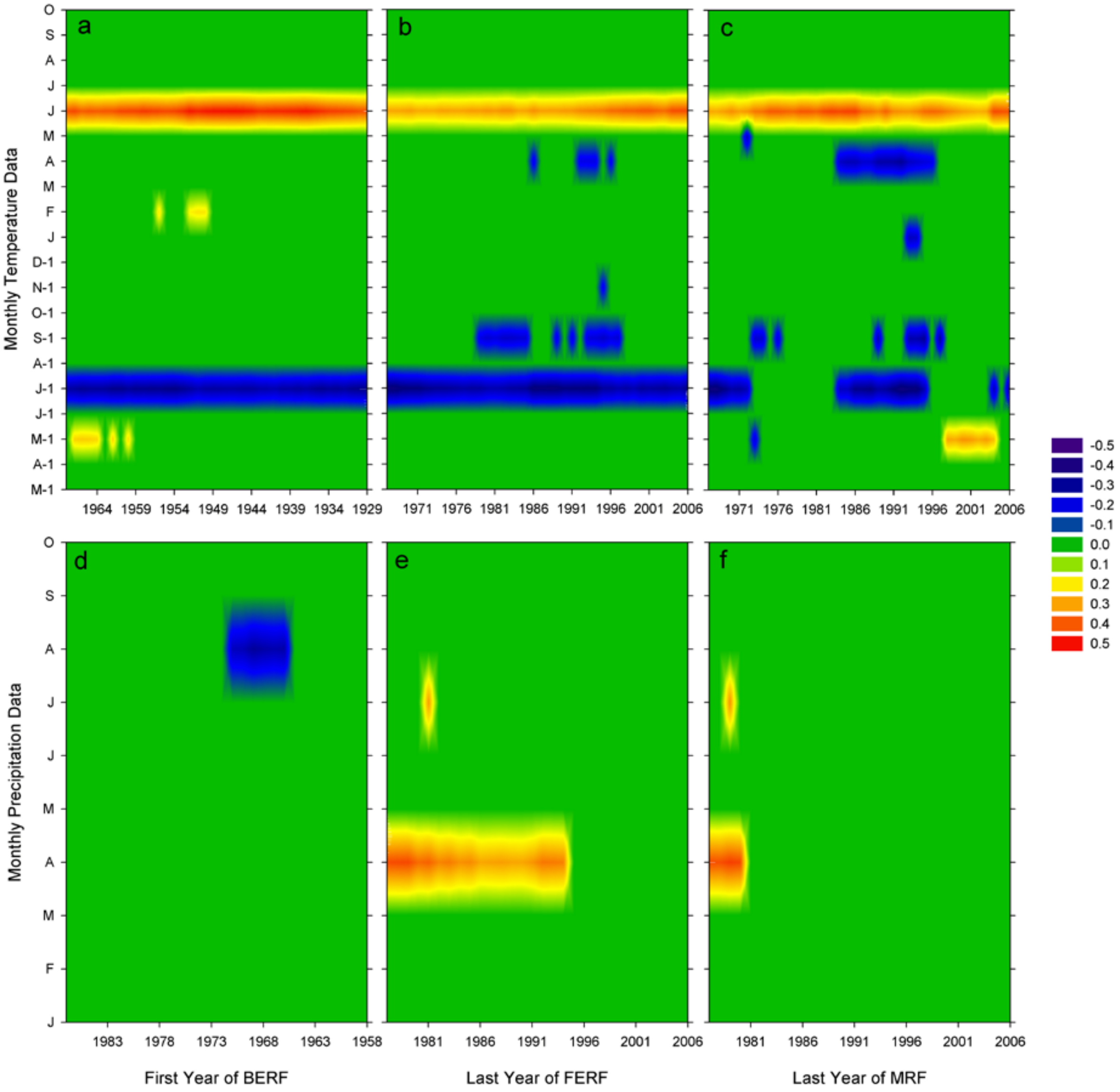

Figure 4.4. Climatic response of the POS chronology. (a) Backward and (b) forward evolutionary response functions (BERF and FERF), and (c) moving response functions (MRF) for mean monthly temperatures (previous March to current October; 1927-2006). (d) Backward and (e) forward evolutionary response functions, and (f) moving response functions for total monthly precipitation (current January to October; 1958-2006). Only significant response functions at the 95% confidence interval were graphed. BERF are plotted against the beginning calibration year; FERF and MRF are plotted against the last year of the period. MRF baselength for analysis was 40 years for temperature and 20 years for precipitation.

response functions are more robust than either evolutionary response function (Biondi 2000), this response is not as stable as that with the NEG chronology. Relations between growth of positive responders and monthly precipitation are not time stable. Similar to the NEG chronology, a significant response to April precipitation only exists when the beginning of the precipitation record is included. Temporally stable responses to temperature appear to define the two sub-populations. There were no significant shifts in response to temperature over the period of record. This is contrary to other studies (Jacoby and D'Arrigo 1995; Barber et al. 2000; Wilmking et al. 2004), which have found a weakening or strengthening of relations between tree growth and temperature during the 20th century. As well, despite some studies that found an increase in the significance of the relation between precipitation and tree growth, there was not a stable response for either of the sub-populations at Blueberry (Jacoby and D'Arrigo 1995; Barber et al. 2000).

4.3. Potential Non-Climatic Controls

One of the primary objectives of this thesis was to assess why different sub-populations of white spruce exist at a single site. A number of possibilities have been suggested in the literature, but many involve temperature-induced moisture stress. Studies have found that these stresses affect trees differently resulting in the different growth responses that have been noted (Wilmking et al. 2004; Pisaric et al. 2007). What is still unclear is why some trees are more impacted by these stresses than others. To investigate this, the influence of microsite conditions and characteristics of the trees themselves were studied.

Characteristics and microsite conditions of 42 trees at Blueberry were measured to assess similarities/dissimilarities between individuals (Table 4.3). The forest canopy at the study site was composed of mature white spruce (mean age = 243 ± 91 years) with a few standing dead snags. The oldest tree was 429 years old and the youngest tree was 99. These dates represent minimum ages because the pith was not cored for each tree and the cores were collected above ground level. Despite their age, the trees were small (mean height = 5.9 m ± 1.6 m; mean DBH = 14.05 cm ± 4.43 cm) compared to sites in the southern Mackenzie Delta. The tallest tree was 10.15 m and the shortest was 3.18 m. Measurements of the distance from each tree to its nearest neighbour (mean = 3.28 m ± 1.67 m) indicate that above ground competition for resources such as light is minimal at the site. Finally, measurements of active layer (which is the maximum thaw depth) within 2 m of each tree revealed a site average depth of 52 cm ± 7.2 cm at the end of the 2007 growing season. There was a maximum thaw depth of 71 cm and a minimum thaw depth of 31 cm. All of these characteristics were normally distributed.

The mean of each tree characteristic and environmental variable for each sub-population were calculated (Table 4.4). A Mann-Whitney U and Kruskal-Wallis test were used to determine if there were significant differences of the measured ecological variables between each of the sub-populations. Non-parametric tests were used due to the low number of positive responders and uneven sample sizes.

Table 4.3. Measured characteristics of the 42 trees at the Blueberry site.

Tree Number	Age [a]	Height (m) [b]	DBH (cm)	Nearest Neighbour (m)	Active Layer Depth (cm) [c]
1	280	7.80	22.0	2.25	60
2	311	6.19	16.1	0.72	72
3	214	6.65	16.9	0.72	54
4	142	4.32	9.6	2.5	47
5	136	5.75	10.7	5.47	56
6	99	5.12	10.3	1.74	52
7	235	6.65	15.9	1.74	57
8	282	4.51	10.3	2.07	60
9	287	3.37	13.0	0.93	63
10	295	3.74	11.1	3.32	49
11	352	7.12	24.9	4.36	46
12	105	4.51	10.8	3.65	54
13	246	7.00	16.3	7.66	50
14	216	5.54	12.4	4.47	47
15	210	6.65	13.0	2.86	52
16	372	6.42	16.6	2.67	51
17	257	5.54	14.1	5.25	57
18	142	7.12	15.9	3.37	47
19	151	7.88	16.4	5.74	45
20	240	5.75	11.8	2.8	39
21	278	5.12	13.1	2.8	31
22	114	4.32	8.4	0.28	39
23	245	9.62	16.4	4.25	41
24	152	5.12	10.4	3.86	51
25	124	3.53	7.0	1.9	62
26	429	6.65	16.7	2.97	55
27	250	7.83	17.9	2.11	61
28	192	3.92	10.0	1.74	52
29	337	6.25	12.8	3.05	55
30	397	3.18	12.3	2.5	53
31	215	5.40	18.9	2.06	52
32	110	4.44	6.8	1.53	53
33	309	7.31	13.5	4.09	55
34	157	7.62	13.8	4.09	58
35	271	5.54	12.6	3.84	52
36	218	3.71	7.4	4.39	55
37	192	4.69	9.1	4.31	52
38	398	7.24	18.4	3.53	49
39	229	5.54	13.1	2.89	43
40	408	7.37	23.4	7.03	52
41	229	10.15	15.9	6.46	49
42	396	5.71	23.9	3.78	51

a - minimum age estimate as pith was not cored for each tree and cores were taken at breast height
b - estimated height from trigonometric functions. A clinometer was used to measure the vertical angle and a tape to measure the distance from the sighting to the base of the tree
c - based on the average of 5 measurements made within 2 m of the base of each tree

Table 4.4. Mean of each measured tree characteristic and microsite variable for each of the identified white spruce sub-populations.

Response Type	N	Mean Age	Mean Height (m)	Mean DBH (cm)	Mean Nearest Neighbour (m)	Mean Depth to Active Layer (cm)
NEG	26	240	6.03	14.27	3.60	52.06
NEUT	13	257	5.84	14.27	2.94	55.20
POS	3	211	5.06	11.10	1.96	36.27

Figure 4.5 reveals no significant differences between sub-populations for age, height, DBH, and nearest neighbour. Previous studies that have identified sub-populations have also found no differences based upon the age or size of the tree (Wilmking et al. 2004; Pisaric et al. 2007). The nearest neighbour measurement approximates possible competitive influence between trees. Contrary to Wilmking et al. (2004), there was no significant difference in the nearest neighbour metric for the three sub-populations of trees examined at the site. In Alaska, Wilmking et al. (2004) concluded that many negative responders were found in high-density stands where competition and water stress may have been higher. In the current study, the only environmental variable that appeared to have statistically significant differences between the sub-populations was the active layer depth between the positive responders and both other sub- populations (POS v. NEG $z = -2.808$ $p<0.01$; POS v. NEUT $z = -2.635$ $p<0.01$) (Fig. 4.5). These differences were confirmed with a significant Kruskal-Wallis one-way analysis of variance between the three sub-populations ($\chi^2 = 12.735$ $p<0.01$). The active layer depth near responding trees was significantly less than neutral and non-responding trees (Fig. 4.6). The shallow active layer near responding trees is possibly related to the greater moss cover in these areas. Moss maintains a low thermal conductivity, which leads to a low ground heat flux, lower ground temperatures and maintains permafrost close to the surface (Smith 1975; Sofronov et al. 2004). These findings seem to contradict previous research where reduced growth in conifers was related to the close proximity of permafrost to the surface and lower soil temperatures (Vaganov et al. 1999; Grossnickle 2000; Vaganov et al. 2006). However, a higher permafrost table around positive responder trees could trap soil moisture near the surface

