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Dendrochronology and treeline dynamics within arctic and alpine localities in western and central Canada

by

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ABSTRACT

The transition from forest to tundra, commonly called treeline, is expected to advance, particularly in northern latitudes. Treeline in two subarctic locales: the western Mackenzie Mountains, Northwest Territories, and the western Hudson Bay Lowlands southeast of Churchill, Manitoba were studied, with the objectives of determining: (i) the historical and current characteristics of the trees at altitudinal and latitudinal treelines, and; (ii) what factors contributed most to the configuration of treeline at its altitudinal and latitudinal limits. Five investigations were undertaken, each employing different methods in order to assess several variables, theorized to be key drivers of pattern and process at treeline. Tree growth was assessed by dendroclimatological techniques at the two study sites. Results demonstrated the primary role of temperature in limiting tree growth, but also identified fine-scale variability in site- and species-specific responses. Winter desiccation and viability of first-year conifer needles were assessed. Minimum epidermal conductance of needles corresponded with June temperatures during the year of needle formation, though varied little with exposure. However, significant correlations were found between viability and needles facing into the predominant wind direction. Seedlings were destructively sampled and aged within forest and at treeline. Seedling establishment was related to inter-specific competition in forest and facilitation at treeline. When seedling age structures were developed for wetland and upland environments and compared with climate, temperature appeared to be the main driver of establishment patterns. Though this influence was moderated in the uplands—most likely due to a thick, continuous lichen mat that represented an inhospitable seedbed. Dendroecology was used to reconstruct recent dynamics of *Picea*, *Larix* and *Abies* within the forest-tundra. Evidence of an advance of treeline position and increase in stand density during the early-mid 20th century was found. Recruitment and reconstructed summer temperatures were significantly correlated, indicating that climate was the reason for change. Collectively, these results suggest a significant potential for subarctic treeline to advance in response to future climate warming—particularly for *Larix*. However, the rate, pattern, and timing of advance will be contingent on heterogeneity of environmental variables at finer scales, especially seedbed, interspecific facilitation/competition, and edaphic characteristics.

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CHAPTER ONE

Subarctic and alpine forest-tundra dynamics in space and time

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> *"In setting up hypotheses on the future treeline development we rely on what we know about the present and past relationships between climatic variables, tree growth, adaptation to rising temperatures, seedling performance and intraspecific and interspecific competition."*
>
> Friedrich-Karl Holtmeier (2010)

INTRODUCTION

This dissertation presents the results of research completed at alpine treeline in the western Mackenzie Mountains of the Northwest Territories, and the latitudinal treeline in the western Hudson Bay Lowlands in northern Manitoba. The fundamental research questions addressed by this investigation were: (i) what are the historical and current characteristics of the trees at altitudinal and latitudinal treelines? And, (ii) what factors have contributed most to the current spatial patterns of treeline at its altitudinal and latitudinal limits? Five scientific investigations were conducted to answer these questions, each utilizing different methodologies within a mechanistic analytical framework. These were: (i) assessment of growth of treeline trees using dendroclimatology, (ii) monitoring the extent of mid-winter desiccation of coniferous foliage, (iii) determination of environmental controls on seedling establishment, (iv) contrasting seedling distribution in wetland and upland environments, and (v) treeline stand reconstruction using dendroecology. Chapters 2–6 present the complete results of these analyses, and chapter 7 provides a synthesis of these results in the context of treeline ecological theory.

The forest-tundra ecotone, climate change and treeline dynamics

Of all naturally occurring ecotones—transitional areas between adjacent ecological systems or between types of vegetation (Risser, 1995)—the forest-tundra is one of the most studied. The term *forest-tundra* describes the transition zone where the subalpine forest and alpine tundra communities meet, and has been extended to include the zone of high-latitude subarctic vegetation between the circumpolar boreal forest and the arctic tundra (Payette *et al.*, 2001). Within the forest-tundra ecotone, lies the treeline or tree limit—defined here as individuals possessing one dominant stem, generally > 2 m in height—tall enough to have its crown coupled with prevailing atmospheric conditions—though species may persist past treeline as prostrate shrubs or krummholz form up to the species line (Slatyer & Noble, 1992).

Numerous explanations for the mechanism that determines treeline position have been proposed. These range from structure-related factors such as frost damage, winter desiccation, and damage by wind-blown snow and ice; growth-related factors such as limited seed development, establishment, and recruitment in low temperatures; a negative carbon balance as a result of short growing seasons; and combinations of these and other factors (Wardle, 1971; Tranquillini, 1979; Grace, 1989; Stevens & Fox, 1991; Hoch & Körner, 2003). Körner (1998; 2003) conducted an extensive review of the treeline literature and found that while some of the aforementioned factors were important at the local scale at some treelines, none offered a universal explanation for the presence of treeline at a global scale. He suggested that growing season temperature limits tree growth and the position of treeline, based on notable similarities in various temperature parameters at treelines world-wide, the most consistent being average growing season temperature (Paulsen & Körner, 2001). However, recent studies suggest temperature during the winter is a more important driver of global and regional treeline position (Kullman, 2007; Harsch *et al.*, 2009). In spite of inconsistent and conflicting evidence for drivers of treeline change, it is evident that air temperature as a limiting factor for treeline location is the most important axiom in global treeline ecology, though our understanding of the specific mechanism by which temperature influences treeline dynamics is still deficient.

While the physiological effects of low temperature could be the main forcing of the *potential* position of treeline in subarctic and alpine environments, the *actual* limits of tree growth are dependent on a synergy of physical and biological agents operating at a variety of spatial and temporal scales (Holtmeier & Broll, 2005) (Fig. 1-1). These include carbon-sink limitation (Hoch & Körner, 2009), competition and herbivory (Cairns & Moen, 2004), and soil moisture availability (Daniels & Veblen, 2004), among many other factors. Moreover, the importance of these and other variables, as well as the magnitude of their interactions, varies between regions and over time.

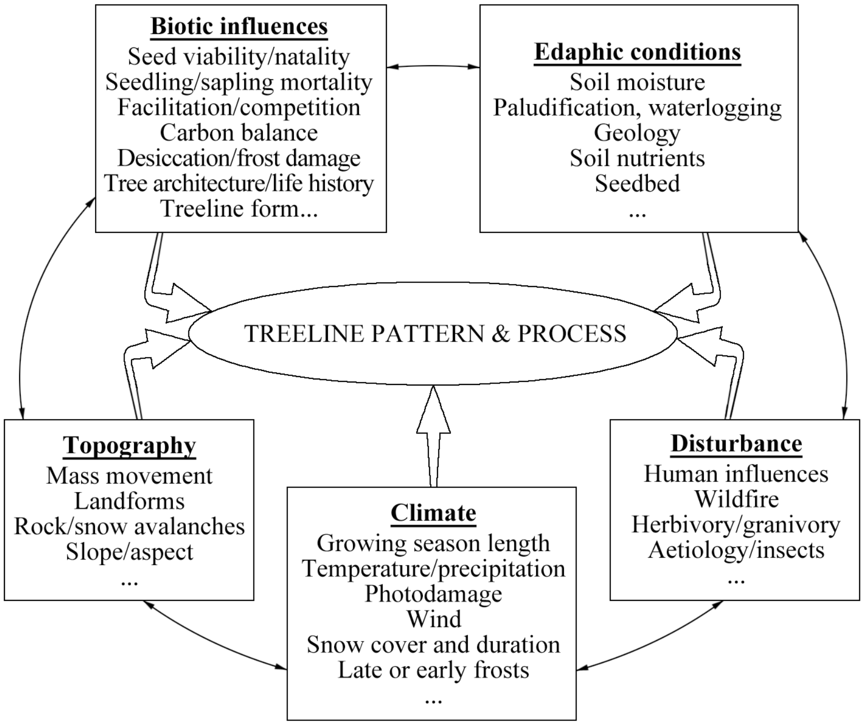

Figure 1-1. Outline of factors that control treeline position at various spatial and temporal scales. Small arrows indicate that these processes are not mutually exclusive and ellipses signify that this is by no means an exhaustive list of treeline-affecting variables.

Trees are not well adapted to subarctic and alpine environments. The tree growth form is well suited to maintain positive growth when competition for solar radiation is of primary importance, though becomes increasingly inappropriate as the treeline is approached and conditions become colder and more extreme (Slatyer & Noble, 1992). Individuals tend to become increasingly multi-stemmed and shrub-like as the tree-species line is approached, and advance of treeline can only occur once conditions have been ameliorated. Indeed treeline has advanced during previous warm periods, as the northwestern arctic coast of North America was rapidly occupied by trees during warming following the Pleistocene-Holocene transition (Payette *et al.*, 2002). *Picea* in particular underwent great changes both in distribution and abundance after the late Pleistocene (Delcourt &

Delcourt, 1992). *Picea* began to spread northward during this time, though was slowed by the slowly melting Laurentide Ice Sheet, and treeline reached its peak elevation and latitude (~200 km north of present treeline) during the warm Hypsithermal around 5.8 ka and retreated to its current position starting around 3.8 ka (Payette *et al.*, 2002). As treeline has advanced with warmer temperatures during Holocene warm periods (MacDonald *et al.*, 2000), and temperatures are expected to increase notably in arctic environments (ACIA, 2004), treeline is expected to shift accordingly—with important consequences for the Earth's climate system in terms of surface albedo, carbon and nutrient cycling, and hydrological cycling (Chapin III *et al.*, 2000). However, actual treeline responses will probably vary significantly at regional, landscape and even local scales and are partly contingent on terrain variability, landscape characteristics and existing vegetation.

STUDY COMPONENTS AND THESIS OUTLINE

Study areas

Hudson Bay Lowlands

The central Canadian study area is located in subarctic Manitoba, near the coast of Hudson Bay. The nearest weather station is 15 km west of Churchill at the airport (lat. 58°45′ N, long. 94°04′ W) with a mean annual temperature of -6.9°C, a mean of -26.7°C in January and 12.0°C in July (all climate normals cover the 1971 to 2000 period) (Environment Canada, 2012). Wind is primarily out of the northwest, with a maximum gust frequency (MGF) of 39%, followed by north (23%) and west (17%) (Environment Canada, 2012). Any winds blowing from a northerly 180° sector from west through east have their course over Hudson Bay which, historically, is only ice-free one month of the year (August), resulting in continental Arctic climatic conditions around Churchill (Rouse, 1991) and continuous permafrost averaging around 80 m thick at Churchill to 25 m at Gillam 175 km to the south (Dredge, 1992). Mean annual precipitation totals 562 mm, 52% of which falls as snow (Environment Canada, 2012).

The study area is at the northern limit of the forest-tundra in east-central Canada. Upland forests are dominated by *Picea glauca* (Moench) Voss with some *Larix laricina* (Du Roi) K. Koch (tamarack) and even fewer *Picea mariana* (Mill) B.S.P., and have a thick ground cover of lichens dominated by *Cladina* spp. (reindeer lichens) and the shrub *Ledum groenlandicum* (Labrador tea). Wetland sites are dominated by *P. mariana* and *L. laricina* and possess a thick ground cover of moss dominated by *Sphagnum* spp. (peat moss), *Hylocomium splendens* (stair-step moss) and *L. groenlandicum*.

Western Mackenzie Mountains

The nearest Environment Canada weather station is at Macmillan Pass, YT (lat. 63°14′ N, lon. 130°02′ W) (1998 to present). Due to the short duration of the Macmillan Pass climate data, gridded climate data were used to estimate climate normals (New *et al.*, 2000). Mean January, July and annual temperatures from 1971–2000 were -26.2, 10.0 and -8.3°C, respectively. Mean annual precipitation totals 339 mm, with about 50% as snow. The area is underlain by discontinuous permafrost ranging from about 2 m thick (Kershaw & Gill, 1979) to greater than 15 m in palsas (Kershaw, 2003).

Ground cover over the study area ranges from extensive mats of *Cladina* spp. to pleurocarpous and acrocarpous mosses. Shrubs are extensive in cover and are dominated by *Betula glandulosa* (dwarf birch), though several *Salix* spp. (willow) are abundant including *Salix reticulata*, *S. commutata* and *S. alaxensis*. Trees are restricted to either individuals or scattered tree islands, with *Abies lasiocarpa* (Hook.) Nutt. occurring most frequently, though individual *P. glauca* trees are found along the Canol Heritage Trail on disturbances resulting from road construction during the early 1940s. Reproduction of *A. lasiocarpa* appears to be primarily asexual within the krummholz stands.

Research objectives

The purpose of this research was to evaluate the response of the forest-tundra ecotone of the western Mackenzie Mountains and the Hudson Bay Lowlands to climatic and environmental change and determine how site-specific environmental factors contribute to dynamics within this ecotone. The primary objectives were to evaluate some key factors that influence treeline dynamics in order to answer the primary research questions. Specifically, these objectives were:

(i) Determine the growth response of trees to climate during the last century, in order to assess historical environmental conditions in order to put this research into a temporal context;

(ii) Evaluate the prevalence of winter desiccation and mortality of coniferous foliage;

(iii) Assess the role of facilitation and competition by conspecific and heterospecific vegetation, as well as environmental characteristics, in influencing seedling establishment;

(iv) Determine the role of climate in seedling establishment in wetland and upland environments;

(v) Elucidate the history of recruitment at treeline, and examine any relationship between the changes in the structure and location of treeline and climate.

The following section describes the five research components that were undertaken in order to fulfill the research objectives. With the exception of the dendroclimatology (Chapter 2) and dendroecology (Chapter 6), all investigations were carried out in Churchill, as winter fieldwork could not be undertaken in the western Mackenzie Mountains due to logistical reasons related to accessibility.

Dendroclimatology at treeline

Radial growth response of trees growing at northern latitudes is highly spatially and temporally variable as growth in a given year depends on numerous factors, such as tree age, climate, endogenous and exogenous stand disturbances, and edaphic influences (Fritts, 2001). Szeicz and MacDonald (1994) found that climatic response of subarctic trees was age-dependent and site-specific, and suggested that as trees age, they could suffer from reduced water efficiency and water translocation mechanisms, which can cause a reduced response to temperature over time. Lloyd and Fastie (2002) found that considerable fine-scale variability in growth response exists at treeline sites in Alaska, and that inverse responses to temperature were more prevalent in trees below the forest margin, compared with treeline trees. The diversity in tree-growth response to such a wide variety of environmental variables at a number of spatial and temporal scales illustrates the need for careful consideration when investigating tree-growth-climate relationships in northern environments.

Steep environmental gradients persist across the treeline ecotone, where vegetation dominated by boreal species transition to predominately tundra taxa, mostly due to changes in microclimate, soil and nutrient cycling (Timoney *et al.*, 1993). In northwestern Canada, Timoney *et al*. (1993) found that the subarctic treeline occurs on the steepest environmental gradient across the forest to tundra transition. In Alaska, Lloyd and Fastie (2002) determined that trees below treeline were more likely to experience declining growth with warmer temperatures after 1950. This mirrored the broader-scale pattern of trees at warmer sites nearer to the centre of the boreal forest responding negatively to increasing warmth (Barber *et al.*, 2000), while those at the cooler boreal forest margin have responded more positively (Jacoby *et al.*, 2000). However, finer-scale studies like that conducted by Lloyd and Fastie (2002) and Paulsen *et al*. (2000) are rare and, to our knowledge, none have included sites from the western Mackenzie Mountains, or Hudson Bay Lowlands. Thus further investigation is required to determine how tree growth proximal and distal to local treelines is responding to warming, and if these responses are indeed indicative of a hemispherical pattern of environmental change during the 20th century.

