THE REPRODUCTION, ESTABLISHMENT, AND GROWTH OF WHITE SPRUCE IN
THE FOREST TUNDRA ECOTONE OF THE INUVIK-TUKTOYAKTUK REGION

by

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ABSTRACT

Climate is considered one of the most important factors controlling tree reproduction, establishment, and growth at the treeline. As climate change continues the latitudinal treeline is expected to shift northwards. The main objective of this research was to characterize the ecological patterns and processes of *Picea glauca* (Moench.) Voss. (white spruce) in the Tuktoyaktuk region of the Northwest Territories, Canada. In particular, this study aims to determine how climate influences white spruce tree reproduction, establishment, and growth throughout the forest-tundra transition zone.

A total of four forest stand sites and eight tree island sites, examined in the early 1990s, were located and re-examined in the summer of 2009. Cone production has increased since the early 1990s and cone production decreases northward across the forest-tundra. Germination rates significantly decrease with increasing latitude but have not significantly changed since they were last examined 15 years ago.

In June 1994 seedlings were transplanted at three tree island sites, survivorship of these seedlings ranged from 3 to 20%. A search for true seedlings was also completed, however, none were found. Basal cores were obtained from numerous individuals within each of the sites and an age structure was developed. Establishment of individuals coincided with decades classified as cool and wet.

The yearly diameter growth of each tree was determined via ring width measurements and using principal component analysis two chronologies were built, one for forest stands and one for tree islands. The chronologies were correlated to climate data of temperature and precipitation from the Inuvik airport. In general, growth was negatively correlated to previous growing season temperature and positively correlated to current season temperature.
Results from this study indicate that tree islands are not likely to be important in supplying viable seed for the infilling of trees in the forest tundra, rather infilling will more likely occur from increased seed production in trees at or just south of treeline. Under proposed climate change scenarios the establishment of new seedlings will likely be negatively affected by the warmer and drier conditions, whereas the radial growth of individuals will likely increase with warming temperatures.
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1.1 Introduction to the Study

The northern treeline is one of the most prominent biogeographical boundaries in the world (Callaghan et al. 2002), yet a comprehensive understanding of the mechanisms controlling tree reproduction, growth, and survival at the treeline has not yet been established (Grace et al. 2002). Climate is considered one of the most important factors controlling treeline dynamics (Grace et al. 2002). Between 1906 and 2005, global temperatures have increased approximately 0.74°C (IPCC 2007), the effects of which are predicted to be greatest in Arctic and Subarctic regions of the world (ACIA 2004). This warming trend is likely to cause a northward treeline expansion (Starfield and Chapin 1996, ACIA 2004). The implications of an advancing treeline include a decrease in the albedo of areas currently covered by tundra vegetation, an increase in terrestrial carbon sequestration, and an alteration of biodiversity in the Arctic ecotone (Grace et al. 2002, Chapin et al. 2005). Understanding potential responses of treeline to climate change is therefore essential.

The main objective of this research was to characterize the ecological patterns and processes of *Picea glauca* (Moench.) Voss. (white spruce) throughout the forest tundra ecotone in the Tuktoyaktuk region of the Northwest Territories, Canada. This research is part of the larger PPS Arctic Canada project (Present day processes, Past changes and Spatiotemporal variability of biotic, abiotic and socio-environmental conditions and resource components along and across the Arctic delimitation zone in Canada). PPS Arctic Canada is a division of PPS Arctic, which studies the effects of climate change on the position, structure, and consequences of change of the treeline at Arctic sites around the globe. The PPS Arctic project is a component of the 2007-2008 International Polar Year (IPY). The IPY is a program focused on scientific research in the
Arctic and Antarctic. This research will significantly contribute to the larger PPS Arctic Canada project which in turn will provide policy relevant knowledge about environmental change in the forest-tundra transition zone.

The purpose of this chapter is to provide background information regarding the treeline and its relationship to climatic conditions, to describe the objectives of this research, and to provide an outline concerning the structure of this thesis.

1.2 Background

1.2.1 Treeline

The boreal forests of the northern hemisphere are circumpolar and stretch from Fennoscandia and Russia to Alaska and across all of Canada (Bonan et al. 1995). The interface between the boreal forest and the Arctic tundra is the largest vegetation transition on Earth, spanning over 13,000 km (Callaghan et al. 2002a). Timoney et al. (1992) divided the forest-tundra transition into three zones: the low subarctic open crown forest, the high subarctic forest-tundra and the low Arctic tundra (Figure 1.1). The low subarctic open crown forest is characterized by a 1000:1 forest-to-tundra cover ratio (Timoney et al. 1992). The northern boundary of this zone is the limit of continuous closed crown forest (Payette 1983). North of this boundary is the transition zone between boreal forest and shrub tundra, or the high subarctic forest-tundra zone (Timoney et al. 1992). Northwards across this zone the canopy opens, tundra vegetation increases, forested stands become limited to protected valleys and lowlands, trees become shorter, and there is an increased occurrence of krummholz. Krummholz are clusters of tree individuals that exhibit a prostrate or shrubby growth form and are less than two meters in height (Payette 1983). This zone is characterized by a forest-to-tundra ratio of 1:1 (Timoney et al. 1992). The northern limit of this zone is marked by the northern limit of trees that are greater
than two meters in height; this limit is referred to as the treeline (Payette 1983). The low Arctic


tundra zone is located north of the treeline. This zone is characterized by a 1:1000 tree-to-tundra


cover ratio in which individuals of coniferous species typically occur in isolated populations,


also known as tree islands, and have a krummholz growth form (Timoney et al. 1992). The tree


islands are often the northernmost extent of a particular tree species, referred to as a tree species


limit (Payette 1983).


1.2.2 Climate


Global climate has warmed approximately 0.74°C over the past 100 years (IPCC 2007). This increase has not been uniform across the planet. The average Arctic temperature has increased at almost twice the rate as that of the rest of the world over the past few decades (ACIA 2004). Temperatures, especially in winter, have increased sharply in most regions of the Arctic in recent decades (ACIA 2004). Winter temperature increases over the past half century have been around 3-4°C (ACIA 2004) and the highest Arctic air temperatures in the past 400 years occurred in the 20th century (Overpeck et al. 1997, Serreze et al. 2000). In northwestern North America a significant warming trend has been documented in the Yukon and Alaska (Zhang et al. 2000). Specifically, surface-air temperatures have risen 0.31 ± 0.03°C per decade in northwestern North America (Keyser et al. 2000).


1.2.3 Treeline and Climate


A variety of studies have addressed the response of latitudinal treeline to climate change in North America (e.g. Payette et al. 1985, Lescop-Sinclair and Payette 1995, Gervais and MacDonald 2000, Sturm et al. 2001, Gamache and Payette 2004, Gamache and Payette 2005, Shiyatov et al. 2005, Caccianiga and Payette 2006, Shiyatov et al. 2007), many of which addressed changes in growth, density, and distribution of high latitude forests (Table 1.1). A
variety of methods were used to assess changes at treeline including dendrochronological dating (Lescop-Sinclair and Payette 1995, Suarez et al. 1999, Gamache and Payette 2004, Gamache and Payette 2005), assessment of sexual reproduction and recruitment (Suarez et al. 1999, Gamache and Payette 2005, Caccianiga and Payette 2006), and repeat photography (Sturm et al. 2001). Results from these studies indicate a general trend of treeline advancement associated with climate warming.

In making predictions of changes at treeline it should be noted that the complex interaction of climate, disturbance, and recruitment may not act in precisely the same way in a warmer climate (Holtmeier and Broll 2007). Global predictions of treeline shifts are also problematic due to the regional differences in the factors that influence treeline position. The models which assess the impacts of global warming predict that the tundra may decrease to one-third of its present size over the next century due to the displacement of tundra by boreal forest (Skre et al. 2002, ACIA 2005). These predictions are based on the assumptions that CO₂ levels will double over the next century and that annual mean temperatures will rise between 1.5 and 4°C (Skre et al. 2002). Starfield and Chapin (1996), using a change of 3°C this century, calculated that any significant change from tundra to forest would take at least 150 years. Similarly, Rupp et al. (2000) modeled the effects of climate change on subarctic vegetation and concluded that a change of 2°C over a century would cause significant forest advancement onto the tundra and a substantial increase in the frequency and extent of forest fires within 200 years.

In general, models predict that the treeless gaps in the present forest-tundra zone will become forested and that the treeline will shift northwards hundreds of kilometres (Callaghan et al. 2002). However, predictions made from models can result in different outcomes depending on their assumptions and the number of variables initially included (Skre et al. 2002). Thus, an
adequate understanding of the influential dynamics at the landscape scale is needed in order for
global or regional models to more accurately predict treeline shifts.

Boreal forest advancement onto the tundra due to climate warming will have significant
global consequences. As tree density in the forest-tundra increases there will be alterations in the
exchanges of carbon dioxide (CO$_2$), methane (CH$_4$), and nitrous oxide (N$_2$O) and an overall
increase in carbon (C) storage and a reduction in CH$_4$ emissions (Harding et al. 2002). Harding et
al. (2002) concluded that the substitution of tundra by forest will cause a reduction in emissions
of important greenhouse gases to the atmosphere and significantly alter the radiative forcing of
the earth-atmosphere system. However, greenhouse gas exchange is very sensitive to changes in
soil moisture; therefore, any changes in trace gas exchange will be dependent on the feedback
mechanisms between tree migration and soil moisture (Harding et al. 2002). Also, before any
substantial increases in tree density occur, there will likely be increases in emissions of CO$_2$ and
CH$_4$ due to the Low Arctic Tundra warming and the ice-rich permafrost melting (Oechel et al.

Feedbacks between the physical climate and vegetation are important. Climate affects the
structure of vegetation, but vegetation also affects climate by converting short wave energy into
long wave energy, sensible heat, or by influencing evapotranspiration (Grace et al. 2002).
Coniferous forests are more effective in converting incoming energy into heat than alpine or
Arctic vegetation because they shed their snow, while snow remains on the ground over treeless
areas (Grace et al. 2002). The albedo of the boreal forest is low, while tundra has a high albedo;
thus, the boreal forest heats up the atmosphere more than the tundra (Foley et al. 1994, Chapin et
al. 2005). An expansion of the boreal forest onto the tundra due to climatic warming will in turn
cause more warming due to the lower albedo of the forest. Chapin et al. (2005) predict that
atmospheric heating will amplify by two to seven times if the current trends of shrub and tree expansion continue.

1.3 Research Objectives

The objectives of this research are to 1) assess the reproduction, establishment, and growth of *Picea glauca* (white spruce) throughout the forest-tundra ecotone and 2) determine if these variables have changed since they were last examined 15 years ago. Assessing white spruce growth and reproduction using the temperature gradient across the forest-tundra ecotone as a proxy for a 3°C increase in average summer temperatures, can demonstrate the potential for changes as temperatures warm. Examining these variables in white spruce since they were last assessed 15 years ago will determine the response of treeline to recent climate warming in the Tuktoyaktuk region of the Northwest Territories (NWT), Canada.

1.4 Structure of Dissertation

This dissertation is composed of six chapters. The next chapter provides a general description of the sites examined in this study in order to understand the differences between the forest stands and tree island sites in terms of the growth form, density, and vitality of *P. glauca*. The pertinent soil properties across the latitudinal gradient are also described.

The third chapter examines the reproduction of *P. glauca* throughout the forest-tundra ecotone in the Tuktoyaktuk region of the Northwest Territories, Canada. The differences in the reproductive capacity of individuals across the forest tundra ecotone and since they were last examined, 15 years ago, are assessed.

The fourth chapter focuses on the establishment of *P. glauca*. The recent and transplanted establishment success of seedlings is assessed and the long term establishment patterns of individuals in forest stands and tree islands are determined. The relationship between
establishment patterns and the instrumental climate records from Inuvik and the
dendrochronological reconstructed records from northwestern North America are examined.

In the fifth chapter the radial growth rates of individuals throughout the forest-tundra
ecotone are assessed in relation to climatic conditions and the differences in the climate-growth
relationship between forest stands and tree islands is examined.

In the sixth and final chapter a summary and conclusions are made regarding the
reproduction, establishment, and growth of *P. glauca* throughout the forest-tundra ecotone in the
Tuktoyaktuk region of the NWT, Canada and directions for further research is suggested.
1.5 Figures and Tables

Figure 1.1 Representation of the forest-tundra transition zones and limits according to Timoney et al. (1992) and Payette (1983). Obtained from McLeod (2001).
Table 1.1 Studies that have addressed changes in growth, density, and distribution of high latitude forests in North America.

<table>
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<th>Study Area</th>
<th>Tree species</th>
<th>Results</th>
<th>Reference</th>
</tr>
</thead>
</table>
| Northern Quebec             | *Picea mariana*    | - height growth of treeline trees decreased with increasing latitude  
- treeline trees have experienced an acceleration of height growth since the 1970s                                                            | Gamache and Payette (2004)       |
| Northern Quebec             | *Picea mariana*    | - treelines advanced due to the establishment of seed-origin spruce                                                                                                                                     | Gamache and Payette (2005)       |
| Eastern coast of Hudson Bay | *Picea glauca*     | - responded to recent favourable climatic conditions  
- active recruitment of new individuals at the treeline  
- shift in growth form of krummholz to trees                                                                                                      | Caccianiga and Payette (2006)    |
| Northwest Alaska (Noatak National Preserve) | *Picea glauca* | - the forest/tundra ecotone shifted about 80 to 100 m into the tundra in last 200 years  
- growth rates and tree establishment on the tundra have increased since 1970                                                                          | Suarez et al. (1999)            |
| Arctic Alaska               | Three deciduous shrubs: *Betula nana, Salix sp.* and *Alnus crispa*.  
*Picea glauca* | - increase in shrub abundance along latitudinal temperature gradients  
- increase in the extent and density of the forest at the treeline                                                                                       | Sturm et al. (2001)             |
CHAPTER 2: DESCRIPTION OF RESEARCH SITES IN THE FOREST TUNDRA ECOTONE OF THE INUVIK-TUKTOYAKTUK REGION

2.1 Introduction

As climate warms it is expected that the treeless gaps in the present forest-tundra zone will become forested, there will be a shift in growth form from krummholz to trees, and the treeline will shift northward hundreds of kilometres (Callaghan et al. 2002). Central to this prediction is an increase in the reproductive capacity, establishment, and growth of trees located throughout the forest tundra ecotone. A comprehensive understanding of the mechanisms controlling tree reproduction, establishment, and growth in the forest-tundra has not yet been established (Grace et al. 2002). Climate, in particular temperature, is considered the primary factor controlling treeline dynamics, however, there are a large number of variables including wind, soil nutrients, microclimate, topography, and disturbances that affect various aspects of a tree species performance (Sveinbjornsson et al. 2002). Describing these variables at the sites examined in this study provides an underlying basis for the following chapters in which the reproduction, establishment, and growth of *P. glauca* is assessed in terms of climate.

The objectives of this chapter are to 1) describe physical and biological characteristics of the sites examined in this study and to understand the differences between the forest stands and tree island sites, and 2) assess the growth form, density, and vitality of *P. glauca*, and pertinent soil properties across the latitudinal gradient. Understanding the current density, growth form, and vitality of individuals, as well as the soil properties across a latitudinal gradient will determine how these variables relate to deteriorating climate conditions northward across the forest tundra ecotone and how they could possibly change with climate warming.
2.2 Material and Methods

2.2.1 Study Area

A total of 12 sites were examined in the Tuktoyaktuk region of the NWT, Canada during the summer of 2009 (Figure 2.1). In 1993, a transect was established in this region that stretches from the northern forest-tundra to the northernmost limit of white spruce (McLeod 2001). Each site was labelled with an upper case letter (R=Richards Island, T=Tuktoyaktuk peninsula) and a number (e.g. T1 and T2 refer to sites 1 and 2 along the Tuktoyaktuk peninsula) (as per Mcleod 2001). Sites were labelled to represent the latitudinal gradient, with site T1 being the most northerly and site T10 the most southerly. Both sites on Richard Island are further north of the treeline than those on the Tuktoyaktuk peninsula. A total of 10 sites (T1 through T10) were established on the Tuktoyaktuk peninsula and 2 sites (R1 and R2) were established on Richards Island. In the summer of 2009 a total of eight tree island sites were examined, two on Richard’s Island (R1, R2) and six on the Tuktoyaktuk peninsula (T1 through T6). In addition, four forest stand sites (T7 through T10), each consisting of 3 plots, were examined. The original Site T2 could not be located; however, a tree island in the same general location as the original coordinates was used and is referred to as site T2.

The location of each sampling site was recorded by GPS, including coordinates and elevation. Photos of each site were obtained and notes were taken to describe the topography, the site boundaries (hills, lakes, large creeks, or rivers), the relative position of trees, any other aspects of the sites that will help in the future relocation and re-measurement.

2.2.2 Climate

A significant climatic gradient exist in the study area. Lantz (2008), using temperature loggers across a latitudinal gradient in the Mackenzie Delta region throughout the summer of
2005, found a decrease of approximately 3°C for every degree of increasing latitude. Monthly climate normals of precipitation and temperature from 1971 through 2000 from Inuvik and Tuktoyaktuk were obtained from Environment Canada (2009).

2.2.3 Stand Structure

The number of tree islands at each tree island site and the number of individuals within each tree island were recorded. The growth form of individuals were described based on the terminology of Lavoie and Payette (1992, Figure 2.2). A sixth growth form, infranival erect which resembles miniature trees, was also used (McLeod 2001).

All individuals within each of the tree island sites and all individuals within the plots in the forest stand sites were examined. Based on their height, erect individuals were classified as follows: seedlings (height less than 15 cm), saplings (height between 15 and 199 cm), and trees (equal to or greater than 2 m tall) (PPS Arctic Protocols 2008). A clinometer was used to determine the heights of any individuals that could not be determined using a tape measure. The stem diameter at the standard height of 1.3 m above ground was measured for all trees. The basal diameter at the root collar, which is the widest point above the swelling of the root bases, was also measured. The greatest length, and the width perpendicular to that direction, of each tree island was measured. At tree island sites where numerous separate tree islands existed, the aerial size of both individual tree islands and the entire tree island site was obtained. The density (#stems/hectare) of seedlings, saplings, and trees within each site were calculated by determining the number of individuals within each plot or tree island and relating that number to the area of the plot. In the forest stand sites the size of the plots were chosen to include a minimum of twenty trees (height >2m) and ranged from 10 to 50 m².
2.2.4 Vitality

The health of each individual was noted. The presence or absence of damage from herbivory was recorded as well as the type of herbivory if it could be determined. Whether or not the apical meristem was damaged was recorded. Based on the extent of herbivory, the damage to the apical meristem, and the overall health, each individual was placed in one of three vitality classes: dead, reduced, or healthy.

2.2.5 Vegetation

The vegetation composition within the tree islands and forest stand sites was assessed by laying out transects on the ground spanning the length and width of the tree islands or 100 m in the forest stands. The dominant functional group or species (mosses and lichens were recorded as functional groups and all other plants were indentified to the species level) for each of the ground-, field-, shrub-, and tree- layers were recorded. Each of the layers corresponds to the height of vegetation with the ground layer being on the ground, the field layer is <25 cm, the shrub layer is 25 cm to 199 cm, and the tree layer is ≥2 m. For tree islands, the dominant functional group or species were recorded every 1 m along the transect. In the forest stands the dominant species or functional group was recorded every 2 m. All of the plant identifications were made using Porsild and Cody (1980).

2.2.6 Soils

Soil samples (5 cm x 10 cm x 10 cm depth) were collected at each of the sites. Three soil samples were taken from each tree island and from each plot within the forest stand sites. The moisture (dry, mesic, wet), and slope were noted for each sample. All soil samples were kept as cool as possible until returning to Inuvik at which time they were refrigerated.
In the laboratory, soil samples were sieved to 2 mm. The samples were then sent to the Ministry of Forest & Range Research Branch in Victoria, BC to be analyzed for total nitrogen (N), total carbon (C), and pH.