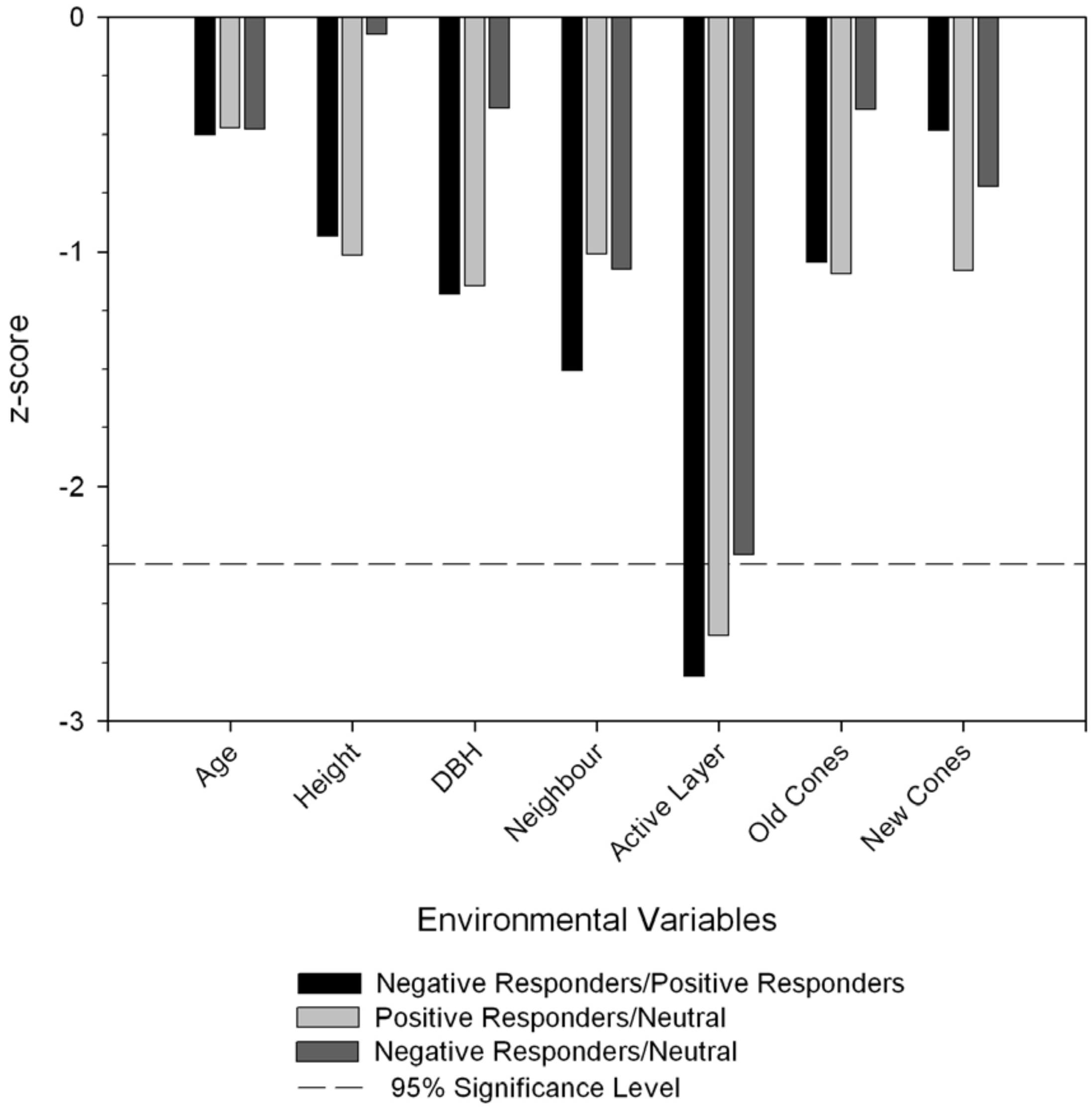

Figure 4.5. Computed z-scores from a Mann-Whitney U test for differences between the sub-populations of white spruce and ecological variables. The dashed line represents the 95% significance level.

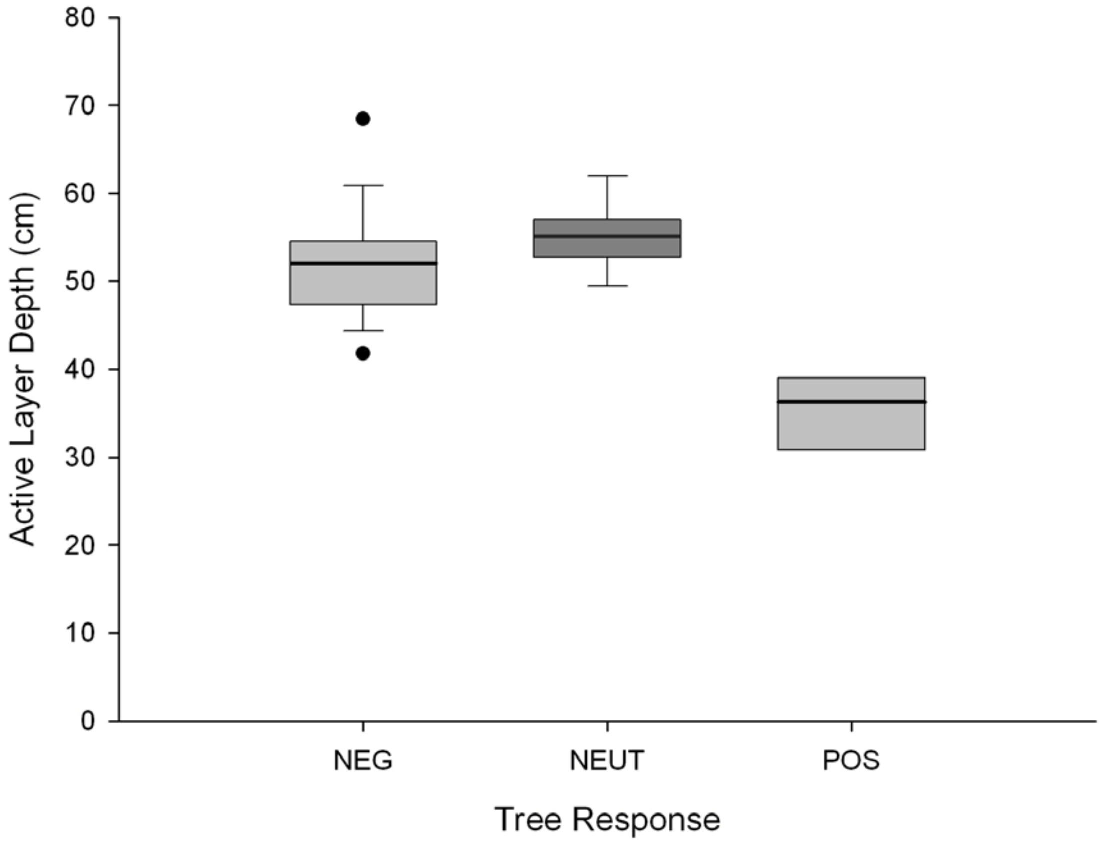

Figure 4.6. Boxplot showing the mean (thick black line), upper and lower quartiles (top and bottom of boxes) and the 5th and 95th percentiles (bars) of active layer depth for each of the three sub-populations of white spruce found at the study site. Outliers are represented by black dots.

and within the shallow depth of tree roots observed at the site. There is evidence that active layer depth in permafrost environments have been steadily increasing since the middle of the 20th century (Frauenfeld et al. 2004). Permafrost controls subsurface and surface hydrology limiting the amount of infiltration of spring runoff from snowmelt and absorption of precipitation (Hinzman et al. 1991; Juday et al. 1998). Changes in seasonal thaw depth could also alter the water-storage capacity of soils (ACIA 2004). In areas of low annual precipitation, such as the Mackenzie Delta, an increase in active layer depth is likely to lead to drying of soils (Juday et al. 1998; ACIA 2004).

Several pits were excavated near the study area to determine the rooting depth of the nearby trees. All of the white spruce trees exhibited diffuse and very shallow root systems similar to published accounts (Strong and La Roi 1983; Nienstaedt and Zasada 1990). At the study site, there were few roots deeper than 40 cm below the surface. The shallow root depths coupled with increased active layer depth, could lead to moisture stress, as trees cannot access water at greater depths (Kane et al. 1991). However, as observed at the site, moss cover can buffer soil temperatures and limit the depth of the active layer. This could lead to saturation of the active layer and increased availability of soil water at an accessible depth for roots (Hinzman et al. 1991; Kane et al. 1991).

Thus, the presence of a thick moss cover may limit the depth of the active layer during the growing season. This may increase soil moisture content in the rooting zone and possibly explain the occurrence of the positive responder sub-population. Given the small sample size, further research is needed to support this conclusion.

Along with the environment, another potential non-climatic control of the different growth responses identified at Blueberry could be the underlying blueprints of each individual tree. Although no data was collected during this study to quantify the genotypes of the white spruce populations at the site, recent literature possibly indicates that genetically different populations of white spruce exist in northwestern North America (Anderson et al. 2006). These genetic differences may play an important role in the divergence issue.

It has been well established that plants with restricted ranges in cool environments have low optimal temperatures for growth and limited potential for acclimation to high temperatures (Berry and Bjorkman 1980). Although distributed across much of Canada, white spruce are optimally adapted to temperature and precipitation conditions in local environments based on genecological tests of open-pollinated white spruce populations in Quebec (Andalo et al. 2005). Within the Mackenzie Delta, these genetic differences may be linked to the last glaciation when spruce populations existed at refugia in Alaska and south of the Laurentide Ice Sheet (Ritchie and MacDonald 1986; Anderson et al. 2006). After glaciation, the populations, which would have been adapted to different climatic conditions through long-term evolutionary processes, appear to have re-vegetated northwest North America from these two refugia (Larsen 1980b; Hopkins et al. 1981; Ritchie and MacDonald 1986). New genetic evidence and a study that concludes the proposed rates of spread from southern refugia were too fast, lend support to the possibility that small populations of white spruce could have survived the last glacial maximum in Alaska (Clark et al. 2001; Anderson et al. 2006). Anderson et al. (2006) sequenced chloroplast DNA (cpDNA) and found a very high diversity of halotypes (haploid genotypes) in Alaska. They conclude that since the mutation rate of cpDNA is extremely slow, there would not be enough time for this diversity of halotypes to evolve if white spruce migrated to this area after the end of the last glaciation. These northern populations of white spruce then expanded during the Holocene, at the same time southern populations also expanded northward. These two populations probably met somewhere in northern British Columbia (Anderson et al. 2006).

It is possible the sub-populations found at the study site and at many other sites across the circumpolar north (Wilmking et al. 2005), represent a mixing of two different white spruce populations. One adapted to warmer conditions having survived in refugia south of the Laurentide Ice Sheet and the other adapted to the much colder conditions of Alaska refugia. The close proximity of the Alaskan refugia suggests they could comprise the majority of the Mackenzie Delta population while genetic information from southern refugia may be more limited. Due to a lack of speciation, mixing with viable offspring would take place among the populations. These would represent the three different sub-populations at these sites: the cold-adapted negative responders, which are not tracking recent warming trends; the warmer adapted positive responders, which follow the warming trends with increased radial growth; and the neutral population, a mixture that does not show either trend significantly. It is plausible that the genetic composition of trees at Blueberry differ significantly enough that interactions with environmental factors lead to sub-populations of trees with very different growth trends.

4.4. Reproductive Ecology

The earlier analyses investigated the climatic and environmental factors that may be responsible for the development of sub-populations at Blueberry. However, it is unknown if the climatic and environmental conditions that lead to these sub-populations have an impact on their reproductive ecology as well. To investigate this, cone counts and seed viability tests were conducted. Cone counts revealed that all trees had low numbers of cones (mean old cones = 12 ± 13 cones; mean 2007 cones = 14 ± 21 cones) (Table 4.5). The standard deviation for these numbers was extremely high because many of the trees had no cones present. Cones were collected from nine trees at the site so the number of viable seeds could be determined (Table 4.6). There were 541 seeds collected from 35 cones. The average number of seeds per cone was 15 ± 8. The percentage of viable seeds (seeds that contained a complete endosperm and embryo) was low with an average of 31% ± 16%.

There were no significant differences between the sub-populations when considering the number of cones. A comparison among number of seeds between sub-populations could not be conducted due to a lack of sample depth for each group. However, some site-wide observations were made. The combination of numbers of cones on the trees and the percentage of viable seed indicates that trees at the study site have low reproductive capability. This is supported by data that suggests white spruce in good years can produce between 8000 and 12000 cones per tree, although yields in the north are much less (Nienstaedt and Zasada 1990; Lamontagne et al. 2005). The annual variability of cones produced by white spruce in the boreal forest is high, ranging from zero up to 3500 cones per tree during mast years at study sites in southwestern Yukon Territory (Dale et al. 2001; Lamontagne and Boutin 2007). Comparisons between sites near the edge of their range with sites in the middle of their range are difficult, but the number of cones produced by trees located at marginal sites would be expected to be much lower. Counts conducted by the Forest Resource Division, Government of NT on

Table 4.5. Cone counts of 42 trees conducted in late August 2007 at Blueberry.