This study was designed to examine the spatial and temporal variability in growth and climate response of trees at and near treeline in the western Mackenzie Mountains, Northwest Territories, and the Hudson Bay Lowlands in northern Manitoba. Specifically, three questions were proposed:

(i) Is there variation in growth trends and/or climatic response of treeline trees across different regions?

(ii) Is there variation in growth trends and/or climatic response between trees growing at and adjacent to treeline?

(iii) Are there commensurate growth responses to climate change during the 20th century?

Using an increment borer, tree cores were obtained from tree islands at 13 sites along the Canol-Heritage Trail in the western Mackenzie Mountains, and from three local diffuse treelines near Churchill in the western Hudson Bay Lowlands during 2008 and 2009. In total, 108 trees from the Mountains and 170 from the Lowlands were measured and sampled. Cores were sanded and polished and annual rings were counted, measured and crossdated using standard dendrochronological techniques (Stokes & Smiley, 1996). Standardized ring-width chronologies were constructed for each site, analyzed for long-term growth trends, and compared with historical climate data. This investigation is presented in its entirety in Chapter 2.

Winter desiccation of coniferous foliage

Winter desiccation of foliage is believed to contribute to the stress of conifers at treeline. At high altitudes and latitudes, cuticular development can be restricted by a short, cool growing season (Wardle, 1971; Tranquillini, 1979). Increased cuticular transpiration can result in severe winter dehydration, and it has been suggested that winter desiccation is a primary determining factor for the range limits of treeline trees (Kullman, 2007; Holtmeier & Broll, 2011). Strong winds can transport snow grains at high velocities, which abrade the cuticles of needles and damage stomata, leading to increased water losses, particularly at the end of winter (Hadley *et al.*, 1991; van Gardingen *et al.*, 1991).

It seems logical to assume a direct relationship between an environmental factor and a plant performance parameter if the two variables are found to vary concomitantly along an ecotone. However, such co-variation does not necessarily represent a causal mechanism, as indirect effects of an environmental factor (e.g., summer temperature) could have a greater effect on a parameter of interest (e.g., tree growth) through its effects on another factor (e.g., needle maturation). Thus determining how plant performance can be affected by its environment is often quite difficult, and studies can be further complicated by non-linear processes, difficult to predict synergistic interactions, and fortuitous co-variation between environment and vegetation (Sveinbjörnsson *et al.*, 2002).

Several studies on coniferous foliage and environmental conditions around Churchill, Manitoba, were completed during the 1980s and 1990s (Scott *et al.*, 1987b; Scott *et al.*, 1987a; Scott & Hansell, 1992; Scott *et al.*, 1993; Scott & Hansell, 2002). However, to our knowledge, there have been no studies on winter effects on treeline vegetation in the Churchill area in 20 years or more, nor have there been comparable studies on finer scale treelines (<100 m from forest to tundra) in the area. Therefore, the purpose of this study was to compare metrics of needle health within open forest, the forest-tundra ecotone and tundra, and determine the presence of winter desiccation and its relevance to treeline dynamics in the Churchill region. Specifically, the aim was to answer the following questions:

(i) How does needle health vary:
  a. within and above the mid-winter snowpack?
  b. with orientation to regional wind patterns?
  c. in forest-facing and tundra-facing margins of trees?
  d. through time as a function of environmental conditions during needle formation?

(ii) Is there a link between winter desiccation and/or frost drought, and recent treeline dynamics?

During the mid-winters of 2008–2010, the most recent production of needles formed during the preceding growing season were sampled at several heights and orientations from three randomly selected *P. glauca* trees in each zone: forest, forest-tundra ecotone, and tundra. Snowpack was also sampled in each zone. Epidermal conductance, needle viability and water content were calculated (Baig & Tranquillini, 1980; Hadley & Smith, 1983) and compared among zones. This investigation is presented in its entirety in Chapter 3.

Environmental controls on seedling establishment

Growing season temperature is often considered to be the primary driver of changes in treeline position across the circumboreal (Hoch & Körner, 2009), though climate is only one facet of environmental variation (Holtmeier & Broll, 2005). As treeline heterogeneity increases from global to smaller scales, so does the influence of local biotic and abiotic factors on spatial variability of seedling establishment and survival, and therefore tree recruitment. Temporal scale is also an important factor in treeline sensitivity, as annual to sub-seasonal establishment and recruitment dynamics of younger life stages are increasingly influenced by numerous factors other than weather and climate (Holtmeier & Broll, 2007). As the factors controlling treeline position are strongly scale-dependent (Kupfer & Cairns, 1996), assessment of treeline response to changing climate at regional and finer scales requires a more comprehensive approach than at the circumboreal scale (cf. Körner & Paulsen, 2004).

The presence of ground cover appears to be crucial for survival of seedlings as it can reduce sky exposure and low-temperature photo-inhibition (Germino *et al.*, 2002). Furthermore, shrub shading of the ground can reduce mid-day soil temperatures and make them more tolerable to new seedlings (Keyes & Maguire, 2008). However, while most studies suggest facilitation is the dominant mode of neighbor interactions in stressful environments like those found at treeline [following the Stress Gradient Hypothesis *sensu* Bertness & Callaway (1994)], some contradictions to this premise have been found (e.g., Forbis, 2009), which suggests a site-scale evaluation of micro-environmental facilitation is warranted.

Churchill represents a relatively pristine and easily accessible forest-tundra landscape, and its diffuse treeline form (Harsch & Bader, 2011), could respond swiftly to current and anticipated warming (ACIA, 2004). While there have been a number of studies concerning population dynamics and spatial patterns of mature trees (Scott & Hansell, 2002; Harper *et al.*, 2011; Mamet & Kershaw, 2012), little research has been done into fine-scale biotic and abiotic influences on coniferous seedling establishment at treeline in the area. The objectives of this study were to:

(i) Evaluate establishment and fecundity metrics in forest and treeline sites;

(ii) Characterize the micro-environment in which seedlings establish;

(iii) Determine which factors are most important in influencing seedling establishment.

In 2008, seedlings were destructively sampled within the forest and ecotone from three sites around Churchill. Dominant plant cover around each seedling was recorded. During early October, > 100 cones per species per site were taken and used for germination trials. In order to determine habitat preference by seedlings, the habitat preference index of Duncan (1983) was calculated using the vegetation survey and occurrence of seedlings aged one to seven years (cf. Germino *et al.*, 2002). This investigation is presented in its entirety in Chapter 4.

Seedling abundance in upland and wetland environments

Mean growing season temperature is the primary factor limiting tree growth within the forest-tundra (Mamet & Kershaw, 2011) and radial growth of mature trees has been responding favorably, in many cases, to increased temperatures (D'Arrigo *et al.*, 2008). However, it is the successful germination and survival of tree seedlings rather than increasing growth of mature trees, which are likely the most crucial processes in treeline advance poleward and to higher elevations with climate warming (Holtmeier & Broll, 2007). Thus while radial growth of mature trees responds more rapidly to increases in temperature (Holtmeier & Broll, 2005), it is the recruitment of individuals in the forest-tundra and pertinent environmental factors which must be assessed in order to evaluate spatial forest cover dynamics (Smith *et al.*, 2009).

To my knowledge there have been no studies specifically on recent local seedling establishment around Churchill. The Churchill region is predicted to warm significantly during the next 100 years (Gagnon & Gough, 2005) and the potential for treeline movement and feedbacks with climate (MacDonald *et al.*, 1998) makes the area a prime location for investigation of forest cover dynamics. Uplands around Churchill are often dominated by a lichen mat, which could inhibit establishment (Houle & Filion, 2003). In contrast, mosses and sedges dominate wetland environments in the area, which could be more suitable to successful establishment of seedlings (Black & Bliss, 1980). Thus seedbed must be taken into consideration when evaluating local seedling establishment. The objective of this study was to examine:

(i) Which environmental variables most influence seed-based regeneration;

(ii) Compare recent history of seedling establishment between wetland and upland sites within the forest-tundra near Churchill.

Within an area of 134 m^2 at two sites, a wetland and upland environment, seedlings and saplings were destructively sampled. Static age structures developed for each species were converted to standardized residuals by means of curve fitting following established techniques (Hett & Loucks, 1976). The residuals are a measure for the number of individuals that established and survived up to the year of sampling. These residuals were compared to a time-series of temperature and precipitation in order to assess the influence of climate on seedling establishment and survival. This investigation is presented in its entirety in Chapter 5.

Dendroecological stand analysis

There have been numerous studies of treeline responses to climate change during the last several decades. In some regions, the treeline has advanced (Kullman, 2002; Lloyd & Fastie, 2003). Other studies have found increases in stand density without advance of the treeline (Payette & Filion, 1985; Szeicz & MacDonald, 1995). Some studies suggest that the treeline cannot advance without disturbances such as fire (Johnstone & Chapin, 2006) or thermokarst (Lloyd *et al.*, 2003), or that treeline position is moderated by disturbances such as herbivory (Cairns *et al.*, 2007) and granivory (Castro *et al.*, 1999). In some regions, there could be a change in the dominant treeline species from coniferous to deciduous (Landhäusser *et al.*, 2010). In other areas, there could be a change from stunted individuals (krummholz) to upright growth forms (Lescop-Sinclair & Payette, 1995; Vallée & Payette, 2004). The treeline has receded in some areas (Payette, 2007), remained unchanged in others (Butler *et al.*, 1994) and in some regions, is thought not to be in equilibrium with the present climate (Johnstone & Chapin, 2003). Such treeline variability is mediated by species-specific and environmental controls at a range of scales (Holtmeier & Broll, 2007). Further research is necessary to determine these controls and to improve understanding of feedbacks between climate and treeline dynamics with potential warming of subarctic and alpine regions.

The objectives of this study were to:

(i) Identify episodes and rates of establishment and mortality of treeline individuals across the forest–tundra transition at several sites at the alpine treeline in the western Northwest Territories and the latitudinal treeline in northern Manitoba

(ii) Infer changes in the structure and location of the treeline from these data;

(iii) Examine any relationship between these changes and climate

(iv) Investigate causes of variability between sampling sites and study areas.

Cores and cross-sectional disks from living trees and dead snags were obtained from tree islands at 13 sites along the Canol-Heritage Trail in the western Mackenzie Mountains, and from three local diffuse treelines near Churchill in the western Hudson Bay Lowlands during 2008 and 2009. Saplings were also destructively sampled in these locales. In total, 245 trees and 288 saplings from the Mountains and 318 trees and 608 saplings from the Lowlands were measured and sampled. Cores and cross-sectional disks were sanded and polished and annual rings were counted, measured and crossdated using standard dendrochronological techniques (Stokes & Smiley, 1996). Age structures were developed for each zone at each site and were statistically analyzed to assess whether densities increased, decreased, or remained constant. Data were also compared to determine whether or not treeline has advanced, receded, or remained constant. This investigation is presented in its entirety in Chapter 6.

SYNTHESIS

The methods used in each of these investigations have been used elsewhere, and been utilized effectively in forest-tundra environments. However, it is rare to see the combination of these techniques within a single study area, and over such a short time period. Therefore, this study is unique in its integration of numerous techniques, and the results produced new insight into how treeline ecosystems respond to climate change in western and central Canada. Moreover, the establishment of long-term monitoring plots to be re-sampled in the future will allow the data collected and relationships derived from each investigation to be used in modeling future landscape change—which could then be evaluated by future studies.

This thesis concludes with a seventh chapter that highlights the significance of these investigations and some potential applications. In addition to summarizing the results and main conclusions from each of the component investigations, this final chapter explores their linkages within the context of treeline theory, and identifies potential avenues for future research on subarctic and alpine treeline dynamics.

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CHAPTER TWO

Age-dependency, climate and environmental controls of recent tree growth trends at subarctic and alpine treelines[1]

"*There is a certain irony in the use of tree rings as records of past climate, with all its complexities and subtleties, in that it rests on a very simple observation for which only an increment corer, sandpaper, and a low-power dissecting microscope are needed.*"

Malcolm K. Hughes (2011)

INTRODUCTION

Arctic and subarctic regions have experienced pronounced changes in climate during the 20th century, and the two decades from 1988 to 2008 were the warmest of the last millennium (Ogurtsov *et al.*, 2011). This warming has resulted in a variety of responses in temperature-limited terrestrial ecosystems, particularly in treeline environments. Trees growing at the cold subarctic and alpine margins of the boreal forest, hereafter referred to as "treeline", have fallen under close scrutiny in recent decades as they provide a means of understanding past and present ecosystem productivity, as high- to low-frequency signals of biotic and abiotic forcings are preserved at an annual resolution in the woody tissue of trees (Luckman, 2007). Recent evidence suggests that future climate warming and feedbacks will be greatest in arctic and alpine regions (Chapin III *et al.*, 2005), and growth of treeline trees is expected to respond positively to warming in areas where there is sufficient soil moisture (Wilmking *et al.*, 2005), and negatively in moisture-stressed areas (cf. Lloyd & Fastie, 2002). Positive feedbacks could

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include increased respiration or CO_2 acclimation, while negative feedbacks could include increased productivity and CO_2 sequestration (Harding *et al.*, 2002), and alteration of the solar radiation budget through increased fire emissions (Harden *et al.*, 2000), among many others. Such variability in feedbacks illustrates the need to assess the response of treeline trees to past climate in order to forecast future response to the predicted warming trend.

Radial growth response of trees growing at northern latitudes is highly spatially and temporally variable as growth in a given year depends on numerous factors, including tree age, climate, endogenous and exogenous stand disturbances, and edaphic influences, among others (Fritts, 2001). Szeicz and MacDonald (1994) found that climatic response of subarctic trees was age-dependent and site-specific, and suggested that as trees age, they could suffer from reduced water efficiency and water translocation mechanisms, which can result in a reduced response to temperature over time. Lloyd and Fastie (2002) found that considerable fine-scale variability in growth response exists at treeline sites in Alaska, and that inverse responses to temperature were more prevalent in trees below the forest margin, compared with treeline trees. Particularly prevalent in the tree-ring literature is research into the so-called “divergence problem” in which subarctic and alpine trees exhibit decreased sensitivity to temperature since the middle of the 20th century [for a review see D'Arrigo *et al.*, (2008) and references contained therein]. This phenomenon refers to the tendency for temperature-limited trees within northern sites to record a weaker response to mean temperature in recent decades—expressed as an offset between warmer instrumental temperatures and their underestimation in reconstructions based on tree rings (D'Arrigo *et al.*, 2008). Numerous explanations for this divergence have been proposed, at a variety of scales, such as moisture stress (Barber *et al.*, 2000), non-linear or threshold responses (D'Arrigo *et al.*, 2004), local pollution (Wilson & Elling, 2004), differential response to maximum and minimum temperatures (Wilson & Luckman, 2003), sub-site tree-specific responses (Wilmking *et al.*, 2005) and detrending end effects (Melvin, 2004; Loehle, 2009). However, more empirical evidence is needed to properly evaluate these hypotheses (D'Arrigo *et al.*, 2008). Nonetheless, the diversity in tree-growth response to such a wide variety of environmental variables at a number of spatial and temporal scales illustrates the need for careful consideration when investigating tree-growth-climate relationships in northern environments.

Steep environmental gradients persist across the treeline ecotone (Timoney *et al.*, 1993), where vegetation dominated by boreal taxa transition to predominately tundra species, primarily due to changes in microclimate, soil and nutrient cycling (Timoney *et al.*, 1993). In northwestern Canada, Timoney et al. (1993) found the subarctic treeline occurs on the steepest environmental gradient across the forest to tundra transition. Indeed, mean monthly soil temperatures have been observed to differ by up to 3.9°C across treeline around Churchill, Manitoba during the peak of the growing season (July-August) (Mamet and Kershaw, unpublished data). Results of a study by Scott *et al*. (1987) southwest of Churchill, found that tree growth within the forest-tundra (tree islands) was much greater than growth within open forest during the second half of the 20th century.