2.2.7 Data Analysis

All analyses were conducted using R 2.10. To assess changes in stature across the forest-tundra ecotone the proportion of individuals in each height class (seedling, sapling, tree) were regressed against distance from treeline. The estimated distance north of treeline was determined using the treeline position reported by Timoney (1992) (as per McLeod 2001). The density of seedlings, saplings, and trees were regressed against the distance from treeline to determine the change across the forest-tundra ecotone.

The proportion of individuals within each tree island and forest stand plot classified as healthy, reduced, or dead were regressed against distance from treeline. The vitality data were also grouped into forest stand sites and tree island sites and a one way ANOVA (α=0.05) was used to determine if the proportion of individuals classified in each of dead, reduced, or healthy were different between the two areas.

The sites were combined based on their location within the forest tundra ecotone and an ANOVA (α=0.05) was used to determine if total N and C, carbon to nitrogen (C/N) ratio, and pH differed between the forest stand sites and the tree island sites. In addition, total N and C, C/N, and pH were regressed against distance from treeline in order to assess how they change across a latitudinal gradient.
2.3 Results

2.3.1 Study Area

A total of 12 sites were examined in the Tuktoyaktuk region, NWT, Canada (Figure 2.1). The northernmost tree island was at site R1 at 69°28′37.8″N 134°18′23.2″W and is located 53 km north of the treeline. The southernmost site was at site T10 at 68°17′07.0″N 133°15′14.7″W and is located 60 km south of the treeline.

The physical characteristics of each of the sites differ in elevation, location, aspect, and surface conditions (Table 2.1). The majority (11 out of 17) of the tree islands were located on slopes, although some were also located on hilltops and valley bottoms. Most of the slopes on which tree islands were located had a southerly aspect, but they were also found on east, west, and north facing slopes with protected valleys. The majority of tree islands were roughly circular in shape and ranged in size from ~40 m² to ~5400 m². The soils were mostly a moist moss layer, ranging in thickness from 5 to 20 cm, although some tree islands were situated on well drained gravel and sand. The latitude, longitude, distance from treeline, elevation, location, aspect, and surface conditions of each of the tree islands and the forest stands is summarized in Table 2.1. See Appendix 1 in McLeod (2001) for detailed descriptions of each tree island and forest stand site.

2.3.2 Climate

The monthly climate normals from 1971 through 2000 (data from 2001 through 2010 was not available) from Inuvik and Tuktoyaktuk demonstrate the difference in temperature and precipitation caused by increasing one degree in latitude, from the high subArctic forest to Low Arctic tundra along the coast of the Beaufort Sea (Figure 2.3). Mean summer (June, July, August) temperatures at Inuvik (12.2°C) are warmer that at Tuktoyaktuk (8.6°C). Inuvik also
receives more annual precipitation than Tuktoyaktuk (248 mm vs 167 mm, respectively). The majority of precipitation in this region is in the form of snow. Yearly snowfall at Inuvik (168 mm) is greater than at Tuktoyaktuk (95 mm).

### 2.3.3 Stand Structure

The number of tree islands, the growth forms, and the density of seedlings, saplings, trees, and total individuals at each site were highly variable (Table 2.2). Six of the eight tree island sites examined had only one tree island present. At site T6, eight tree islands were found and at site T2 there were three tree islands. The total number of individuals per tree island varied from three to 744. Growth forms observed include mat, infranival cushion, infranival erect, erect whorled, supranival skirted and tree. Tree Islands T5 and T1 had the greatest total stem density of all the sites. The density of seedlings, saplings, and trees were regressed against the distance from treeline, for the forest stand sites only, to confirm that the density of individuals within the forest stand sites decreases northward. Tree island sites were not included in this regression as they have high stem densities and would skew the results into indicating that densities increase northward across the forest-tundra. Results of the simple linear regression indicate that the density of trees, saplings, and seedlings significantly decrease northward across the forest-tundra (Figure 2.4 and Table 2.3).

Regressing the proportion of individuals within each site classified as trees (>200 cm), saplings (15-199 cm), and seedlings (<15 cm) against distance from treeline demonstrated that the stature of individuals decreased significantly northward across the forest tundra (Figure 2.5). The proportion of individuals classified as trees significantly decreases northward, whereas the proportion of individuals classified as saplings significantly increases northward and no relationship was found with seedling proportions and distance from treeline (Table 2.4).
2.3.4 Vitality

The proportion of individuals in each vitality class were not significantly correlated to distance from treeline (Figure 2.6 and Table 2.5). The proportion of individuals classified as dead and reduced were not significantly different between forest stands and tree islands, but a higher proportion of individuals are healthier in forest stand sites compared to tree island sites (Figure 2.7).

2.3.5 Vegetation

The dominant functional group or species found at each of the different layers are similar for all sites (Table 2.6) The ground layer in the tree islands and forest stands in the Tuktoyaktuk region were dominated by various species of moss and litter. The field layer primarily consisted of *Arctostaphylos rubra* (Rehd. & Wils.) Fern., *Vaccinium vitis-idaea* L., *V. uliginosum* L., *Empetrum nigrum* L., *Dryas integrifolia* M. Vahl, *Lupinus arcticus* Wats., *Equisetum variegatum* Schleich., *Cassiope tetragona* (L.) D.Don, *Ledum decumbens* (Ait.) Lodd., and various ramineae species. The principal species in the shrub layer were *Betula glandulosa* Michx., *Salix* spp. L., and *Alnus crispa* (Ait.) Pursh. The tree layer was dominated by *Picea glauca* (Moench) Voss., however there were five tree island sites in which no individuals greater than 2 m were found.

2.3.6 Soils

Total C, N, and C/N were not significantly related to distance from treeline (Figure 2.8 and Table 2.7). The pH, however, increased significantly with distance from treeline.

Classifying the sites based on their location within the forest tundra showed that forest stand sites had significantly higher total C and N than tree island sites (Table 2.8). However, the
C/N ratio was not significantly different between forest stands and tree islands. The pH of tree islands was significantly higher than the pH of forest stands.

2.4 Discussion

Tree growth is partly determined by temperature and moisture, and has been shown to decrease northward across the forest-tundra (Vowinckel et al. 1975, Scott et al. 1987). Shoot growth for white spruce is at its optimal level when day-night air temperatures are between 18 and 22°C (Grossnickle 2000). Thus the annual growth of individual trees is reduced across the forest-tundra due to the short and cool growing season (Sveinbjornsson et al. 2002).

The northern portion of this study area, encompassing all of the tree islands, is located in the low Arctic ecoclimatic region (Ecoregions Working Group 1989). In this area, summers are short, with the frost free period typically being 25 to 50 days, cool, and has a relatively high humidity. The winter season is extremely cold with mean temperatures below 0°C for 38 to 40 weeks. Total annual precipitation is usually less than 200 mm. The forest stand sites in this study are located in the high subarctic ecoclimatic region (Ecoregions Working Group 1989). In this region summers are cool, moist, and the frost free period ranges from 50 to 90 days. The winters are cold and approximately 36 to 38 weeks have mean daily temperatures below 0°C. The majority of precipitation occurs in the summer and early fall, ranging from 250 to 350 mm.

The difference in temperature and precipitation between Inuvik and Tuktoyaktuk are reflected in the differences between forest stand sites and tree islands, respectively. The number of individuals classified as trees (>2 m) significantly decreases northward across the forest tundra ecotone. However, the number of individuals classified as saplings (15-199 cm) increases from south to north. The individuals classified as saplings, however, are not true saplings in age, but usually exhibit alternate growth forms such as supranival skirted, erect whorled, infranival
cushion, or mat (as per Lavoie and Payette 1992). White spruce at the most northern sites, located on Richard’s Island, only had mat, infranival cushion, and infranival erect growth forms. Not only does the height growth of trees decrease with increasing latitude, the density and vitality of individuals also decreases with increasing latitude.

Temperature is not the only factor limiting tree growth and health. Other climatic influences such as blowing snow, strong winds, and desiccation above the snowpack all diminish the ability of trees to survive and grow, contributing to the development of the treeline (Stevens and Fox 1991, Hadley and Smith 1986). These influences partially account for the presence of dwarf shrubs and trees with a krummholz growth form beyond the treeline (Stevens and Fox 1991). Krummholz are not simply a phenotypic response of trees to the environment. Some are genetically determined forms and therefore may be less adaptable to a changing environment (Grace 1989, Callaghan et al. 2002). McLeod (2001) found that all tree islands in this region had live individuals greater than 200 years of age with the oldest occurring at site T3 (433 years). The age of the tree islands suggests that there is potential for genetic differences between the forest and tree island trees. The ability of the stunted growth forms rather than upright trees to survive beyond the treeline is also due to the relationship between productive tissues and their support structures (Grace et al. 2002). The majority of a tree’s biomass is found in woody tissue that supports the productive leaves and roots (Grace et al. 2002). This productivity to structure ratio is low relative to the high productive tissue to support structure ratio exhibited by dwarf vegetation (Stevens and Fox 1991). The low ratio exhibited by trees is unfavourable in adverse climatic conditions and helps to explain their northern limit as climate deteriorates with increasing latitude (Grace et al. 2002).
The microclimate is probably one of the most important influences on the position of the treeline (Wardle 1974). Once established, the presence of a tree influences the surrounding snow depth, wind velocities, and soil temperature, thus promoting the further establishment of seed and their own longevity (Wardle 1974). The majority of tree islands examined in this study were located on south facing slopes, protected from strong northern winds, or hilltops. Differences in topography (valleys, hills, and slopes) in parts of eastern Canada explain the variances in distribution and density of trees (Lavoie and Payette 1992). Even in the very flat northwestern areas of Siberia tree distribution is often associated with small differences in height and slope of the land (Callaghan et al. 2002).

Competition for nutrients is a limiting factor for plant growth on the tundra (Chapin and Shaver 1996). In particular, nitrogen is the critical limiting factor of boreal tree species growth (Tamm 1991). Rates of nutrient cycling depend on soil temperature, soil moisture, and vegetation, and are all related to varying microtopography (Holtmeier and Broll 2005). The current study demonstrated that total nitrogen and carbon is greater in forest stand sites than in tree islands. The results are similar to those of Rochelle (1998) who described that the majority of variation in soil C is due to landscape position, and that soil C is limited underneath tree islands. Similarly, Seastadt and Adams (2001) found decreases in soil C under tree islands compared to forests. Sveinbjornsson et al. (1995) showed that soil N decreases with elevation. Nitrogen is considered the most limiting nutrient to white spruce growth near treeline in the Brooks Range, Alaska (Shulze et al. 1994). Soil nutrient availability is lower at tree island sites than forest stand sites. These differences are most likely due to reduced mean soil temperatures in tundra compared to forests (Epstein et al. 2004). The availability of below ground resources, in particular nitrogen, is known to decrease in cool soil conditions (Holtmeier and Broll 2007).
Soil pH affects the availability of soil nutrients and a variety of biochemical processes (Walker et al. 1998). Community vegetation composition is different on soils that are base saturated relative to soils with exchangeable acidity (Walker et al. 2002). Results of this study show that soil pH is significantly greater in tree island sites compared to forest stand sites. These results agree with Timmoney (1992) who found that soil pH positively correlated with latitude across the forest tundra ecotone. The approximate optimum range of pH for white spruce growth is from 4.7 to 6.5 (Nienstaedt and Zasada 1990). Thus, as pH increases northward across the forest tundra the ability for white spruce growth decreases once pH levels become greater than 6.5. Walker et al. (2002) found that maximum temperature and soil pH were the two variables which significantly influence community species richness both directly and indirectly through their effect on other environmental variables. When soil pH is low, nutrient availability decreases (Foth 1990). When soil pH is high, micronutrients and the macronutrient P are limited (Foth 1990). Thus, vegetation composition and species richness is influenced by pH, however, the general reasons behind community differences on soil of different pH is not fully understood (Gough et al. 2000).

Despite observing a significant difference in soil pH and nutrients between forest stand and tree islands sites, the dominant functional groups or species of non-arboreal vegetation are similar throughout the forest tundra ecotone. In this study changes in tree height growth, density, and health throughout the forest-tundra are not matched by changes in the dominant species of shrubs and herbs. This is also true in other locations on the Seward Peninsula the majority of species found north of the treeline are also present in the understory of forested areas south of the treeline (Epstein et al. 2004). Similarly, in northern Quebec Morisset et al. (1983) concluded that most Arctic and boreal taxa occur on both sides of the treeline. In a study of historic
vegetation response to climate change Cwynar and Spear (1991) concluded that shrub and herb populations behaved independently of changes in spruce populations.

2.5 Conclusion

The objective of this chapter was to determine the changes in variables across the forest-tundra, including growth form, density, and vitality of *P. glauca*, soil nutrients, and surrounding vegetation. The height and health of *P. glauca* individuals is generally less in tree islands than forest stand sites and the density of individuals significantly decreases across the forest tundra ecotone. Significant differences in soil nutrients and pH were also found between forest stands and tree islands but the general vegetation composition was similar throughout the forest tundra ecotone. Temperature is considered the primary factor influencing tree dynamics at their latitudinal limit (Grace et al. 2002). As climate warms, it is expected that the treeline will advance northward onto the tundra (Callaghan et al. 2002). In order to assess this prediction the reproduction, establishment, and growth of *P. glauca* near treeline needs to be examined in relation to climate. However, any observable differences in treeline dynamics may also be attributable to differences in tree health, density, and growth form, as well as soil nutrients, microclimate, and topography.
2.6 Figures and Tables

Figure 2.1 Location of the study sites. Line represents approximate location of the treeline. Modified from McLeod (2001).
Figure 2.2 Growth forms of spruce. Dashed line indicates the snow-air interface. Obtained from Lavoie and Payette (1992).
Table 2.1 Physical characteristics of *Picea glauca* sites examined in the Tuktoyaktuk region. Modified from McLeod (2001). Site locations are shown in Figure 2.1.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Distance from Treeline (km)</th>
<th>Elevation (m)</th>
<th>Location</th>
<th>Aspect</th>
<th>Surface Conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1</td>
<td>69°28′37.8″</td>
<td>134°18′23.2″</td>
<td>53</td>
<td>60</td>
<td>15 slope</td>
<td>southwest</td>
<td>drained, sandy</td>
</tr>
<tr>
<td>R2</td>
<td>69°22′54.1″</td>
<td>134°01′48.6″</td>
<td>45</td>
<td>44</td>
<td>slope of hollow</td>
<td>south</td>
<td>drained, sandy</td>
</tr>
<tr>
<td>T1</td>
<td>69°23′12.3″</td>
<td>133°29′27.3″</td>
<td>49</td>
<td>3</td>
<td>base of 4 slope</td>
<td>southeast</td>
<td>moist moss</td>
</tr>
<tr>
<td>T2</td>
<td>69°19′18.6″</td>
<td>133°52′36.3″</td>
<td>37</td>
<td>28</td>
<td>hilltop</td>
<td>none</td>
<td>well drained</td>
</tr>
<tr>
<td>T3</td>
<td>69°18′49.1″</td>
<td>132°48′46.3″</td>
<td>31</td>
<td>39</td>
<td>12 slope</td>
<td>south</td>
<td>moist moss</td>
</tr>
<tr>
<td>T4</td>
<td>69°29′00.1″</td>
<td>132°11′21.8″</td>
<td>29</td>
<td>0</td>
<td>hilltop</td>
<td>none</td>
<td>well drained gravelly sand</td>
</tr>
<tr>
<td>T5</td>
<td>69°11′04.4″</td>
<td>133°01′23.1″</td>
<td>40</td>
<td>39</td>
<td>5 slope crest</td>
<td>south</td>
<td>moist moss</td>
</tr>
<tr>
<td>T6</td>
<td>69°17′47.9″</td>
<td>132°33′27.5″</td>
<td>40</td>
<td>27</td>
<td>hilltop, slopes&lt;10, bench in hill, valley bottom</td>
<td>all directions</td>
<td>well drained gravelly sand to poorly drained organic soils</td>
</tr>
<tr>
<td>T7</td>
<td>69°15′20.0″</td>
<td>131°47′27.6″</td>
<td>5</td>
<td>16</td>
<td>Slope and upland</td>
<td>south</td>
<td>moist moss</td>
</tr>
<tr>
<td>T8</td>
<td>69°11′19.2″</td>
<td>131°27′25.3″</td>
<td>-8</td>
<td>7</td>
<td>slope, valley bottom, and upland area</td>
<td>south, and none</td>
<td>moist moss</td>
</tr>
<tr>
<td>T9</td>
<td>69°06′30.9″</td>
<td>130°58′37.6″</td>
<td>-25</td>
<td>0</td>
<td>upland area</td>
<td>none</td>
<td>moist moss layer</td>
</tr>
<tr>
<td>T10</td>
<td>68°17′07.0″</td>
<td>133°15′14.7″</td>
<td>-60</td>
<td>7</td>
<td>upland area</td>
<td>None</td>
<td>moist moss layer</td>
</tr>
</tbody>
</table>
Figure 2.3 Climate Normals (1971-2000) for Inuvik and Tuktoyaktuk (data obtained from Environment Canada 2009).
Table 2.2 The number of tree islands, growth forms and mean density (#/ha) of trees, saplings, seedlings, and total individuals found at each of the examined sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Number of Trees (number of islands)</th>
<th>Growth forms*</th>
<th>Trees (#/ha)</th>
<th>Saplings (#/ha)</th>
<th>Seedlings (#/ha)</th>
<th>Total (#/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1</td>
<td>n/a</td>
<td>m, inc, ine</td>
<td>0</td>
<td>50</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td>R2</td>
<td>n/a</td>
<td>m, inc, ine</td>
<td>0</td>
<td>n/a</td>
<td>0</td>
<td>n/a</td>
</tr>
<tr>
<td>T1</td>
<td>19 (1)</td>
<td>m, inc, ine, ew</td>
<td>0</td>
<td>4750</td>
<td>0</td>
<td>4750</td>
</tr>
<tr>
<td>T2</td>
<td>12-774 (3)</td>
<td>inc, ine, ew, sns</td>
<td>479</td>
<td>590</td>
<td>0</td>
<td>634</td>
</tr>
<tr>
<td>T3</td>
<td>12 (1)</td>
<td>inc, ine, ew, sns</td>
<td>0</td>
<td>1133</td>
<td>0</td>
<td>1133</td>
</tr>
<tr>
<td>T4</td>
<td>n/a</td>
<td>m, ine</td>
<td>0</td>
<td>730</td>
<td>0</td>
<td>730</td>
</tr>
<tr>
<td>T5</td>
<td>44 (1)</td>
<td>inc, ine, ew, sns</td>
<td>5833</td>
<td>12500</td>
<td>0</td>
<td>18333</td>
</tr>
<tr>
<td>T6</td>
<td>3-66 (16)</td>
<td>m, inc, ine, ew, sns</td>
<td>618</td>
<td>548</td>
<td>266</td>
<td>1560</td>
</tr>
<tr>
<td>T7</td>
<td>n/a</td>
<td>ew, sns, tr</td>
<td>42</td>
<td>66</td>
<td>0</td>
<td>109</td>
</tr>
<tr>
<td>T8</td>
<td>n/a</td>
<td>ew, sns, tr</td>
<td>390</td>
<td>218</td>
<td>50</td>
<td>601</td>
</tr>
<tr>
<td>T9</td>
<td>n/a</td>
<td>sns, tr</td>
<td>332</td>
<td>569</td>
<td>12</td>
<td>577</td>
</tr>
<tr>
<td>T10</td>
<td>n/a</td>
<td>tr</td>
<td>937</td>
<td>706</td>
<td>88</td>
<td>1643</td>
</tr>
</tbody>
</table>

*After Lavoie and Payette (1992), m= mat, inc = infranival cushion, ine = infranival erect, ew = erect whorled, sns = supranival skirted, tr=tree. See Figure 2.2
Figure 2.4 The density (#/m$^2$) of individuals classified as trees (≥200 cm), saplings (15-199 cm), or seedlings (<15 cm) regressed against distance from treeline. Negative values on the x-axis indicate south of the treeline and positive values indicate north of the treeline. See Table 2.3 for regression results.