Tree Number	Old Cones	2007 Cones
1	20	4
2	10	5
3	0	0
4	0	0
5	10	12
6	3	0
7	2	4
8	0	0
9	0	0
10	7	0
11	50	100
12	10	20
13	12	50
14	3	20
15	0	0
16	3	0
17	45	35
18	30	50
19	20	20
20	15	17
21	30	50
22	5	0
23	40	6
24	10	18
25	0	0
26	25	15
27	15	0
28	0	0
29	31	23
30	4	0
31	4	3
32	0	0
33	20	50
34	8	42
35	0	0
36	0	0
37	8	33
38	0	0
39	7	0
40	3	3
41	8	0
42	26	8

Table 4.6. Assessment of the seed viability of white spruce trees at Blueberry.

Tree Number [a]	**No. Cones Collected** [b]	**No. of Seeds** [c] **Total**	 **Empty**	 **Viable**	**%** [d]
2	2	48	43	5	10
12	4	8	7	1	13
14	3	13	5	8	62
17	8	137	81	56	41
21	4	53	32	21	40
24	5	84	63	21	25
29	4	58	40	18	31
37	4	125	72	53	42
42	1	15	12	3	20

a - number of tagged tree (corresponds to Table 4.4)
b - total number of cones collected from each tree
c - number of seeds collected from the cones for each tree. The total number is the sum of viable seeds (complete endosperm and embryo) and empty seeds (any seed not considered viable)
d - percentage of viable seeds for each tree

12 white spruce located on the uplands near Inuvik in 2007 found an average of 395 ± 211 new cones on each tree. These trees were much larger than trees in the Delta and probably younger, indicating that the limitations on cone production may be attributable to both a poor environment and age of the tree. However, white spruce are known to experience mast years when large amounts of cones are produced (Dale et al. 2001; Lamontagne and Boutin 2007). Therefore, additional years of observations are required to support these preliminary conclusions.

The seed data supports the conclusion that reproductive capacity at Blueberry is limited, regardless of the sub-population to which a tree belongs. Previous studies have reported finding between 32 and 130 seeds per cone compared to the average of 15 seeds per cone at Blueberry (Nienstaedt and Zasada 1990; Messaoud et al. 2007). Further, the number of viable seeds per cone has been reported to be more than double (12-34 viable seeds/cone) in non-controlled pollinations (Nienstaedt and Zasada 1990), than the average of 5 viable seeds/cone found at Blueberry. Similar to observations of cones from Blueberry, (Owens and Molder 1979) found a large number of normal, but empty seeds while investigating the sexual reproduction of white spruce. They attribute the abortion of the female gametophyte to two primary causes, environmental factors and self-pollination. Both affected late embryo development, but not initial fertilization. Both of these factors could have had an effect at the study site due to a marginal environment and a small number of individuals, increasing the possibility of self-pollination.

All of the trees at the site appear to have limited reproductive capability and there appears to be no difference among the three sub-populations. A short growing season, cold temperatures and low amounts of precipitation at Blueberry could mean that trees must allocate limited energy supplies between growth and reproduction.

4.5. Summary

This chapter examined the growth response to climate of the three sub-populations identified at Blueberry. Several non-climatic factors were investigated as possible reasons that trees were responding differently within a single site. Finally, the influence of climatic and environmental conditions on the reproductive ecology of trees was considered.

Each of the 42 white spruce trees were grouped into one of the three sub-populations (negative responders, neutral and positive responders) based upon their growth response to recent climatic trends. The response of each sub-population chronology to temperature and precipitation over the period of overlap was examined. Negative responders had a significant, inverse relation to previous June and July temperature that was temporally stable over the entire record. The positive responders showed a less consistent response to previous growing season temperatures, but a positive correlation to current June temperatures that was stable from 1927-2006. Although both sub-populations had a significant correlation to April precipitation, the DENDROCLIM analysis revealed that the response is not temporally stable for either population and is only significant when values from 1958-1961 were included in the calculation. The temperature and tree growth relations support the hypothesis of temperature-induced moisture stress afflicting the NEG sub-population, whereas the POS sub-population had greater radial growth because of a positive response to June temperatures.

An investigation of non-climatic factors that may influence tree growth response to climate revealed no significant differences in age, height, DBH and distance to nearest neighbour. However, positive responders were associated with a significantly shallower active layer depth than both the neutral and negative responder sub-populations. This difference was attributed to increased access to soil moisture late in the growing season, due to the shallow rooting depth of all trees at the site. The primary reason for the shallow active layer depth appears to be the influence of a well-developed moss cover around the responding trees.

There was no significant difference among sub-populations in relation to the number of cones produced. An analysis of the viability of the seed crop in collected cones also found no differences among the sub-populations. However, both cone counts and seed analysis revealed that the reproductive potential of the site appears to be low.

Chapter 5
Intra-Annual Tree Growth Response

5.1. Introduction

Determining which variables influence tree growth requires an investigation at multiple temporal scales. This chapter presents an investigation of tree growth across short temporal scales. The influence of seasonal weather is discussed in relation to high-resolution tree growth records obtained using automatic dendrometers. Analysis of these records will provide insight into the intra-annual response of subarctic trees to short-term variations in weather conditions. The specific objectives addressed by this chapter are:

1. Describe the phenology of growth of white spruce trees in this region.
2. Examine the short-term weather conditions that influence tree growth at treeline in the Mackenzie Delta, NT.
3. To produce a conceptual model of the climatic/environmental factors that influence tree growth within the Mackenzie Delta, NT.

5.2 Weather Data

The first step in understanding intra-annual tree growth is to investigate the weather conditions during the study period. Meteorological conditions were recorded at Blueberry from August 2006 to December 2007. Site data was supplemented with data from the Inuvik Climate meteorological station (Climate ID: 2202578) from January 2006 to August 2007. Missing data between May 19, 2007 and June 20, 2007 were also gap-filled using data from Inuvik. Correlation of records from the Inuvik and Blueberry weather stations for the period from 21 June 2007 to 31 December 2007 indicate that this data is capturing similar trends and is valid for gap-filling. Daily mean (r = 0.99, $p<0.01$)

(Fig. 5.1), maximum ($r = 0.99$, $p<0.01$) and minimum air temperatures ($r = 0.98$, $p<0.01$), relative humidity ($r = 0.96$, $p<0.01$) and snow cover were used for gap-filling. All precipitation data was taken from the Inuvik hourly records.

Daily averages of meteorological variables reveal the weather patterns at the study site from January 2006 to December 2007 (Fig. 5.2 and 5.3). The warmest mean daily temperatures occur in early to mid-July, which coincides with the peak in solar insolation (Fig. 5.2a and d). With its location above the Arctic Circle, this is the period when Blueberry experiences 24-hour daylight. Similarly, the lowest mean daily temperatures of the year occur in February when the sun does not rise above the horizon. However, diurnal temperature gradients still exist. The records of maximum and minimum air temperatures follow similar patterns (Fig. 5.2b and c). The maximum daily temperature is below zero from October to April in part due to the presence of arctic high-pressure air masses during the winter months (Dyke 2000). The highest maximum temperature (29.7°C) during the study period was recorded on 10 July 2007. This is slightly less than the extreme maximum from the Inuvik temperature record (1948-2007) of 32.8°C recorded on 11 July 1999. The minimum air temperatures rarely exceed 15°C during the summer. The lowest minimum air temperature (-44.9°C) was recorded on 23 February 2007. Overall, both 2006 and 2007 were 2.6°C warmer than the 1971-2000 climatic normal. In 2006, this was influenced by a warm February, September, October and December while in 2007 it was influenced more by warmer temperatures in January, April and November. The lowest relative humidity measurements occur during late May and early June, but the measurements were usually above 50% (Fig. 5.3a). From

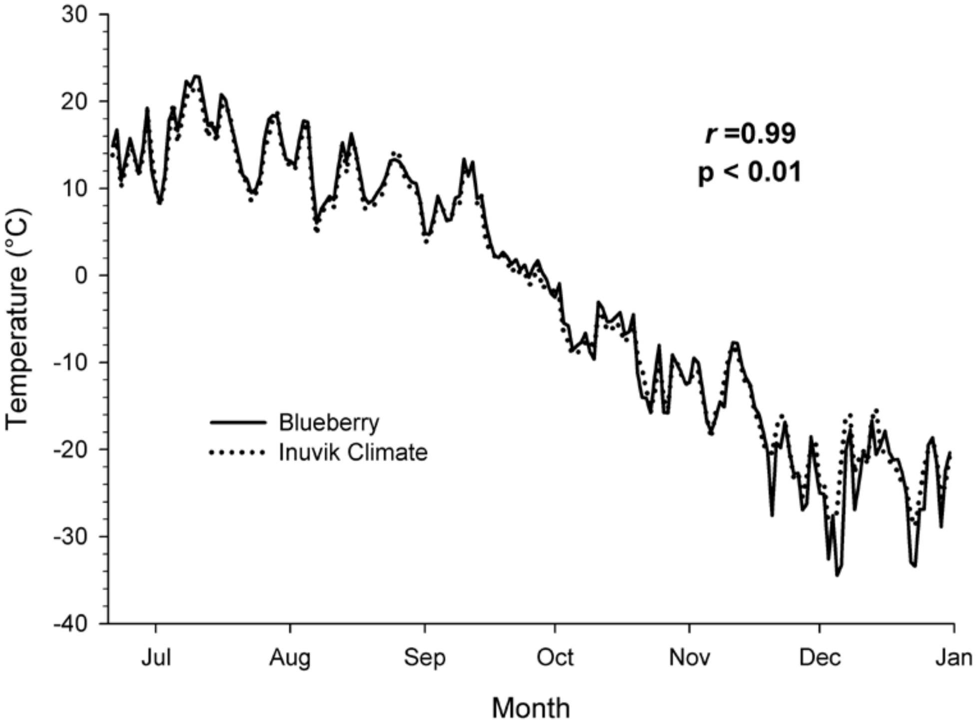

Figure 5.1. Comparison of the mean daily air temperature records for the period 21 June 2007 to 31 December 2007 from the Inuvik Climate weather station (dotted line) and the station installed at Blueberry (solid line).