Scott *et al*. (1987) hypothesized this difference was due to different strategies in biomass accumulation along the stem (e.g., basal rosettes in forest-tundra trees and height growth in open forest trees), which could supersede the notable regional influence of frontal activity on tree growth in the area (Scott *et al.*, 1988). Tree growth in the area does not appear to be impeded by wind-blown snow abrasion (Scott *et al.*, 1993). In Alaska, Lloyd and Fastie (2002) found considerable variations in tree growth between trees below and at treeline over distances less than 75 m. They found that trees below treeline were more likely to experience declining growth with increasing temperature after 1950, which mirrored the broader-scale pattern of trees at warmer sites nearer to the centre of the boreal forest responding negatively to increasing warmth (Barber *et al.*, 2000), while those at the cooler boreal forest margin have responded more positively (Jacoby *et al.*, 2000). However, finer-scale studies like that conducted by Lloyd and Fastie (2002) and Paulsen *et al*. (2000) are rare and, to our knowledge, none have included sites from continental mountains (Mackenzie Mountains, NWT) or continental lowlands (Hudson Bay Lowlands, MB). Thus further investigation is required to determine how tree growth that is proximal and distal to local treelines is responding to warming, and if these responses are indeed indicative of a hemispherical pattern of environmental change during the 20th century.

This study was designed to examine the spatial and temporal variability in growth and climate response of trees at and near treeline in the western Mackenzie Mountains, Northwest Territories, and the Hudson Bay Lowlands in northern Manitoba. Specifically, three questions were proposed: (1) is there variation in growth trends and/or climatic response of treeline trees across different regions? (2) Is there variation in long-term growth trends and/or climatic response between trees growing at and adjacent to treeline? And, (3) are there commensurate growth responses to climate change during the 20th century?

MATERIALS AND METHODS

Study areas

Study sites within the Mackenzie Mountains were located along the Canol Heritage Trail, which runs approximately 370 km from Macmillan Pass, northeast to Norman Wells in the Northwest Territories (Fig. 2-1). The trail follows the abandoned, and now unusable, service road built for the Canol Pipeline during the early 1940s. This area was chosen due to its relative ease of access and, despite development during the 1940s, remains a relatively pristine treeline environment. The Churchill area was also chosen based on accessibility to an unaltered, natural treeline. Historically, some areas were mined west of Churchill (Bamburak, 2000), and some subsistence logging has occurred in burned forests southeast of Churchill. However, most of these activities were small in scale and none have occurred within or near (within 2 km) any of the sites sampled for this study. In addition, large disturbances such as wildfire, anthropogenic influences, insect infestations, slope failure, and winter avalanches have been infrequent or non-existent at all study sites.

The Mackenzie Mountains reach altitudes of ~2000 m.a.s.l., and treeline often occurs between 800 and 1500 m.a.s.l., depending on aspect and edaphic characteristics. There was a shift from open forests of *Abies lasiocarpa* (Hook.)

Nutt. (subalpine fir) with some *Picea glauca* (Moench) Voss. (white spruce) in the Yukon west of Macmillan Pass, to scattered islands of *A. lasiocarpa* and few *P. glauca* near the border in the Northwest Territories. Macmillan pass (63.2°N, 130.0°W, 1380 m.a.s.l.), mean January, July and annual temperatures from 1971–2000 were -26.2, 10.0 and -8.3°C, respectively (New *et al.*, 2000). Mean annual precipitation totals 339 mm, with about 50% as snow.

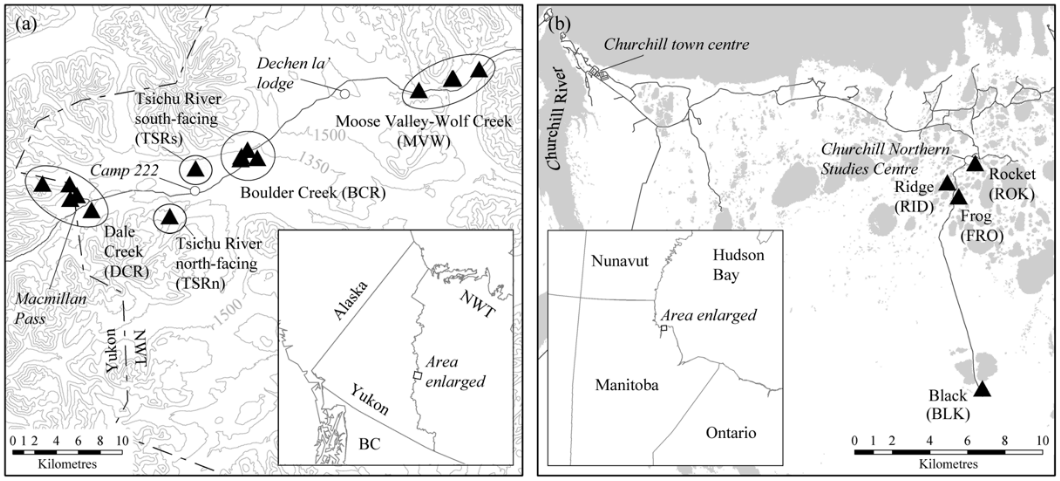

Figure 2-1. Location of the (a) western Mackenzie Mountains and (b) western Hudson Bay Lowlands study areas (inset) and the sampling sites in each region. The solid gray line (a), which runs from southwest to northeast, is the Canol Heritage trail. The contour interval in (a) is 150 m.

The study area of the Hudson Bay Lowlands had a peak elevation of 39 m.a.s.l. Uplands were dominated by *P. glauca* with some *Larix laricina* (Du Roi) K. Koch (tamarack), while wetland environments further south were predominantly *Picea mariana* (Mill.) B.S.P. (black spruce) and *L. laricina* in bogs, and *P. glauca* on hummocks. Much of the area lies on remnant beach ridges formed during isostatic rebound (Dredge, 1992), and the land is still rising at approximately 11.4 mm year^{-1} (Wolf *et al.*, 2006). Mean January, July and annual temperatures were -26.7, 12.0 and -6.9°C, respectively. Mean annual precipitation is 562 mm with 52% as snow (Environment Canada, 2012).

Field methods

Trees were sampled from 13 tree islands in the Western Mackenzie Mountains and four sites southeast of Churchill (Fig. 2-1; Table 2-1). Eleven of the 13 tree islands in the mountains were grouped into three study sites based on similar exposure and elevation. The remaining two stands were approximately north- and south-facing, respectively, and therefore were analyzed separately for differences in aspect. Study plots were established in order to sample a minimum of 30 individuals of each species present at each study site. In the mountains, elliptical plots of a known length and width were set up to sample as many tree island stems as possible (i.e., approximately the same size as the island), while rectangular plots were arranged at random within the open forest and adjacent treeline near Churchill (30 m initial width; plot was extended as necessary—see below). One plot was established per zone (proximal and distal to treeline), and plot areas differed in order to satisfy the objective of including at least 30 individuals of each species. Since the density of stems differed among plots, the final areas sampled were unique to each site (Table 2-1). Trees were bored at chest height (~1.3 m). Tree height, diameter at breast height (dbh), basal diameter, number of cones and dominant plant species cover were recorded for each sample where applicable.

Laboratory methods

All samples were dried at ~25°C and then mounted on wooden blocks. Cores were sanded with progressively finer grits of sandpaper until individual xylem cells were visible (Stokes & Smiley, 1996). Samples were dated and measured using a stereomicroscope and Velmex slide stage micrometre with a digital encoder (Velmex Inc., Bloomfield, New York, USA), at 0.001 mm resolution. Crossdating was conducted using light rings (rings with unusually few latewood cells) (Yamaguchi, 1991) and narrow marker years (Fritts, 2001). Crossdating was statistically verified using the program COFECHA (Grissino-Mayer, 2001).

Table 2-1. Description of study sites. Type of treeline indicates whether the site was located at a western Mackenzie Mountains alpine treeline or at arctic treeline in the Hudson Bay Lowlands of northern Manitoba. Elevation refers to the approximate elevation of each site. Values of tree density are means (where applicable) of two to five sampling plots at each site. All mean values are ± one standard error.

Study site	TT[a]	Lat.[b]	Lon.[c]	Z[d]	A[e]	TD[f]	NP[g]	TA[h]
WMM[i]								
DCR	Alpine	63°15′ N	130°01′ W	1449 ± 28	ENE - NNW	1333 ± 453	5	855
BCR	Alpine	63°19′ N	129°45′ W	1345 ± 19	SE - SSE	1652 ± 1119	4	557
MVW	Alpine	63°26′ N	129°28′ W	1376 ± 31	E - S	3656 ± 757	5	79
TSRn	Alpine	63°15′ N	129°51′ W	1408	ENE	990	1	141
TSRs	Alpine	63°18′ N	129°50′ W	1310	SSW	891	1	236
HBL								
RID	Arctic	58°43′ N	93°50′ W	22 ± 0.1	NE	1669 ± 35	2	903
ROK	Arctic	58°43′ N	93°49′ W	17 ± 0.1	S	567 ± 5	2	1950
FRO	Arctic	58°42′ N	93°50′ W	23 ± 0.1	WSW	283 ± 127	2	900
BLK	Arctic	58°37′ N	93°48′ W	36 ± 0.1	NNE	684 ± 12	2	645

[a] Treeline type

[b] Latitude

[c] Longitude

[d] Elevation (m)

[e] Azimuth refers to aspect for alpine treelines and direction of decreasing tree density (i.e., direction of forest to tundra transition) for arctic treelines

[f] Tree density (trees/ha)

[g] Number of plots

[h] Total area (m^2)

[i] WMM = Western Mackenzie Mountains, DCR = Dale Creek, BCR = Boulder Creek, MVW = Moose Valley-Wolf Creek, TSRn = Tsichu River: north-facing, TSRs = Tsichu River: south-facing, HBL = Hudson Bay Lowlands, RID = Ridge, ROK = Rocket, FRO = Frog Pond, BLK = Black.

The complete data set of crossdated ring width series was sub-sampled in order to create chronologies that were homogeneous with respect to series length. Only series originating before 1920 were used in order to maintain constant sample depth during post-Little Ice Age warming (MacDonald *et al.*, 2009), and to exclude younger trees whose climate response might differ from old trees (cf. Szeicz & MacDonald, 1994). A ring-width chronology was constructed for each species at each site, including only series that were highly correlated to the master dating series (r > 0.3281; using 50-year segments), and standardized using basal area increments (BAI) (Biondi & Qeadan, 2008). Ring-widths were standardized using the Dendrochronology Program Library (dplR) in the statistical software R (Bunn, 2008; R Development Core Team, 2011). The BAI standardization method was chosen in order to effectively visualize long-term growth trends within the chronologies, and avoid some of the pitfalls associated with other "conservative" standardization techniques. For example, the Regional Curve Standardization method (RCS) (Cook & Kairiukstis, 1990) requires large sample sizes (Cook *et al.*, 1995)—and the modified negative exponential or straight line with slope ≤ 0, cannot differentiate between growth trends due to age-size effects and those due to climatic influence (Cook *et al.*, 1995). The BAI method has proven useful for retention of low-frequency climatic trends in growth, and was therefore utilized in this study (Biondi & Qeadan, 2008).

Ring-width in a given year can be influenced by growth during the previous year, resulting in chronologies with a strong autocorrelation (Fritts, 2001). This "persistence" is desired when visualizing long-term trends in a chronology, thus BAI chronologies are advantageous for that type of analysis. However, the presence of autocorrelation results in data that are not independent, precluding the use of parametric statistics for climate comparisons. Therefore a second set of chronologies was constructed for each site using a two-stage detrending process with the program ARSTAN (Holmes, 1992). First, a negative exponential curve or alternatively a linear regression line was fitted to the raw data and, second, a cubic spline of a relative stiffness of 128-years was fitted to the resulting indices (Cook & Peters, 1981). For standardization, each ring-width series was converted into dimensionless indices by dividing observed values by the modeled values. Final chronologies (RES) were created by averaging residuals from autoregressive modeling of the standardized measurement series (Fritts, 2001), thus making observations independent to meet the requirements of most statistical analyses (Legendre & Legendre, 1998).

Data analyses

Using linear regression to estimate growth trends during the last 150 years (the interval of greatest sample depth), multi-decadal growth trends of each BAI chronology were compared. This time period was divided into three intervals of equal length (1851–1900, 1901–1950, and 1950–2000), and a fourth period (1980–present) was used to evaluate recent growth trends.

Gridded climate data at 0.5x0.5° intervals covering the 1901–2006 period were obtained from the Climate Research Unit (CRU) (New *et al.*, 2000) for each sampling site. Bootstrapped correlation- and response-functions, in which coefficients of two data sets were repeatedly computed (1000 iterations) from randomly selected subsets of the complete data set, were calculated between temperature and precipitation, and the RES indices at each site using DendroCLIM 2002 (Biondi & Waikul, 2004). Precipitation data were only available from 1929 for Churchill, and therefore all analyses cover the 1930–2006 period for consistency. Fifty-year sliding correlations were used to evaluate the temporal relations between growth and climate.

RESULTS

A total of 108 trees from the Mackenzie Mountains (Table 2-2) and 170 from the Hudson Bay Lowlands (Table 2-3) were included in the chronologies (Fig. 2-2). At the Ridge and Rocket sites, nearly all *P. glauca* proximal to treeline were established after 1930, too young to be included in the analyses and therefore excluded. At the Black site, only two treeline *P. glauca* were found, which precluded construction of a sufficiently replicated chronology. Chronology length ranged from 121 to 254 years, with a mean of 191 ± 48 years (± one standard error), and from 181 to 237 years (218 ± 84 years) for the Mackenzie Mountains and Hudson Bay Lowlands, respectively. Chronologies were typically longer at lower elevations and distal to treeline (Tables 2-2 and 2-3).