Table 2.3 Results of linear regression of the density of trees, saplings, and seedlings against distance from treeline.

<table>
<thead>
<tr>
<th>Density of Individuals</th>
<th>F</th>
<th>R$^2$</th>
<th>p-value $^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trees (&gt;200 cm)</td>
<td>11.039</td>
<td>0.477</td>
<td><strong>0.0077</strong></td>
</tr>
<tr>
<td>Saplings (15-199 cm)</td>
<td>6.663</td>
<td>0.340</td>
<td><strong>0.0273</strong></td>
</tr>
<tr>
<td>Seedlings (&lt;15 cm)</td>
<td>0.618</td>
<td>0.030</td>
<td>0.4316</td>
</tr>
</tbody>
</table>

$^*$Bold text indicates p-values<0.05
Figure 2.5 The proportion of individuals classified as trees (≥200 cm), saplings (15-199 cm), or seedlings (<15 cm), regressed against distant from treeline. Positive values on the x-axis represent north of treeline, negative values represent south of the treeline. See Table 2.4 for regression results.

Table 2.4 Results of regression for the proportion of individuals classified as trees, saplings or seedlings against distant from treeline.

<table>
<thead>
<tr>
<th>Height Class</th>
<th>F</th>
<th>$R^2$</th>
<th>p-value*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trees (≥200 cm)</td>
<td>11.14</td>
<td>0.5298</td>
<td><strong>0.0102</strong></td>
</tr>
<tr>
<td>Saplings (15-199 cm)</td>
<td>11.74</td>
<td>0.5440</td>
<td><strong>0.0090</strong></td>
</tr>
<tr>
<td>Seedlings (&lt;15 cm)</td>
<td>4.29</td>
<td>0.2679</td>
<td>0.0719</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values<0.05
Figure 2.6 The proportion of individuals classified as dead, reduced, or healthy in relation to distance from treeline. Negative values on the x-axis indicate south of the treeline and positive values indicate north of the treeline. See Table 2.5 for regression results.

Table 2.5 Results for regression of the proportion of individuals classified as dead, reduced, or healthy against distance from treeline.

<table>
<thead>
<tr>
<th>Vitality Class</th>
<th>F</th>
<th>R²</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead</td>
<td>0.5135</td>
<td>0.0603</td>
<td>0.494</td>
</tr>
<tr>
<td>Reduced</td>
<td>1.9584</td>
<td>0.0962</td>
<td>0.199</td>
</tr>
<tr>
<td>Healthy</td>
<td>4.0236</td>
<td>0.2515</td>
<td>0.079</td>
</tr>
</tbody>
</table>
Figure 2.7 The proportion of individuals classified as dead, reduced, or healthy in forest stands and tree island sites. (* p-value<0.05)
Table 2.6 The dominant species or functional groups for each of the tree, shrub, field, and ground layers at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Tree (&gt;2 m)</th>
<th>Shrub (0.25-2 m)</th>
<th>Field (&lt;25 cm)</th>
<th>Ground</th>
</tr>
</thead>
<tbody>
<tr>
<td>T10</td>
<td>Pic gla</td>
<td>Sal, Pic gla,</td>
<td>Led dec, Vac vit, grass, Lup arc</td>
<td>litter, moss</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aln cri</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T9</td>
<td>Pic gla</td>
<td>Sal, Bet gla,</td>
<td>Led dec, Vac vit, Vac uli, Arc rub</td>
<td>litter, moss</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aln cri</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T8</td>
<td>Pic gla</td>
<td>Sal, Bet gla</td>
<td>Vac uli, Arc rub, Emp nig, Equ var</td>
<td>litter, lichen, moss</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T7</td>
<td>Pic gla</td>
<td>Bet gla, Sal,</td>
<td>Emp nig, Led dec, Arc rub, Equ var</td>
<td>moss, lichen</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aln cri</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T6</td>
<td>Pic gla</td>
<td>Sal, Bet gla</td>
<td>Arc rub, Emp nig, Cas tet</td>
<td>moss, lichen</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T5</td>
<td>Pic gla</td>
<td>Pic gla, Sal,</td>
<td>Emp nig, Vac vit, Arc rub, Equ var</td>
<td>moss, litter</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bet gla</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T4</td>
<td>Pic gla, Bet gla</td>
<td>Pic gla, Vac vit, Dry int</td>
<td>litter, lichen</td>
<td></td>
</tr>
<tr>
<td>T3</td>
<td>Sal, Pic gla</td>
<td>Arc rub, Vac vit, Emp nig, Led dec, Dry int</td>
<td>litter, moss</td>
<td></td>
</tr>
<tr>
<td>T2</td>
<td>Pic gla</td>
<td>Sal</td>
<td>Arc rub, Vac vit, grass, Lup arc</td>
<td>litter, moss</td>
</tr>
<tr>
<td>T1</td>
<td>Bet gla, Sal,</td>
<td>Vac vit, Led dec, Arc rub, Cas tet</td>
<td>moss</td>
<td></td>
</tr>
<tr>
<td>R1</td>
<td>Pic gla</td>
<td>Pic gla, Dry int, Arc rub, Cas tet</td>
<td>litter</td>
<td></td>
</tr>
<tr>
<td>R2</td>
<td>Pic gla</td>
<td>Pic gla, Dry int, Arc rub, Cas tet</td>
<td>litter</td>
<td></td>
</tr>
</tbody>
</table>

Figure 2.8 Total N and C, C/N, and pH in relation to distant from treeline. Negative values on the x-axis indicate south of the treeline and positive values indicate north of the treeline. See Table 2.7 for regression results.

Table 2.7 Results of linear regression of total N and C, C/N, and pH against distance from treeline.

<table>
<thead>
<tr>
<th>Soil Property</th>
<th>F</th>
<th>$R^2$</th>
<th>p-value*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total N</td>
<td>1.695</td>
<td>0.0118</td>
<td>0.198</td>
</tr>
<tr>
<td>Total C</td>
<td>2.834</td>
<td>0.0306</td>
<td>0.097</td>
</tr>
<tr>
<td>C/N</td>
<td>-0.011</td>
<td>0.3403</td>
<td>0.562</td>
</tr>
<tr>
<td>pH</td>
<td>30.41</td>
<td>0.3365</td>
<td>8.825e-07</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values < 0.05

Table 2.8 ANOVA results comparing each of total C and N, C/N, and pH between tree islands and forest stands.

<table>
<thead>
<tr>
<th>Soil Property</th>
<th>Mean±Standard Error</th>
<th>F</th>
<th>p-value*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tree Island</td>
<td>Forest Stand</td>
<td></td>
</tr>
<tr>
<td>Total N</td>
<td>0.568±0.136</td>
<td>1.606±0.153</td>
<td>22.05</td>
</tr>
<tr>
<td>C/N</td>
<td>22.695±0.244</td>
<td>25.214±0.157</td>
<td>19.76</td>
</tr>
<tr>
<td>pH</td>
<td>6.870±1.285</td>
<td>5.637±1.599</td>
<td>1.225</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values < 0.05
CHAPTER 3: THE REPRODUCTIVE CAPACITY OF WHITE SPRUCE IN THE FOREST TUNDRA ECOTONE OF THE INUVIK-TUKTOYAKTUK REGION

3.1 Introduction

A northward decrease in the regenerative capacity of trees is thought to be the primary cause of the vegetation zonation throughout the forest-tundra ecotone (Sirois 2000). Throughout the majority of its range, *Picea glauca* (Moench) Voss, primarily reproduces sexually (Nienstaedt and Zasada 1990). Vegetative reproduction, by the process of layering, usually occurs at the range limit of *P. glauca* (Elliot-Fisk 1983, Timoney 1992, Nienstaedt and Zasada 1990). McLeod (2001) found that 62% to 94% of individuals within tree islands in the Tuktoyaktuk region originated from layering rather than sexual reproduction. The prominence of vegetative reproduction in tree island sites is in part due to the relatively inexpensive energy demand compared to sexual reproduction, as establishment from layering is more certain than from seed (Cook 1985). Sexual reproduction is correlated with the temperatures and length of growing season, both of which decrease northward across the forest-tundra (Legere and Payette 1982). As temperatures and growing season increase so does the energy available for cone production, seed ripening, germination, and seedling establishment (Legere and Payette 1982).

The general location of the treeline across North America coincides reasonably well with the mean July 10°C isotherm of air temperature (Grace et al. 2002). This correlation has been considered strong evidence that temperature is one of the most important factors controlling treeline dynamics (Grace et al. 2002). Temperatures, especially in winter, have increased sharply in most regions of the Arctic in recent decades (ACIA 2004). In north-western North America a significant warming trend has been documented in the Yukon and Alaska (Zhang et al. 2000). Specifically, surface-air temperatures have risen 0.31 ± 0.03°C per decade in north-western
North America (Keyser et al. 2000). This warming trend is expected to cause a northward treeline expansion (Starfield and Chapin 1996, ACIA 2004).

Climate change models generally predict that the treeless gaps in the present forest-tundra will become forested and that the treeline will shift northwards hundreds of kilometres (Callaghan et al. 2002). Central to this prediction is an increase in the reproductive capacity of tree species at treeline in response to increased temperatures and growing season length. In order to assess this prediction, cone production and seed viability of *P. glauca* were examined across a latitudinal gradient, spanning approximately a 3°C temperature change, and compared to data along the same gradient from the early 1990s. The responses of these variables across the temperature gradient and over the past 15 years will help determine the potential reproductive responses of *P. glauca* to a changing climate.

This chapter will focus on the reproduction of *P. glauca* throughout the forest-tundra ecotone in the Tuktoyaktuk region of the Northwest Territories, Canada. The objectives are: 1) to assess the reproductive capacity in the tree island sites compared to sites in the low subarctic forest-tundra, and 2) to determine if the reproductive capacity has changed since the sites were last examined in the early 1990s.

### 3.2 Methods

#### 3.2.1 Study Area

A total of 12 sites were examined in the Tuktoyaktuk region of the NWT, Canada (Figure 3.1). In 1993, a transect was established in this region that stretched from the northern forest-tundra to the species northernmost limit (McLeod 2001). A total of 10 sites (T1 through T10) were established along this transect. In addition to these sites two more tree island sites were established on Richard’s Island (R1 and R2). In September 2008, 7 tree island sites (R1,
R2, T1, T2, T3, T4, and T5) were re-examined. Site T6 has 16 tree islands and was excluded in 2008 due to time constraints. In the summer of 2009 a total of eight tree island sites were examined, two on Richard’s Island (R1, R2) and eight on the Tuktoyaktuk peninsula (T1 through T6). In addition, four forest stand sites (T7 through T10), each consisting of 3 plots, were re-examined.

3.2.2 Climate

A strong climatic gradient exists across the study area. Lantz (2008), using temperature loggers across a latitudinal gradient in the Mackenzie Delta region throughout the summer of 2005, found a decrease of approximately 3°C for every degree of increasing latitude. Monthly climate normals of precipitation and temperature from 1971 through 2000 from Inuvik and Tuktoyaktuk were obtained from Environment Canada (2009).

In order to determine the reproductive response of *P. glauca* to climate warming since the sites were last examined 15 years ago, homogenized temperatures for Inuvik were obtained from Environment Canada’s Adjusted Historical Canadian Climate Data (AHCCD 2009) (Vincent 1998, Mekis and Hogg 1999, Vincent and Gullet 1999, Vincent et al. 2002, Mekis and Hopkinson 2004, Mekis 2005, Devine and Mekis 2008, Vincent and Mekis 2009), which has been designed for climate change analyses. This database contains daily mean, maximum, and minimum temperatures and extends from 1926 to 2005. A regression analysis was completed on this data in order to assess any changes in temperature over this time period. There was an obvious break in the temperature trend starting in 1977, therefore two separate regression analysis were completed using data prior to 1977 and post 1977. Homogenized precipitation data was also available for Inuvik from 1958 to 2007. The data consists of rainfall, snowfall, and total
precipitation. Regression analysis was completed on this data to see if any changes in precipitation occurred over this time period.

3.2.2 Reproductive Capacity

At all sites the presence or absence of cones from the current year was noted. The number of male and female cones on each individually-measured tree was estimated. The abundance of each of male and female cones per tree were classified as low (less than 10), medium (10-50), or high (more than 50) (PPS Arctic Protocols 2008).

Female cones were collected as close the end of the growing season as possible as this is the natural time of seed maturation. Cones were collected on a per tree basis (PPS Arctic Protocols 2008). At tree island sites where few trees produced cones, all cones were collected. At tree island sites where cones were plentiful from 5 to 50 cones were collected from each individual. At forest stand sites, cones were collected from at least 20 individuals with a minimum of 5 cones per tree.

Cones were stored in paper bags for several weeks at room temperature to allow for ripening of the seed (Caron et al. 1993). Seeds were removed from the cones by shaking, imbibed for 24 hours, de-winged, and stored for two to three weeks at 2 to 5°C (McLeod 2001). Germination trials were not conducted at each site in every year due to a lack of cone production, the ripeness of cones, and the availability to visit each site. Germination trials were completed by placing up to 100 seeds on moist filter paper in Petri dishes (100 x 15 mm). The tests were conducted at the UBC Department of Botany Greenhouses under constant light conditions with temperatures ranging from 22 to 28°C. Seeds were deemed germinated when the radical was at least the same length as the seed (PPS Arctic Protocols 2008). All seeds that exhibited moulding
were immediately removed from the Petri dishes. The germination trials continued for four
weeks.

Soil samples (5 cm x 10 cm x 5 cm depth) were collected throughout the summer of 2009
to test for germinable seedbank as an indication of the potential for future seed germination and
seedling establishment. At each tree island site 6 soil samples were taken: 3 inside and 3 (5 m
from the edge) outside of each tree island. At sites with numerous tree islands (T6) the soil
samples were taken at the first tree island found. In the forest stand sites, six soil samples were
randomly taken within each plot. In the laboratory, soil samples were loosened and spread in
plastic dishes (10 cm x 10 cm). The samples were kept moist, and under constant light conditions
at temperatures ranging from 22 to 28°C for 4 weeks. Every other day the samples were
examined to assess if any seeds had germinated. A seed was considered germinated when the
radical was at least the same length as the seed (PPS Arctic Protocols 2008).

3.2.3 Data Analysis

All analyses were conducted using R 2.10. Simple linear regression was used to assess
trends in temperature and precipitation over time. To assess changes in reproduction across the
forest-tundra ecotone male and female cone production and seed viability were regressed against
distance from treeline. A randomized-complete-block-design analysis of variance (RCBD-
ANOVA), blocking for the variability due to sites, was used to assess if cone production varied
among the years for which data are available (1993, 1994, and 2009). In 2009, cone production
was assessed using classes. A chi-squared test was used to determine how the proportions of
these classes varied between sites. Proportions from site T10, the furthest south forest stand site,
were used as the expected values. Each of the classes was also regressed against distance from
treeline to assess cone production across the forest-tundra ecotone. Cone production data were
grouped into forest stand sites and tree island sites and a Student’s t-test was used to determine if the proportions of individuals classified in each of low, medium, and high were different between the two areas. An RCBD-ANOVA, blocking for the variability introduced by sites, was used to assess if seed germination was different between sample years. Similarly, germination rates across the forest-tundra ecotone were assessed using an RCBD to remove the variability due to years. A pairwise t-test (bonferroni adjustment) was then used to determine which sites were significantly different form one another.

3.3 Results

3.3.1 Climate

The monthly climate normals from 1971 through 2000 from Inuvik and Tuktoyaktuk show the change in temperature and precipitation caused by increasing one degree in latitude, from high subarctic forest to shrub tundra along the Beaufort Sea coast (Figure 3.2). Mean summer temperatures from Inuvik and Tuktoyaktuk are noticeably different (12.2 vs. 8.6°C). Inuvik also receives more annual precipitation than Tuktoyaktuk (248 vs 167 mm).

A warming trend $0.34 \pm 0.07°C$ per decade is exhibited by the homogenized annual temperatures recorded at Inuvik airport from 1926 through 2005 (Figure 3.3). Mean daily, mean daily maximum, and mean daily minimum temperatures all significantly increase with time (Table 3.1). Prior to 1977 there was relatively little increase in temperature ($0.04 \pm 0.09°C$ per decade); however after 1977 a large temperature increase of $0.59 \pm 0.11°C$ per decade occurred (Figure 3.3). Regression results for temperature trends are presented in Table 3.1. In contrast to the temperature change, no trend in precipitation from 1958 through 2006 was found (Figure 3.4).
3.3.2 Reproductive capacity

All sites, except T1, produced male cones in each sample year (Table 3.2). No female cones were produced at site T1 in any of the sample years. Site T5 did not produce any female cones in 1993 or 2008. All other sites produced female cones in all sample years.

Quantitative data on cone production from the early 1990s were available from sites T6, T5, T3, and T1. There was a significant difference in female cone production at these sites (F=6.21, p-value = 0.03); cone production was slightly higher in 2009. (Figure 3.5). In contrast, to the slight increase in female cone production, male cone production has not changed (F=0.88, p-value=0.46).

For the 2009 cone data, the chi-square analysis showed that each site relative to site T10 produced significantly different proportions of female cones (Figure 3.6, Table 3.3). Similarly, every site relative to T10, except T9, produced significantly different proportions of male cones (Figure 3.6).

The proportion of individuals classified as having low, medium, or high cone production were regressed against distance from treeline indicating an overall decrease in female cone production northward across the forest-tundra and no change in male cone production (Figure 3.7 and Table 3.4). There was no significant correlation between the proportion of individuals classified as having low female cones and distance from treeline. The proportion of individuals with medium female cones was significantly correlated to distance from treeline, but those with high cone production was not. None of the classes of male cone production was correlated with distance from treeline.

Germination rates of *P. glauca* seeds in 2009 ranged from 0.1 to 19.3% in forest stand sites and 0 to 0.5% in tree island sites (Table 3.5). In the early 1990s, germination rates were
similarly low, ranging from 0.5 to 21.5\% in forest stand sites and 0 to 8\% in tree island sites. Comparing germination among all years showed there were no significant differences between any of the years (F=2.34, p-value=0.06). The data were then divided into two groups: germination rates in 1993, 1994, and 1995 were combined and compared against those in 2008 and 2009 to determine if rates may have changed over time. Results indicated that germination rates have not significantly changed between the two time periods (F=3.63, p-value=0.06).

After accounting for the variability due to years, there was a significant difference in germination rates between sites across the forest-tundra ecotone (F= 5.26, p<0.001). Site T10 had significantly higher germination rates than all of the tree island sites and site T7 (Table 3.6). There were no other significant differences between any sites.

Germination rates in each sampled year relative to distance from treeline varied among sampled years (Table 3.7). No significant relationship was found in 1994 and 2008, but rates in 1993, 1995, and 2009 were all significantly related to distance from treeline (Figure 3.8). Sorting the data into 2 groups by averaging the 1993, 1994, and 1995 data and comparing them to the average of the 2008 and 2009 data showed that germination rates from both the early 1990s and the late 2000s are significantly correlated with distance from treeline (Figure 3.9).

In the early 1990s no germinable seedbank was found (McLeod 2001). Similarly, in 2009 no seeds germinated from the collected soil samples.