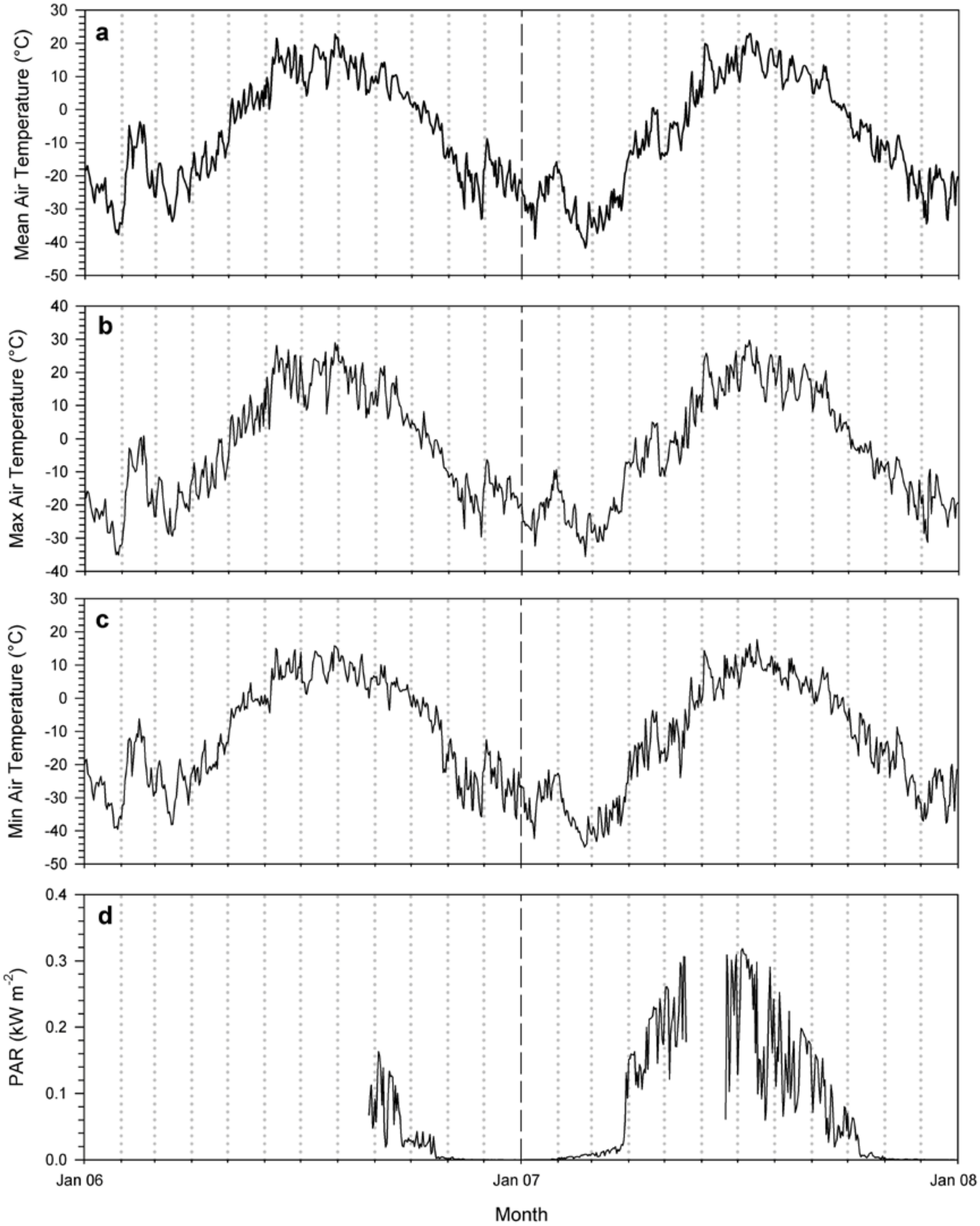

Figure 5.2. Daily (a) mean, (b) maximum and (c) minimum air temperatures and (d) mean incoming radiation (PAR - 400 to 700 nm). Temperature data from 1 January 2006 to 26 August 2006 and from 19 May 2007 to 20 June 2007 are from the Inuvik Climate meteorological station. No PAR data was available to fill these gaps. All other data are from the Blueberry weather station. Dashed vertical line marks the start of year. Dotted vertical lines mark the beginning of each month.

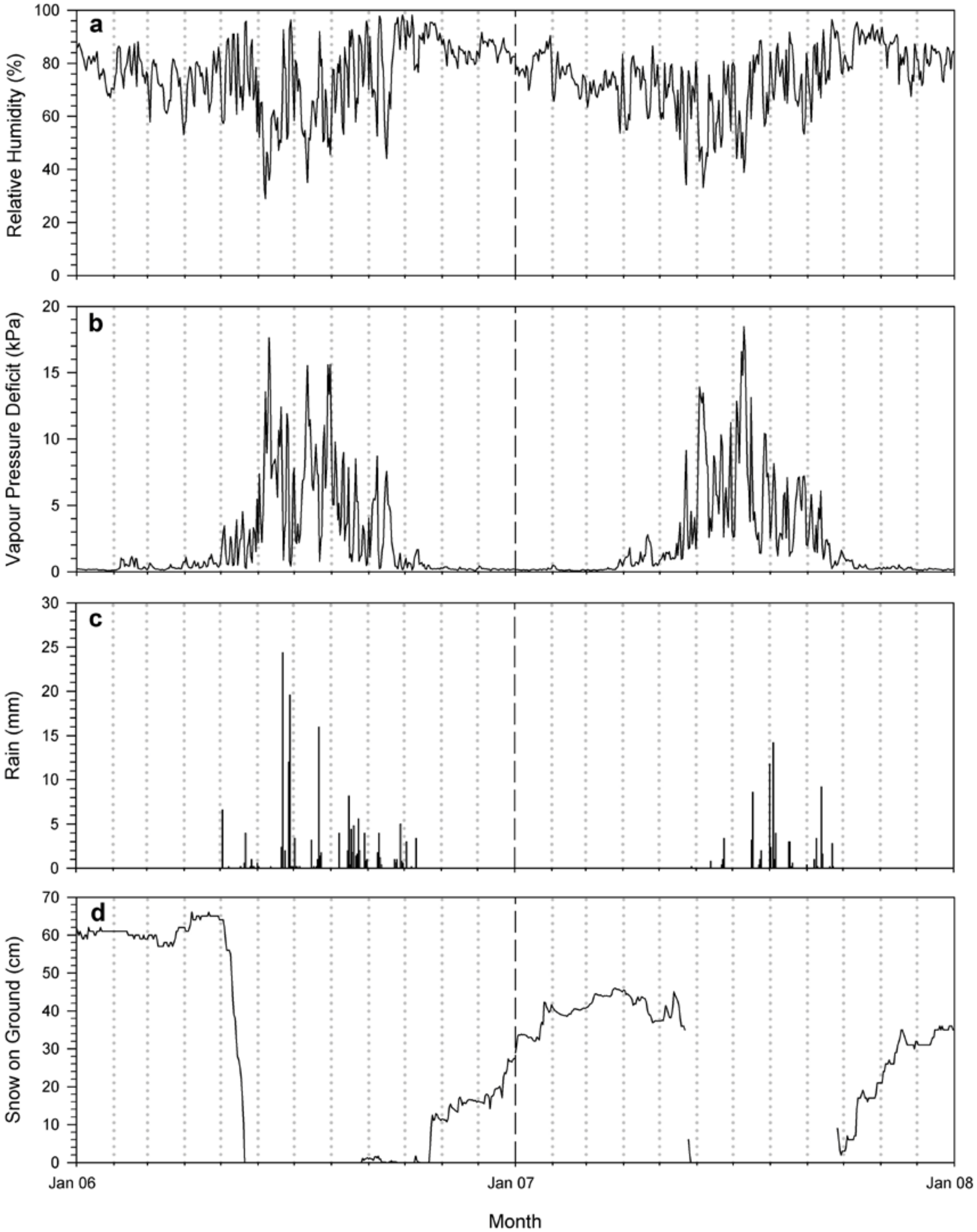

Figure 5.3. Daily (a) mean relative humidity, (b) vapour pressure deficit, (c) daily total rainfall and (d) snow depth measurements. Relative humidity and snow depth data from 1 January 2006 to 26 August 2006 and from 19 May 2007 to 20 June 2007 as well as the entire rainfall record from the Inuvik Climate meteorological station. All other data are from the Blueberry weather station. Dashed vertical line marks the start of year. Dotted vertical lines mark the beginning of each month.

minimums in early summer, relative humidity increased reaching its peak at the beginning of October and then decreases through winter until snowmelt. Relative humidity and temperature define the vapour pressure deficit (VPD), which is a measurement of the atmospheric demand for moisture. The VPD record is dominated by seasonal patterns with low deficits from October to April and the highest deficits in June and July depending on the amount of precipitation received (Fig. 5.3b). The precipitation measurements are divided into rain and snow depth (an approximate cumulative record of snowfall). Rain occurred between May and October with the largest rain events generally occurring in June/July. August and September had the most days of rainfall, but the total amounts were less than during June/July (Fig. 5.3c). This is consistent with the early summer paths of low-pressure systems originating from the Gulf of Alaska and bringing heavy precipitation compared to systems originating in the Beaufort Sea which are more frequent during the rest of the year, but are generally colder and drier (Dyke 2000). There was significantly more precipitation received in 2006 than 2007 with the greatest daily rainfalls occurring on 22 June 2006 (24.4 mm) and 28 June 2006 (19.6 mm). In 2006, there was 37.4 mm more precipitation than the climate normal (1971-2000) compared to 2007 when there was 102.5 mm less than average. The differences between the two years can be attributed to the large amount of precipitation received in June 2006 compared to below average precipitation from February to July in 2007. Snowfall can occur as early as late August, but accumulation does not usually begin until October (Fig.5.3d). Snow depth increases over the winter and peaks in early May when maximum temperatures begin to exceed 0°C and snowmelt begins. There was no snow remaining on the ground by the beginning of June in both years. The snowpack was approximately 20 cm deeper in 2006 than in 2007.

An environmental characteristic influenced by weather is the depth of the thaw layer (Fig. 5.4). At Blueberry, the average depth to permafrost was 20 cm below the surface in late June and it decreased to between 60 and 70 cm by the end of August. The rate of thaw was similar in both 2006 and 2007, but the site active layer was 10 cm deeper in 2006. The increased amount of precipitation in 2006, especially in June may have contributed to this difference. Taking an average of the two seasons, the thaw rate was calculated to be approximately 4 cm per week.

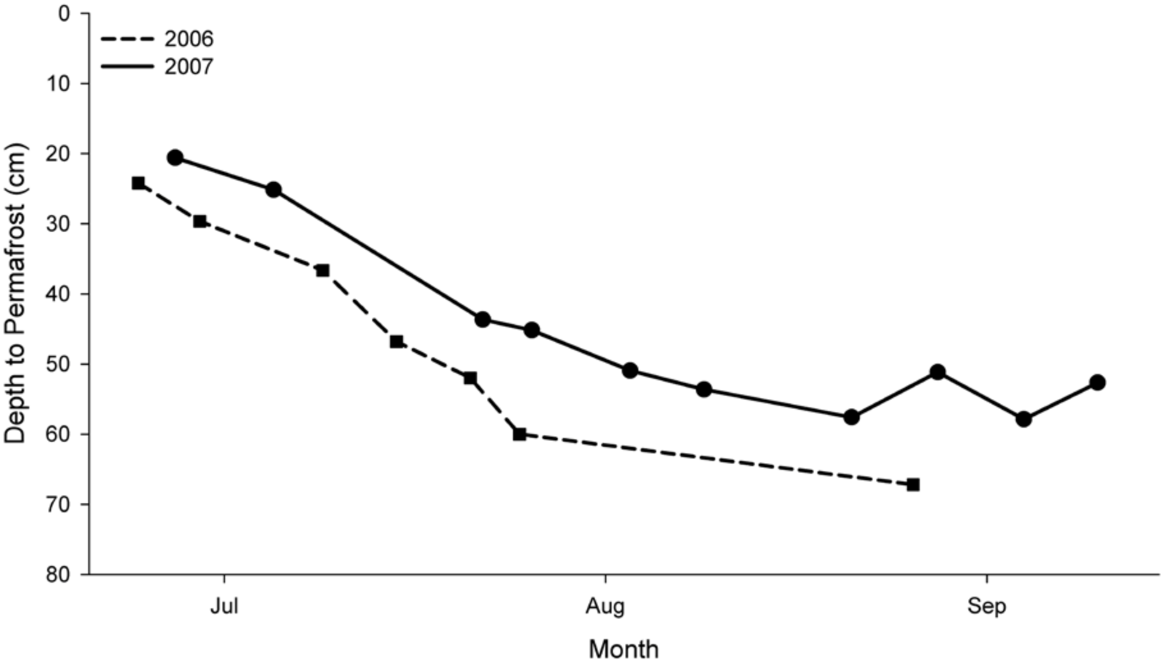

Figure 5.4. Thaw layer depths at Blueberry from late June to early September 2006 and 2007.

5.3. Dendrometer Measurements

Automatic point dendrometers were installed on trees at Blueberry in 2006 and 2007. The dendrometers record expansion and contraction of the tree stem. The averaged hourly stem variations reveal a record dominated by diurnal variations (Fig. 5.5). In 2006, 3 trees were instrumented with dendrometers. All three trees showed similar patterns of stem variation, although at different magnitudes. Pearson correlations revealed that Tree 1 and Tree 7 had the greatest similarity (r = 0.94), followed by Tree 1 and Tree 5 (r = 0.61), while Tree 5 and Tree 7 were the least similar (r = 0.44). Tree 7 showed the greatest increase in stem radius over the growing season. Although 14 trees were instrumented in 2007, only 2 (Tree 1 and Tree 5) are presented because 11 of the dendrometers were installed too late in the growing season and the dendrometer on Tree 7 malfunctioned. The high frequency patterns were similar between the two trees (r = 0.89), but there was a difference in the magnitude of the stem variations. In 2007, both trees had a similar amount and rate of radial increase.