Table 2-2. Statistical characteristics of residual chronologies produced from trees established within the western Mackenzie Mountains prior to 1920

Species:	*Abies lasiocarpa*				*Picea glauca*
Site:	DCR[a]	BCR	TSR		MVW
Sample:	<1920	<1920	S-facing	N-facing	<1920
CL[b]	1828-2009	1815-2008	1805-2006	1886-2006	1755-2008
NY[c]	182	194	202	121	254
ML[d]	128	113	106	76	138
NT[e]	32	30	20	11	15
NR[f]	39	42	36	22	22
MRW[g]	0.40	0.36	0.52	0.56	0.64
MS[h]	0.22	0.26	0.21	0.22	0.21
SD[i]	0.20	0.20	0.23	0.27	0.31
FOA[j]	0.80	0.78	0.78	0.80	0.81
MCC[k]	0.49	0.50	0.43	0.48	0.55
EPS[l]	0.92	0.93	0.91	0.82	0.86

[a] DCR=Dale Creek, BCR=Boulder Creek, TSR=Tsichu River, MVW=Moose Valley/Wolf Creek

[b] Chronology length

[c] Number of years

[d] Mean series length (years)

[e] Number of trees

[f] Number of radii

[g] Mean ring width (mm)

[h] Mean sensitivity

[i] Mean standard deviation calculated from standard chronology (Grissino-Mayer, 2001)

[j] First order autocorrelation removed to form whitened chronology

[k] Mean series correlation to master series (50-year segments)

[l] Expressed Population Signal 1901 to 2006, which represents the degree to which a particular sampling portrays the hypothetical perfect chronology (Briffa & Jones, 1990)

Table 2-3. Statistical characteristics of residual chronologies produced from trees established within the Hudson Bay Lowlands prior to 1920

Species:	*Picea glauca*					*Picea mariana*		*Larix laricina*	
Site:	RID[a]	ROK	FRO		BLK	BLK		BLK	
Zone:	Dt[b]	Dt	Dt	Tr	Dt	Dt	Tr	Dt	Tr
Sample:	<1920	<1920	<1920	<1920	<1920	<1920	<1920	<1920	<1920
CL[c]	1784-2008	1600-2008	1743-2008	1852-2008	1884-2008	1777-2008	1802-2008	1846-2008	1829-2008
NY[d]	225	409	266	157	125	232	207	163	180
ML[e]	125	241	119	111	102	117	119	94	117
NT[f]	29	33	21	11	21	15	17	15	8
NR[g]	46	51	35	21	32	17	21	19	8
MRW[h]	0.43	0.40	0.36	0.29	0.48	0.32	0.23	0.50	0.19
MS[i]	0.20	0.18	0.20	0.21	0.21	0.21	0.21	0.27	0.27
SD[j]	0.22	0.19	0.18	0.14	0.25	0.19	0.11	0.29	0.11
FOA[k]	0.85	0.81	0.83	0.80	0.84	0.89	0.80	0.79	0.74
MCC[l]	0.50	0.53	0.41	0.47	0.53	0.43	0.45	0.56	0.47
EPS[m]	0.90	0.92	0.88	0.86	0.93	0.88	0.90	0.93	0.70

[a] RID=Ridge, ROK=Rocket, FRO=Frog, BLK=Black

[b] Dt=distal to treeline, Tr=treeline

[c] Chronology length

[d] Number of years

[e] Mean series length (years)

[f] Number of trees

[g] Number of radii

[h] Mean ring width (mm)

[i] Mean sensitivity

[j] Mean standard deviation calculated from standard chronology (Grissino-Mayer, 2001)

[k] First order autocorrelation removed to form whitened chronology

[l] Mean series correlation to master series (50-year segments)

[m] Expressed Population Signal 1901 to 2006, which represents the degree to which a particular sampling portrays the hypothetical perfect chronology (Briffa & Jones, 1990)

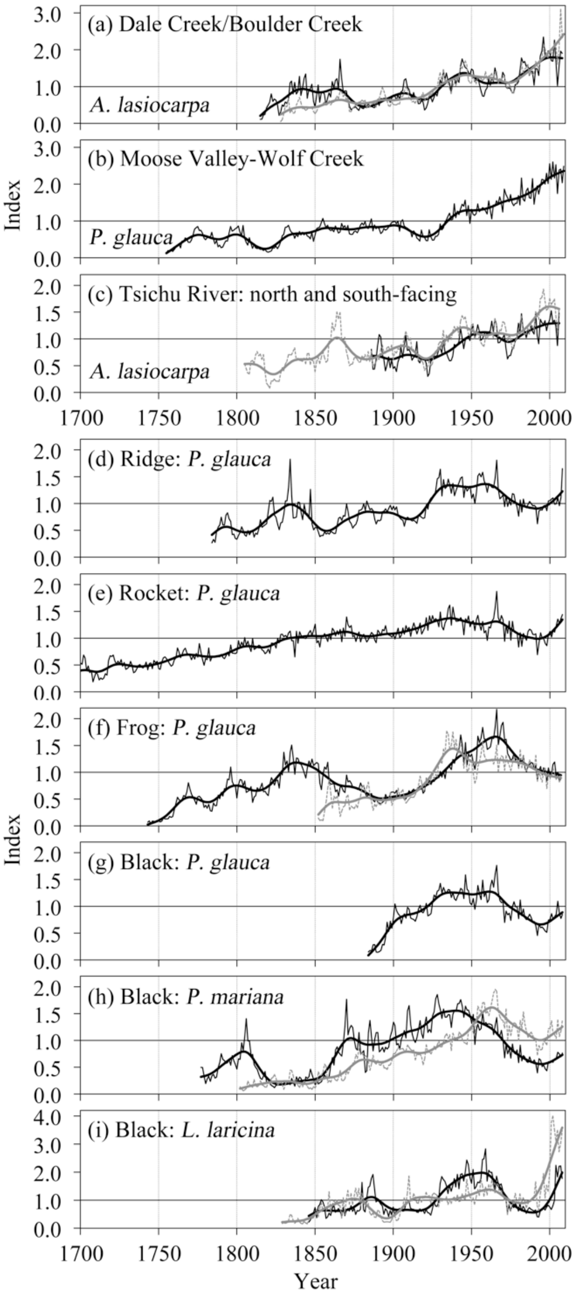

Figure 2-2. BAI indices for (a–c) the Mackenzie Mountains and (d–i) Hudson Bay Lowlands. The thick line is a 15-year smoothing spline fit to the data to emphasize low-frequency trends. (a, b, d–i) The solid black line is the chronology developed from trees distal to treeline. The dashed grey line is the chronology developed from trees at treeline. (c) The solid black line is the north-facing index, and the dashed grey line is the south-facing chronology. Note the change in scale in the y-axis for the Lowland sites.

Despite lower sample depth for some indices, the mean Expressed Population Signal (EPS) during the 20th century—the degree to which a given chronology portrays the hypothetical "perfect" chronology, exceeded 0.8 for 13 of

14 chronologies, and was above 0.85, a threshold for a sufficiently replicated chronology [as suggested by Wigley *et al*. (1984)], for 12 chronologies. Therefore, despite some variation during the 20th century and lower EPS values before 1900 (Fig. 2-3), most chronologies were acceptable for comparison to the 1901–2006 climate record. Only the Black *L. laricina* treeline index demonstrated intermediate EPS values (Fig. 2-3j). Therefore results based on this chronology should be interpreted carefully.

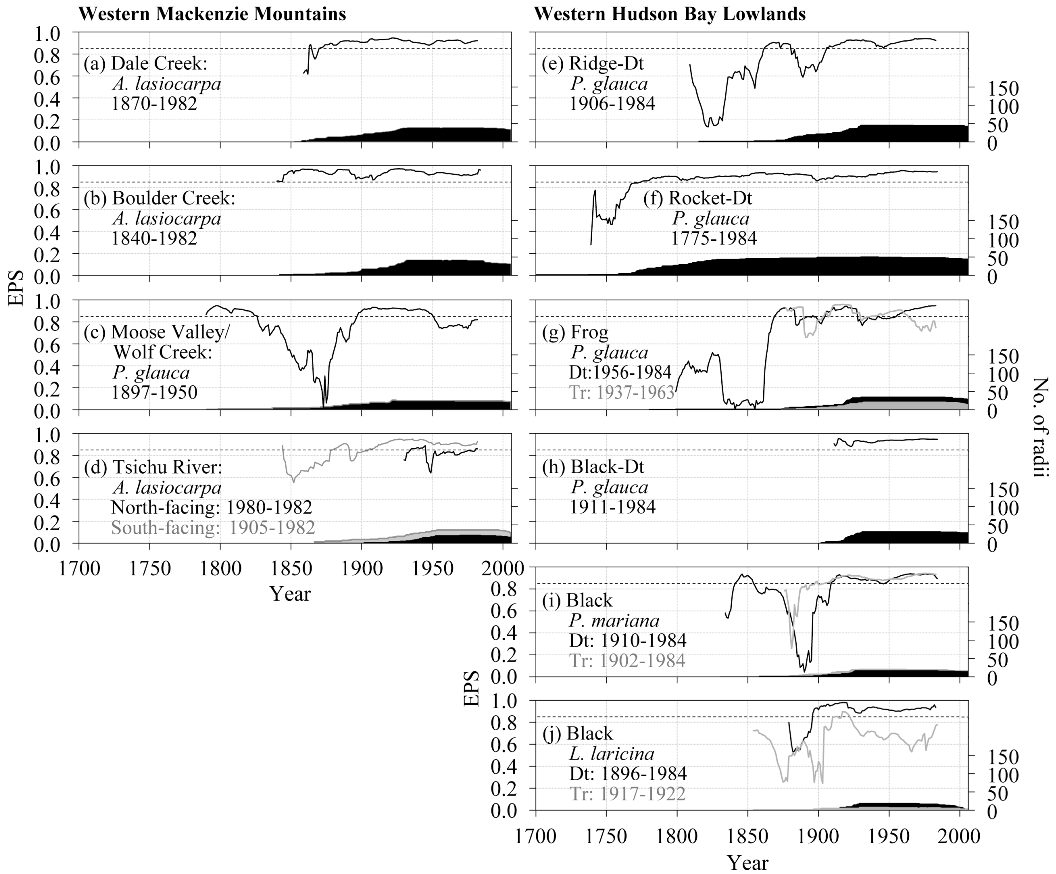

Figure 2-3. Expressed Population Signal (EPS) statistics for species sampled in the (a–d) western Mackenzie Mountains and (e–j) western Hudson Bay Lowlands (HBL). EPS statistics were computed using a 50-yr moving window with one-year time-steps. The shaded region is the sample depth (no. of radii), and for the HBL black represents distal to treeline (Dt) and grey represents treeline (Tr) chronologies. The most recent time period when EPS values were > 0.85 is shown for each species.

Climate/growth relationships in the Western Mackenzie Mountains

Low-frequency growth trends were similar among *A. lasiocarpa* of the region during the 20th century (Figs. 2-2a and 2-2c). Few trends in growth were found during 1851–1900, though almost all species exhibited positive growth trends during 1900–2006 (Table 2-4).

Table 2-4. Growth trends from 1851 to present for trees from the western Mackenzie Mountains and Hudson Bay Lowlands. Standardized regression coefficients (β) are shown for each site and species for three time periods. Coefficients in bold are significant at $P < 0.05$

Site	1851–1900	1901–1950	1951–2000	1980–2006
Western Mackenzie Mountains				
Dale Creek (*Al*)[a]	0.002	**0.018**	**0.013**	**0.030**
Boulder Creek (*Al*)	**-0.008**	**0.017**	**0.017**	0.014
Moose Valley/Wolf Creek (*Pg*)	0.000	**0.012**	**0.018**	**0.029**
Tsichu River (north–facing) (*Al*)	–	**0.007**	0.003	0.005
Tsichu River (south–facing) (*Al*)	-0.004	**0.011**	**0.012**	**0.020**
Regional-*Al* (pre-1920)[b]	-0.002	**0.018**	**0.016**	**0.027**
Regional-*Al* (all)	-0.002	**0.010**	**0.012**	**0.020**
Regional-*Pg* (pre-1920)[c]	0.000	**0.012**	**0.018**	**0.029**
Regional-*Pg* (all)	0.000	**0.007**	**0.012**	**0.021**
Hudson Bay Lowlands				
Ridge (Dt-*Pg*)[d]	**0.010**	**0.017**	**-0.012**	0.004
Rocket (Dt-*Pg*)	0.001	**0.006**	**-0.008**	**0.007**
Frog (Dt-*Pg*)	**-0.010**	**0.020**	**-0.014**	**-0.009**
Frog (Tr-*Pg*)	**0.004**	**0.022**	**-0.005**	**-0.013**
Black (Dt-*Pg*)	–	**0.011**	**-0.016**	-0.002
Black (Dt-*Pm*)	**0.014**	**0.012**	**-0.020**	-0.002
Black (Tr-*Pm*)	**0.007**	**0.008**	**-0.014**	-0.003
Black (Dt-*Ll*)	0.006	**0.033**	**-0.035**	**0.034**
Black (Tr-*Ll*)	**-0.010**	**0.008**	-0.001	**0.102**
Regional-*Pg* (pre-1920)	0.000	**0.010**	**-0.011**	0.003
Regional-*Pg* (all)	0.000	**0.006**	**-0.003**	**0.012**
Regional-*Pm* (pre-1920)[e]	0.000	**0.011**	**-0.011**	-0.002
Regional-*Pm* (all)	0.000	**0.009**	**-0.010**	0.002
Regional-*Ll* (pre-1920)	0.002	**0.013**	**-0.013**	**0.044**
Regional-*Ll* (all)	0.002	**0.010**	**-0.009**	**0.033**

[a] *Al=A. lasiocarpa*, *Pg=P. glauca*, *Pm=P. mariana*, *Ll=L. laricina*

[b] The regional chronologies are a composite of all ring-width series in a region for a given species.

[c] Includes only series from the Moose Valley/Wolf Creek sites

[d] Dt=distal to treeline, Tr=treeline

[e] Includes ring-width series from two sites within one kilometre of the Black site (Mamet & Kershaw, 2011). See text for details.

Growth of *A. lasiocarpa* was typically correlated with temperature during autumn and July (Figs. 2-4a and 2-4b). Some inter-site variability was evident as Dale Creek tree growth had some negative correlations with precipitation, while growth at Boulder Creek was not significantly correlated with precipitation. There were also differences between aspects, as each chronology responded differently to precipitation and temperature during spring and summer (Fig. 2-4d). Growth of *P. glauca* and *A. lasiocarpa* was negatively correlated with temperature during summer and precipitation in January (Fig. 2-4c). *P. glauca* growth was also negatively correlated with temperature during January and April, and positively correlated with temperature and precipitation during June.

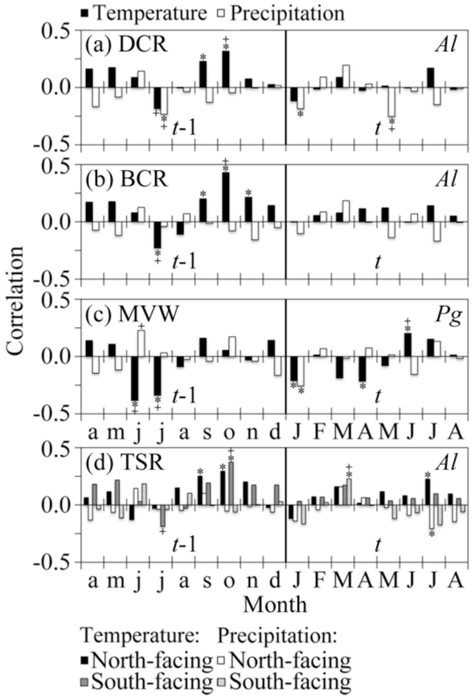

Figure 2-4. Correlation between mean monthly temperature and precipitation and the residual chronologies (RES) from the western Mackenzie Mountains for the 1930−2006 period. Species include *A. lasiocarpa* (*Al*) and *P. glauca* (*Pg*). Uppercase letters indicate comparisons with climate of the year of ring formation (*t*) and lowercase letters indicate comparisons with climate during the year preceding ring formation (*t*-1). *Significant at $P < 0.05$. +Significant variables after response-function analyses. Note the change in the legend for (d). See Table 2-1 for site codes.

Moving correlations

Growth response at Dale Creek appeared to change throughout the 20th century, and climate sensitivity appeared to diminish in recent years, with intermittent growth/climate correlations (Fig. 2-5a). At Boulder Creek, growth correlated with fewer climate variables, but had positive temperature correlations during spring and winter, and negative precipitation correlations during the growing season (Fig. 2-5b). In contrast with Dale Creek, positive correlations with October precipitation occurred at Boulder Creek. Response of *P. glauca* varied markedly from that of *A. lasiocarpa* (Fig. 2-5c). Few positive correlations were observed during the early record, and more during mid-century. Correlations with April temperature persisted throughout the later 20th century (Fig. 2-5c).

North-facing *A. lasiocarpa* at Tsichu River were less climate-sensitive than south-facing trees (Figs. 2-5d and 2-5e). North-facing trees had some correlation with temperature during spring and autumn, and precipitation during July mid-century. As well, correlations with July temperature (positive) and January precipitation (negative) occurred in recent decades. South-facing trees were correlated with temperature and precipitation intermittently throughout the 20th century (Fig. 2-5e).