3.4 Discussion

The northern limit of a species distribution is often related to a reduction in their reproductive capacity due to colder temperatures and a shorter growing season (Lavoie and Payette 1996). The reproductive capacity of *P. glauca* depends on the climatic conditions of the current and the previous year as their reproductive cycle last 2 years (Owens and Blake 1985). A series of events
must occur in order for successful sexual reproduction to be completed. These include the production of gametes (pollen and ovules), the dispersal of a male gamete (pollen) to a female, fertilization, development of viable seed, dispersal of this seed to a suitable substrate, and lastly successful germination and establishment of the seedling (Sveinbjörnsson et al. 2002). Environmental interference at any of these steps greatly reduces a tree species chance of successful sexual reproduction. It is for this reason that tree species at their range limit more commonly reproduce by layering, or vegetative reproduction, than by sexual reproduction (Sveinbjörnsson et al. 2002).

Cone production at a species range limit may be less frequent than in southern locations (Sveinbjörnsson et al. 2002). Reduced cone production at northern latitudes is also caused by blowing snow or large snow loads damaging the cone producing shoots (Hadley and Smith 1986, Hadley and Smith 1987). Wind speeds and their subsequent damage to cones producing shoots are understandably higher on the tundra than in the forest as the forest obstructs airflow (Chapin III F.S et al. 2000, Eugster et al. 2000). Sirois (2000) studied cone crops of *Picea mariana* (Mill.) BSP, and found that the number of trees producing cones significantly decreased northward along a latitudinal gradient.

In the early 1990s, McLeod (2001) found that the production of female and male cones both significantly decreased northward. In 2009 each tree was classified according to the number of cones it produced (10 or less, 10 to 50, more than 50). In general both female and male cone production was higher in the more southern forest stand sites compared to the more northern tree island sites. This implies that the total female and male cone crop does in fact decrease northwards across the forest tundra in association with increasing climatic stress.
In this study female cone production by adult trees of *P. glauca* increased since the early 1990s, whereas male cone production has not changed. Quantitative data from the early 1990s for female and male cone production was only available from four sites. Thus, the production of cones in 2009 compared to the early 1990s is limited in terms of the number of sample sites and thus not statistically reliable. *Picea glauca* is a mast seeding conifer. Mast seeding is the synchronous and highly variable production of seed crops by a population (Lamontagne and Boutin 2007) and could explain the observed variability in cone production between years and between sites.

Warm dry summer conditions result in high levels of viable seeds for *P. glauca* (Zasada et al 1992). As temperature decreases northward it is expected that germination rates would decrease in association with this temperature gradient. Temperature, however, is not the only factor that affects seed viability. Other physical factors such as the availability of nutrients and water are also important (Tamm 1991, Sveinbjörnsson et al. 2002). A variety of disturbances, such as fire, herbivores, pests and parasites also affect seed production and viability (Payette et al. 1985, Caccianiga et al 2008).

In addition to the physical and biological factors, internal factors are also extremely important in determining the production of viable seed. Self pollination in spruces causes the gametophyte to stop growing and results in empty seeds and reduced germination (Fowler and Park 1983). This often occurs when stand density is low and may partly explain the rarity of successful sexual regeneration within the forest-tundra (Caron et al. 1990). Many individuals within the tree island sites originated by vegetative reproduction (McLeod 2001), making them genetically identical, thus increasing the probability of self pollination and subsequently reducing germination rates. An even more prominent limiting factor to sexual reproduction is the low
viability of pollen in the forest-tundra (Elliott-Fisk 1983), which could explain the increased proportion of unfilled seeds at the northern-most sites. The proportion of filled seeds and successful germination have also been associated with the regional variation in heat sum (Sirois 2000). Numerous studies have shown that successful germination of boreal species is temperature limited (Black and Bliss 1980, Hobbie and Chapin 1998, Sirois 2000). *P. glauca* within the forest-tundra ecotone of the Keewatin region, Nunavut produced cones that yielded no viable seed or pollen (Elliot-Fisk 1983). Zasada et al. (1978) reported that *P. glauca* north of the Arctic Circle in Alaska regularly failed to produce mature seeds, particularly during summers when heat sum requirements for embryo maturation were not met. Sirois (2000) studied seed crops of (*Picea mariana* along a latitudinal gradient and found that the number of seeds extracted per cone, the percentage of filled seeds, and the germination of filled seeds decreased significantly northward.

Germination rates have not significantly changed since they were last examined in the early 1990s. The lack of change between the two time periods is reflected in the fact that climatic conditions have not drastically altered in the last 15 years. Inuvik summer temperatures (June, July, August) averaged over 1993, 1994, and 1995 were 13.2 ± 0.62°C compared to 11.9 ± 0.73°C for 2007, 2008, and 2009. Similarly Tuktoyaktuk summer temperatures were not different between the two time periods, 9.9 ± 0.09°C for the early 1990s compared to 8.9 ± 0.67°C for the late 2000s. Despite the lack of observable temperature differences between the two time periods from which cones were collected there has been a large temperature increase, since 1977, of 0.59 ± 0.11°C per decade at Inuvik airport. The lack of change in germination rates over time may simply be accounted for by the interannual climate variation or perhaps the directional change in temperature may not have been sufficient enough to induce change.
Germination rates did, however, vary across the forest tundra gradient. Sites T10, T9, and T8, the three most southern sites, had significantly greater germination rates than the rest of the sites. Overall, germination rates significantly decreased northward across the forest tundra. The decline in seed viability is most likely associated with the deterioration of climatic conditions and decreased temperatures beyond treeline, represented by the climatic differences between Inuvik and Tuktoyaktuk.

The germinability of *P. glauca* seed reported in this study is much lower than that presented in a variety of studies from more southerly locations. Germination rates of 94% were reported in northern Quebec (O’Connell 2006), 45% in interior Alaska (Zasada 1971), 89 to 95% in central Ontario (Caron et al. 1993), and 64% in southern Ontario (Fowler and Park 1983). Lower germination rates found in this study reflect the effect of climatic limitations to successful sexual reproduction throughout the forest-tundra ecotone.

No *P. glauca* seeds germinated from soil samples in 2009 or in the early 1990s. Seed is shed annually by *P. glauca* and loses viability within a few years (Nienstaedt and Zasada 1990), making it unlikely to have a germinable seedbank. In addition to a short period of viability, cone production and viable seeds are limited in northern locations, making it unlikely for a seedbank to be present. No seedbank was found for *P. glauca* in the forest tundra of the NWT (Elliot 1979), nor in the forest-tundra of Nunavut (Johnson 1975). Similarly, Payette et al. (1982) found no germinable seedbank of *Picea mariana* or *Larix laricina* at the treeline in northern Quebec.

3.5 Conclusions

As climate continues to warm it is predicted that the treeless gaps in the present forest-tundra will become forested and that the treeline will expand northwards (Callaghan et al 2002). Treeline expansion could result from a continuous expansion of the species border (Delcourt and
Delcourt 1987) or it could occur from outlying populations, such as tree islands, acting as nodes of expansion (Scott and Hansell 2002). Studying the reproductive capacity of *P. glauca*, using the forest-tundra ecotone in the Inuvik-Tuktoyaktuk region as a proxy for a 3°C increase in average summer temperatures, demonstrated the potential for increased reproduction as temperatures warm. No changes in reproductive capacity were observed throughout the forest tundra ecotone since they were last assessed, 15 years ago, despite the increase in temperatures since 1977. This lack of change indicates that the reproductive capacity of *P. glauca* individuals on the tundra will have a slow response to changes in temperature and that temperature is probably not the principal limiting factor for sexual reproduction. Currently, individuals within tree island sites are producing cones in abundance, yet the viability of seeds from these sites is very low. This suggests that the production of viable seeds is an important bottleneck to the tree islands acting as nodes of treeline expansion. The majority of individuals within the tree islands are probably genetically identical or closely related, resulting in self-pollination and aborted seed. Germination rates will therefore not increase with increasing temperatures unless an outside seed source becomes available. *Picea glauca* throughout the forest tundra ecotone in the Mackenzie Delta region, NWT, will likely have a positive reproductive response to climate warming, but it is unlikely that the tree islands will act as nodes of expansion unless there is seed input from southern sources.
3.6 Figures and Tables

Figure 3.1 Location of the study sites. Line represents approximate location of the treeline. Modified from McLeod (2001).
Figure 3.2 Climate Normals (1971-2000) for Inuvik and Tuktoyaktuk (data obtained from Environment Canada 2009).
Figure 3.3 Annual temperatures for Inuvik airport: mean daily maximum, mean daily, and mean daily minimum temperatures. Trendlines represent 1926 through 1976, and 1977 through 2005. See Table 3.1 for regression results. Data obtained from Environment Canada’s Adjusted Historical Canadian Climate Data (AHCCD) (2009).

Table 3.1 Regression results for mean daily maximum, mean daily, and mean daily minimum annual temperatures for Inuvik airport; 1926 through 2005 (all), 1926 through 1976 (<1977), and 1977 through 2005 (≥1977).

<table>
<thead>
<tr>
<th>Temperature and Year</th>
<th>R²</th>
<th>F-statistic</th>
<th>P-value*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean &lt;1977</td>
<td>0.0002</td>
<td>0.0086</td>
<td>0.9263</td>
</tr>
<tr>
<td>Mean ≥1977</td>
<td>0.0588</td>
<td>1.6878</td>
<td>0.2049</td>
</tr>
<tr>
<td>Mean (all)</td>
<td>0.2004</td>
<td>19.5477</td>
<td>3.14e-05</td>
</tr>
<tr>
<td>Maximum &lt;1977</td>
<td>0.0054</td>
<td>0.2662</td>
<td>0.6082</td>
</tr>
<tr>
<td>Maximum ≥1977</td>
<td>0.0672</td>
<td>1.9445</td>
<td>0.1746</td>
</tr>
<tr>
<td>Maximum (all)</td>
<td>0.1478</td>
<td>13.5277</td>
<td>0.0004</td>
</tr>
<tr>
<td>Minimum &lt;1977</td>
<td>0.0033</td>
<td>0.1601</td>
<td>0.6908</td>
</tr>
<tr>
<td>Minimum ≥1977</td>
<td>0.0432</td>
<td>1.2191</td>
<td>0.2793</td>
</tr>
<tr>
<td>Minimum (all)</td>
<td>0.2457</td>
<td>25.4019</td>
<td>2.94e-06</td>
</tr>
</tbody>
</table>

*Bold text indicates P-values <0.05.
Figure 3.4 Annual Precipitation at Inuvik Airport between 1955 and 2006: total precipitation, rainfall, and snowfall. Data obtained from Environment Canada’s Adjusted Historical Canadian Climate Data (AHCCD) (2009).
Table 3.2 The proportion (%) of individuals within each site producing female and male cones in 1993, 1994, 1995, 2008, and 2009 (Data from 1993, 1994, and 1995 are from McLeod 2001).

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
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<th></th>
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<tbody>
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<td>R1</td>
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<td>M</td>
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<td>P</td>
<td>M</td>
<td>P</td>
<td>M</td>
<td>M</td>
<td>P</td>
<td>M</td>
<td></td>
</tr>
<tr>
<td>R2</td>
<td>45</td>
<td>P</td>
<td>M</td>
<td>M</td>
<td>P</td>
<td>M</td>
<td>P</td>
<td>M</td>
<td>M</td>
<td>P</td>
<td>M</td>
<td></td>
</tr>
<tr>
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<td>49</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
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</tr>
<tr>
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<td>M</td>
<td>M</td>
<td>-</td>
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<td>M</td>
<td>M</td>
<td>M</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>T3</td>
<td>37</td>
<td>15</td>
<td>11</td>
<td>M</td>
<td>P</td>
<td>60</td>
<td>60</td>
<td>58</td>
<td>M</td>
<td>P</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>T4</td>
<td>34</td>
<td>F</td>
<td>F</td>
<td>-</td>
<td>P</td>
<td>63</td>
<td>F</td>
<td>F</td>
<td>-</td>
<td>P</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>T5</td>
<td>31</td>
<td>0</td>
<td>5</td>
<td>13</td>
<td>0</td>
<td>25</td>
<td>21</td>
<td>M</td>
<td>7</td>
<td>P</td>
<td>28</td>
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</tr>
<tr>
<td>T6</td>
<td>29</td>
<td>27</td>
<td>35</td>
<td>M</td>
<td>-</td>
<td>61</td>
<td>42</td>
<td>42</td>
<td>M</td>
<td>-</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td>T7</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>84</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>75</td>
<td></td>
</tr>
<tr>
<td>T8</td>
<td>-8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>100</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>98</td>
<td></td>
</tr>
<tr>
<td>T9</td>
<td>-25</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>44</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td>T10</td>
<td>-60</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>60</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>60</td>
<td></td>
</tr>
</tbody>
</table>

*+km=distance north of treeline, -km=distance south of treeline, M=many individuals with cones, F= few individuals with cones, P=cones Present, - = no data.
Figure 3.5 The proportion of individuals producing female cones at sites T6, T5, T3, and T1 in 1993, 1994, and 2009. Error bars represent standard error of the mean.
Figure 3.6 The proportion of individuals within each site classified as having low, medium, and high levels of female cones (top) and male cones (bottom) in 2009. Error bars represent standard error of the mean. T10 was used as the expected proportions. See Table 3.3 for Chi-square results.
Table 3.3 Chi-square results for the proportion of individuals producing low, medium, and high levels of female and male cones in 2009. Proportions from T10 were used as expected values.

<table>
<thead>
<tr>
<th>Site</th>
<th>Female cones</th>
<th></th>
<th>Male cones</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$X^2$</td>
<td>p-value*</td>
<td>$X^2$</td>
<td>p-value*</td>
</tr>
<tr>
<td>T9</td>
<td>9.595</td>
<td>0.0082</td>
<td>2.935</td>
<td>0.2305</td>
</tr>
<tr>
<td>T8</td>
<td>160.7</td>
<td>&lt;0.0001</td>
<td>16.79</td>
<td>0.0002</td>
</tr>
<tr>
<td>T7</td>
<td>98.53</td>
<td>&lt;0.0001</td>
<td>7.252</td>
<td>0.0266</td>
</tr>
<tr>
<td>T6</td>
<td>39.59</td>
<td>&lt;0.0001</td>
<td>31.52</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>T5</td>
<td>56.93</td>
<td>&lt;0.0001</td>
<td>95.26</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>T4</td>
<td>153.8</td>
<td>&lt;0.0001</td>
<td>129.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>T3</td>
<td>140.0</td>
<td>&lt;0.0001</td>
<td>15.04</td>
<td>0.0005</td>
</tr>
<tr>
<td>T2</td>
<td>10.47</td>
<td>0.0053</td>
<td>63.30</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>T1</td>
<td>100.0</td>
<td>&lt;0.0001</td>
<td>225.0</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values <0.05.
Figure 3.7 The proportion of individuals within each site producing low, medium, and high levels of female cones (top) and male cones (bottom) in 2009, regressed against distance from treeline. Positive values on the x-axis indicate north of the treeline and negative values indicate south of the treeline. See Table 3.4 for regression results.
Table 3.4 Results of linear regression of female and male cone production classes against distance from treeline.

<table>
<thead>
<tr>
<th>Cone class</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>R²</td>
</tr>
<tr>
<td>Less 10</td>
<td>1.098</td>
<td>0.1206</td>
</tr>
<tr>
<td>10 to 50</td>
<td>20.99</td>
<td>0.7241</td>
</tr>
<tr>
<td>More 50</td>
<td>0.006</td>
<td>0.0008</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values < 0.005


<table>
<thead>
<tr>
<th>Site</th>
<th>Distance from treeline (km)</th>
<th>1993</th>
<th>1994</th>
<th>1995</th>
<th>2008</th>
<th>2009</th>
</tr>
</thead>
<tbody>
<tr>
<td>R2</td>
<td>45</td>
<td>0</td>
<td>0</td>
<td>7.1</td>
<td><strong>0.32±0.005</strong></td>
<td>0</td>
</tr>
<tr>
<td>R1</td>
<td>53</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td><strong>0.25±0.02</strong></td>
<td>0</td>
</tr>
<tr>
<td>T1</td>
<td>49</td>
<td>no cones</td>
<td>no cones</td>
<td>no cones</td>
<td>no cones</td>
<td>no cones</td>
</tr>
<tr>
<td>T2</td>
<td>37</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
<td>not ripe</td>
<td><strong>0.50±0.26</strong></td>
</tr>
<tr>
<td>T3</td>
<td>31</td>
<td>0.6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td><strong>0.33±0.19</strong></td>
</tr>
<tr>
<td>T4</td>
<td>29</td>
<td>1.6</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td><strong>0.08±0.05</strong></td>
</tr>
<tr>
<td>T5</td>
<td>40</td>
<td>no cones</td>
<td>8</td>
<td>0</td>
<td>no cones</td>
<td><strong>0.13±0.08</strong></td>
</tr>
<tr>
<td>T6</td>
<td>40</td>
<td>0.7</td>
<td>5.3</td>
<td>0</td>
<td>-</td>
<td><strong>0.28±0.09</strong></td>
</tr>
<tr>
<td>T7</td>
<td>5</td>
<td>-</td>
<td>0.5</td>
<td>2.5</td>
<td>-</td>
<td><strong>0.14±0.09</strong></td>
</tr>
<tr>
<td>T8</td>
<td>-8</td>
<td>-</td>
<td>1</td>
<td>18</td>
<td>-</td>
<td><strong>0.29±0.47</strong></td>
</tr>
<tr>
<td>T9</td>
<td>-25</td>
<td>-</td>
<td>6</td>
<td>33</td>
<td>-</td>
<td><strong>0.54±0.83</strong></td>
</tr>
<tr>
<td>T10</td>
<td>-60</td>
<td>30</td>
<td>5.5</td>
<td>21.5</td>
<td>-</td>
<td><strong>19.3±3.52</strong></td>
</tr>
</tbody>
</table>

- = site not visited that year
Table 3.6 P-values* for the pairwise t-test (bonferroni adjustment) for differences in germination rates between sites. Values of 1 represent all p-value ≥ 1 after the bonferroni adjustment.

<table>
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<tr>
<th>Sites</th>
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<th>R2</th>
<th>T1</th>
<th>T2</th>
<th>T3</th>
<th>T4</th>
<th>T5</th>
<th>T6</th>
<th>T7</th>
<th>T8</th>
<th>T9</th>
<th>T10</th>
</tr>
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<tbody>
<tr>
<td>R1</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R2</td>
<td>1</td>
<td>-</td>
<td></td>
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</tr>
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<td>-</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>T3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td>1</td>
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</tr>
<tr>
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<td>1</td>
<td>-</td>
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<td>T9</td>
<td>0.13994</td>
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<td>0.13512</td>
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<td>0.15394</td>
<td>0.17074</td>
<td>0.40813</td>
<td>0.31942</td>
<td>0.64302</td>
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<td><strong>0.00588</strong></td>
<td>0.28700</td>
<td>1</td>
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</table>

*Bold text indicates p-values <0.005
Table 3.7 Regression results for germination rates in each sample year regressed against distance from treeline.