Previous intra-annual tree growth analysis with dendrometers has found that only the main period of growth should be used to assess climate relations due to measurement variability exceeding actual radial growth near the end of the growing season (Deslauriers et al. 2007b). To determine the main period of growth in the record, raw measurements were examined for the point when the slope of the stem radius variations decreases (Fig. 5.5). Previous studies have identified this point as the beginning of latewood formation and cell wall thickening, processes which contribute little to radial expansion (Deslauriers et al. 2003b; Vaganov et al. 2006; Deslauriers et al. 2007b). The main period of stem

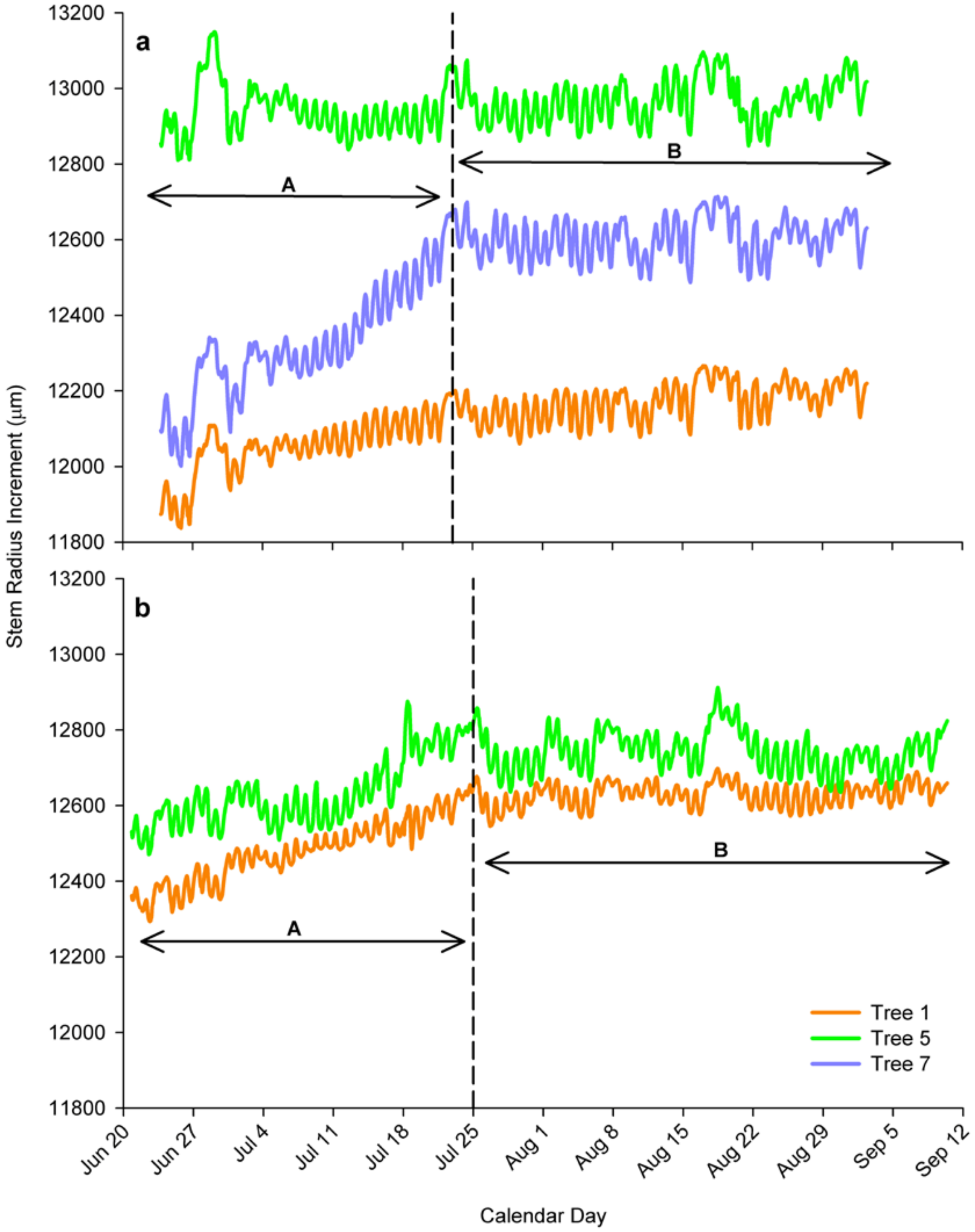

Figure 5.5. Hourly stem variation records measured by automatic dendrometers in (a) 2006 and (b) 2007. The dashed vertical lines mark the division between the growth periods. In 2006, period A was from the 23 June to 23 July and period B was from 24 July to 2 September. In 2007, period A was from 20 June to 25 July and period B was from 26 July to 10 September.

growth was identified as period A in Figure 5.5. The period that was associated with reduced cell production and increased cell wall thickening was identified as period B.

In 2006, the period of stem growth lasted from 23 June to 23 July, and the period of cell wall thickening continued from 24 July and continued until at least 2 September when the dendrometers were removed. In 2007, the period of stem growth lasted from 20 June to 25 July and cell wall thickening began 26 July to at least the 10 September (when dendrometers were removed). The period of stem growth identified in both years did not capture the entire growing season, as dendrometers were not installed until late June, while cambial division probably begins in early June based on phenology surveys conducted in the Inuvik region and the disappearance of snow at the site. However, it is notable that there is similarity (difference of 2 days) in the timing of the end of cell production in both 2006 and 2007. This occurred despite different meteorological conditions during the growth period in 2006 and 2007. Mean air temperatures were not significantly different, although 2007 was slightly warmer. There were significantly different amounts of precipitation during June and July (88.8 mm in 2006 and 20.8 mm in 2007). In both years, August had a similar amount of precipitation (~ 40 mm) but neither tree responded with additional growth during that month. The termination of growth despite conditions in which growth could continue is in agreement with observations made by Juday et al. (2008) and further confirms that conifers are unidirectional species. Once trees finish cellular division, they do not commence again until the next growing season begins.

Daily measurements captured by the dendrometers are composed of three different phases: (1) contraction, (2) expansion and (3) growth or stem radial increment

(SRI) phase, which make up the stem circadian cycle. The SRI may exceed the previous day’s maximum stem radius (ΔR+ cycle) or fail to exceed it (ΔR- cycle) (see Fig. 3.14). The frequency of these cycles was calculated and compared across the identified periods during the growing season and between trees (Fig. 5.6).

In 2006, Tree 1 and Tree 7 had a greater proportion of ΔR+ cycles compared to ΔR- cycles when comparing the period of cell expansion (period A) to the period of cell wall thickening (period B). Tree 5 had fewer observations of ΔR+ during period A compared to period B. Combining the frequency of both types of SRI cycles for all tree in 2006 reveals there were significantly more ΔR+ occurrences during the period of xylem cell production and expansion than during the period of cell wall thickening ($\chi 2 = 7.38$; $p < 0.01$). This supports the identification of 23 July as the termination of the main period of stem growth during 2006.

In 2007, Tree 1 and Tree 5 showed an increased frequency of ΔR+ in period A compared to period B. Overall, there was a lower frequency of ΔR+ occurrences in 2006 compared to 2007. However, unlike 2006, there was no significant difference between the identified main period of growth and the period of latewood formation and cell wall thickening. This may be a result of the low overall growth for both trees during 2007. Trees have low annual growth rates, such as those in northern regions make it difficult to define when exactly the main period of growth ends, especially during climatically marginal years.

Comparisons of the frequency of SRI cycles for each of the identified periods in the growing season lend support to the identification of the main periods of growth. It is

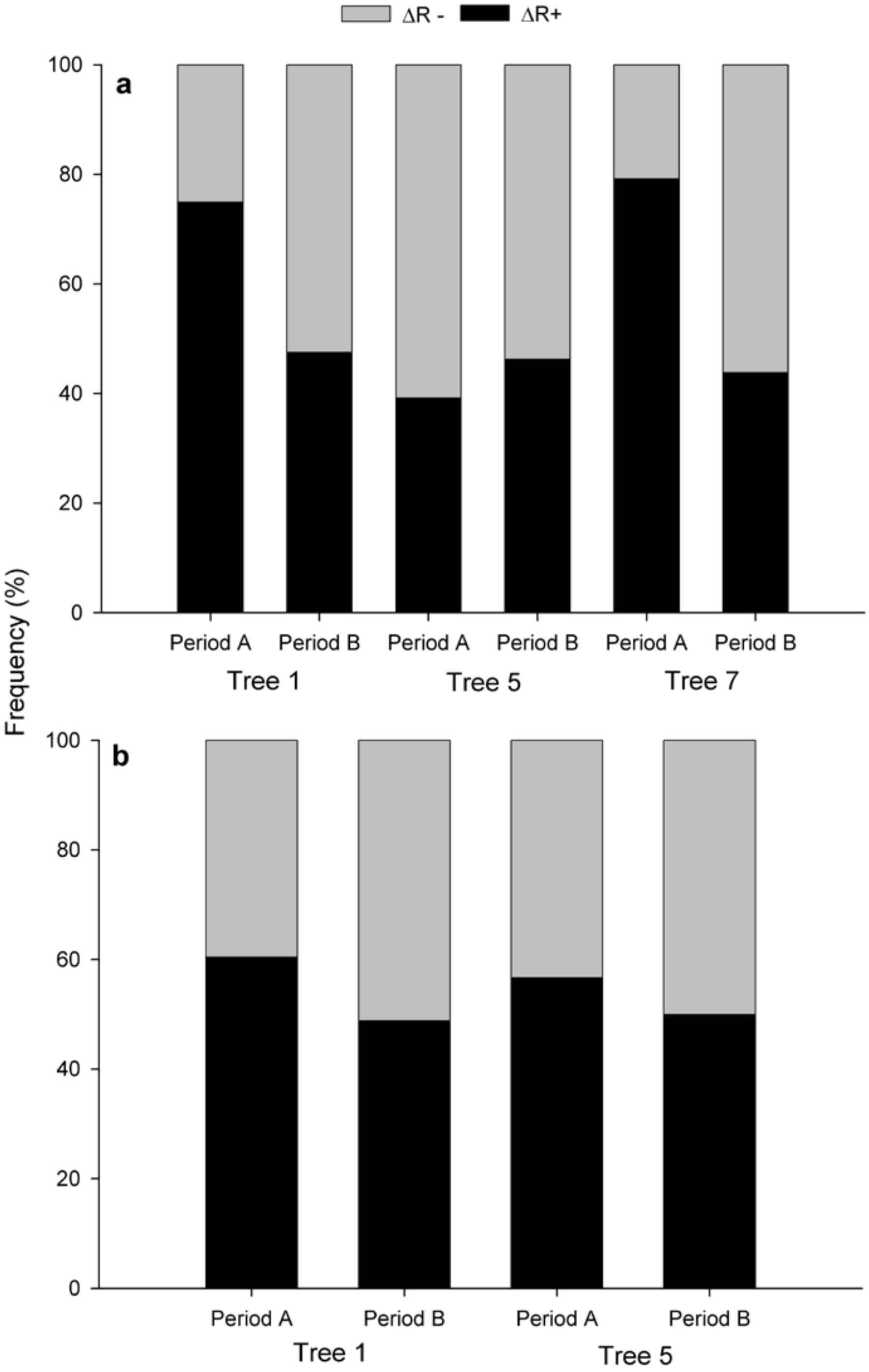

Figure 5.6. Frequency distribution (%) of ΔR+ (black) and ΔR- (grey) during the period of cell division and expansion (period a) and the period of cell wall thickening (period b) from the white spruce trees at Blueberry from (a) 2006 and (b) 2007.

clear that during the period defined by xylem cell division and expansion, most trees experience more ΔR+ cycles than in the cell wall thickening period.