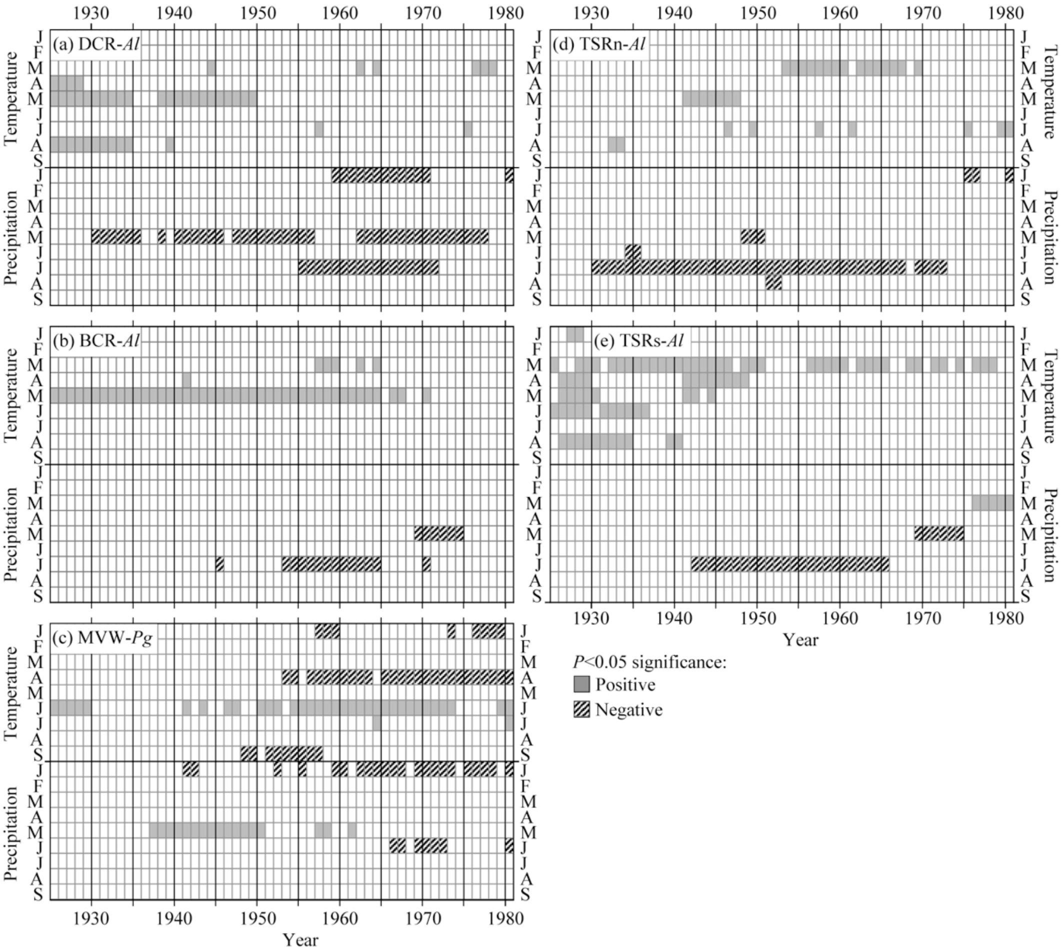

Figure 2-5. Correlations calculated within a 50-year sliding window with one-year time-steps, between the residual chronologies (RES) for each species, and monthly temperature and precipitation within the western Mackenzie Mountains (1901−2006). Species include *A. lasiocarpa* (*Al*) and *P. glauca* (*Pg*). See Table 2-1 for site codes.

Climate/growth relationships in the Hudson Bay Lowlands

Growth trends were variable during 1851–1900 and 1980–2006, though all species showed similar growth trends during the 20th century: positive from 1901–1950 and negative from 1951–2000 (Figs. 2-2d–2-2i; Table 2-4). The greatest growth of any species occurred in *L. laricina* from 1980–2006, particularly at treeline.

Growth of most trees was positively correlated with temperature during summer and autumn (Fig. 2-6). Rocket *P. glauca* growth distal to treeline was negatively correlated with temperature in January and May (Fig. 2-6b), and *L. laricina* growth at Black was also negatively correlated with May temperature (Figs. 2-6h and 2-6i). There was no clear pattern in the growth-precipitation relationship across sites. However, *P. glauca* was typically negatively correlated with January precipitation, while *P. mariana* and *L. laricina* were positively correlated with precipitation during March. As well, Black *Picea* distal to treeline was negatively correlated with summer precipitation (Figs. 2-6e and 2-6f).

Moving correlations

Growth response through time differed between and within sites, though there were some similarities among species (Fig. 2-7). Most *P. glauca* had some correlation with temperature during summer and spring, and late summer and January precipitation throughout the record (Fig. 2-7a). There was no consistent temperature or precipitation correlation for treeline *P. mariana* during the 20th century (Fig. 2-7g). *P. mariana* growth distal to treeline had more climate correlations than treeline individuals (Figs. 2-7f and 2-7g). In recent decades, *P. mariana* growth distal to treeline was positively correlated with summer temperature and January precipitation. Similarly, *L. laricina* growth was consistently correlated with temperature in spring (negative), and July (positive) (Figs. 2-7h and 2-7i). Recently, *L. laricina* growth distal to treeline positively correlated with September temperature and February precipitation, while *L. laricina* at treeline were positively correlated with late spring temperature.

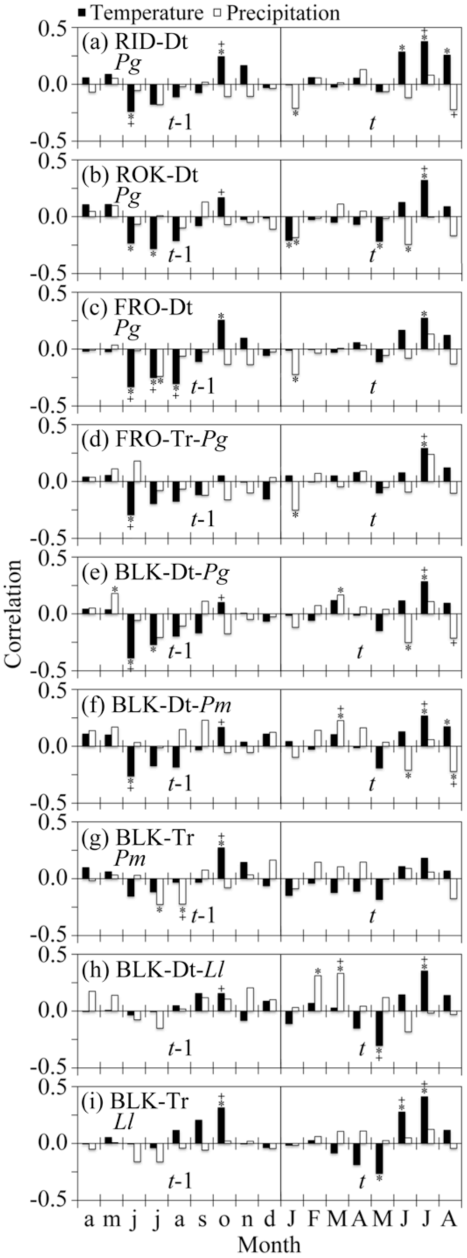

Figure 2-6. Correlation between mean monthly temperature and precipitation, and residual chronologies (RES) from the Hudson Bay lowlands for the 1930−2006 period. Dt=distal to treeline and Tr=treeline. Species include *P. glauca* (*Pg*), *P. mariana* (*Pm*) and *L. laricina* (*Ll*). Uppercase letters indicate comparisons with climate of the year of ring formation (*t*) and lowercase letters indicate comparisons with climate during the year preceding ring formation (*t*-1). *Significant at P < 0.05. +Significant variables after response-function analyses. See Table 2-1 for site codes.

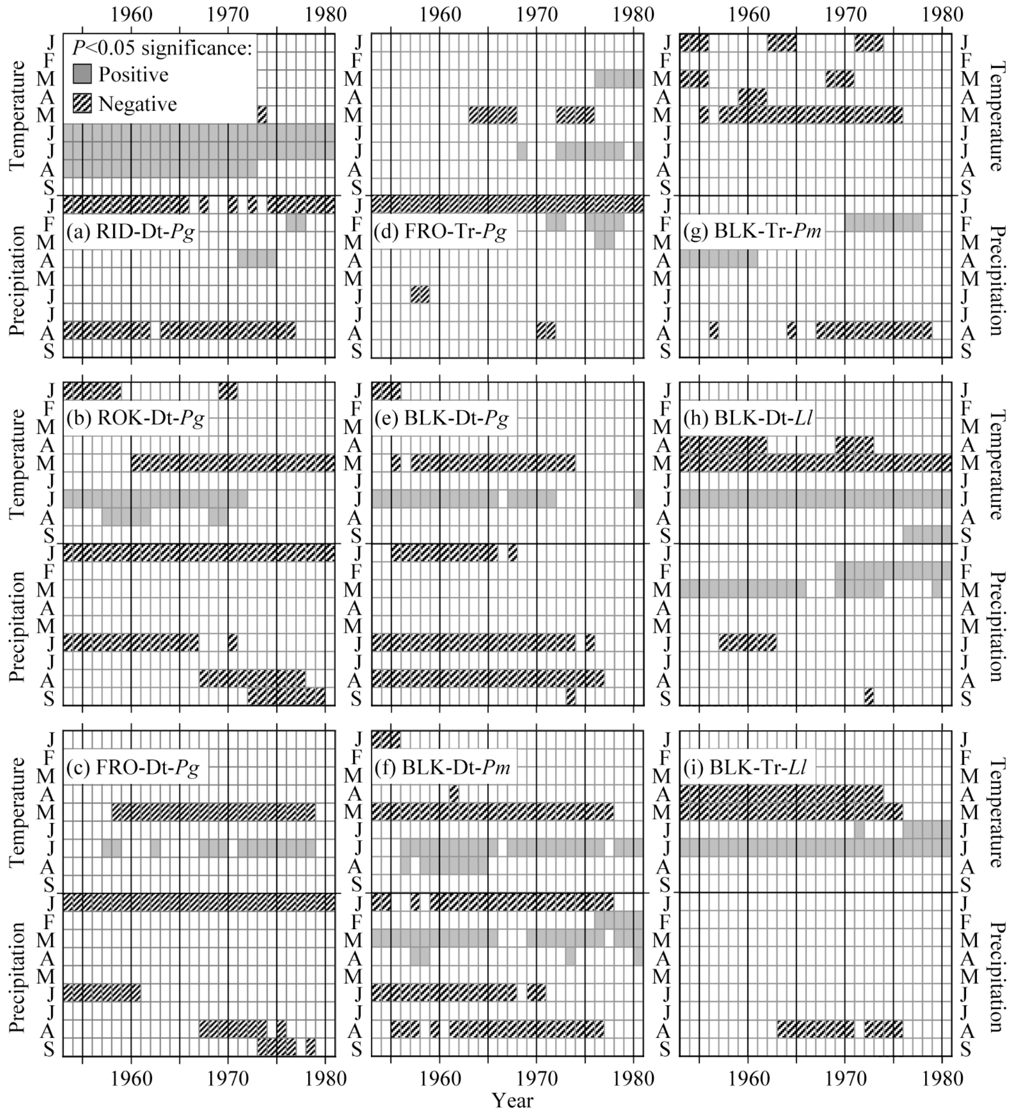

Figure 2-7. Correlations calculated within a 50-year sliding window with one-year time-steps, between the residual chronologies (RES) for each species and monthly temperature and precipitation within the western Hudson Bay lowlands (1930–2006). Species include *P. glauca* (*Pg*), *P. mariana* (*Pm*), and *L. laricina* (*Ll*). See Table 2-1 for site codes.

Regional long-term growth trends

To compare growth of each species in a region as a whole, all series of a given species were combined into single BAI indices (Fig. 2-8). A separate chronology was created for series established prior to 1920 (OLD), and for all series (ALL), and compared to growing season temperatures. Since there were few *P. mariana* and *L. laricina* trees sampled in the Hudson Bay Lowlands, those chronologies were supplemented with cores from two sites within one kilometre of the Black site (Mamet & Kershaw, 2008; Mamet & Kershaw, 2011).

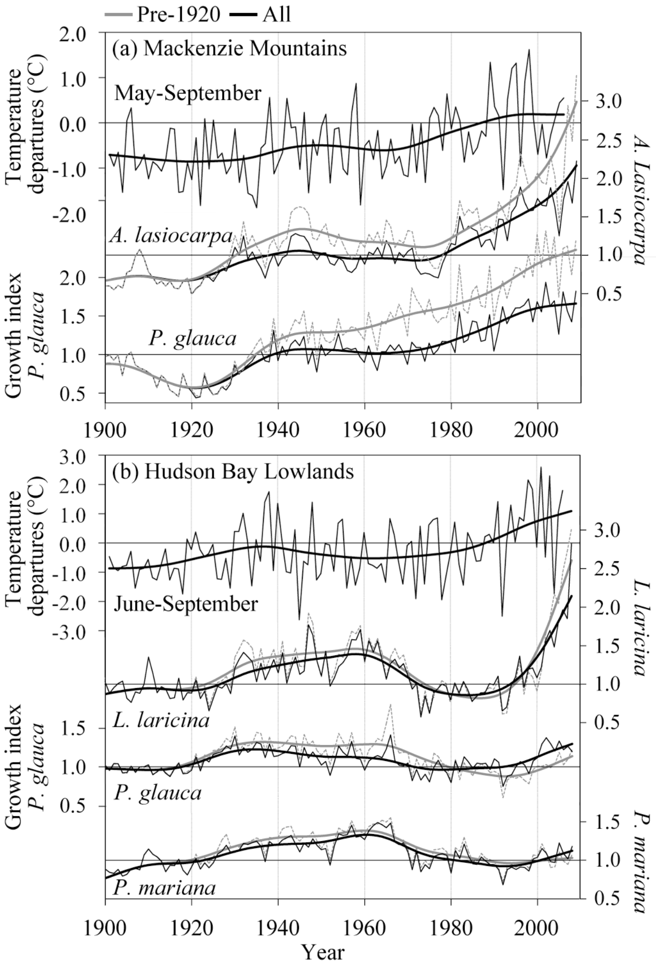

Figure 2-8. Relationship between regional tree growth dynamics and climatic change during the 20th century around the western Mackenzie Mountains and western Hudson Bay Lowlands. Top: mean temperatures during (a) May–Sept. for the region bounded by 63° N, 130° W and 64° N, 129° W, and (b) June–Sept. for the region bounded by 58° N, 94° W and 59° N, 93° W, from New *et al*. (2000). The thin line is temperature departures w.r.t. the 1971–2000 mean and the thick line is a smoothing spline. Bottom: BAI indices for each species. The thin grey lines (with thick grey smoothing splines) represent chronologies derived from trees established prior to 1920, and the thin black lines (with thick black smoothing splines) show chronologies derived from all sampled trees across the region.

Western Mackenzie Mountains

Growth trends within the Mackenzie Mountains corresponded among heterospecifics, and all chronologies had significant positive growth trends since 1900, regardless of sub-chronology series lengths (Table 2-4). However, there was a notable divergence between the ALL and OLD chronologies following 1920, when the ALL chronologies were reduced substantially (Fig. 2-8a). Growth trends of all chronologies corresponded with growing season temperatures since 1951 (Fig. 2-8 and Table 2-5).