<table>
<thead>
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<th>year</th>
<th>F</th>
<th>R²</th>
<th>p-value*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>193.1</td>
<td>0.965</td>
<td>&lt;0.0001</td>
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<tr>
<td>1994</td>
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<td>0.1637</td>
<td>0.1912</td>
</tr>
<tr>
<td>1995</td>
<td>22.19</td>
<td>0.6894</td>
<td>0.0008</td>
</tr>
<tr>
<td>2008</td>
<td>3.18</td>
<td>0.3464</td>
<td>0.1248</td>
</tr>
<tr>
<td>2009</td>
<td>11.79</td>
<td>0.5412</td>
<td>0.0064</td>
</tr>
<tr>
<td>93, 94, 95</td>
<td>45.62</td>
<td>0.8202</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2008, 2009</td>
<td>11.8</td>
<td>0.5413</td>
<td>0.0064</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values<0.05

Figure 3.8 The percentage of seeds that germinated at each site in 1993, 1994, 1995, 2008, and 2009 regressed against distance from treeline. Positive values on the x-axis indicate north of the treeline and negative values indicate south of the treeline. See Table 3.7 for regression results.
Figure 3.9 The percentage of seeds that germinated at each site in the early 1990s and the late 2000s regressed against distance from treeline. Positive values on the x-axis indicate north of the treeline and negative values indicate south of the treeline. See Table 3.7 for regression results.
4.1 Introduction

There are numerous factors that affect the establishment of *Picea glauca* (Moench) Voss. (white spruce) at northern latitudes. Seedling establishment and survival depends on a combination of adequate moisture, sufficient surface soil temperatures, ample below ground resources, and a suitable substrate (Sveinbjornson 2000). Seedling establishment at treeline and beyond in the tundra occurred from the late 19th century to the mid 20th century in northern Canada (Morin and Payette 1984, Lamb 1985, Payette and Filion 1985, Szeicz and MacDonald 1995, MacDonald et al. 1998), Alaska (Cooper 1986, Suarez et al 1999, Lloyd and Fastie 2002, Wilmking et al 2004), and Russia (Esper and Schweingruber 2004). Dendrochronology can be used to date the establishment of trees and measure the impact of climate on tree recruitment (MacDonald et al. 1998). Numerous studies have used this method and concluded that there was an increased recruitment of treeline spruce after 1880 (Payette and Filion 1985, Payette et al. 1985, Scott et al 1987, Szeicz and MacDonald 1995b).

The general location of the treeline across North America coincides reasonably well with the mean July 10°C isotherm of air temperature (MacDonald et al 2008, Grace et al. 2002). This correlation has been considered evidence that temperature is one of the most important factors controlling treeline dynamics (Grace et al. 2002). Temperatures, especially in winter, have increased sharply in most regions of the Arctic in recent decades (ACIA 2004). In north-western North America a significant warming trend has been documented in the Yukon and Alaska (Zhang et al. 2000). Specifically, average surface-air temperatures have risen 0.31 ± 0.03°C per decade in north-western North America (Keyser et al. 2000). It is predicted that increasing
temperatures due to recent warming will lead to increased establishment of individuals throughout the forest-tundra and a northward expansion of the treeline (Callaghan et al. 2002).

In order to better understand the predicted treeline expansion this chapter is focused on the establishment of *P. glauca* throughout the forest-tundra ecotone in the Tuktoyaktuk region of the Northwest Territories, Canada. The objectives are to 1) evaluate the recent natural and transplanted establishment success of seedlings and 2) examine the long term establishment patterns of individuals in forest stands and tree islands in relation to the instrumental climate records from Inuvik and climate reconstruction from dendrochronological records from north-western North America. Determining the influence of climate factors on the establishment of white spruce throughout the forest-tundra will provide insight into how establishment may change under predicted future climate change scenarios.

### 4.2 Methods

#### 4.2.1 Study Area

A total of 11 sites were examined in the Tuktoyaktuk region of the NWT, Canada (Figure 4.1). In 1993, a transect was established in this region that stretched from the northern Boreal forest to the species northernmost limit (McLeod 2001). This transect corresponds to approximately a 3°C change in average annual temperature (Lantz 2008). In the summer of 2009, four forest stand sites (T10, T9, T8, and T7), each consisting of three plots, and six tree islands sites (T6, T5, T4, T3, T2, T1 and R1) were located and examined. Sites are numbered according to latitude, with site R1 and T1 being the northernmost and site T10 the southernmost.

#### 4.2.2 Climate

Homogenized climate data for Inuvik were obtained from Environment Canada’s Adjusted Historical Canadian Climate Data (AHCCD 2009) (Vincent 1998, Mekis and Hogg 1999,
Vincent and Gullet 1999, Vincent et al. 2002, Mekis and Hopskinson 2004, Mekis 2005, Devine and Mekis 2008, Vincent and Mekis 2009), which has been designed for climate change analyses. This database contains daily mean, maximum, and minimum temperatures and extends from 1926 to 2005. Homogenized precipitation data were also available for Inuvik from 1960 to 2006. The data consist of rainfall, snowfall, and total precipitation.

To obtain information on climatic conditions prior to the instrumental record it is necessary to use proxy records. Reconstructed climatic data were obtained from Szeicz and MacDonald (1995, 1996). Using P. glauca ring widths from alpine treeline in northwest Canada, Szeicz and MacDonald (1995) reconstructed June-July temperatures from 1638-1988. Szeicz and MacDonald (1996) produced a 930-year ring-width chronology for P. glauca in the Campbell Dolomite Upland, near Inuvik, NWT and determined that periods of increased precipitation were associated with high radial growth.

4.2.3 Recent Establishment Success

In order to assess recent establishment success a search for true seedlings, established from seed rather than vegetatively, at all of the sites was completed. A seedling was classified as such if it was less than 15 cm in height (PPS Arctic Protocols 2008). Within the forest stand sites a 100 m transect was laid out. The direction and starting point of the transect was chosen in such a way as to capture the best possible representation of tree density in the area. Every 2 m along this transect a 10 cm x 10 cm quadrat was placed on the ground, centered on the transect, to search for true seedlings. Two transects were also positioned through the length and width of each of the tree island sites and seedlings were searched for using the same 10 cm x 10 cm quadrat at 1m intervals.
Seedling survival was determined through transplant studies. In 1993 seeds were collected in the Inuvik region (site T10). These seeds were germinated and grown in the greenhouse over the winter and transplanted in June, 1994 (McLeod 2001). Seedlings were transplanted at ten random spots both inside and in a circular arrangement one meter outside of three tree island sites: T1, T3, and T5. At each tree island site 30 to 40 seedlings were transplanted inside and outside the tree island. The survival of transplanted seedlings was checked at the end of the 1994, 1995, and 2009 growth seasons. The numbers of living seedlings both inside and outside the tree islands were recorded and the height, crown diameter, and a nodal count of each individual were obtained.

To determine if the survivorship, height, crown diameter, and number of nodes of seedlings varied inside vs. outside of the tree islands a RCBD-ANOVA, to block for the variability due to sites, was used. Analysis was completed in R 2.10.

4.2.4 Historic Establishment Patterns

At each of the forest stand sites (T9, T8, and T7) from 15 to 50 trees were cored, all individuals above 2m in height were cored within each plot. In the tree island sites (T6, T5, T3, T4, T2, T1 and R1) the number of individuals cored ranged from 1 to 30, depending on the number of individuals within the tree island. Using an increment borer one tree core was taken from each tree as close as possible to the base of the tree (above the root collar). Cores were stored in sealed plastic straws and mounted on thin wooden moulding as soon as possible. The height and diameter of the tree where the core was taken was also recorded.

In the forest stand sites, 5 to 12 small individuals (15 - 200 cm in height) were cut down and basal disks obtained. As tree islands in this region are few in number, isolated, and in a
stressed state, basal disks were only obtained at site T2 where there were numerous small individuals.

Handling of cores and disks, preparation, and age reconstruction was completed using standard dendrochronology techniques (Cook and Kairiukstis 1990). The tree-ring cores and disks were sanded with increasingly finer sandpaper, up to 600 grit, in order to produce visible rings. The tree-ring cores and disks were microscopically examined and visually cross-dated to identify rings with unusual (very small or large) growth. Ring-width measurements were conducted using a Velmex slide and Measure J2X (0.001 mm resolution). The accuracy of the tree ring dates were statistically verified using the application of COFECHA software (Grissino-Meyer 2001). COFECHA creates a master tree-ring chronology by averaging all tree ring-width measurements. The measurements from each core were then assessed against the master chronology using a correlation analysis to ensure the proper calendar year is assigned to each ring and to detect errors to be corrected. A tree-ring chronology was built for each site throughout the forest tundra ecotone, by averaging the ring widths of the correctly dated and highly correlated ring-width series.

For the subset of cores that did not intercept the pith (n = 44 of 171), the number of rings to pith was estimated geometrically (Duncan 1989). For the cores taken above the stem base, the age of the tree at the coring height was estimated using the height-age regressions developed from small individuals that had been sectioned at ground level. This estimation should introduce little error; coring was carried out within 30 cm from the ground, and 51% and 80% of corrections were less than 10 years and 20 years, respectively.

The establishment dates of individuals were grouped based on the location of the sites within the forest-tundra ecotone. Forest stand sites T9, T8, and T7 were grouped together and
tree island sites T5, T3, T4, T2, T1, and R1 were combined. The number of individuals dated in each of the forest stands ranged from 23 to 38 (Table 4.1). The majority of individuals dated in the tree islands came from site T2 (Table 4.1), as this was the largest tree island site. Two histograms, one for forest stands and one for tree islands were made to depict the decadal pattern of seedling establishment. Due to the error associated with estimating basal age, establishment histograms were made using ten year age classes (Szeicz and MacDonald 1995, McLeod 2001). The decadal pattern of seedling establishment developed for the tree islands is probably not representative of all tree island sites but biased towards T2. Therefore, two more establishment pattern histograms were made, one for all the tree islands excluding T2 and one for site T2 on its own.

4.2.5 Establishment-Climate Relationship

Each decade was classified by temperature and precipitation based on the instrumental and reconstructed climate records (as per McLeod 2001). For the instrumental records, summer temperatures and precipitation levels for each decade were classified as above or below the average of temperature of 12.3°C and precipitation of 106.8 mm for the extent of the record (1926-2005). Szeicz and MacDonald (1995) reconstructed June-July temperatures and each decade was classified as above or below the average of 14.3°C for the extent of the record. Szeicz and MacDonald (1996) associated Picea glauca ring widths to changes in moisture conditions. Each decade was classified based on ring widths. Decades of above average (1.031 mm) ring width were classified as wet and decades of below average ring width were classified as dry. Using a Chi Square Test of Independence (α=0.05) the decadal pattern of establishment was compared to the decadal temperature (warm or cool), moisture (dry or wet), and temperature/moisture (warm and dry, warm and wet, cool and dry, or cool and wet) patterns.
This comparison was used to determine if the patterns of establishment are independent of the temperature and moisture patterns.

4.3 Results

4.3.1 Climate

Inuvik’s instrumental climate record for temperature is available from 1926 through to 2005 and from 1959 to 2006 for precipitation. Inuvik annual temperatures, relative to climate normals, were high (> -9°C) in the late 1920s, low (< -9°C) in the 1930s, high in the 1940s and 1950s, average in the 1960s, and have continuously increased since the 1970s, peaking in both the late 1980s and 1990s (Figure 4.2). Prior to 1977 there was relatively little increase in temperature (0.04 ± 0.09°C per decade); however after 1977 a large temperature increase of 0.59 ± 0.11°C per decade occurred (Figure 4.2). In contrast to the temperature change, no trend in precipitation from 1958 through 2006 was found (Figure 4.3).

In order to assess climatic conditions prior to the instrumental record it was necessary to use reconstructed data (Figure 4.4). Based on the reconstructed temperatures, the early 1700s were very cool, 1750 through 1780 were warm, 1790 through 1870 were cool, and from 1920 onwards temperatures were very warm. Using ring width as a proxy for precipitation (larger rings associated with increased precipitation), the early 1700s were moist, as were 1770 through 1810, while 1820 through 1850 were very dry, and 1920 through 1940 were moist. Since 1940 precipitation has remained around the average for the instrumental record.

4.3.2 Recent Establishment Success

No true seedlings were found along the transects in either the forest stands or the tree island sites. However, numerous seedlings were found within the forest stand plots at each of site T10, T9, and T8.
The number of transplanted seedlings that survived after 15 growing seasons ranged from 0 to 18% inside the tree islands and from 6 to 23% outside the tree islands (Table 4.3). There was no significant difference in the survivorship of transplanted seedlings inside compared to outside of the tree islands (F=3.20, p=0.23). The total number of surviving seedlings decreased throughout the years, after 15 growing seasons from 4 to 12 seedlings survived (Figure 4.5).

The average height, crown diameter, and number of nodes of the transplanted seedlings differed outside versus inside in each of the tree islands. The height of transplanted individuals were significantly greater inside than outside the tree islands (F=9.46, p-value<0.001). Similarly, the crown diameter (F=7.30, p-value<0.001) and the number of nodes (F=10.72, p-value<0.001) were both larger inside compared to outside of the tree islands. However, the increased height, crown diameter, and number of nodes found within the tree islands can be attributed to the differences inside versus outside at tree island T3 (Table 4.4). At site T3 each of height, crown diameter, and number of nodes were greater inside versus outside. At site T5 there is no significant difference in the three variables between inside and outside. These variables were not compared inside versus outside at site T1 as only 2 seedlings were found, both outside, at this tree island site.

The number of nodes of the transplanted individuals ranged from 1 to 15. This was unexpected as the number of nodes usually represents the age of a sapling/seedling (ie. one node per year of life) (Fritts 1976).

4.3.3 Historic Establishment Patterns

The establishment patterns presented here are those of surviving individuals at the time of sampling. Whether individuals established from seed or from layering were not differentiated,
but it is assumed that the majority of individuals in the tree islands established from layering and
the majority of individuals in the forest stands established from seed (McLeod 2001).

In the forest stand sites few individuals established prior to 1800 (Figure 4.6). The
majority of individuals established between 1850 and 1950, with the greatest number
establishing in 1870-1879 and 1900-1909. There are a few young individuals (<20 years) that
established and no individuals less than 10 years of age were recorded.

In the tree island sites only two individuals established prior to 1800 (Figure 4.7). These
individuals were located in sites T5 and T2. The majority of individuals established between
1870 and 1950. Very few individuals established after 1950. The establishment pattern of site T2
was very similar to that of the tree islands as the majority of individuals included in the tree
island establishment pattern were from site T2. The establishment patterns of all the tree island
sites excluding site T2 were also similar, with the majority of individuals establishing between
1850 and 1950.

4.3.4 Establishment-Climate Relationship

A Chi-square test of Independence was used to determine whether the decadal pattern of
seedling establishment was independent of the decadal temperature and moisture patterns (Table
4.5). The pattern of seedling establishment in the forest stands, tree islands, tree islands
excluding site T2, and site T2 alone were all not independent of the decadal temperature pattern
but were all independent of the decadal precipitation pattern. The pattern of seedling
establishment in the forest stands, tree islands, and tree islands excluding site T2 were not
independent of the temperature and moisture pattern, but establishment patterns in site T2 were
independent of the temperature/moisture patterns.
4.4 Discussion

The establishment of trees on the tundra is both indirectly and directly prevented by cold temperatures (Hobbie and Chapin 1998). Seed germination is dependent on temperature, while seedling growth and survivorship is limited by the supply of below ground resources (Hobbie and Chapin 1998). Resource limitation, particularly nitrogen availability, is directly related to the cool soil conditions (Holtmeier and Broll 2005). An additional factor that limits seed germination and establishment of trees on the tundra is the availability of suitable substrate (Hobbie and Chapin 1998). DeLong et al. (1997) found that exposed mineral soil is the best substrate for seedling establishment. Exposed mineral soil is moist, thus permitting rapid root development. It is also free of dense vegetation; providing seedlings with plenty of light (DeLong et al. 1997).

*Picea glauca* establishment and overwinter survival are associated with vegetation cover and temperature (DeLong et al. 1997). Hobbie and Chapin (1998) found that *P. glauca* seedlings grew significantly more in terms of above ground biomass by reducing below ground biomass of other species, implying that seedling growth is limited by competition for below ground resources. Seedlings also showed an increase in biomass with warming after 3 years, suggesting that cold temperature directly limits the growth of *P. glauca* at the treeline (Hobbie and Chapin 1998). Seedling survival and growth is reduced by late spring frosts (Groot and Carlson 1996) and high vapour deficits (Marsden et al 1996); therefore, white spruce seedlings should benefit from shelter that can improve temperatures and vapour deficits (Groot 1999).

Despite all of the limitations associated with seedling establishment, 3% to 20% of transplanted seedlings survived. Survivorship did not vary between outside or inside of the tree islands. The number of nodes usually represents the age of a sapling/seedling (ie. one node per year of life) (Fritts 1976), however the number of nodes differed between transplanted
individuals of the same age. This exemplifies how slow growing individuals of white spruce are at their northernmost limit. At site T3, the height, crown diameter, and number of nodes were greater inside than outside. There was no difference in these variables inside compared to outside at site T5 and no transplanted seedlings survived inside the tree island at site T1. Sites T5 and T1 were much denser than site T3. Site T5 had 1.83 individuals m\(^{-2}\), T1 had 0.475 individuals m\(^{-2}\) and T3 had only 0.113 individuals m\(^{-2}\). This could help to explain the increased growth of individuals inside T3 compared to T5. In a very dense tree island seedling growth will be inhibited by competition for below ground resources and light. Outside of the tree islands, the seedlings will not have the same degree of shelter to ameliorate low temperatures and high vapour deficits. A moderate density of trees would therefore promote seedling survival and growth.

The oldest individuals of *P. glauca* were found within the forest stand sites rather than in tree island sites. Szeicz and MacDonald (1995) found a similar pattern of the oldest individuals being found in the Forest-Tundra rather than at their range limits in the Mackenzie Mountains, NWT. In forest stands the lack of individuals establishing from 2000-2009 is due to the fact that they were not sampled, as numerous seedlings were found within the forest stand sites. The lack of establishment in the tree island sites during the last few decades is due to the lack of viable seed and establishment of true seedlings (see Chapter 3) as well as to the process of layering. In the layering process a live branch from a well established individual is partially buried and continues to grow, becoming erect and eventually forming adventitious roots at which point it is considered an established individual (McLeod 2001). Thus, at the time of establishment the individual may already be many years old.
Timing of establishment was similar in both forest stands and tree islands. The earliest establishment period for both was in the 1770s. Based on the reconstructed climate data (Figure 4.4), this was a period of relatively warm and wet conditions, conditions warm enough to allow establishment of individuals in the tree islands.

The establishment pattern of the forest stands and tree islands were similar in that the majority of individuals established between 1850 and 1950. This coincides well with the end of the Little Ice Age (ca. 1850). Increased establishment resulting in increased stand density following the Little Ice Age has been observed from sites in central Canada (MacDonald et al 1998), northern Quebec (Payette et al 1985), Churchill (Scott et al. 1987), and the treeline of the Mackenzie Mountains (Szeicz and MacDonald 1995). Increased establishment can be attributed to increased temperatures of 1 to 2°C since the closing of the Little Ice Age (ACIA 2004). Warmer summer temperatures promote increased radial growth and seed development due to higher rates of photosynthesis and the subsequent increase in carbohydrate supply (Kramer and Kozlowski 1979). Increased seed development leads to increased seedling establishment and survival.

Despite the observed increase in establishment following the Little Ice Age which may be due to warmer climatic conditions, the decadal pattern of seedling establishment coincided with decades that were classified as cool and wet. Conditions beneficial for establishment may differ from those required for high growth rates (Wirth 2010). Growth rates of adults are highly dependent on temperature and also depend on active layer thickness, soil temperature, and nutrient supply (Dyrness et al 1989). Seedling survival during the early stages is sensitive to soil moisture, which depends on climate, microtopography, and organic layer thickness. The initial limitation to establishment has been attributed to water stress as a result of poor root to soil
contact (Marsden et al. 1996). Other climatic variables such as temperature and precipitation seasonality and changes in length of growing season may also be important in recruitment and establishment of individuals (McLeod 2001).

The establishment of white spruce may be limited by both the negative influence of lichens on seed regeneration (Scott et al. 1987), and drought stress induced by warmer temperatures, as reported in Alaska (Barber et al. 2000, Lloyd and Fastie 2003). Seedling establishment is often limited to moist, protected sites with a positive feedback to further recruitment (Caccianiga et al. 2008). Another limitation to seedling establishment and survival may be due to the indirect effects of climate change, acting to increase competition from other plants (Stevens and Fox 1991) and alter the frequency and severity of disturbances (Briffa et al. 1998).