The average beginning of each phase can provide insight into the periods of each day that have the greatest influence on tree growth (Table 5.1). In 2006, the daily circadian cycle began with a contraction phase (1) between 0800 and 0830 hours with a standard deviation of about 1 hour and 40 minutes. This response was consistent between instrumented trees. In 2007 the trees began phase 1 closer to 0900 hours and showed a lower standard deviation of around 1 hour and 30 minutes. The contraction phase continues until the middle of the evening (~ 11 hours) when the expansion phase (2) begins. In 2006, the second phase usually began between 1900 and 2000, with a standard deviation of 1 hour and 35 minutes, while in 2007 it began between 1900 and 1930 and had a similar standard deviation as 2006. The expansion phase continues for about 9 hours until it exceeds the previous day’s maximum radius, which is considered the growth or SRI phase (3). At the study site in 2006, the trees began phase 3 early in the morning around 0330, but with a large standard deviation of 2 hours and 15 minutes. In 2007, the trees began phase 3 around 0400 with the same standard deviation. This phase is the shortest of the three and lasted for approximately 4 hours, until contraction begins again. Deslauriers et al. (2003) found that balsam fir trees from the boreal forest of Quebec began contraction at approximately the same time, but the phase only lasted for 9 hours, with expansion beginning 2 hours earlier (between 1630 and 1700). The trees at Blueberry continued the expansion phase for 2 hours longer than trees from Quebec, which began the SRI phase between 0030 and 0100 hours. A possible reason for these differences in phase length could be related to photoperiod. During the main period of

Table 5.1. Temporal characteristics of the phases of growth and stem radius increment (SRI) characteristics for 2006 and 2007.

Tree-year	**Tree 1 - 2006**	**Tree 5 - 2006**	**Tree 7 - 2006**	**Tree 1 - 2007**	**Tree 5 - 2007**
Period of Analysis [a]	23 June - 2 Sept	23 June - 2 Sept	23 June - 2 Sept	20 June - 9 Sept	20 June - 9 Sept
Phase Characterisation [b]					
Beginning of Phase 1	8:04 ± 1:42	8:16 ± 1:56	8:32 ± 1:41	8:54 ± 1:35	9:12 ± 1:18
Beginning of Phase 2	19:22 ± 1:28	19:00 ± 1:43	19:48 ± 1:37	19:18 ± 1:26	18:59 ± 1:31
Beginning of Phase 3	3:28 ± 2:02	3:40 ± 2:27	3:20 ± 2:10	4:01 ± 1:52	4:12 ± 2:28
SRI Statistics					
No. of poitive SRI [c]	41	30	41	45	43
Mean SRI (μm)	20.43	35.99	32.86	17.10	29.07
SD of SRI (μm)	21.72	36.24	30.37	13.23	33.13

a - period of analysis for both the phase and SRI characteristics
b - average time that each phase began during the entire period of analysis
c - number of positive SRI cycles extracted during the entire analysis period

growth at Blueberry, the sun is always above the horizon, compared to the Quebec forests where the sun is above the horizon for a maximum of about 16 hours per day. In Inuvik, daily maximum temperatures do not usually occur until later in the evening, which is also the time of greatest atmospheric moisture demand. Increased moisture demand leads to the contraction of the stem. Expansion and subsequent growth does not begin until both temperatures and the vapour pressure deficit decrease.

The stem radial increment (SRI) records of the trees provide additional information about growth trends. Table 5.1 includes the number of positive SRI cycles recorded for each tree in 2006 and 2007. Most trees were very similar with about 40-45 positive SRI cycles. However, in 2006 Tree 5 had only 30 positive SRI cycles. The mean SRI ranged from 17.10 μm in Tree 1 in 2007 to 35.99 μm in Tree 5 in 2006, but high standard deviations indicate these values are variable.

Figure 5.7 plots the daily stem radius variation as well as the cumulative SRI for each of the instrumented trees for both 2006 and 2007. In 2006, Tree 7 had the largest cumulative SRI (527.5 μm), followed by Tree 1 (300.4 μm), while Tree 5 had the lowest cumulative SRI (85.4 μm). In 2007, both trees had similar cumulative SRI, but Tree 1 grew slightly more (309.0 μm) than Tree 5 (281.5 μm). When examining the daily variation of stem radius, there is more variation in both years near the beginning of the record than near the end. This appears to be associated with the greatest increase in the cumulative record of growth and may be representative of the explosive growth that typifies northern conifers (Vaganov et al. 2006). The largest single day increase in SRI was 189.5 μm in Tree 7 on 17 July 2006. The records reveal that these trees are very slow growing with no tree exceeding a millimeter of growth over either season. On many days,

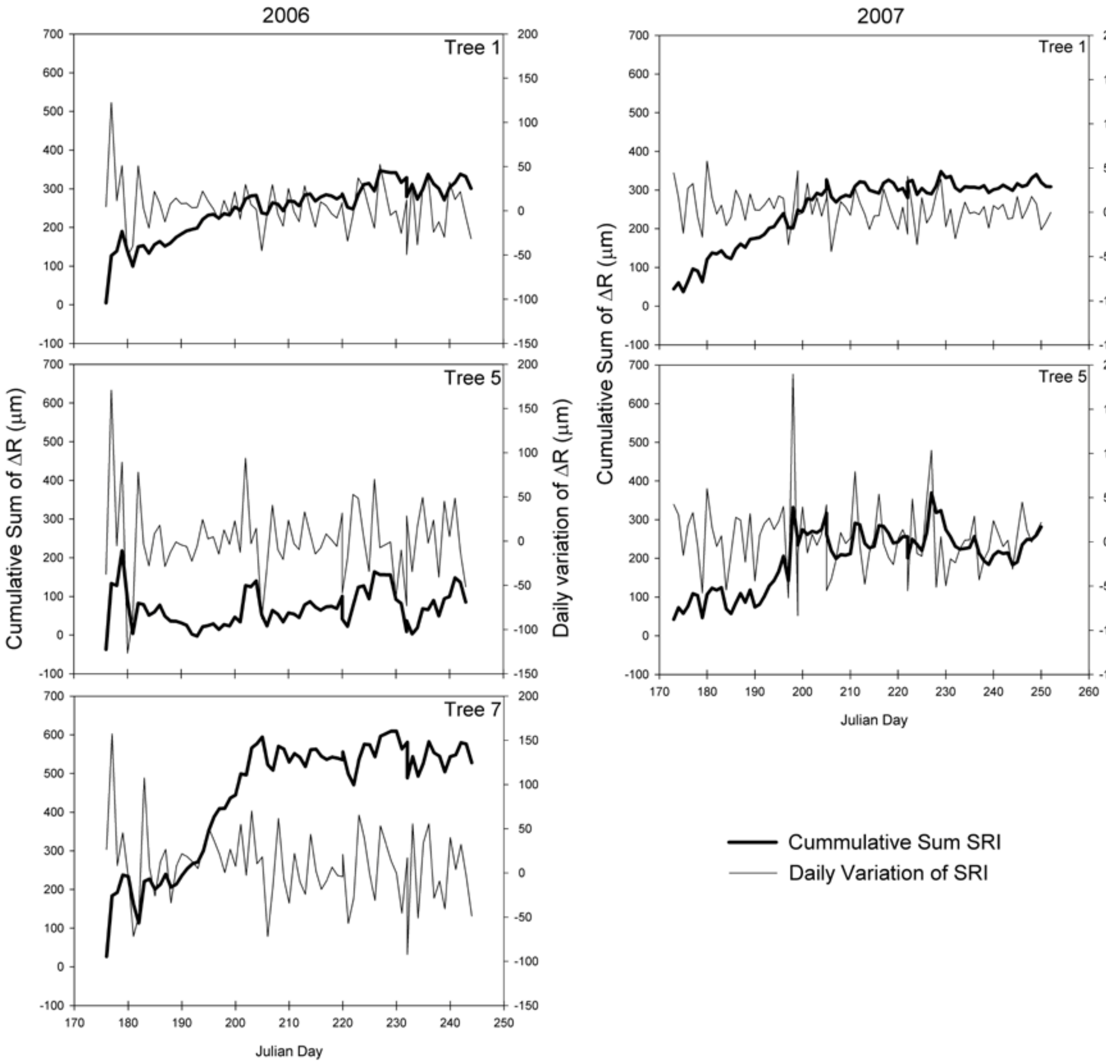

Figure 5.7. Comparisons of the daily stem radius variation (grey line) and cumulative SRI (black line) (both measured in μm) for each of the instrumented white spruce trees at Blueberry for 2006 (left column) and 2007 (right column).

a negative daily variation was observed. This means that the stem radius did not exceed the previous day’s maximum and thus is interpreted as no growth.

5.4. Tree Growth and Weather Correlations

To determine the influence of weather conditions on the growth of white spruce, a Pearson correlation analysis between the SRI of each tree and measured weather variables was conducted (Fig. 5.8 and 5.9). Correlations are limited to the main period of growth defined by cell division and expansion (period A) in 2006 and 2007.

In 2006, the measured weather variables were mean temperature (T_{mean}), maximum temperature (T_{max}), minimum temperature (T_{min}), relative humidity (RH), vapour pressure deficit (VPD) and precipitation (P). In 2007, volumetric water content (VWC) and the incoming photosynthetically active radiation (PAR) were also measured. Each variable was processed following the stem phase divisions: (1) contraction, (2) expansion, (3) SRI and (4) the entire circadian cycle. The phase average of each variable was calculated for each day of the main period of stem growth. This means that for each day, there are four T values (T_1, T_2, T_3 and T_4). Each of these was correlated against the mean daily SRI value.

This analysis was used to determine which weather variables influence the short-term growth responses of trees at Blueberry and if there were differences between individuals from different sub-populations. However, the limited number of dendrometers with data from the main period of stem growth did not capture an individual from each population. Tree 1 was a negative responder, while Tree 5 and Tree

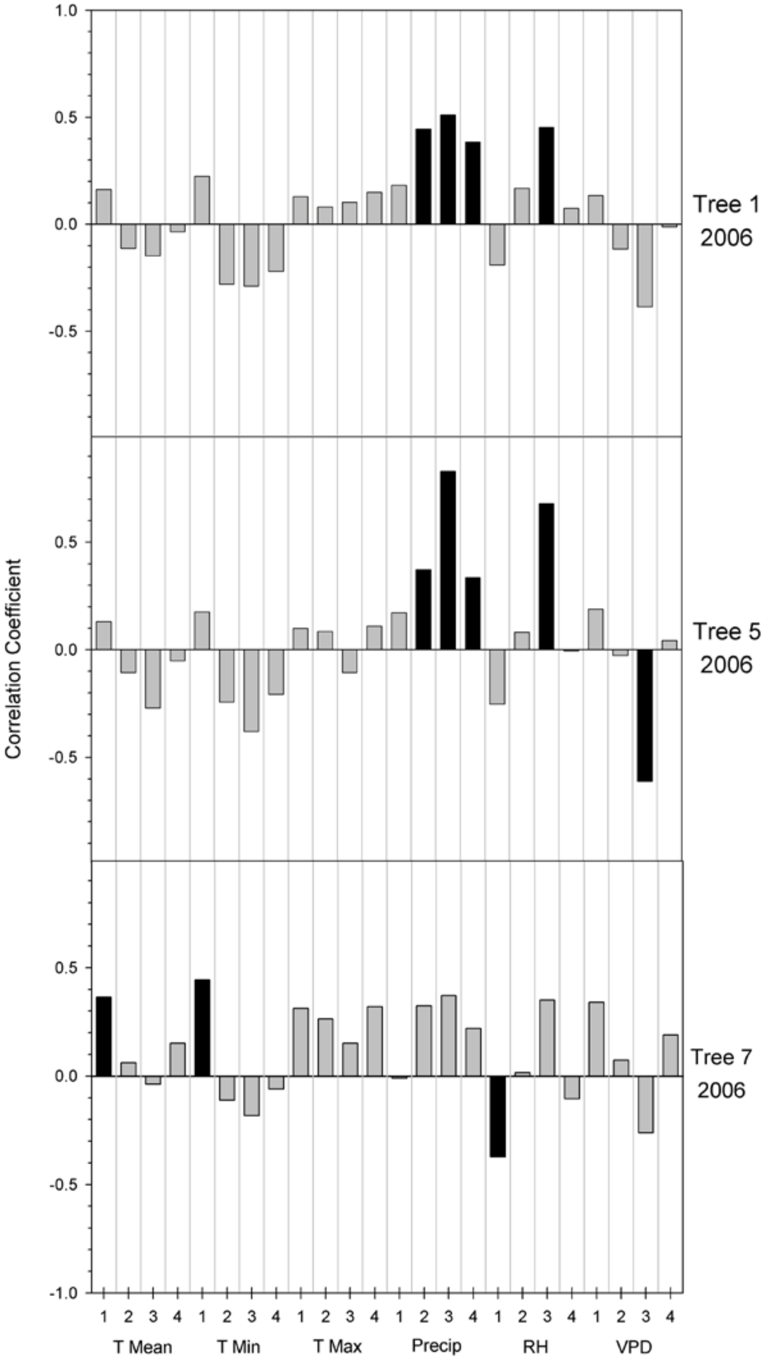

Figure 5.8. Simple Pearson correlation coefficients between the daily SRI and weather variables for each phase of the daily growth cycle (1 = contraction, 2 = expansion, 3 = SRI, 4 = circadian cycle) from the 3 trees during the main period of stem growth in 2006. Correlations significant at $p \leq 0.05$ are shown in black.