Table 2-5. Results of tree growth/growing season temperature statistical comparisons during the 20th century. Values represent *P*-values generated by each Spearman's rank correlation test (rho). Values of rho have been converted to Z-scores in order to test significance ($P < 0.05$). Bold text indicates comparisons where the null hypothesis was rejected (i.e., statistically significant)

CR[a]	TI	*Al*	*Pg*	*Pm*	*Ll*
WMM					
OLD:	1901−1950	*Z*=1.55; *P*=0.061	*Z*=1.62; *P*=0.053	−	−
	1951−2006	**_Z_=2.10; _P_=0.018**	**_Z_=3.05; _P_=0.001**	−	−
	1901−2006	**_Z_=3.39; _P_<0.001**	**_Z_=4.24; _P_<0.001**	−	−
ALL:	1901−1950	**_Z_=1.67; _P_=0.048**	*Z*=1.51; *P*=0.066	−	−
	1951−2006	**_Z_=2.34; _P_=0.010**	**_Z_=3.46; _P_<0.001**	−	−
	1901−2006	**_Z_=3.50; _P_<0.001**	**_Z_=4.25; _P_<0.001**	−	−
HBL					
OLD:	1901−1950	−	**_Z_=4.22; _P_<0.001**	**_Z_=2.37; _P_=0.009**	**_Z_=4.38; _P_<0.001**
	1951−2006	−	*Z*=0.11; *P*=0.456	*Z*=0.87; *P*=0.192	**_Z_=2.27; _P_=0.012**
	1901−2006	−	*Z*=1.06; *P*=0.145	*Z*=0.51; *P*=0.304	**_Z_=3.03; _P_=0.001**
ALL:	1901−1950	−	**_Z_=4.43; _P_<0.001**	**_Z_=2.47; _P_=0.007**	**_Z_=3.90; _P_<0.001**
	1951−2006	−	**_Z_=4.31; _P_<0.001**	*Z*=0.30; *P*=0.382	**_Z_=3.03; _P_<0.001**
	1901−2006	−	**_Z_=3.91; _P_<0.001**	*Z*=0.84; *P*=0.201	**_Z_=3.53; _P_<0.001**

[a] CR = chronology, TI = time interval, *Al* = *A. lasiocarpa*, *Pg* = *P. glauca*, *Pm* = *P. mariana*, *Ll* = *L. laricina*

Hudson Bay Lowlands

All chronologies had good correspondence with each other for most of the 20th century, until the late 1970s when the ALL and OLD *Picea* chronologies diverged (Fig. 2-8b). Growth in both *P. mariana* chronologies was reduced relative to the other species. As well, OLD *P. mariana* growth had a negative trend, while the ALL chronology had a positive trend in recent years—though neither was significant (Table 2-4). All species exhibited no growth trends from 1851–1900, positive from 1901–1950, negative from 1951–2000, and then variable in recent decades. Growth of *L. laricina* increased markedly during the last 30 years, with positive trends several times greater than the rest of the chronologies. Contrary to the *Picea* chronologies, recent OLD *L. laricina* growth was greater than ALL. Moreover, ALL *L. laricina* growth was significantly correlated with temperature, as were ALL *P. glauca* (Table 2-5). The *P. mariana* chronologies typically had the lowest correlations with growing season temperatures.

DISCUSSION

Western Mackenzie Mountains

Patterns of tree growth and the relationship with climate varied among sites, species, aspects, and over time. Within the mountains, growth increased almost without exception during the 20th century. This pattern was concurrent with 20th century warming, though interspecific climate responses were unique and non-stationary through time. *A. lasiocarpa* responded primarily to July and autumn temperatures of the previous year, which suggests that a cool summer combined with a warm autumn can lead to increased carbon storage, mycorrhizal root growth, and/or maturation of needles, shoots, and buds, improving growth the following year (Tranquillini, 1979). Higher elevation trees at Dale Creek also responded negatively to precipitation during January and May, which could be indicative of heavy mid-winter snowfall resulting in a late-lying snowpack and delay in the onset of growth the following spring (Vaganov *et al.*, 1999), which was further delayed by spring snowfall. Aspect influences growth during summer, when north-facing *A. lasiocarpa* respond negatively to precipitation, which could lead to waterlogged soils from lower evapotranspiration; while south-facing trees could benefit from increased March rainfall—due to higher evaporative demands from earlier occurrence of snow melt, soil thaw and growth initiation. *P. glauca* growth was more sensitive to growing season conditions as indicated by the positive correlation with July temperature, though trees could become susceptible to moisture stress without an equal amount of rain, as indicated by correlations with previous-year's summer temperature (negative) and precipitation (positive) (Fig. 2-4c). *P. glauca* also appeared to be affected by late-lying snowpack due to enhanced January precipitation, potentially related to warmer temperatures (Vaganov *et al.*, 1999).

Within the mountains, it seems most trees have become rather less climate sensitive based on the number of significant correlations during the early 1900s, compared to the latter half of the century. Enhanced precipitation has typically been negatively correlated with growth, and only seems beneficial for south-facing trees. Moreover, the greatest growth trends have occurred since 1980—the warmest period on record for the region—when moisture stress and growth declines have been observed at other temperature-sensitive treelines (e.g., Briffa *et al.*, 1998; Jacoby *et al.*, 2000). Perhaps this recent trend is related to a changing seasonality in growth response due to warmer springs (Groisman *et al.*, 1994), or related to a signal not associated with meteoric water supply, such as snowpack redistribution by wind and its duration on the ground, or mechanical damage due to snow creep and/or pressure (Höller *et al.*, 2009). It could also be due to reduced capacity for water translocation through a tree with age, due to increasing root to shoot ratios, development of non-conductive heartwood, and a progressively thinning sheath of new xylem (Kozlowski, 1971). However, such parameters were beyond the scope of this study and further research is necessary to test such hypotheses.

Hudson Bay Lowlands

Growth responses were highly variable among sites and species in the Hudson Bay Lowlands. Growth across the region, almost without exception, switched from a positive trend in 1901–1950, to negative from 1951–2000 (Table 2-4). Most notably perhaps, is that all *P. glauca*—with the exception of Rocket—had either negative or no trends since 1980, in spite of recent warming. Growth of *L. laricina* was greatest in recent years, particularly at treeline. Such a range in growth can be explained in part by climate, topography and edaphic characteristics. Almost all *P. glauca* exhibited typical growth responses to temperature during summer and autumn, and January precipitation (see above for explanations), which has been found in other studies (Girardin *et al.*, 2005; Tardif *et al.*, 2008; Mamet & Kershaw, 2011), and appears to be relatively stable through time (Fig. 2-7). The variety of responses to precipitation found in this study is likely related to differing surface and internal drainage at the study sites. For example, the Ridge site was located on a north-south trending beach ridge relict from isostatic rebound (Dredge, 1992), and had a thin organic soil layer over carbonate sands and gravels—optimal habitat for *P. glauca* (Nienstaedt & Zasada, 1990). However, the distal to treeline sampling area on the southwestern flank of the ridge had a significantly thicker (two-tailed t-test: P = 0.004) organic layer compared to at treeline, which had impeded drainage due to a shallow active layer over impermeable permafrost. The sampling area distal to treeline at the Black site also had a thick organic layer and permafrost, and was also negatively correlated with August precipitation, though soils were thicker in the treeline sampling area. This could explain the negative response to precipitation, and the response of Black *P. glauca* in June, as precipitation could lead to further water logging. Water logging has also been observed at the Rocket site; though it is due to the spring melt of snow, which could be exacerbated by June rainfall. The presence of permafrost beneath all sites can impede drainage and has likely led to the consistent negative growth response of *P. glauca* to precipitation throughout the 20th century (Figs. 2-7a–2-7e).

Growth of *P. mariana* differed across the treeline ecotone, likely due to edaphic factors. The Black treeline ecotone occurred on the edge of a kame delta composed of carbonate sands and gravels deposited at the end of the last glaciation (Dredge, 1992), with the distal to treeline sampling area on the raised periphery of the delta, and treeline on the surrounding lichen-spruce bog. Thick, poorly drained organic soils of the bog are nutrient-poor, anaerobic and acidic relative to delta soils due to paludification. The distal to treeline *P. mariana* trees on the delta are therefore more likely to respond positively to growing season temperatures without a superseding edaphic influence, while treeline trees are probably limited more by subsurface influences (Crawford *et al.*, 2003) (Fig. 2-6).

Recent growth of *L. laricina* was unprecedented and responded primarily to July and autumn temperatures across the ecotone. Moreover, treeline *L. laricina* growth has become increasingly sensitive to June temperature, which could be a response to a lengthening growing season. As well, negative correlation of *L. laricina* growth with May temperature suggests adverse effects during growth initiation when roots of trees are still encased in frozen soil while air temperatures are above zero (Girardin *et al.*, 2005). In contrast to the growth response of *Picea*, distal to treeline *L. laricina* demonstrated positive correlations to late-winter precipitation (Fig. 2-6h), which is curious considering the expected negative association between late-lying snowpack and growth (Vaganov *et al.*, 1999). One plausible explanation for this relationship, is that late-lying snow does not adversely affect growth initiation and could act to protect against winter desiccation which can result from increased transpiration rates of shoots, photo-inhibitory stress and short-term fluctuations in shoot temperatures, leading to xylem embolism (Mayr & Charra-Vaskou, 2007). Conversely, none of the Black chronologies were correlated with January precipitation, which might suggest late-lying snow does not limit Black tree growth. Timing of snowfall and snowpack duration are important factors regulating growth during the later growing season. Evidently the complex spatial and temporal synergistic effects between winter precipitation and temperature, warrants further research into these ecological influences and their effect on growth in the Lowlands.

Regional growth responses during the 20th century

In the vicinity of both the subarctic and alpine treelines, the temporal pattern of long-term growth trends agreed with growing season temperature patterns during most of the 20th century (Fig. 2-8). This suggests that, despite site-specific environmental influences, regional long-term growth trends are responding strongly to temperature—albeit more so for some species than others (Table 2-5). However, there does appear to be an age-related growth suppression recently, which has been found in other studies (Szeicz & MacDonald, 1994; Carrer & Urbinati, 2004). However, interpretation of these suppressions is complicated by what may be the presence of detrending end effects (Melvin, 2004). End effects likely explain the growth suppression in the Mackenzie Mountains ALL chronologies, though not the Churchill chronologies. When other conservative standardization techniques were applied to the same series (negative exponential or line of slope ≤ 0; RCS), the results were virtually identical chronologies for Churchill, but the ALL suppression was reversed with OLD for the Mackenzie chronologies (data not shown). This is probably due to a significantly greater density of stems in the tree islands within the Mackenzies (Table 2-1), resulting in shading and reduced growth for the early record of younger trees within the stands. Therefore, when radii from the younger trees were included in the chronology, there was a notable suppression in the chronology immediately after 1920. In spite of this suppression, a greater correlation existed between the ALL chronologies and growing season temperatures. And while there could be an age-dependent trend in the Mackenzie chronologies, it is impossible to resolve it from potential detrending end effects. Clearly, further research is necessary to evaluate recent growth dynamics in the Mackenzie Mountains.

With the exception of Mackenzie Mountains chronologies and Hudson Bay *L. laricina*, OLD chronologies had noticeable growth suppression during the

1980s–2000s, particularly *P. glauca*. Moreover, comparison of the ALL indices yielded greater climate correlations at both locales (Table 2-5), contrary to other studies (Szeicz & MacDonald, 1994). These results suggest that including younger trees in a ring width chronology could enhance the long-term climate signal, though this effect is site- or region-specific. Trees of advanced age likely respond to factors other than climate, and two explanations are hypothesized here. First, as a tree develops, its root system grows into different soil environments resulting in different growth conditions (Pittock, 1982). Second, water translocation could be reduced due to a number of factors: increased tree height, increasingly complex hydraulic path length through stems and branches, and reduced allocation to roots, among others (Ryan & Yoder, 1997). These theories lend credence to the idea that individual trees could respond inversely to temperature (cf. Wilmking *et al.*, 2005), and as this study suggests, species- and site-specific traits can influence the magnitude and direction of the response.

CONCLUSIONS

Periods of enhanced growth have been observed elsewhere during the 20th century at a number of temperature-sensitive sites at treeline (e.g., Jacoby *et al.*, 2000). The same phenomena were observed in the western Northwest Territories and northern Manitoba in this study. However, site- and species-specific traits mitigated what ostensibly is a regional temperature forcing of tree growth at both locales. Growth trends typically did not differ between treeline and adjacent trees, but differed considerably between study areas. Nearly all chronologies within the Mackenzie Mountains experienced significant positive growth trends since the

1980s, while in the Hudson Bay Lowlands, only *L. laricina* (and *P. glauca* at one site) responded similarly within the same interval. Specific climate responses differed across the treeline ecotone within the Hudson Bay Lowlands, probably related to topography, vegetation density and edaphic characteristics. Growth of *P. glauca* was most likely to suffer from moisture stress or adverse effects from enhanced snowfall, though all species appeared to be responding primarily to summer and autumn temperatures. An exception was treeline *P. mariana*, which demonstrated little climate correlation, probably related to paludification (Crawford *et al.*, 2003). Most notably perhaps, was that *L. laricina* demonstrated the highest correlation with climate and greatest growth trends in recent years, which is paralleled by recent increases in *Larix* establishment across the circumboreal (Peñalba & Payette, 1997; Treter, 2000; MacDonald *et al.*, 2008; Mamet & Kershaw, 2012; among others). And despite the suppressed growth in older trees of most species in recent years, *Larix* > 85 years old demonstrated the greatest growth of all chronologies during recent decades. As the climatic response of most trees appeared to be variable through time, future research should focus on continued monitoring of growth to determine if current growth trends will continue with projected warming, or if the current exception of moisture stress as a limiting factor at treeline could become the norm.

The results of this study confirm temperature as the main forcing of recent tree growth patterns observed within continental treeline, though factors such as topography, near-surface permafrost, paludification, as well as age-dependent and autecological traits mitigate regional-scale responses. Some aspects of this study are in agreement with what has been found in some areas (Jacoby *et al.*, 2000), while it contrasts with the work of others (Lloyd & Fastie, 2002). While this study has answered some questions about tree growth at treeline, in lieu of predicted warming and a variety of growth responses found by others, several more questions have been revealed: (1) Will the current positive growth trend demonstrated by several species across the study areas continue? (2) Do these temperature-induced growth increases have the potential to have a negative feedback with warming? (3) Will some trees become primarily limited by moisture stress? And (4) to what extent will growth response and/or moisture stress be mitigated by ongoing paludification in some areas? In order to answer these and other questions that may arise, future monitoring of treeline populations is crucial due to the age-dependent and interspecific nature of growth response to climate, and should consider detrending end-effects in any further dendroclimatological research.

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CHAPTER THREE

Environmental influences on needle health of *Picea glauca* at treeline, Churchill, Manitoba[2]

"Damage through abrasion is significant. It may cause water stress, defoliation, death of needles, and a consequent reduction in the photosynthetic area of the plant. Whether the thickness of cuticle is a major determinant of susceptibility to damage is open to question."