### 4.5 Conclusions

Temperature is considered the primary factor influencing tree dynamics at their latitudinal limit (Grace et al. 2002). As climate warms, it is expected that the treeline will advance northward onto the tundra (Callaghan et al. 2002). In order to assess the validity of this prediction for treeline in the Tuktoyaktuk region of the NWT, Canada, the recent establishment success and the climate-establishment relationship of *P. glauca* throughout the forest tundra ecotone was assessed.

Assuming that seed viability increases with climate warming, seedling establishment on the tundra will also likely increase. Establishment, however, is dependent on a suitable substrate and moisture and nutrient availability. Thus establishment will only increase with warming if warming also increases nutrient availability, a situation that is likely to occur (Hobbie and Chapin 1998). Although no true seedlings were found in the tree islands, numerous seedlings were found in the forest stand sites. This study showed that transplanted seedlings can in fact
establish and survive on the tundra, although survivorship was low, supporting the notion that a lack viable seeds is the major limiting factor for tree islands to act as nodes of treeline expansion.

In this study the establishment of *P. glauca* coincided with decades classified as cool and wet, indicating that adequate soil moisture is an important factor affecting establishment. Establishment in decades classified as warm and dry may be inhibited by water stress and increased competition from other plants that grow more favorably under warmer and drier conditions. The establishment of individuals also coincided with the closing of the Little Ice Age suggesting that the warmer conditions at this time promoted the establishment of individuals throughout the forest tundra ecotone. However, only live individuals were sampled in this study, thus the establishment of individuals coinciding with the closing of the Little Ice Age may be due to older individuals not surviving to be sampled. In a warmer and drier climate the initial recruitment and establishment may be reduced but the growth and reproductive rates will likely increase, eventually leading to increased establishment.
4.6 Figures and Tables

Figure 4.1 Location of the study sites. Four forest stand sites (T10, T9, T8, and T7) and three tree island sites (T6, T5, T3, and T2) were examined in this study. Line represents approximate location of the treeline. Modified from McLeod (2001).

Table 4.1 The number of dated individuals from each site that were added to decadal pattern of seedlings establishment histograms for each of forest stands and tree islands.

<table>
<thead>
<tr>
<th>Forest Stands</th>
<th># of dated individuals</th>
<th>Tree Islands</th>
<th># of dated individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>T9</td>
<td>39</td>
<td>T6</td>
<td>8</td>
</tr>
<tr>
<td>T8</td>
<td>30</td>
<td>T5</td>
<td>4</td>
</tr>
<tr>
<td>T7</td>
<td>23</td>
<td>T4</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>92</td>
<td>T3</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T2</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R1</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>65</td>
</tr>
</tbody>
</table>
Figure 4. 2 Annual temperatures for Inuvik airport: mean daily maximum, mean daily, and mean daily minimum temperatures. Trendlines represent 1926 through 1976, and 1977 through 2005. See Table 4.2 for regression results. Data obtained from Environment Canada’s Adjusted Historical Canadian Climate Data (AHCCD) (2009).

Table 4.2 Regression results for mean daily maximum, mean daily, and mean daily minimum annual temperatures for Inuvik airport; 1926 through 2005 (all), 1926 through 1976 (<1977), and 1977 through 2005 (≥1977).

<table>
<thead>
<tr>
<th>Temperature and Year</th>
<th>R²</th>
<th>F-statistic</th>
<th>P-value*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean &lt;1977</td>
<td>0.0002</td>
<td>0.0086</td>
<td>0.9263</td>
</tr>
<tr>
<td>Mean ≥1977</td>
<td>0.0588</td>
<td>1.6878</td>
<td>0.2049</td>
</tr>
<tr>
<td>Mean (all)</td>
<td>0.2004</td>
<td>19.5477</td>
<td>3.14e-05</td>
</tr>
<tr>
<td>Maximum &lt;1977</td>
<td>0.0054</td>
<td>0.2662</td>
<td>0.6082</td>
</tr>
<tr>
<td>Maximum ≥1977</td>
<td>0.0672</td>
<td>1.9445</td>
<td>0.1746</td>
</tr>
<tr>
<td>Maximum (all)</td>
<td>0.1478</td>
<td>13.5277</td>
<td>0.0004</td>
</tr>
<tr>
<td>Minimum &lt;1977</td>
<td>0.0033</td>
<td>0.1601</td>
<td>0.6908</td>
</tr>
<tr>
<td>Minimum ≥1977</td>
<td>0.0432</td>
<td>1.2191</td>
<td>0.2793</td>
</tr>
<tr>
<td>Minimum (all)</td>
<td>0.2457</td>
<td>25.4019</td>
<td>2.94e-06</td>
</tr>
</tbody>
</table>

*Bold text indicates P-values <0.05.
Figure 4.3 Annual Precipitation at Inuvik Airport between 1955 and 2006: total precipitation, rainfall, and snowfall. Data obtained from Environment Canada’s Adjusted Historical Canadian Climate Data (AHCCD) (2009).
Figure 4.4 Reconstructed temperature and precipitation in ten year classes from 1700 to 1980. Ring widths are used as a proxy for precipitation. Thick black line indicates average. Data obtained from Szeicz and MacDonald (1995, 1996).

Table 4.3 Survivorship of transplanted seedlings inside and outside of tree islands after 1, 2 and 15 growing seasons.

| Site | Inside Tree Island | | | | | Outside Tree Island | | | |
|------|-------------------|---|---|---|---|-------------------|---|---|---|---|
| T1   | 8/30 (27%) | 6/8 (75%) | 0/6 (0%) | 0/30 (0%) | 13/31 (42%) | 7/13 (54%) | 2/7 (29%) | 2/31 (6%) |
| T3   | 19/31 (61%) | 14/19 (74%) | 5/14 (36%) | 5/31 (16%) | 14/31 (45%) | 8/14 (57%) | 7/8 (88%) | 7/31 (23%) |
| T5   | 20/40 (50%) | 17/20 (85%) | 8/17 (41%) | 8/40 (18%) | 17/40 (43%) | 14/17 (82%) | 4/14 (29%) | 4/40 (10%) |
Figure 4.5 The total number of transplanted seedlings surviving at the end of the 1994, 1995, and 2009 growing seasons in site T1, T3, and T5. Seedlings were grown from seed collected south of Inuvik and transplanted in June 1994.

Table 4.4 Means and standard error and t-test results for difference between means, for height, crown diameter, and number of nodes inside versus outside of tree islands T5 and T3.

<table>
<thead>
<tr>
<th></th>
<th>Mean ± Standard Error</th>
<th>Test Statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>inside</td>
<td>outside</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T5</td>
<td>15.12±2.34</td>
<td>14±2.38</td>
<td>0.336</td>
</tr>
<tr>
<td>T3</td>
<td>33.25±5.38</td>
<td>12.08±1.529</td>
<td>3.779</td>
</tr>
<tr>
<td>T1</td>
<td>9.7±1.4</td>
<td>9.7±1.4</td>
<td>0.081</td>
</tr>
<tr>
<td>Crown Diameter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T5</td>
<td>9.5±1.21</td>
<td>8.63±2.67</td>
<td>0.298</td>
</tr>
<tr>
<td>T3</td>
<td>21.33±2.72</td>
<td>9.4 ±0.47</td>
<td>4.318</td>
</tr>
<tr>
<td>T1</td>
<td>3.5±2.5</td>
<td>3.5±2.5</td>
<td>3.623</td>
</tr>
<tr>
<td>Number of Nodes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T5</td>
<td>8±1.15</td>
<td>8.25±2.87</td>
<td>0.081</td>
</tr>
<tr>
<td>T3</td>
<td>13.17±1.49</td>
<td>6.83±0.91</td>
<td>3.623</td>
</tr>
<tr>
<td>T1</td>
<td>4.0±2.0</td>
<td>4.0±2.0</td>
<td>4.0±2.0</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values<0.05
Figure 4.6 The decadal pattern of seedling establishment in a) forest stand sites (T9, T8, and T7), b) tree island sites (T6, T5, T4, T3, T2, T1, and R1), c) tree island sites excluding T2, and d) site T2.
Table 4.5 Chi-square Test of Independence results comparing the decadal pattern of seedling establishment to the decadal temperature and moisture patterns.

<table>
<thead>
<tr>
<th>Climate Variables</th>
<th>Establishment</th>
<th>Forest Stands</th>
<th>Tree Islands</th>
<th>Tree Islands (without T2)</th>
<th>T2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X²</td>
<td>p-value</td>
<td>X²</td>
<td>p-value</td>
<td>X²</td>
</tr>
<tr>
<td>Temperature</td>
<td>6.532</td>
<td>0.011</td>
<td>10.253</td>
<td>0.001</td>
<td>6.2061</td>
</tr>
<tr>
<td>Moisture</td>
<td>0.546</td>
<td>0.460</td>
<td>0.008</td>
<td>0.930</td>
<td>0.0839</td>
</tr>
<tr>
<td>Temperature/Moisture</td>
<td>14.747</td>
<td>0.002</td>
<td>12.209</td>
<td>0.007</td>
<td>8.4</td>
</tr>
</tbody>
</table>

*Bold text indicates p-values < 0.05*
CHAPTER 5: THE CLIMATE-GROWTH RELATIONSHIP OF WHITE SPRUCE IN THE FOREST TUNDRA ECOTONE OF THE INUVIK-TUKTOYAKTUK REGION

5.1 Introduction

There are numerous factors which influence the growth of *Picea glauca* (Moench) Voss. at northern latitudes, these include but are not limited to temperature, precipitation, light levels, winds, and nutrient supply. Numerous studies have found positive relationships between ring widths and growing season temperatures (Garfinkel and Brubaker 1980, Jacoby and Cook 1981, Scott et al. 1988, D’Arrigo et al. 1992, Schweingruber et al. 1993, Szeicz and MacDonald 1995) and it is widely accepted that summer temperatures are the primary factor controlling tree growth in boreal latitudes (Garfinkel and Brubaker 1980, Cropper and Fritts 1981, D’Arrigo et al. 1992).

The general location of the treeline across North America coincides well with the mean July 10°C isotherm of air temperature (Bonan et al. 1995, Grace et al. 2002). This correlation has been considered strong evidence that temperature is one of the most important factors controlling treeline dynamics (Grace et al. 2002). Temperatures, especially in winter, have increased sharply in most regions of the Arctic in recent decades (ACIA 2004). In north-western North America a significant warming trend has been documented in the Yukon and Alaska (Zhang et al. 2000). Specifically, surface-air temperatures have risen 0.31 ± 0.03°C per decade in north-western North America (Keyser et al. 2000). It is predicted that increasing temperatures due to recent warming will lead to greater tree growth and a northward expansion of the treeline (Callaghan et al. 2002).

In order to better understand the predicted treeline expansion this chapter will focus on the radial growth of *P. glauca* throughout the forest-tundra ecotone in the Tuktoyaktuk region of the Northwest Territories, Canada. The objectives were to 1) assess how the radial growth rates of individuals throughout the forest-tundra ecotone relate to climatic conditions and 2) determine if
the climate growth relationship is different between forest stands and tree islands. Determining the influence of climate factors on the radial growth of white spruce throughout the forest-tundra will provide insight into how the growth of individuals may change under predicted future climate change scenarios.

5.2 Methods

5.2.1 Study Area

A total of 8 sites were examined in the Tuktoyaktuk region of the NWT, Canada (Figure 5.1). In 1993, a transect was established in this region that stretched from the northern forest-tundra to the species northernmost limit (McLeod 2001). This transect corresponds to approximately a 3°C change in average annual temperature (Lantz 2008). In the summer of 2009, four forest stand sites (T10, T9, T8, and T7), each consisting of three plots, were located and examined. The three forest stand plots were located along a 100 m transect, which was chosen to accurately represent the density of trees in the region. The size of the plots were chosen to include a minimum of ten trees (>2 m in height) and were located at the 0 m, 50 m, and 100 m points along the transects. In addition to the forest stand sites, four tree islands sites (T6, T5, T3, and T2) were also located and re-examined in the summer of 2009. Sites are numbered according to latitude, with site T2 being the northernmost and site T10 the southernmost (Figure 5.1).

5.2.2 Sampling

At each of the forest stand sites (T10, T9, T8, and T7) from 30 to 60 trees were cored, while in the tree island sites (T6, T5, T3, and T2) the number of individuals cored ranged from 4 to 50, depending on the number of individuals within the tree island. To assess diameter growth two cores were taken, perpendicular from one another, from each tree at the standard height of
Cores were labelled in such a way as to link them to the tree data and stored in sealed plastic straws until they could be mounted and dried on wooden moulding.

Handling of cores, preparation, and age reconstruction was completed using standard dendrochronology techniques (Cook and Kairiukstis 1990). The tree-ring cores were sanded with increasingly finer sandpaper, up to 600 grit, in order to produce visible rings.

**5.2.3 Chronology Development**

The tree-ring cores were microscopically examined and visually crossdated to identify rings with unusual (very small or large) growth. Ring-width measurements were conducted using a Velmex slide and Measure J2X (0.001 mm resolution). The accuracy of the tree ring dates were statistically verified using the application of COFECHA software (Grissino-Meyer 2001).

COFECHA creates a master tree ring chronology by averaging all tree ring-width measurements. The measurements from each core were then assessed against the master chronology using a correlation analysis to ensure the proper calendar year is assigned to each ring and to detect errors to be corrected. A tree ring chronology was built for each site throughout the forest tundra ecotone, by averaging the ring widths of the correctly dated and highly correlated ring-width series.

As two cores were taken from each individual tree, the two radial measurements for each year were averaged. The individual ring width measurement series were transformed using a multi-step process into standardized indices using ARSTAN software (Cook 1985). First, ARSTAN was used to fit a negative exponential curve to each series to remove the non-climatic trends of growth-effects, such as increasing circumference, changes in physiological processes due to age, and changes in growth conditions from stand dynamics (Cook and Briffa 1990, Cook and Holmes 1996). Each series was detrended a second time by fitting a cubic smoothing spline.
with a 50% frequency cut-off of 50 years (Cook and Peters 1981, Cook and Briffa 1990). This second detrending removes variances of low frequencies (i.e. longer wavelengths) with a transition to little or no removal of variance of high frequencies (i.e. shorter wavelengths) to facilitate analyses of climate-growth relationships (Cook and Holmes 1996). Cut-offs of 98 and 20 years were also tested, but 50 years was used as it retained the high frequency variance of interest while still remaining relatively conservative. The indices for each series were derived by dividing the actual ring-width measurement by the curve-fitted value in each year (Cook and Briffa 1990, Cook and Kairiukstis 1990). Autoregressive moving-average models were applied to the indices to remove autocorrelation effects or the statistical dependence of tree-ring widths on values of previous years (Cook and Briffa 1990). This process is referred to as pre-whitening. An overall site chronology was then built by averaging each year’s pre-whitened index values using a biweight robust mean. The biweight mean enhances the common signal contained in the data (Mosteller and Tukey 1977, Cook and Briffa 1990, Goldblum and Rigg 2005). These chronologies were then re-whitened by reincorporating the pooled autoregression value to the residual chronologies (Cook and Holmes 1986, Cook and Krusic 2005). The program ARSTAN builds a set of three chronologies: a standard chronology (un-whitened), a residual chronology (pre-whitened), and the ARSTAN chronology (re-whitened) (Cook 1985).

ARSTAN provides an output of statistics that were used to describe the variation within and between site chronologies. These statistics include the signal to noise ratio (SNR), mean sensitivity (MS), and standard deviation (SD). The SNR is an expression of the strength of the observed common signal among trees; MS is a measure of the relative difference in width between adjacent rings; and, SD represents the variability among all ring widths at the site. In general, higher SNR, MS, and SD are believed to indicate a greater climatic influence on tree
growth (Cook and Kairiukstis 1990). Based on the SNR, MS, and SD the residual chronologies were chosen and used for further analysis.

The residual chronologies were truncated to exclude years outside the period from which temperature (1926-2005) and precipitation (1960-2006) data were not available. This resulted in eight standardized chronologies corresponding to four forest stand sites T10, T9, T8, T7, and four tree island sites T6, T5, T3, and T2. Pearson’s moving product correlations were executed on every chronology against all the other chronologies in order to assess the degree of correlation between the chronologies.

To assess if growth had changed over time each residual ring-width chronology was regressed over time. The residual chronologies were also divided into two time periods based on the negative phase (before 1970) and the positive phase (1971 to present) of the Arctic Oscillation Index (Thompson and Wallace 1998). The percent change of radial growth was calculated between the two time periods.

5.2.4 Principal Component Analysis

A principal component analysis (PCA) was completed in R.2.1.0 to develop regional chronologies. PCA is often used in dendroclimatology as it extracts the dominant variation in ring-width series (Cook and Briffa 1990). Three PCAs were conducted on the ring-width series. The first using a matrix of the ring-widths from all sites, the second from a matrix of only the forest stand sites (T10, T9, T8, and T7), and the third from a matrix of only the tree island sites (T6, T5, T3, and T2).

For ‘all sites’, the PCA loadings of each of the first three components were plotted against each other in order to assess how the variance explained by each component may relate to one another. Each of the first, second, and third component loadings were correlated with distance
from treeline in order to see if the variance explained by these components is related to the spatial distribution of the sites.

Using the first principal components from the PCA of each of the forest stands and tree islands, two new chronologies were developed that represent yearly ring width variations in forest stands and tree islands, respectively.

### 5.2.5 Climate-Growth Relationship

Homogenized climate data for Inuvik were obtained from Environment Canada’s Adjusted Historical Canadian Climate Data (AHCCD 2009) (Vincent 1998, Mekis and Hogg 1999, Vincent and Gullet 1999, Vincent et al. 2002, Mekis and Hopkinson 2004, Mekis 2005, Devine and Mekis 2008, Vincent and Mekis 2009), which has been designed for climate change analyses. This database contains daily mean, maximum, and minimum temperatures and extends from 1926 to 2005. Homogenized precipitation data were also available for Inuvik from 1960 to 2006. The data consist of rainfall, snowfall, and total precipitation.

Relationships between climate and radial growth were assessed using the standardized residual chronologies developed for each of the sites and the first, second, and third principal component scores for ‘all sites’ and the first principal components for ‘forest stands’ and ‘tree islands’. Correlations were calculated between each of the 13 chronologies and the climatic variables of mean, minimum, and maximum monthly temperatures, and total precipitation, rainfall, and snowfall.

The relationships between the chronologies and climate variables were correlated to 18 separate months, extending over two growing seasons, from April of the previous year to September of the current year. Conditions outside of the growing seasons conditions were included because climatic conditions prior to cambial activity influence the amount of wood
produced while the cambium is active (Fritts 1976). The analyses were conducted using Pearson moving product correlation analysis ($\alpha = 0.05$).

Climate-growth relationships were also assessed based on the phase of the Arctic Oscillation (AO). The AO has mainly been in the positive phase since the early 1970s (Thompson and Wallace 1998). The shift to the positive phase is linked to increasing surface air temperatures and changes in precipitation (Serreze et al. 2000). In order to determine the possible effects of the AO on tree growth throughout the forest tundra ecotone blocked correlations based on the phase of the AO were completed. Correlations were calculated for both the negative phase (before 1970) and the positive phase (1971 to present) between both mean temperature and total precipitation and the first principal component scores for ‘all sites’, ‘forest stands’, and ‘tree islands’.