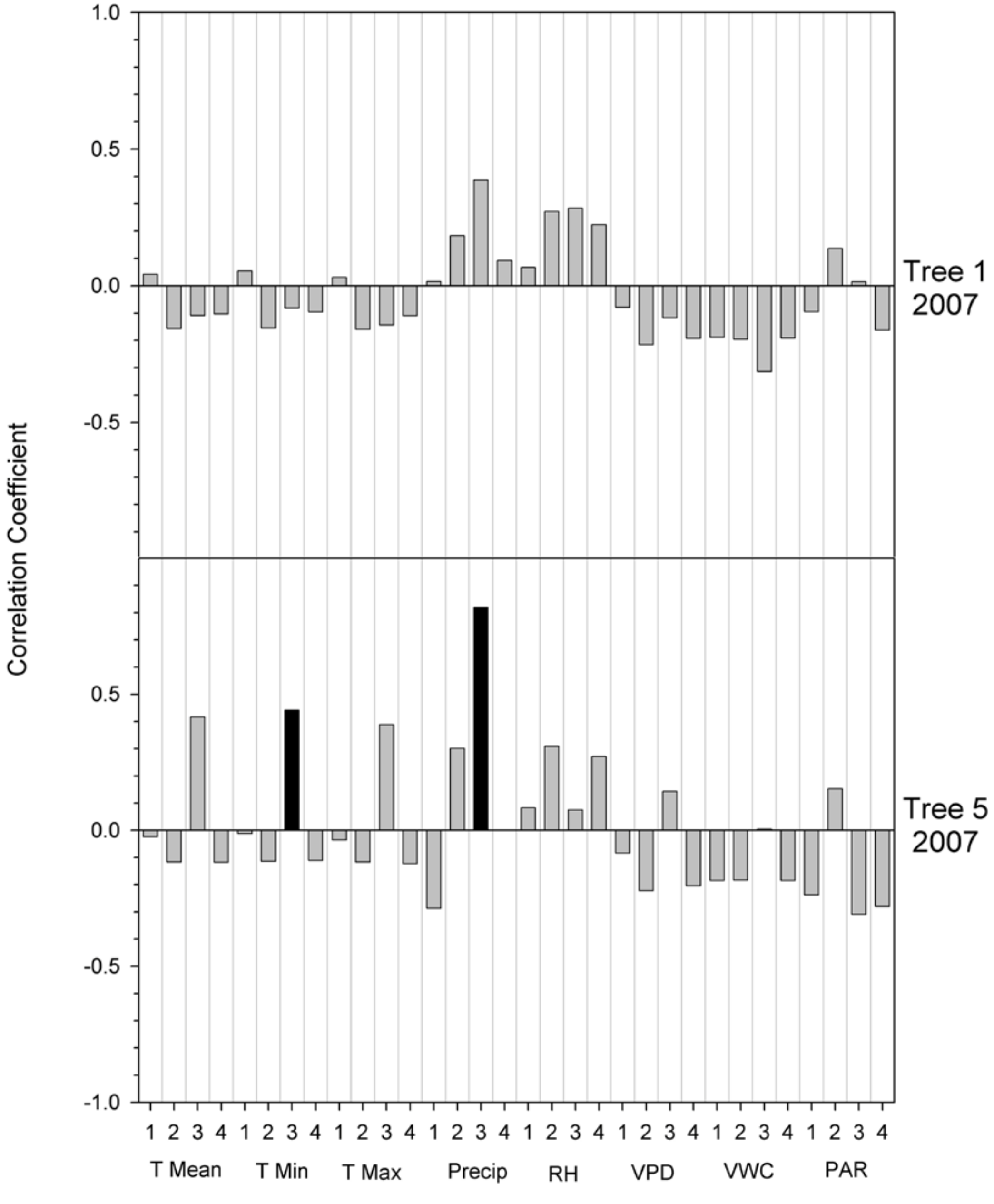

Figure 5.9. Simple Pearson correlation coefficients between the daily SRI and weather variables for each phase of the daily growth cycle (1 = contraction, 2 = expansion, 3 = SRI, 4 = circadian cycle) from the 2 trees during the main period of stem growth in 2007. Correlations significant at $p \leq 0.05$ are shown in black.

7 were neutral. The results may provide some insight into the response of trees at the site, but the full range of variability was probably not captured in this dataset.

In 2006, Tree 1 and Tree 5 had the most similar response to weather with significant positive response to P_2, P_3 and P_4 as well as a significant positive response to RH_3 (Fig. 5.8). Both also had a negative response to VPD_3, but it was only significant in Tree 5. No temperature variables were significant in either of these trees, but they both seem to show a positive response

to all T_{max} phases and a negative response to T_{min} in all phases. Tree 7 had a much different response from the other two trees. Tree 7 had no significant response to any precipitation variable and showed significant positive response to $T_{mean\ 1}$ and $T_{max\ 1}$ as well as a significant negative response to RH_1.

In 2007, Tree 1 and 5 responded quite differently than they had in 2006 (Fig. 5.9). Tree 1 had no significant relations with any weather variables. However, it did show a similar positive response to precipitation. Tree 5 continued to show a significant positive response to P_3, but also showed a significant positive response to $Tmin_3$, compared to the negative relation in 2006. Neither tree had a significant response to VWC.

The growth of Tree 1 correlated most positively to precipitation and relative humidity during the expansion and SRI phases and had no significant response to any temperature variables. Tree 1 was classified as a negative responder according to its growth response to climate. The positive intra-annual growth response to precipitation and relative humidity (which are closely related) seems to support the earlier conclusion that negative responders may be impacted by temperature-induced drought stress and thus at fine temporal scales they respond to available moisture. However, this does not appear to translate into a long-term response to precipitation during the growing season. These findings are supported by studies that have suggested that drought stress may lead to increased importance of precipitation for tree growth (Barber et al. 2000; D'Arrigo et al. 2008).

Although Tree 5 and Tree 7 were classified as neutral, they responded quite differently from each other. Tree 7 had the largest amount of cumulative SRI in 2006, which may have been because of the strong response to contraction phase (daytime) temperatures. This tree also had no significant response to precipitation. Tree 5 had the lowest amount of growth in both 2006 and 2007. Tree 5 had positive significant responses to precipitation in the expansion and SRI phases and exhibited significant responses to RH_3 (positive) and VPD_3 (negative) in 2006. However, these responses are related because a high relative humidity leads to the calculation of a low vapour pressure deficit (VPD). Physiologically, a high VPD inhibits cell enlargement because it increases transpiration and can lead to a reduction of cell turgor pressure (Kozlowski et al. 1997; Deslauriers et al. 2003a). In 2007, Tree 5 responded very differently than Tree 1, showing positive responses to temperatures and precipitation in the expansion phase. Positive responses to temperatures during the SRI phase have been identified as extremely important to the radial cell enlargement and cell size in conifers (Antonova et al. 1995). Other studies using dendrometers have also found that temperatures in the expansion phase had a significant relation with SRI (Downes et al. 1999; Deslauriers et al. 2003b).

These results seem to indicate that some trees respond more significantly to temperature than others. This may be an indication of differences within sub-populations, although low sample numbers and only two years of measurements limit the conclusions that can be drawn from the data. The negative responder had significant correlation to precipitation and the neutral trees responded differently to weather conditions in both years. This may support the earlier conclusion of the neutral population representing a genetic cross of positive responder and negative responder populations. Finally, many of the significant responses were between SRI and weather in the expansion phase. This reveals the importance of weather conditions in the early morning, between 0330 and 0830 hours, on radial stem growth.

5.5. Conceptual Model of Tree Growth

A conceptual model of the factors that influence tree growth for the sub-populations of positive responders and negative responders at Blueberry was developed to provide a synthesis of the results. With additional data collection, it may be possible to use these identified inputs in the development of a non-linear mechanistic model (Anchukaitis et al. 2006). These non-linear models could provide accurate estimations of tree growth and in turn provide increased confidence in reconstructions of past climate or predictions of future growth based on projected climatic change.

The model has four main components: (1) environmental factors, (2) climate response factors, (3) weather response factors and (4) genetic influences that combine to influence growth in each of the sub-populations (Fig. 5.10). The environmental factors focus on the significant difference of active layer depth between the positive responders and negative responders. Blueberry has a very open canopy and snow depth was considered consistent across the site, indicating that the factor that influences the active layer depth is the vegetation. It was observed that the ground cover around the positive

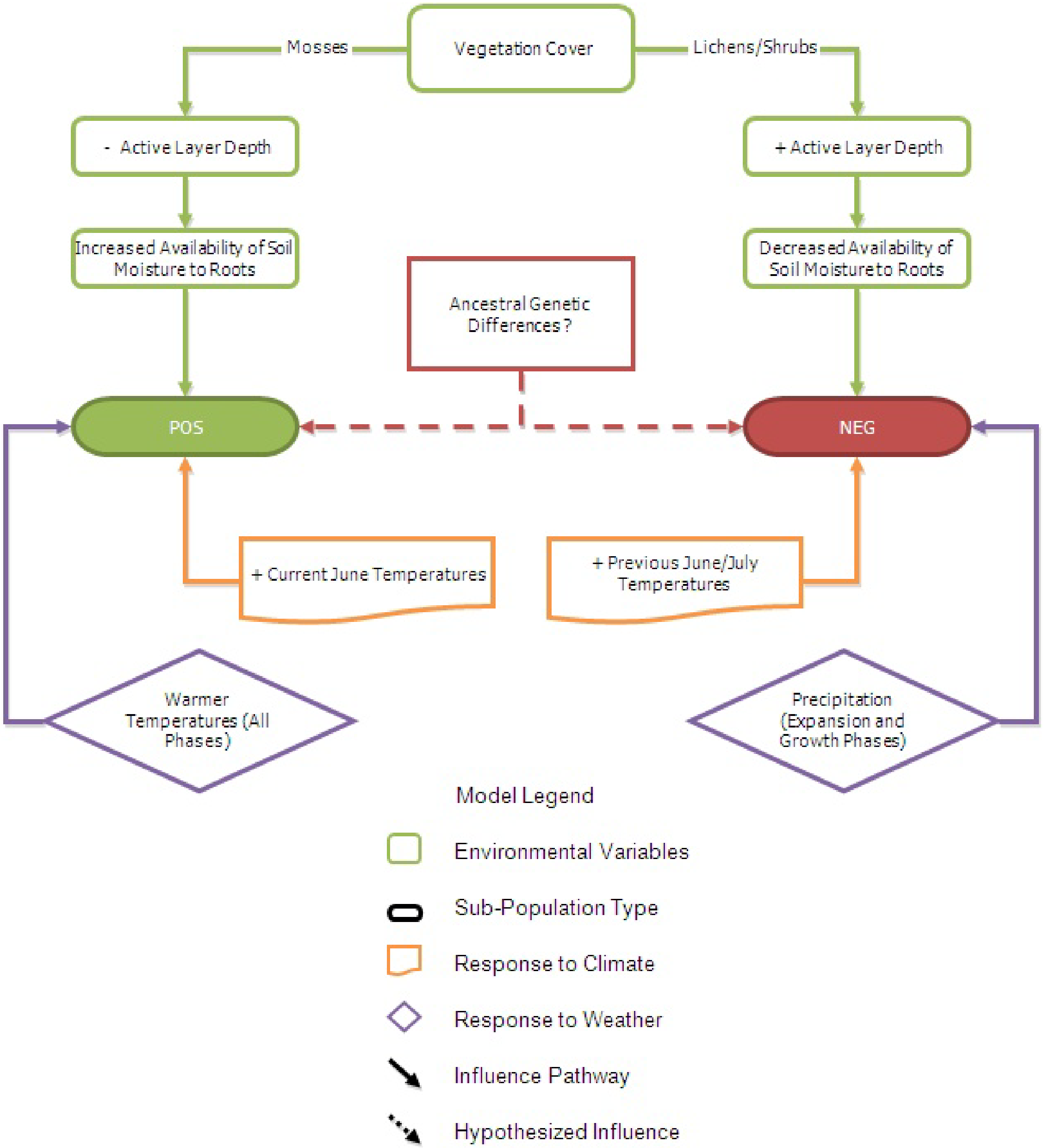

Figure 5.10. Conceptual model of factors that influence the growth of two sub-populations (Positive responders - POS and Negative responders - NEG) at Blueberry.