John Grace (1993)

INTRODUCTION

Winter desiccation of foliage is believed to contribute to the stress of conifers at treeline. At high altitudes and latitudes, cuticular development can be restricted by a short and cool growing season (Wardle, 1971; Tranquillini, 1979). Increased cuticular transpiration can result in severe winter dehydration, and it has been suggested that winter desiccation is a primary determining factor for the range limits of treeline trees (Tranquillini, 1979; Kullman, 2007; Holtmeier & Broll, 2011). Winter desiccation is associated with two processes that can occur simultaneously, though independent of each other: frost-drought and abrasion by wind blown snow grains. Frost-drought occurs because soil water is frozen or just cold, and is unavailable to the plant, though transpiration proceeds—even in winter (Michaelis, 1934). Furthermore, increased winter desiccation can occur when the epidermis of needles fails to fully develop as a result of a lack of warmth during the short growing season, and consequently needles are poorly protected against cuticular transpiration during the following winter (Wardle, 1971; Tranquillini,

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1979). Strong winds can transport snow grains at high velocities, which abrade the cuticles of needles and damage stomata, leading to increased water losses, particularly at the end of winter (Hadley *et al*., 1991; van Gardingen *et al*., 1991). In either case, dehydration would likely be most severe during cold winters with low precipitation for two reasons: (i) the rooting zone remains frozen longer, during which time the supply of water to the needles is prevented, and (ii) needles that might normally be snow-covered and protected from extremely cold temperatures and wind-blown snow abrasion, instead can be exposed to the elements and susceptible to tissue damage and water loss (Grace, 1977; Cairns, 2001).

Climatic changes during the last 20 to 30 years have resulted in increased scrutiny on marginal environments like the treeline ecotone, as they are most likely to transform with warming (cf. Harsch *et al*., 2009). Numerous studies have suggested a causal linkage between temperature and metrics of treeline dynamics such as fecundity, establishment, recruitment, radial and height growth, and treeline movement, among others (Batllori *et al*., 2009; Holtmeier & Broll, 2010; Kharuk *et al*., 2010). It seems logical to assume a direct relationship between an environmental factor and a plant performance parameter if the two variables are found to vary concomitantly along an ecotone. However, such co-variation does not necessarily represent a causal mechanism, as indirect effects of an environmental factor (e.g., summer temperature) can have a greater effect on a parameter of interest (e.g., tree growth) through its effects on another factor (e.g., needle maturation). Thus determining how plant performance can be affected by its environment is often quite difficult, and studies can be further complicated by non-linear processes, difficult to predict synergistic interactions, and fortuitous co-variation between environment and plants (Sveinbjörnsson *et al*., 2002).

Several studies on coniferous foliage and environmental conditions around Churchill, Manitoba, were completed during the 1980s and 1990s (Scott *et al*., 1987a; Scott *et al*., 1987b; Scott & Hansell, 1992; Scott *et al*., 1993; Scott & Hansell, 2002). Scott *et al*. (1993) found that wind-blown snow abrasion and needle loss represented a noticeable limitation to growth above the snowpack, and that trees needed to achieve at least 80 cm in height over seven to eight years in order to successfully mitigate passage through the abrasion zone. Abrasion was alleviated by tree and branch density, as woodlands (scattered groupings of erect trees) and open forest (>95% full-crowned trees) were virtually free of snow abrasion, and snow load on branches was the dominant winter stress in those treed environments (Scott *et al*., 1993; Scott & Hansell, 2002). Temperature and moisture extremes in the tundra caused height growth to be reduced in the prostrate trees established there, which meant that the stem of a terminal bud of a tundra tree will be forced to spend a substantial number of winters in the abrasion zone, leaving it more vulnerable to damage (Scott *et al*., 1987a). Thus there is evidence that supports the idea that a synergy of processes operating during the summer (e.g., height growth, needle development) and winter (frost drought and winter desiccation) play a role in treeline dynamics around Churchill, which has been suggested by studies from other regions (Baig & Tranquillini, 1980; Hadley & Smith, 1983, 1987; Kayama *et al*., 2009; Nagano *et al*., 2009; among others).

Despite the hypothesis that treeline around Churchill would not likely advance with warming, unless there was a disturbance resulting in secondary succession (Scott *et al.*, 1987b), recent evidence suggests that treeline advancement has resumed during the warm period of the last 30 years (Mamet & Kershaw, 2011a). However, several studies suggest the effects of not only summer conditions, but also winter environments cannot be ignored in searching for regional mechanisms for the treeline phenomenon (Kullman, 2007; Kharuk *et al.*, 2010; Holtmeier & Broll, 2011; Kirdyanov *et al.*, 2012). Further, to our knowledge, there have been no studies on winter effects on treeline vegetation in the Churchill area in 20 years or more, nor have there been comparable studies on finer scale treelines (<100 m from forest to tundra) in the area. Therefore, the purpose of this study was to compare metrics of needle health within open forest, the forest-tundra ecotone and tundra, and determine the presence of winter desiccation and its relevance to treeline dynamics in the Churchill region. Specifically, the aim was to answer the following questions—how does needle health vary: (1) within and above the mid-winter snowpack? (2) with orientation to regional wind patterns? (3) in forest-facing and tundra-facing margins of trees? (4) through time as a function of environmental conditions during needle formation? And (5) is there a link between winter desiccation and recent treeline dynamics?

MATERIALS AND METHODS

Study Area

Sampling was completed during mid-winter (late February/early March) of 2008–2010 at four sites east of the Churchill town site (58°45′ N, 93°04′ W) (Fig.

3-1; Table 3-1). Tree populations at the four sites were dominated by *Picea glauca* (Moench) Voss. (white spruce), with scattered *Larix laricina* (Du Roi) K. Koch. (tamarack). *Picea mariana* (Mill.) B.M.P. were very rare at the four sites, though become increasingly prevalent further inland as a thicker layer of peat has accumulated following post-glacial isostatic rebound, making conditions more conducive for *P. mariana* establishment (Dredge, 1992; Wolf *et al.*, 2006). *Rhododedron groenlandicum* (Oeder) Kron & Judd (Labrador tea) and *Betula glandulosa* Michx. (dwarf birch) dominate the understory in treed environments across the region. Mean January, July and annual temperatures are -26.7, 12.0 and -6.9°C, respectively (1971−2000 normal). An average of 562 mm of precipitation falls annually with 52% as snow (Environment Canada, 2012).

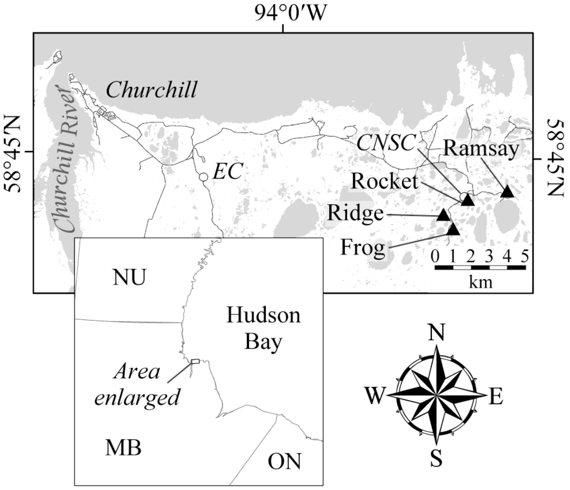

Figure 3-1. Location of the sampling sites southeast of Churchill, Manitoba. Open circles show the locations of the Environment Canada weather station (EC) and the Churchill Northern Studies Centre (CNSC). Site descriptions are given in Table 1.

Needle collection

During the winter field season at each of the four sites, the most recent production of needles or "branchlets" formed during the preceding growing season were sampled at several heights and orientations from three randomly selected *P. glauca* trees in each zone: forest, forest-tundra ecotone, and tundra. Using pruning shears, a branchlet was removed from each tree >15 cm depth into the snowpack, within the abrasion zone (0–80 cm above the snow surface), and >1.5 m above the snow surface. This sampling was replicated three times on each tree to represent three cardinal directions: northwest–the dominant wind direction, south–greatest receipt of solar radiation and hence, greatest potential for solar desiccation (cf. Hadley *et al.*, 1991), and east as a control. As the tundra is by definition, "treeless", and only stunted individuals were found, samples were only collected from within the snowpack and in the abrasion zone [collected each season: $n_{P.\ glauca}=36$, $n_{\text{branchlets}}=288$ (4 sites × 72 branchlets per site)].

Table 3-1. Characteristics of each site from which needles were sampled from 2008 to 2010.

Site	Abbreviation	Elevation (m.a.s.l.)	Zone[a]	Orientation[b]	Ecotone length (m)	Canopy openness (%)[c]
Frog pond	FRO	16	F	248°	36	91.6±1.6
			E			91.5±1.2
			T			100.0[d]
Ramsay Lake	RAM	18	F	136°	67	79.6±7.2
			E			81.2±10.
			T			100.0
Ridge	RID	22	F	38°	49	63.8±8.3
			E			83.6±7.4
			T			100.0
Rocket	ROK	16	F	190°	103	53.2±9.4
			E			83.2±6.3
			T			100.0

[a] F=forest, E=ecotone, T=tundra

[b] Bearing in which tree density decreases (i.e., forest transitions to tundra)

[c] Determined through analysis of hemispherical photos taken at each site (n=18 per site) (Frazer *et al.*, 1999)

[d] Canopy openness was assumed to be 100% within the tundra as there was no tree cover

Since not all sites were oriented with the gradient of decreasing tree density into the northwest, in 2010 branchlets were collected from the forest and tundra-facing aspects of each tree, in addition to the three cardinal directions described previously. However, due to logistical constraints, this double sampling was only completed at one site (Rocket). Following collection in the field, all branchlets were placed in sealed Ziploc© bags, kept in the dark at 5°C or cooler, until laboratory processing.

Snowpack

Mid-winter snowpack sampling was carried out from 28 February to 6 March 2008 and 2009, and included snow pits and snow cores obtained using an Adirondack snow sampler (McClung & Schaerer, 2006), within the three zones at each site. Due to time constraints, no snowpack survey was completed in 2010. Only the snow cores were analyzed for this study. Heat Transfer Coefficient (HTC) was calculated following Kershaw (1991; 2001), in order to compare thermal properties of snow among sites.

Soil temperature

To measure soil temperature at 10 cm depth, HOBO microloggers (HOBO H8 Pro, Onset Computer Corporation, Cape Cod, MA, USA; with a measuring range of –30 to +50°C and a resolution of 0.2°C, measured hourly) were deployed within the forest and at treeline. Loggers were initiated 22 June 2008, and data were collected during October and June each year. Due to logistical constraints, loggers were not deployed within the tundra zone at each site.

Needle water content and viability

Percent water content (WC) was determined from measurements of fresh and dry weights (*f.w.* and *d.w.*) determined using a Scientech® SA210 precision weigh balance (Scientech, Inc., Boulder, Colorado, U.S.A) following Hadley & Smith (1983):

$$\mathrm{WC} = \frac{f.w.\text{-}d.w.}{d.w.} \times 100 \tag{1}$$

Dry weights were measured after three days of drying at 105°C. Needle viability was determined by computing the percent of needles remaining green (>50% of needle area) after five days at room temperature (2008: 18.5±2.3°C, 2009: 18.3±3.4°C, 2010: 18.5±1.9°C) and 9.7–11.3% relative humidity (cf. Hadley & Smith, 1983) as determined at five minute intervals using a Campbell Scientific® HMP45C-L temperature and relative humidity probe (Campbell Scientific Canada Corp., Edmonton, Alberta, Canada).

Epidermal conductance

Transpiration rates were determined gravimetrically from the excised branchlets. The cut ends of the each branchlet were sealed with paraffin wax in order to prevent water loss through the cut. Water loss through the stem was assumed to be minimal (Baig & Tranquillini, 1980). Following determination of fresh weight, branchlets were weighed at 24-hour intervals for five days in a darkened room at ambient conditions before dry weight determination (Baig and Tranquillini, 1980). Determinations of needle surface area (SA) were completed using cross-sectional needle geometries computed for *Picea* by Bond-Lamberty *et al*. (2003), and the mean needle length (l) for each branchlet by:

$$\mathrm{SA} = 2l\left(\sqrt{1.35^2 + 1}\right) \tag{2}$$

Epidermal conductance was calculated as needle transpiration per unit surface area (g m^{-2} s^{-1}) divided by the water vapor concentration gradient (g m^{-3}) between the needle interior and the surrounding environment, assuming 100% relative humidity within the needle and similar needle and air temperatures (Anfodillo *et al.*, 2002). Epidermal conductance was expressed in m s^{-1} 10^{-5} as recommended by Kerstiens (1996). Minimum epidermal conductance (g_{min}) was determined by fitting a least-squares regression line to the relationship between epidermal conductance and time since full stomatal closure was assumed to have occurred. It is impossible to determine if all stomata closed, as some could have been damaged or non-functional. Therefore the term epidermal conductance was used to include both cuticular and any residual stomatal conductance components following closure (van Gardingen *et al.*, 1991). The intercept of the regression line when t=0 provides an unbiased estimate of g_{min} (van Gardingen *et al.*, 1991). Data obtained during the period before full stomatal closure had a curvilinear relationship and were excluded from the regression.

Data analyses

Statistical tests were performed using SigmaStat version 3.5 (Systat Software Inc., Son Jose, CA, U.S.A.). Preliminary one-way ANOVA suggested there was no difference in each needle metric among zones between sites. Therefore similar zones were combined, and statistical differences in needle metrics among azimuths, heights, and zones were investigated by one-way ANOVA at a regional scale.

RESULTS

Environmental conditions

Mean daily air temperatures from 22 June to 15 September (growing season) were 11.8°C, 12.3°C, and 9.8°C, in 2007, 2008 and 2009, respectively. Air temperatures during 2009 were 1.1°C cooler than the 1971–2000 normal of 10.9°C, and significantly cooler than 2007 and 2008 ($F_{2,254} = 7.087$, $P = 0.001$). Air temperatures were also warmer than within the soil, and soil temperatures increased significantly from forest to within the ecotone in both 2008 ($F_{3,856} = 49.707$, $P < 0.001$) and 2009 ($F_{3,856} = 47.993$, $P < 0.001$) (Fig. 3-2a).

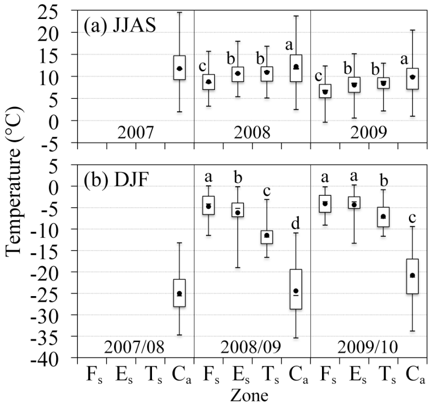

Figure 3-2. Temperature of the air and at 10 cm soil depth across the forest-tundra ecotone. (a) Growing season temperatures from 22 June to 15 September (JJAS) and (b) winter temperatures from 1 December to 28/29 February. Fs=forest soil, Es=ecotone soil, Ts=tundra soil, Ca=Churchill air temperature. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each zone is indicated as a solid circle. Different lowercase letters at the top of each box stand for intra-year differences based on a one-way ANOVA followed by a Holm-Sidak post hoc comparison. No soil temperature measurements were available prior to 22 June 2008. Statistical differences are significant at $P < 0.05$.

Mid-winter air temperatures (December–February) were similar in 2007/08 (–25.0°C) and 2008/09 (–24.4°C), though significantly warmer during 2009/10 (–20.7°C) ($F_{2,266} = 15.639$, $P < 0.001$). Mid-winter of 2009/10 was also 3.9°C warmer than normal (–24.8°C). Mid-winter air temperatures were significantly cooler than soil temperatures (2008/09: $F_{3,896} = 723.249$, $P < 0.001$; 2009/10: $F_{3,894} = 785.992$, $P < 0.001$), and soil temperatures decreased from forest to tundra (Fig. 3-2b).