5.3 Results

5.3.1 General Chronology Statistics

A total of eight residual chronologies, one per site, were developed across the latitudinal gradient, T10 being the most southern site and T2 being the most northern (Table 5.1). The number of trees used to develop the chronology ranged from 2 at site T5 to 52 at site T9. The overall series length ranged from 60 years at site T3 to 218 years at both sites T8 and T9. The mean sensitivity (MS), the standard deviation (SD), and the signal-to noise ratio (SNR) differed between each site. Sites with higher MS, SD, and SNR indicate that these chronologies have good qualities to study the correlation between radial growth and climatic factors. At sites with relatively few trees (T6, T5, and T3) the SNR were very low, and sites with more trees had higher SNR.
All of the forest stands were significantly and positively correlated to one another (p-values <0.01, Table 5.2). The tree island sites were also correlated to one another (p-value <0.05), however not as strongly as the forest stand sites. The most southern site (T10) was not significantly correlated to the two most northern sites (T3 and T2), and site T2 is not correlated to the three most southern sites (T10, T9, and T8).

There was less variability in the standardized chronologies for the forest stand sites (Figure 5.2) than for the tree island sites (Figure 5.3). Regression analysis revealed that there is no significant trend in ring widths over time at any of the sites.

The percent change in radial growth, from the residual chronologies, between the negative phase (before 1970) and positive phase (1971 to present) of the AO was very low at all sites but differed slightly between the sites (Table 5.3). Growth in all of the forest stand sites and two of the tree island sites has decreased since the early 1970s, whereas growth at the two northernmost sites has increased.

**5.3.2 Principal Component Analysis**

Three PCAs were completed on matrices including ring widths from: 1) all sites, 2) forest stand sites, and 3) tree island sites. For each of the PCAs the first principal component accounted for the majority of the variance (Figure 5.4).

For all sites, the first principal component accounted for 52.1% of the total variance (Figure 4). Its components exhibited negative values at all of the sites (Table 5.4); indicating that annual growth is positively correlated among all sites throughout the study area. The second principal component (PC2) accounted for 15.6% of the variance (Figure 5.4), its components did not exhibit similar signs among sites (Table 5.4). Site T9 and site T8, two forest stand sites, were strongly positive with PC2, and two tree island sites, T5 and T2, were strongly negative. The rest
of the sites were close to zero indicating they were not significantly influenced by the second principal component. This suggests that in certain years growth in the southern area (T9 and T8) tends be low or high relative to growth in the northern area (T5 and T3) of the forest-tundra ecotone. The third principal component (PC3) accounted for 12.9% of the variance (Figure 5.4) and, like PC2, its components did not have similar signs among sites (Table 5.4). Site T10 and site T3 were strongly inversely correlated relative to each other, while the rest of the sites were weakly correlated to PC3 (r < 0.30, Table 5.4). Again this indicates that in certain years growth at the most southern sites (T10) is low or high relative to growth at one of the most northern sites (T3). These relationships were depicted by plotting the site loadings for each pair of the principal components (Figure 5.5). Correlating the first principal component to distance from treeline resulted in no significant relationship (r = -0.3553, p-value = 0.3878), nor did the correlations between the second principal component (r = -0.5022, p-value = 0.2047) and the third principal component (r = -0.6252, p-value = 0.0974) and distance from treeline. The lack of significant correlations suggests that the possible relationships observed for PC2 and PC3 may be non-linear.

The first principal component from the PCA preformed on the forest stands accounted for 67.2% of the variance (Figure 5.4). Its components exhibited negative values at all of the sites (Table 5.3). Approximately 55.2% of the variance was explained by the first principal component from the PCA preformed on the tree islands (Figure 5.4) and its components exhibited negative values at all sites (Table 5.3). The first principal components for the tree islands were more variable than those for forest stands (Table 5.3).

The first, second, and third principal components for all sites were plotted against time (Figure 5.6) in order to later be used to determine if climate is associated with the inter-annual
variation in the principal component scores through time. Similarly, the first principal component scores for forest stands and tree islands were plotted against time (Figure 5.7).

5.3.3 Climate-growth Relationships

5.3.3.1 Individual Sites

Each of the eight residual site chronologies correlated to mean monthly temperatures for 18 months resulted in all sites exhibiting some general trends (Figure 5.8). There was a negative correlation between ring widths in the current year and mean temperature in the previous growing season (June, July, and August). There was also a slight positive relationship between ring width and mean temperatures in the current growing season (June, July, and August). Ring-widths in two tree islands, sites T5 and T2, were consistently limited by temperature as indicated by significant positive correlations with temperatures in both the previous summer and fall and current summer.

Each of the eight residual chronologies correlated to total monthly precipitation over an 18 month period did not exhibit any general trends (Figure 5.9). Sites T9, T8, and T6 were significantly negatively correlated to precipitation in August and December of the previous year. Site T10 was positively correlated to precipitation in October of the previous year and July and August of the current year. Site T7 was also correlated to precipitation in August of the current year. No significant correlations were found at site T5. Site T3 was negatively correlated with precipitation in August and September of the previous year and positively correlated with August of the current year. Site T2 was only positively correlated with October precipitation in the previous year.

The correlations between all of the individual chronologies and minimum and maximum monthly temperatures, as well as snowfall and rainfall are not presented here because they
provide no additional information, as any significant relationships found were also observed with mean monthly temperatures and total monthly precipitation.

5.3.3.2 All Sites

Based on the PCA loadings and the amount of variance explained by each of the components, all three principal components were deemed useful for climate correlations. The three principal components were compared with climate data to determine if climate was associated with the inter-annual variation in the principal component scores through time. The first three principal component scores for all sites showed very different significant correlations to mean monthly temperatures over 18 months (Figure 5.10). The first principal component scores showed a negative correlation to mean temperatures in June and July of the previous year and in May of the current year. There was a positive correlation between the first component scores and mean temperatures in July of the current year. This trend was similar to that observed throughout the standardized sites chronologies, indicating that the variance explained by the primary component could be attributed to mean monthly temperature. The second principal component was positively correlated to mean temperatures in July of the previous growing season. The third principal component was negatively correlated to mean temperatures in August of the previous year.

The first three principal component scores for all sites showed different responses when correlated to total precipitation over an 18 month period showed (Figure 5.10). The first principal component was positively correlated to December precipitation in the previous year. There were no correlations with the second component. The third principal component scores were positively correlated to precipitation in August of the previous year and negatively correlated to precipitation in December of the previous year and July of the current year.
The correlation results between the first three principal components for all sites and minimum and maximum monthly temperatures and monthly rainfall and snowfall are not presented. Any significant correlations found were also observed with mean monthly temperatures and total monthly precipitation thus these correlations provide no additional information.

5.3.3.3 Forest Stands and Tree Islands

The correlations between first principal component scores and temperature for the forest stands were similar to the correlations for all sites in that they were negatively correlated to mean temperatures in June and July of the previous year and positively correlated with July of the current year (Figure 5.12). For tree islands the first principal component scores were positively correlated to mean temperatures of September in the previous year and negatively correlated to mean temperatures in May of the current year (Figure 5.12). This suggests that temperatures in the fall of the previous year and the spring of the current year influence tree growth in tree islands whereas summer temperatures are more influential on tree growth in forest stands.

Growth in forest stands and tree islands had slightly different responses to total precipitation (Figure 5.13). Growth in forest stands was negatively correlated to August precipitation of the current year, whereas growth in tree islands was strongly positively correlated to precipitation in August of the previous year.

There was a positive correlation between growth in forest stands and June rainfall of the previous year and between growth in tree islands and August rainfall of the previous year (Figure 5.14). This indicates that rainfall in the previous year is important for tree growth in both forest stands and tree islands but that early summer precipitation is more influential on tree growth in forest stands, whereas late summer precipitation is more influential at tree island sites.
Growth in forest stands was positively correlated to July and December snowfall in the previous year and negatively correlated to February snowfall of the current year (Figure 5.15). Growth in tree islands was positively correlated to snowfall in August and June of the previous and current year, respectively (Figure 5.15). This suggests that snowfall in the previous growing season will increase tree growth in the current year throughout the forest tundra. Heavy winter (February) snowfall will inhibit tree growth in the forest stands, but late spring snowfall (June) will increase tree growth in tree islands.

5.3.3.4 Arctic Oscillation Phases

Mean temperature correlations with the first principal components from all sites, forest stand sites, and tree islands were completed from both the negative phase (1951-1970) and the positive phase (1971-2005) of the AO (Figure 5.16). For all sites, forest stands, and tree islands there were more significant correlations with mean temperature in the negative phase than found in the positive phase of the AO.

Correlations between total precipitation and the first principal components from all sites, forest stand sites, and tree islands were completed for both the negative phase (1951-1970) and the positive phase (1971-2005) of the AO (Figure 5.17). There were significant positive correlations with December total precipitation of the previous year for all sites and forest stands in the negative phase. For tree islands significant negative correlations were found in the positive phase to July and August precipitation of the current year.

5.4 Discussion

The basis of all plant growth is photosynthesis, in which plants capture light energy and use it to form simple sugars from carbon dioxide and water while producing oxygen (Kozlowski et al 1991). There are several processes governing photosynthetic rates (Sharpe 1983). The initial
transfer of light energy through the electron transport chain and into chemical energy (light reactions), and the subsequent fixing of $\text{CO}_2$ (dark reactions) that occur in photosynthesis are basically independent of temperature (Sharpe 1983). However, the reactions that follow in which the actual formation of photosynthates occurs are temperature dependent and their rates are greatly reduced in cold environments (Sharpe 1983). In addition to the effect temperature has on the photosynthetic process it also affects the rate of consumption of the produced photosynthates (Kolari et al. 2007). The demand of photosynthates for growth is reduced in cold temperatures, hence, colder temperatures will actually inhibit photosynthetic production (Savitch et al. 2002).

In this study, the positive response of growth throughout the forest tundra to current summer temperature indicates that warm temperatures increase the rates of net photosynthesis and enhance growth in treeline environments during the growing season. These results are similar to numerous studies carried out in northern Canada and Alaska during the past 40 years which found positive relationships between ring widths and growing season temperatures (Garfinkel and Brubaker 1980, Jacoby and Cook 1981, Scott et al. 1988, D’Arrigo et al. 1992, Schweingruber et al. 1993, Szeicz and MacDonald 1995).

Results from this study also indicate that climatic conditions in the summer of the previous year strongly influence white spruce growth throughout the forest-tundra ecotone, particularly in forest stand sites. There were strong negative correlations found between ring width and the previous June, July, and August growing temperatures, meaning that warmer temperatures in the previous growing season will lead to the formation of smaller rings. This suggests that the previous growing season condition contributes to the photosynthetic reserves for the year of ring formation (Zahner 1969, Fritts 1976, Kozlowski et al. 1991). The photosynthetic reserves from
the previous year, used for growth in the current year, may be depleted by warmer temperatures that increase evapotranspiration demands and increased respiration rates (Kozlowski et al. 1991).

Low temperatures near the end of the growing season can cause early termination of growth, increasing reserves available for growth in the next year (Garfinkel and Brubaker 1980). In this study ‘tree islands’ responded positively to previous fall temperatures after radial growth has ceased. When growth ceases photosynthates are put in reserve, to be used for next year’s growing season, rather than using them for late season growth (Garfinkel and Brubaker 1980). Warm autumn temperatures may help to ensure translocation and storage of photosynthates to be used for growth in the next season.

Summer temperatures are thought to be the primary factor controlling the position of the northern treeline (Starfield and Chapin 1996, MacDonald et al. 1998, Grace et al. 2002). Numerous studies have demonstrated that tree growth is limited by temperature. Using multivariate statistical comparisons, Garfinkel and Brubaker (1980), found that radial growth of white spruce in the Brooks Range of Alaska is positively influenced by warm growing season temperatures. Similarly, Cropper and Fritts (1981) found positive correlations between over 100 tree-ring chronologies and summer temperatures in Alaska and north-western Canada. Using correlation and response function coefficients, Chin et al. (2004) found that conditions in the summer and fall of the previous year and the summer of the current year strongly influenced white spruce growth. The relationship between temperature and growth found in these studies suggest that warmer temperatures in the forest tundra region should lead to increased tree growth.

The Arctic Oscillation (AO) is a large-scale annular mode of atmospheric circulation that has largely been in the positive phase since approximately 1970 (Thompson and Wallace 1998).
Increasing surface air temperatures and changes in precipitation have been linked to the positive phase of the AO (Serreze et al. 2000). As cold temperatures limit tree growth, it is expected that radial growth should have increased since the 1970s as the sites are no longer as limited by temperature. However, examining the percent difference between average growth rates, from the residual chronologies, within each site revealed that at most sites growth is actually less in the positive phase than in the negative phase.


Climate-growth relationships were also assessed in both the positive and negative phase of the AO. Significant negative correlations between tree growth and mean temperatures in the previous growing season and positive correlations with the current growing season temperatures, for the negative phase of the AO, were observed. The general temperature-growth relationship is still apparent in the positive phase (1971 to present) but not as significant as those relationships in the negative phase. This indicates that cooler temperatures are more influential on tree growth.
at the latitudinal limit and/or the relationship between temperature and growth is losing its strength as climate warms.

The correlations between radial growth and total precipitation, rainfall, and snowfall were strong for some months, but these responses do not follow clear seasonal trends and are more difficult to interpret than the temperature correlations. The high variability found with precipitation data may be due to the short record (1960 to present) or the distance from the sites to where the precipitation data were recorded (up to 60 km). The relationship of high latitude trees to precipitation, particularly winter precipitation, is not fully understood (Garfinkel and Brubaker 1980). This study found a slight negative correlation with the previous year’s growing season precipitation and a positive correlation with the current seasons. These results support those of Garfinkel and Brubaker (1980) who found a positive correlation of growth to precipitation in the current summer months suggesting that internal water stress is a limitation to photosynthesis at subarctic treeline sites, particularly when temperatures are high.

Continuous permafrost prevents drainage, creating treeless bogs or muskegs (Sveinbjörnsson et al. 2002). The continuous permafrost line is often near the treeline implying that flooding could be one of the limiting factors for tree growth beyond a tree species latitudinal limit (Sveinbjörnsson et al. 2002). Excessive soil water limits photosynthesis due to the poor aeration of the roots, impeding water uptake (Grossnickle 2000). However, no evidence of flooding was observed at the sites in the summer during which the samples for this study were taken. Soil moisture is more difficult to access in cool soil conditions and white spruce is a determinant species that will finish growing as soon as it encounters a threshold of moisture stress (Juday 2008). A lack of moisture results in stomatal closure and the subsequent reduction
of photosynthetic gains (Goldstein et al. 1985). In essence, tree growth is limited by both an excess and a scarcity of water.

The impact of moisture availability on ring widths has long been known (Sceizc and MacDonald 1995). Water stress is most strongly shown in earlywood cells, indicating that ring widths are sensitive to precipitation early in the growing season. Radial growth is also sensitive to temperature during the previous growing season (Zahner 1968). Moisture stress caused by high temperatures in the summer preceding ring growth can cause decreases in photosynthesis and increases in leaf senescence (Kozlowski et al. 1991) which decreases early wood formation in the subsequent year due to a lack of resources (Sceizc and MacDonald 1995).

Growth throughout the forest tundra, particularly in ‘forest stands’, is influenced by winter precipitation. These results correspond with Vaganov et al. (1999), who studied tree growth across the forest tundra ecotone in Siberia, and found that increased winter precipitation strongly influenced radial growth. The increase in winter precipitation leads to increased spring snowpack and delayed snowmelt, which in turn prevents the seasonal thaw of permafrost from reaching a depth which trees can access soil water. This delays the initiation of cambial activity thus reducing total radial growth (Vaganov et al. 1999). This relationship has also been observed in other tree ring studies (Briffa et al. 2002). No data on snow depth or evidence of the delay in snow melt dates was obtained for the sites in this study. The greater the snow depth, implied from the negative correlations with snowfall, not only reduces total radial growth but also protects smaller trees and insulates the soils so they are warmer in the winter.

The negative correlation of growth in both ‘forest stands’ and ‘tree islands’ to May temperature is likely due to winter desiccation (Girardin and Tardif 2005; Scott et al. 1993; DeLucia 1986). Above average May temperatures lead to an early onset of the growing season,
resulting in the thawing of foliage preceding the thaw of soil. This means the roots of the trees are still encased in frozen soil, inhibiting water intake. Transpiration, however, has been activated, resulting in severe water stress which if prolonged will lead to death of foliage (Levitt 1980, Garfinkel and Brubaker 1980). D’Arrigo et al (2003) found negative correlations between radial growth and spring air temperature, showing that northern white spruce trees experience drought related stress in the spring.

The PCA results support the mixed response hypothesis, outlined by Brubaker (1980), in which trees in different regions will respond differently to the same climate variation. According to this hypothesis the first principal component from the PCA results from a common growth response at all sites to a regionally uniform climate variable. This study showed that temperature is the primary control on growth of P. glauca, regardless of the position of the trees within the forest tundra. Temperatures influenced growth at all the tree island and forest stand sites in a similar way: negative correlation to the previous season and a positive correlation to current season.

According to the mixed response hypothesis the second principal component, from the PCA, results from differential south-north responses to regionally uniform climatic variations (Brubaker 1980). In some years forest stand trees will have an opposite growth response to tree island sites. Loadings on the second component, however, indicate more of a gradient in the growth rather than a distinct division between the northern and southern sites. This is expected as the sites are located along a latitudinal gradient with a relatively gradual change in temperature. In order to fully support the mixed response hypothesis, northern and southern sites should respond differently to a region-wide climatic variable.
No opposing correlations were found between growth in the forest stands and tree islands to any of the climatic variables. There were however slight differences in the climate-growth response of forest stands to tree islands. Temperatures in the fall of the previous year and the spring of the current year influence tree growth in tree islands whereas summer temperatures and winter precipitation are more influential on tree growth in forest stands. Growth in tree islands is likely more limited by photosynthetic reserves from the previous fall (Garfinkel and Brubaker 1980) and more susceptible to winter desiccation due to an earlier onset of the growing season than forest stands (Girardin and Tardif 2005; Scott et al. 1993; DeLucia 1986). Growth in forest stands is more limited by the previous growing season temperature, suggesting that the photosynthetic reserves for the year of ring formation are being depleted by warmer temperatures (Zahner 1969, Fritts 1976, Kozlowski et al. 1991). Growth in forest stands is also more limited by increased snowfall in late winter which delays snowmelt and postpones the onset of the growing season (Vaganov et al. 1999, Briffa et al. 2002).

As the climate-growth relationship is slightly different across the latitudinal gradient, it is expected that the growth in forest stands should be slightly different than in tree islands. Correlations indicates that radial growth between forest stands, which are in the southern portion of the study area, are more highly correlated to one another than to tree islands, which are in the northern part of the study area. This confirms that there is a gradual change in growth spanning the latitudinal gradient and reinforces the mixed response hypothesis.

Tree growth is related by temperature and moisture, and has been shown to decrease northward across the forest-tundra (Vowinckel et al. 1975, Scott et al. 1987). The annual growth of individual trees is reduced across the forest-tundra due to the short and cold growing season (Sveinbjörnsson et al. 2002). In this study however, we did not observe a distinct difference in
growth or climate-growth relationships between the forest stands and tree islands. This could be attributed to the fact that temperature and precipitation are not the only factors limiting tree growth, suggesting that there is another controlling factor on the radial growth of white spruce in this region.

Climatic influences such as blowing snow, strong winds, and desiccation above the snowpack all diminish the ability of trees to survive and grow (Stevens and Fox 1991, Hadley and Smith 1986). Wind speeds are understandably higher on the tundra than in the forest as the forest obstructs airflow (Eugster et al. 2000, Chapin III F.S et al. 2000). Wind speed and abrasion by windblown snow affect the growth of trees throughout the forest-tundra (Scott et al. 1987). Abrasion by windblown snow or ice and dehydration following incomplete cuticle development often leads to extensive winter needle death (Hadley and Smith 1983, 1986, 1989). The winter loss of this photosynthetic tissue may restrict growth during the subsequent growing season as the trees allocate resources to repair of the needles rather than to new xylem cells for radial growth. Payette (2007) found that white spruce at an exposed site in northern Labrador did not respond to monthly temperature or precipitation due to the mechanical defoliation by wind. Tree islands are relatively unprotected from strong winds compared to trees within forest stands, thus defoliation by wind would be more prevalent in the tree islands. This factor may partly account for the different growth responses observed between tree islands and forest stands.