responders was predominantly composed of moss compared to other areas that were covered with a greater proportion of lichens and shrubs. In summer, moss can act as an insulating cover, reducing the ground heat flux and maintaining permafrost close to the surface. The lichens and shrubs do not insulate as well as the moss and the active layer becomes deeper in these locations. It is hypothesized that the close proximity of the permafrost near positive responders allows the diffuse, but shallow roots of the white spruce to access water throughout the growing season, whereas the negative responders become stressed due to lack of available soil water. Low moisture availability may be the reason that the negative responder showed a strong response to precipitation events according to the intra-annual growth analysis. These precipitation events (specifically during the expansion and growth phases between 1900 and 0800 hours) provide needed moisture during the growing season. The positive responders with access to an adequate amount of soil moisture are believed to respond more directly to temperature. Although no positive responders were instrumented with dendrometers, the growth responses of the neutral trees indicate that positive responders may have positive correlation between SRI and mean and minimum temperatures across all of the growth cycles.

The third component of the model is the response to climate over intra-decadal scales. The results showed that the NEG sub-population had a significant negative response to June and July monthly temperatures from the previous growth season. This is attributed to the lack of available soil moisture for these trees. Increased temperatures during the middle of the growing season with no available soil moisture could lead to trees terminating growth early and limiting their storage of photoassimilate for use at the beginning of the following year (Kagawa et al. 2006). This scenario could lead to reduced growth. This is contrasted with the positive responders, which show a strong positive response to current June temperatures. This indicates that the warmer the June temperature, the greater the rate of xylem cell division and expansion, which are the primary influences on the total amount of seasonal radial growth.

Finally, the fourth component of the model is a hypothesized influence of ancestral genetic differences between the two populations. This influence is based on the identification of two different white spruce refugia during the last glaciation (Anderson et al. 2006). There is evidence that plants are optimally adapted to local climatic conditions and often have a difficult time acclimatizing to new climatic conditions, especially species that have adapted to cold environments and then attempt to adapt to warmer temperatures. This may be part of the reason that negative responders are not tracking the high rates of temperature change in this region.

5.6. Summary

This chapter examined the intra-annual growth response of white spruces trees at Blueberry to weather conditions from 2006 and 2007. The main period of stem growth was identified in the raw dendrometer record and the daily variation and cumulative SRI was presented. Finally, a conceptual model of the factors that influence the growth of white spruce at Blueberry was presented.

The weather data revealed that growing season temperatures were similar between 2006 and 2007, but that there was significantly more precipitation during the growing season in 2006 than 2007. Southern air masses moving up the Mackenzie Valley bring the heaviest precipitation to the region in late June/early July (Dyke 2000).

Raw dendrometer data from Blueberry showed that the main period of growth (defined by cell division and expansion) was very short, ending during the last week of July in 2006 and 2007. After this, reversible stem swelling and shrinking exceeds any non-reversible increase in stem size (as the cells commence cell wall thickening). The identification of the main period of growth was supported by a frequency analysis of positive (ΔR+) and negative (ΔR-) SRI cycles.

The average beginning and length of each phase of the stem cycle was calculated. Trees began contraction around 0800 hours and it lasted for approximately 11 hours before expansion began between 1900 and 2000 hours. Stem expansion continued for approximately 9 hours until 0400 when the SRI phase begins. The SRI phase lasted for approximately 4 hours. Compared to other published phase timings, the trees at Blueberry began expansion and growth later, most likely due to the photoperiod length at the study site during the growing season.

Comparisons of daily SRI and cumulative SRI values were made between the instrumented trees for each year. In 2006, Tree 7 had the largest cumulative SRI, while Tree 5 had the lowest radial growth in both 2006 and 2007. Tree 1 experienced a similar SRI for both growing seasons. However, compared to SRI estimates from conifers from the Quebec boreal forest and the Italian Alps (Deslauriers et al. 2003b; Rossi et al. 2006b; Deslauriers et al. 2007a), the amount of growth in all trees at Blueberry was low. Correlations between weather variables averaged for each phase of the stem cycle and daily SRI revealed that Tree 1 (negative responder) had significant correlation to precipitation in the expansion and SRI phase. There were also no significant correlation between SRI and temperature in Tree 1. This was considered an indication of moisture stress. Tree 5 and Tree 7 (both neutral) had very different correlations to the weather in 2006, with Tree 7 showing significant positive response to temperature during the contraction phase and tree 5 showing a similar response to Tree 1. In 2007, Tree 5 had significant positive responses to precipitation, T_{mean} and T_{min} in the growth phase. These were consistent with other studies that had identified temperature during the SRI phase as a primary factor influencing daily SRI (Antonova et al. 1995; Downes et al. 1999; Deslauriers et al. 2003b).

Finally, a conceptual model of the four primary factors that influence the growth of both positive responders and negative responders was developed. These factors were: (1) the difference in active layer depth near the trees, (2) possible growth response to temperature for positive responders and response to precipitation events during the expansion and growth phases for negative responders, (3) positive response to current mean monthly June air temperatures for positive responders and an inverse response to mean monthly previous June/July temperatures for negative responders, and (4) possible genetic differences between the two populations.

Chapter 6

Summary of Results and Conclusions

6.1. Summary of Results

This thesis examines the factors that influence growth of white spruce trees at a single study site located in the Mackenzie Delta, NT. Analysis of tree cores collected from 42 trees at the site indicated that tree growth is responsive to several climatic controls. The most important being June temperatures during the growing season, June/July temperatures in the previous year and April precipitation during the growth year. Interestingly, the climatic controls were not consistent amongst all trees and revealed the presence of different sub-populations of white spruce (negative responder, neutral and positive responder) based on recent climate growth relations. Based on these sub-populations, an investigation of non-climatic influences on tree growth was also conducted to determine if specific controls exist for the identified sub-populations of white spruce on the landscape. Tree growth is not only controlled by long-term variations in climate (annual scales and higher) but can also be influenced across short temporal scales. Thus, the influence of seasonal weather is discussed in relation to high-resolution tree growth records obtained using automatic dendrometers.

6.1.1. Tree Response to Climate

Correlation of ring widths from the averaged sub-population chronologies with climatic variables found that negative responders had a significant negative relation to previous June and July temperatures that was temporally stable over the entire record (1927-2006). The positive responders showed a less consistent response to previous growing season temperatures, but a positive correlation to current June temperatures that was stable from 1927-2006. Although both sub-populations showed a significant response to April precipitation at the beginning of the record (1957-mid 1980s), DENDROCLIM2002 analysis revealed that this response was not temporally stable and that it has become non-significant since this period.

The temperature and tree growth relations lend support to the hypothesis of temperature-induced moisture stress influencing the NEG sub-population, whereas the POS sub-population had greater radial growth because of a positive response to June temperatures.

6.1.2. Tree Response to Non-Climatic Factors

An investigation of non-climatic factors that may influence tree growth response to climate revealed no significant differences in age, height, DBH and distance to nearest neighbour. However, positive responders were associated with a significantly shallower active layer depth than both the neutral and negative responder sub-populations. This difference was attributed to increased availability of soil moisture late in the growing season, due to the shallow rooting depth of all trees at the site. The primary reason for the shallow active layer depth appears to be the influence of a well-developed moss cover around the responding trees.

There was no significant difference among sub-populations in relation to the number of cones produced. An analysis of the viability of the seed crop in collected cones also found no differences among the sub-populations. However, both cone counts and seed analysis revealed that the reproductive potential of the site appears to be low. This may be due to the influence of a marginal environment, which leads to investment of limited energy supplies into either growth or reproduction, but not both.

6.1.3. Tree Response to Weather

Analysis of dendrometer data revealed that the main period of growth (defined by cell division and enlargement) was very short at Blueberry, lasting only until late July in both 2006 and 2007. A frequency analysis of positive (ΔR+) and negative (ΔR-) stem radial increment (SRI) cycles found significantly more ΔR+ during the identified main period of growth than during the period of cell wall thickening, supporting the conclusion that the growing season ends during the last week of July. The beginning and length of each of the stem cycle phases was calculated and revealed the trees at Blueberry spend about 11 hours each day in the contraction phase. Expansion began between 1900 and 2000 hours and lasted for approximately 9 hours until 0400 when the SRI phase began. The SRI phase lasted for about 4 hours. The contraction period is very long at Blueberry and the trees begin expansion and growth later than published phase times from the boreal forest. This was attributed to the photoperiod length during the main period of growth at the study site.

Comparisons of daily SRI and cumulative SRI values were made between the instrumented trees for each year. In 2006, Tree 7 had the largest cumulative SRI, while Tree 5 had the lowest radial growth in both 2006 and 2007. Tree 1 experienced a similar SRI for both growing seasons. Overall, the total amount of seasonal radial growth in all trees at Blueberry was low. Correlations between weather variables averaged for each phase of the stem cycle and daily SRI revealed that Tree 1 (negative responder) had significant correlation to precipitation in the expansion and SRI phase. There were also no significant correlation between SRI and temperature in Tree 1. These responses were considered evidence of a possible temperature-induced moisture stress that has been proposed as a reason for the divergence trend among negative responders. Tree 5 and Tree 7 (both neutral) had very different correlations to the weather in 2006, with Tree 7 showing significant positive response to temperature during the contraction phase and tree 5 showing a similar response to Tree 1. In 2007, Tree 5 had significant positive responses to precipitation, T_{mean} and T_{min} in the growth phase. These were consistent with other studies that had identified temperature during the SRI phase as a primary factor influencing daily SRI (Antonova et al. 1995; Downes et al. 1999; Deslauriers et al. 2003b).

6.2. Conclusions

Several conclusions regarding the factors that influence white spruce growth at this study site can be made:

1. Non-climatic factors such as age, height, DBH and distance to nearest neighbour had no significant influence on tree growth response to climate. However, the depth of the active layer showed a significant difference between positive responders and negative responders. This difference was attributed to increased availability of soil moisture late in the growing season.
2. A significant negative response to previous June and July temperature records (1927-2006) and a significant response to precipitation during the

expansion and SRI phase suggests that temperature-induced moisture stress influences the growth response of the negative responder sub-population.

3. Positive response to growing season June temperatures and hypothesized greater access to soil water due to the shallow active layers may be the reasons that the positive responder sub-population follows current temperature trends. However, this did not appear to increase the reproductive potential of these individuals.
4. Genetic differences among white spruce at the study site may limit the ability of individuals to adjust to climatic trends and may be a possible explanation of separate sub-populations existing on the same landscape.

6.3. Recommendations for future research

This study has identified a number of possible improvements to dendroclimatological studies while also introducing new questions that could form the basis for future areas of research. A combination of micro-coring and dendrometer data will improve the understanding of the phenology of white spruce in this region and increase the understanding of factors limiting growth (Rossi et al. 2006b; Deslauriers et al. 2007a; Rossi et al. 2007). Long-term collection of data will improve the understanding of the variability of this system and could lead to future manipulation experiments, leading to improved hypothesis testing. Installing automatic dendrometers on trees at several different forest assemblages within the Mackenzie Delta could provide interesting comparisons. A genetic analysis of both chloroplast DNA (cpDNA) and mitochondrial

DNA (mtDNA) of individuals from each sub-population could confirm the hypothesis presented in this thesis. Finally, increasing the number of observations of environmental data (active layer depth, cones and seeds) from all three sub-populations would improve the confidence of some conclusions made in this study.

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