Below ground resources, in particular nitrogen, the availability of which decreases in cool soil conditions, is another limitation of tree growth (Holtmeier and Broll 2007). Boonstra et al. (2008) demonstrated the impacts of nitrogen fertilization on the growth of white spruce. They found that growth was accelerated by fertilization with nitrogen and that growth acceleration stopped almost immediately when fertilization was discontinued (Boonstra et al. 2008).
Similarly, Schulze et al. (1994) showed that there is a positive relationship between nitrogen content in needles and growth, concluding that nitrogen is limiting to the growth of treeline spruce. Numerous studies suggest that nutrient availability is lower at treeline sites than within the forest (Sveinbjornsson et al 1995, Loomis et al. 2006). Measurements of nutrient availability were not obtained in this study, however, total N, C, and pH levels of the soils were taken (Chapter 2). Findings indicate that forest stand sites had significantly higher total C and N than tree island sites and that the pH of tree islands was significantly higher than the pH of forest stands. This indicates that forest stand soils are more conducive for white spruce growth than tree island soils (Chapter 2).

5.5 Conclusion

As climate continues to warm it is predicted that the treeless gaps in the present forest-tundra will become forested and that the treeline will expand northwards (Callaghan et al. 2002). In order to assess the validity of this prediction for treeline in the Tuktoyaktuk region of the NWT, Canada the climate-growth relationship of *P. glauca* throughout the forest tundra ecotone was examined. The tree-ring chronologies developed in this study indicate that the primary factor limiting tree growth in northern ecosystems is in fact temperature. There is a general negative correlation to mean temperature in the previous growing season to ring widths in the current year. There is also a positive relationship between ring width and mean temperatures in the current growing season. The same general climate-growth relationships were found in both the periods of negative phase (prior to 1970) and positive phase (1971 to present) of the AO, however the correlations were much higher during the negative phase. Under proposed climate change scenarios, in which temperatures increase, these results indicate that tree growth will
increase. In this study, however, radial growth rates compared before and after 1970 did not confirm this increase.

This study also assessed the difference in the climate-growth relationship between forest stands and tree islands. Results support the mixed hypothesis response of Brubaker (1980) in which trees in different regions will respond differently to the same climate variation. This hypothesis requires that 1) the majority of variance in growth results from a common growth response at all sites to a regionally uniform climate variable, in this case temperature, and 2) that a significant amount of variance in growth can be explained by a differential south-north response to a climatic variable. Although no opposing climate-growth correlations between tree islands and forest stands were found, trees in the two areas did respond slightly differently to some climate variables. Growth in tree islands was positively correlated to late summer rainfall (Aug) and warm fall temperatures (Sept) in the previous year. In the spring (May) of ring formation growth in tree islands was positively correlated to cold temperatures and snowfall. Growth in forest stands was positively correlated to cool and wet summers of the previous year, December snowfall, and warm and dry conditions in the summer of ring formation. In addition, growth was negatively correlated to late winter (Feb, Mar, April) snowfall.

Although temperature was found to be the limiting factor controlling growth across the forest-tundra in this study, there are numerous other factors such as precipitation, soil moisture, light availability, wind, and nutrients that influence tree growth. Some combination of these factors plus the microenvironment (elevation, slope, and aspect) limits the growth of conifers throughout the forest tundra ecotone. Thus in order to fully understand how climate change will affect the growth of treeline trees it is necessary to comprehend the interaction of these variables and their influence on growth.
5.6 Figures and Tables

Figure 5.1 Location of the study sites. Four forest stand sites (T10, T9, T8, and T7) and four tree island sites (T6, T5, T3, and T2) were examined in this study. Line represents approximate location of the treeline. Modified from McLeod (2001).
Table 5.1 General descriptive statistics for the residual chronologies of each site, including the number of trees and radii used to develop the chronology, the time period the chronology covers (series extent), the overall series length, the average length of the series contributing to the chronology (mean length), the mean sensitivity (MS), the standard deviation (SD), and the signal-to-noise ratio (SNR).

<table>
<thead>
<tr>
<th>Site</th>
<th># trees (radii)</th>
<th>Series extent</th>
<th>Series length</th>
<th>Mean length</th>
<th>MS</th>
<th>SD</th>
<th>SNR</th>
</tr>
</thead>
<tbody>
<tr>
<td>T10</td>
<td>29 (52)</td>
<td>1940-2008</td>
<td>69</td>
<td>34</td>
<td>0.19</td>
<td>0.18</td>
<td>5.41</td>
</tr>
<tr>
<td>T9</td>
<td>52 (68)</td>
<td>1791-2008</td>
<td>218</td>
<td>105</td>
<td>0.15</td>
<td>0.13</td>
<td>16.72</td>
</tr>
<tr>
<td>T8</td>
<td>51 (69)</td>
<td>1791-2008</td>
<td>218</td>
<td>91</td>
<td>0.22</td>
<td>0.20</td>
<td>24.32</td>
</tr>
<tr>
<td>T7</td>
<td>29 (46)</td>
<td>1905-2008</td>
<td>104</td>
<td>39</td>
<td>0.15</td>
<td>0.13</td>
<td>7.76</td>
</tr>
<tr>
<td>T6</td>
<td>13 (23)</td>
<td>1920-2008</td>
<td>89</td>
<td>55</td>
<td>0.18</td>
<td>0.16</td>
<td>2.71</td>
</tr>
<tr>
<td>T5</td>
<td>2 (4)</td>
<td>1927-2008</td>
<td>82</td>
<td>73</td>
<td>0.24</td>
<td>0.22</td>
<td>1.52</td>
</tr>
<tr>
<td>T3</td>
<td>4 (7)</td>
<td>1949-2008</td>
<td>60</td>
<td>45</td>
<td>0.28</td>
<td>0.28</td>
<td>2.69</td>
</tr>
<tr>
<td>T2</td>
<td>46 (77)</td>
<td>1945-2008</td>
<td>64</td>
<td>23</td>
<td>0.30</td>
<td>0.26</td>
<td>15.48</td>
</tr>
</tbody>
</table>

Table 5.2 Pearson moving product correlation coefficients between the residual chronologies developed for each site.

<table>
<thead>
<tr>
<th></th>
<th>T10</th>
<th>T9</th>
<th>T8</th>
<th>T7</th>
<th>T6</th>
<th>T5</th>
<th>T3</th>
</tr>
</thead>
<tbody>
<tr>
<td>T10</td>
<td>1.00</td>
<td>0.44**</td>
<td>0.43**</td>
<td>0.46**</td>
<td>0.47**</td>
<td>0.45**</td>
<td>0.04</td>
</tr>
<tr>
<td>T9</td>
<td></td>
<td>1.00</td>
<td>0.91**</td>
<td>0.56**</td>
<td>0.56**</td>
<td>0.44**</td>
<td>0.37**</td>
</tr>
<tr>
<td>T8</td>
<td></td>
<td></td>
<td>1.00</td>
<td>0.67**</td>
<td>0.69**</td>
<td>0.51**</td>
<td>0.46**</td>
</tr>
<tr>
<td>T7</td>
<td></td>
<td></td>
<td></td>
<td>1.00</td>
<td>0.66**</td>
<td>0.54**</td>
<td>0.51**</td>
</tr>
<tr>
<td>T6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.00</td>
<td>0.43**</td>
<td>0.62**</td>
</tr>
<tr>
<td>T5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.00</td>
<td>0.29*</td>
</tr>
<tr>
<td>T3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.00</td>
</tr>
<tr>
<td>T2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* = p-value<0.05 **=p-value<0.01
Figure 5.2 Standardized chronologies for the four forest stand sites (T10, T9, T8, and T7). Bold line indicates 10-year running mean.
Figure 5.3 Standardized chronologies for the four tree island sites (T6, T5, T3, and T2). Bold line indicates 10-year running mean.
Table 5.3 The average ring widths (mm) in the negative (before 1970) and positive (1971 to present) phases of the Arctic Oscillation and the percent change in growth between the two phases.

<table>
<thead>
<tr>
<th>Site</th>
<th>Negative Phase</th>
<th>Positive Phase</th>
<th>Percent Change (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>T10</td>
<td>1.011</td>
<td>0.994</td>
<td>-1.73</td>
</tr>
<tr>
<td>T9</td>
<td>1.003</td>
<td>0.990</td>
<td>-1.26</td>
</tr>
<tr>
<td>T8</td>
<td>1.002</td>
<td>0.988</td>
<td>-1.36</td>
</tr>
<tr>
<td>T7</td>
<td>1.020</td>
<td>0.978</td>
<td>-4.16</td>
</tr>
<tr>
<td>T6</td>
<td>1.017</td>
<td>0.978</td>
<td>-3.80</td>
</tr>
<tr>
<td>T5</td>
<td>1.021</td>
<td>0.969</td>
<td>-5.06</td>
</tr>
<tr>
<td>T3</td>
<td>0.930</td>
<td>0.969</td>
<td>4.17</td>
</tr>
<tr>
<td>T2</td>
<td>0.990</td>
<td>1.008</td>
<td>1.80</td>
</tr>
</tbody>
</table>
Figure 5.4 The proportion of variance explained by each of the principal components (eigenvalues) for PCAs preformed on the ring width indices of all sites (A), forest stand sites (B), and tree island sites (C).
Table 5.4 Site loadings from principal component analysis on all sites, forest stand sites, and tree islands sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>All Sites</th>
<th>Forest Stand</th>
<th>Tree Islands</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
<td>PC3</td>
</tr>
<tr>
<td>T10</td>
<td>-0.2944</td>
<td>-0.0839</td>
<td>0.6346</td>
</tr>
<tr>
<td>T9</td>
<td>-0.3888</td>
<td>0.4599</td>
<td>0.0935</td>
</tr>
<tr>
<td>T8</td>
<td>-0.4316</td>
<td>0.3143</td>
<td>0.0021</td>
</tr>
<tr>
<td>T7</td>
<td>-0.4135</td>
<td>-0.0886</td>
<td>-0.0354</td>
</tr>
<tr>
<td>T6</td>
<td>-0.4102</td>
<td>-0.0223</td>
<td>-0.2337</td>
</tr>
<tr>
<td>T5</td>
<td>-0.3403</td>
<td>-0.2435</td>
<td>0.2720</td>
</tr>
<tr>
<td>T3</td>
<td>-0.3036</td>
<td>-0.0958</td>
<td>-0.6772</td>
</tr>
<tr>
<td>T2</td>
<td>-0.1696</td>
<td>-0.7784</td>
<td>-0.0033</td>
</tr>
</tbody>
</table>

Figure 5.5 Site loadings on the principal components (eigenvectors) plotted against each other for the principal components analysis performed on the matrix of ring-width indices from all sites. The % of variance explained by each principal component is shown in brackets on the axis label. See Table 5.4 for loadings.
Figure 5.6 The first, second, and third principal component scores for all sites plotted against time. Bold line is a 10 year running mean.
Figure 5.7 The first principal component scores for A) forest stand sites and B) tree island sites plotted against time. Bold line is a 10 year running mean.
Figure 5.8 Correlations between mean monthly temperatures and site chronology for 18 months for four forest stand sites (T10, T9, T8, and T7) and the four tree island sites (T6, T5, T3, and T2). Y-axis represents Pearson moving product correlation coefficients. Red bars represent significant (p-values <0.05) correlations.
Figure 5.9 Correlations between mean monthly total precipitation and site chronology for 18 months for four forest stand sites (T10, T9, T8, and T7) and the four tree island sites (T6, T5, T3, and T2). Y-axis represents Pearson moving product correlation coefficients. Red bars represent significant (p-value<0.05) correlations.
Figure 5.10 Correlations between mean monthly temperatures and the first, second, and third principal component scores of all sites for 18 months. Y-axis represents Pearson moving product correlation coefficients. Red bars represent significant (p-values <0.05) correlations.
Figure 5.11 Correlations between mean monthly total precipitation and the first principal component scores of all sites, forest stand sites, and tree island sites for 18 months. Y-axis represents Pearson moving product correlation coefficients. Red bars represent significant (p-values <0.05) correlations.
Figure 5.12 Correlations between the first principal component scores of forest stands and tree islands to mean monthly temperature for 18 months. Y-axis is Pearson moving product correlation coefficients. Red bars are significant (p-values <0.05) correlations.

Figure 5.13 Correlations between the first principal component scores of forest stands and tree islands to total precipitation for 18 months. Y-axis is Pearson moving product correlation coefficients. Red bars are significant (p-values <0.05) correlations.
Figure 5.14 Correlations between the first principal component scores of forest stands and tree islands to rainfall for 18 months. Y-axis values are Pearson moving product correlation coefficients. Red bars are significant (p-values <0.05) correlations.

Figure 5.15 Correlations between the first principal component scores of forest stands and tree islands to snowfall for 18 months. Y-axis values are Pearson moving product correlation coefficients. Red bars are significant (p-values <0.05) correlations.
Figure 5.16 Correlations of mean temperatures with the first principal component scores of all sites, forest stands, and tree islands, in the negative phase (before 1970), and positive phase (1971 to present) of the Arctic Oscillation. Y-axis values are Pearson moving product correlation coefficients. Red bars are significant (p-values <0.05) correlations.
Figure 5.17 Correlations of total precipitation with the first principal components of all sites, forest stands, and tree islands, in the negative phase (before 1970), and positive phase (1970 to present) of the Arctic Oscillation. Y-axis represents Pearson moving product correlation coefficients. Red bars represent significant (p-values <0.05) correlations.
CHAPTER 6: SUMMARY AND CONCLUSIONS

6.1 Introduction

This thesis has focused on the reproduction, establishment, and growth of *Picea glauca* in the Tuktoyaktuk region, NWT, Canada. The main objectives were to:

1. Describe the sites examined in this study and understand the differences between the forest stands and tree island sites by assessing the growth form, density, and vitality of *P. glauca*, and soil properties across the latitudinal gradient (Chapter 2).

2. Assess the reproductive capacity in the tree island sites compared to forest stand sites and to determine if the reproductive capacity has changed since the sites were last examined in the early 1990s (Chapter 3).

3. Evaluate the recent and transplanted establishment success of seedlings and to examine the long term establishment patterns of individuals in forest stands and tree islands in relation to climate (Chapter 4).

4. Determine how the radial growth rates of individuals throughout the forest-tundra ecotone relate to climatic conditions and to assess whether the climate growth relationship is different between forest stands and tree islands (Chapter 5).

6.2 Summary of Results

The height and health of *P. glauca* individuals was generally less in tree islands than forest stand sites and the density of individuals significantly decreased northward across the forest tundra ecotone in the Tuktoyaktuk region. Significant differences in soil nutrients and pH were also found between forest stands and tree islands but the general vegetation composition was similar throughout the forest tundra ecotone.
No changes in reproductive capacity were observed throughout the forest tundra ecotone since they were last assessed, 15 years ago. There was a significant decrease in both cone production and seed viability northward across the forest tundra ecotone. Currently, individuals within tree island sites are producing cones in abundance, yet the viability of seeds from these sites is very low.

No true seedlings were found in the tree islands and numerous seedlings were found in the forest stand sites. This study showed that transplanted seedlings can establish on the tundra, although survivorship was very low. The establishment of *P. glauca* coincided with decades classified as cool and wet and the majority of individuals in both forest stand and tree island sites established between 1850 and 1950.

The tree-ring chronologies developed in this study indicate that the primary factor limiting tree growth in these northern ecosystems was temperature. There was a general negative correlation of mean temperature in the previous growing season to ring widths in the current year. There was also a positive relationship between ring width and mean temperatures in the current growing season. The same general climate-growth relationships were found in both the negative phase (prior to 1970) and the positive phase (1971 to present) of the Arctic Oscillation.

**6.3 Significance of Results**

The lack of change in the reproductive capacity of *P. glauca* over the last 15 years throughout the forest tundra ecotone suggests that temperature may not be the primary limiting factor to sexual reproduction. All sites are producing cones in abundance yet there is a lack of viable seeds, particularly at tree islands sites. Individuals within tree islands sites reproduce primarily through layering and are therefore closely genetically related. This results in a lack of
viable seed. Thus seed viability within tree island sites will not increase with warming temperatures unless an outside seed source becomes available.

If seed viability does increase this will likely increase seedling establishment on the tundra. Establishment, however, is dependent on a suitable substrate and nutrient availability. Thus establishment will only increase with warming if warming also increases nutrient availability, a situation that is likely to occur. The survivorship of transplanted seedlings supports the notion that a lack of viable seeds is the major limiting factor for tree islands to act as nodes of treeline expansion.

The establishment of *P. glauca* coincided with decades classified as cool and wet. In warm and dry decades individual most likely did not establish due to water stress. The establishment of individuals also coincided with the closing of the Little Ice Age suggesting that the warmer conditions at this time promoted the establishment of individuals throughout the forest tundra ecotone.

Temperature was found to be the limiting factor controlling *P. glauca* radial growth across the forest-tundra in this region. A significant amount of variance in radial growth was found between forest stands and tree islands exemplifying the difference in radial growth between the two areas. However, in both areas tree growth is limited by temperature therefore under proposed climate change scenarios, in which temperatures increase, tree growth will also increase.

**6.4 Future Research**

The reproductive capacity, establishment, height growth, density, and health of *P. glauca* decreased northward across the forest tundra ecotone. The decrease in these variables can be attributed to deteriorating climatic conditions, particularly a decrease in temperature. However, there are numerous other factors such as precipitation, soil moisture, light availability, wind, and
nutrients that influence tree reproduction, establishment, and growth. Some combination of these factors plus the microenvironment (elevation, slope, and aspect) limits the reproduction, establishment, and growth of conifers throughout the forest tundra ecotone. In order to gain a better understanding of the reproduction, establishment, and growth of conifer trees it would be beneficial to assess these variables and their effects on treeline dynamics.

The relations between vegetation, snow cover, and air and ground temperatures over the freezing and thawing seasons throughout the forest tundra should be investigated. Changes in snow cover affect ground surface temperatures, ultimately altering vegetation dynamics. Changes in vegetation could in turn alter snow depth working as a feedback mechanism to further vegetation change. It would be beneficial to determine the differences in snow depths and vegetation cover between the forest stands and tree islands as well as assess how the tree islands modify their environment in terms of snow depth and vegetation composition.

The establishment of individuals may be limited by a lack of viable seed, competition from ground vegetation, and/or climatic conditions. Field experiments with seeding and transplant studies extended along the entire transect could determine how the survivorship of seedlings is affected by climatic conditions and ground vegetation.

The sites assessed in this study were examined in the early 1990s as were sites spanning a latitudinal gradient along the Horton River Valley and Anderson River Valley. It would be advantageous to resample the sites in the Horton and Anderson River Valleys in order to determine if the dynamics observed in this study are consistent at a greater regional scale.

6.5 Conclusion

As climate continues to warm it is predicted that the treeless gaps in the present forest-tundra will become forested and that the treeline will expand northwards. In order for treeline expansion
to occur each of reproduction, establishment, and growth of *P. glauca* must respond positively to changing climatic conditions. The decrease in these parameters northward across a latitudinal gradient spanning approximately 3°C change in annual temperature suggests that these variables will respond positively to warming temperatures. Results from this study indicate that under warmer conditions the reproductive capacity of the northern isolated tree islands will not increase unless an outside seed source becomes available, the establishment of individuals may be limited, and the radial growth of individuals will increase. These results suggest that in a warmer and drier climate the initial recruitment and establishment of *P. glauca* may be reduced but the growth and reproductive rates will increase, leading to increased establishment and an eventual expansion of forest into the tundra.
REFERENCES