Snow depth ranged from 64–82 cm in forest to 9–16 cm in tundra, and was significantly different among zones and years ($F_{5,731} = 215.314$, $P < 0.001$) (Fig. 3-3a). The thermal conductivity of the snow as indicated by the Heat Transfer

Coefficient (HTC) was similar between forest and ecotone (range: 0.28–0.66 Wm^{-2}°K^{-1}), but significantly greater within the tundra (1.04–1.90 Wm^{-2}°K^{-1}) ($F_{5,732}$ = 119.109, $P < 0.001$) (Fig. 3-3b).

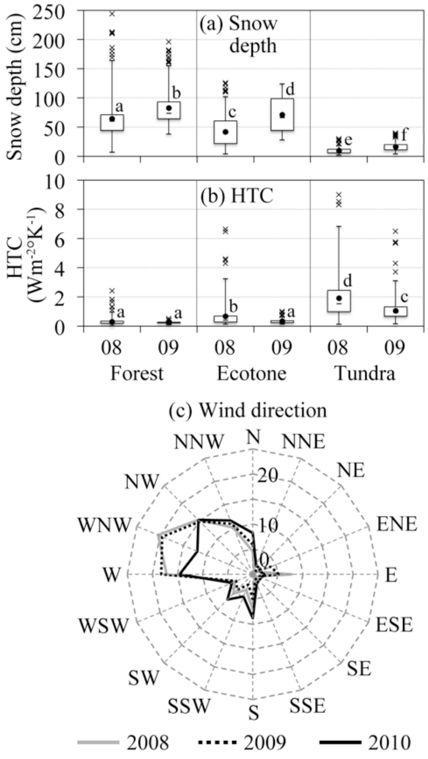

Figure 3-3. Mid-winter snowpack characteristics (2008–2009) and wind direction frequency (2008–2010). (a) Snow depth. (b) Heat Transfer Coefficient (HTC). (c) Wind direction frequency (Environment Canada, 2012). Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each zone is indicated as a solid circle. (a, b) Outliers for each year (± two standard deviations) are indicated by the letter ‘x’. Different lowercase letters at the top of each box stand for differences based on a one-way ANOVA followed by a Holm-Sidak post hoc comparison. Statistical differences are significant at $P < 0.05$.

Mid-winter wind gusts typically originated between west and northwest, with 52.9%, 52.6% and 41.9% frequency during 2007/08, 2008/09 and 2009/10, respectively (Fig. 3-3c). Mean wind speeds were similar at ~23 ± 12 km h^{-1} between mid-winter of 2007/08 and 2008/09, though significantly lower during 2009/10 (20 ± 13 km h^{-1}) ($F_{2,6485}$ = 24.146, $P < 0.001$). Similarly, strong breezes (>

41 km h^{-1} according to the Beaufort Scale) occurred approximately 12% of the time from 2007–2009, but with only 9% frequency during 2009–2010.

Minimum epidermal conductance

Minimum epidermal conductance (g_{min}) varied little among different azimuths, heights and zones (Fig. 3-4). During 2008, g_{min} was significantly greater in northwest-facing tundra needles compared to east-facing needles ($F_{2,61} = 3.254$, $P = 0.045$), and g_{min} of tundra-northwest needles were significantly greater than in the forest or ecotone ($F_{2,75} = 4.556$, $P = 0.014$) (Fig. 3-4a). Though the same patterns were not observed in 2009 (Fig. 3-4b), ecotone needles at a height > 0.8 m had greater values of g_{min} relative to the abrasion zone and snowpack in 2009 ($F_{2,92} = 7.854$, $P < 0.001$) (Fig. 3-4d) and 2010 ($F_{2,45} = 8.474$, $P < 0.001$) (Fig. 3-5).

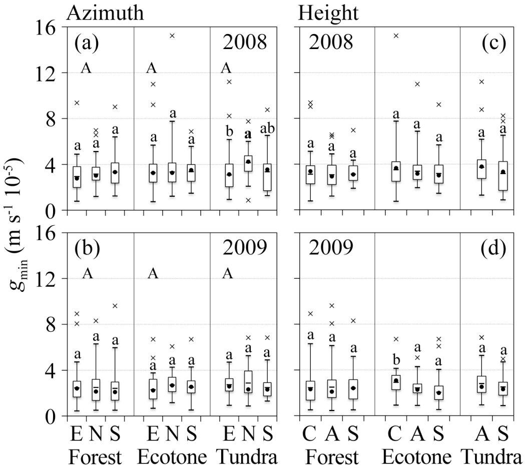

Figure 3-4. Minimum epidermal conductance (g_{min}) among different (a,b) azimuths and (c,d) heights from 2008–2009. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each orientation is indicated as a solid circle. Outliers for each orientation (± two standard deviations) are indicated by the letter 'x'. Different lowercase letters at the top of each box stand for intra-zone differences based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. Values in bold represent differences among similar orientations between years. Different uppercase letters represent differences among zones. Statistical differences are significant at $P < 0.05$. (a,b) E=east, N=northwest, S=south. (c,d) C=> 0.8 m and A=0–0.8 m height above the snowpack, S=> 0.15 m depth into the snowpack.

There was little difference in $g_{\min}$ among needles sampled from the forest- and tundra-facing sides of trees (Fig. 3-5a). The $g_{\min}$ of forest-facing needles within the forest zone was significantly lower than that of tundra-facing needles (t_{48} = -2.052, P = 0.046). Similarly, $g_{\min}$ was similar within ecotone and tundra, and significantly lower in the forest ($F_{2,129}$ = 7.599, P < 0.001). Needles sampled at a height > 0.8 m within the ecotone, exhibited a $g_{\min}$ significantly greater than needles from a similar height within the forest (t_{30} = -4.603, P < 0.001) (Fig. 3-5b).

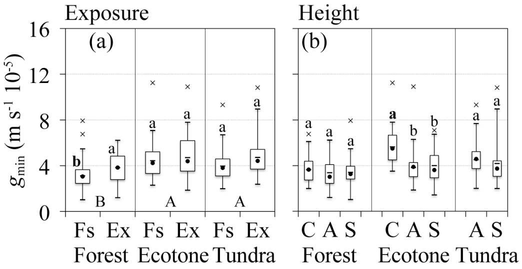

Figure 3-5. Minimum epidermal conductance ($g_{\min}$) among different (a) exposures and (b) heights during 2010. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each orientation is indicated as a solid circle. Outliers for each orientation (± two standard deviations) are indicated by the letter 'x'. Different lowercase letters at the top of each box stand for intra-zone differences based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. Values in bold represent differences among similar orientations between years. Different uppercase letters represent differences among zones. Statistical differences are significant at P < 0.05. (a) Fs=forest-facing, Ex=tundra-facing (exposed). (b) C=> 0.8 m and A=0–0.8 m height above the snowpack, S=> 0.15 m depth into the snowpack.

Annual variation in $g_{\min}$ from 2008 to 2010 was inversely related to temperatures during the June of needle formation in the previous year (Fig. 3-6). Values of $g_{\min}$ were significantly different among years ($F_{2,187}$ = 97.756, P < 0.001), as were June temperatures ($F_{2,2155}$ = 127.641, P < 0.001). Most notably perhaps is that the highest values of $g_{\min}$ (4.6×10^{-5} m s^{-1}) were observed in 2010, when temperatures during the previous June were 3.7°C; 2.9°C cooler than normal. Conversely, the lowest $g_{\min}$ of 2.8×10^{-5} m s^{-1} occurred during 2009 when the previous June was 7.8°C; 1.2°C warmer than normal.

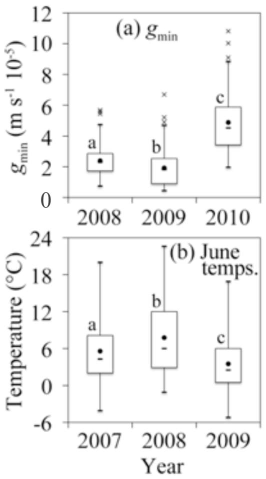

Figure 3-6. (a) Minimum epidermal conductance (g_{min}) at site Rocket and (b) June temperatures (Environment Canada, 2012) from 2007–2010. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each year is indicated by a solid circle. Outliers for each year (± two standard deviations) are indicated by the letter 'x'. Different lowercase letters at the top of each box stand for differences between years based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. Differences are significant at $P < 0.05$.

Needle viability and water content

Mean length of needles produced during 2009 (7.45 ± 0.04 mm; values are ± SE) were significantly shorter than those originating from 2007 (9.42 ± 0.06 mm) and 2008 (9.10 ± 0.04 mm) ($F_{2,3607} = 288.361$, $P < 0.001$). Needle water content and viability were consistent among zones, orientations and years (Table 3-2). There were few correlations between needle viability and water content, and little consistency in correlations from year to year (Table 3-3). However, significant correlations were observed during all three years in northwestern-facing needles within the ecotone zone.

Table 3-2. Water content and viability of *P. glauca* needles collected during mid-winter 2008–2010. Values are ± one standard error. There were no statistical differences among zones, orientations, or years (one-way ANOVA, $P > 0.05$).

		Water content (%)			Viability (%)		
Zone	Orientation	2008	2009	2010	2008	2009	2010
Forest	> 0.8 m	103.2 ± 5.0	100.9 ± 4.2	105.0 ± 8.5	97.5 ± 1.5	96.3 ± 1.4	95.4 ± 1.5
	Abrasion	104.1 ± 1.4	97.0 ± 2.7	102.5 ± 4.0	96.5 ± 2.0	96.4 ± 0.9	94.6 ± 2.4
	Snowpack	98.9 ± 2.8	99.8 ± 3.5	118.1 ± 18.2	94.5 ± 4.4	95.4 ± 1.8	88.2 ± 4.1
Ecotone	> 0.8 m	101.3 ± 1.9	96.9 ± 1.3	111.7 ± 1.5	96.7 ± 2.7	95.1 ± 1.2	97.0 ± 1.1
	Abrasion	101.0 ± 1.6	97.5 ± 1.3	110.2 ± 2.2	98.2 ± 0.8	96.2 ± 0.7	96.7 ± 1.2
	Snowpack	95.4 ± 3.4	96.4 ± 2.2	107.9 ± 9.6	98.6 ± 0.5	95.2 ± 1.9	90.3 ± 6.0
Tundra	Abrasion	100.7 ± 2.3	102.1 ± 3.7	99.6 ± 1.9	99.5 ± 0.1	90.3 ± 2.4	89.5 ± 5.2
	Snowpack	98.6 ± 2.4	96.5 ± 2.7	99.9 ± 2.3	97.6 ± 1.2	92.0 ± 2.1	90.4 ± 5.4
Forest	East	106.9 ± 4.8	94.2 ± 4.4	102.2 ± 5.8	98.4 ± 0.6	92.5 ± 2.2	92.8 ± 1.4
	Northwest	101.6 ± 1.9	103.0 ± 3.4	105.2 ± 6.3	96.1 ± 2.4	97.6 ± 0.5	84.6 ± 4.4
	South	99.1 ± 3.4	100.7 ± 2.2	108.5 ± 6.2	94.7 ± 3.4	98.2 ± 0.4	89.4 ± 5.6
Ecotone	East	98.6 ± 1.6	95.0 ± 1.4	104.3 ± 4.3	98.0 ± 0.9	96.5 ± 0.4	94.7 ± 2.4
	Northwest	103.0 ± 2.9	97.5 ± 2.0	104.3 ± 3.4	96.0 ± 2.9	94.4 ± 1.4	95.4 ± 1.4
	South	96.4 ± 2.5	98.3 ± 1.2	103.8 ± 1.9	99.3 ± 0.2	95.7 ± 1.5	90.8 ± 2.4
Tundra	East	99.4 ± 2.2	98.9 ± 2.6	120.6 ± 7.3	99.9 ± 0.0	92.8 ± 2.2	94.2 ± 4.7
	Northwest	102.1 ± 3.7	101.2 ± 6.5	109.7 ± 10.8	96.1 ± 1.8	92.2 ± 2.8	98.1 ± 1.2
	South	97.9 ± 2.7	98.2 ± 2.2	112.0 ± 2.1	99.6 ± 0.2	88.4 ± 3.2	89.5 ± 6.1

Table 3-3. Correlations between needle viability and percent water content from *P. glauca* needles collected from various orientations across the forest-tundra transition. Only values associated with $P \leq 0.05$ are shown; $P \leq 0.01$ for bold values. F=forest, E=ecotone, T=tundra.

Year	Zone	Orientation	r	n
2008	F	> 0.8 m	**0.558**	33
2008	F	Abrasion	0.434	33
2009	F	Snow	0.408	30
2008	F	Northwest	0.462	28
2008	E	> 0.8 m	**0.865**	35
2008	E	Abrasion	**0.716**	35
2008	E	Northwest	**0.554**	33
2009	E	Northwest	**0.458**	33
2010	E	Northwest	0.806	8
2010	T	Abrasion	0.551	18
2008	T	South	**0.609**	24

DISCUSSION

Epidermal conductance, water content and viability

The mean values of g_{min} obtained in this study were similar to those obtained by others (Sowell *et al.*, 1982; Heinsoo & Koppel, 1998; Anfodillo *et al.*, 2002), and despite notable inter-tree variability in g_{min}, there was very little variation across a gradient of decreasing tree density from 2008 to 2010. However, there was a significant difference in g_{min} between years, and a noticeable correspondence between temporal patterns of g_{min} and early growing season temperatures (Fig. 3-6). This supports the hypothesis of Michaelis (1934) and Wardle (1971) that insufficient maturation of coniferous foliage during the growing season can influence the desiccation resistance of coniferous foliage during the following winter.

There was little variability in g_{min}, needle water content, or viability with either sampling height or orientation to the regional wind patterns, though there was some association between viability and water content across the region (Table 3-3). Based on zone of greatest wind exposure around Churchill and the work of others (Baig & Tranquillini, 1980; Hadley & Smith, 1983; Scott & Hansell, 1992), it was expected that correlations between viability and water content would be greatest within different subsets of the sampling schemes—zone: tundra, azimuth: northwest, and height: abrasion zone. Indeed there were significant correlations observed within these sampling units, though the only consistency among years was for northwest-facing branches within the ecotone. These results are exceptional as none of the sampling sites were oriented with the tree density gradient—parallel to the regional wind direction, yet all sites together reflected what could be interpreted as a regional wind signal within the ecotone. While there was a statistically significant relationship between viability and water content, it is beyond the scope of this study to determine if this phenomena is due to increased abrasion from wind blown snow and ice particles, damage to the stomata, the rubbing together of adjacent needles, or the flexing of leaves in the wind (Grace, 1977; van Gardingen *et al.*, 1991). It is likely a combination of two or more of these actions, though the mechanical abrasion by neighboring needles and branches is probably more important for water loss. This is because it would be expected that northwest-facing needles on the more exposed tundra would experience similar—if not more—water loss, compared with more sheltered ecotone trees, if snow and ice abrasion was the dominant agent. Further, tundra individuals were very short in stature (< 0.8 m) and therefore would not be subject to the same stresses and branch movements as taller trees within the ecotone (cf.

Dean *et al*., 2002). However, further research is necessary to properly evaluate these relationships.

Environmental characteristics

Some research has suggested a link between winter soil temperatures and winter desiccation (Kullman, 2007). Kullman (2007) found that winter desiccation was a primary limiting factor determining the position of treeline in the Swedish Scandes until the late-1980s, when amelioration of winter temperatures occurred. The limiting factor then shifted from winter temperatures and foliage mortality due to winter desiccation, to summer temperatures and their effects on seed viability. Additionally, Cairns (2001) hypothesized that a greater amount of snowfall resulted in longer duration of frozen soils limiting moisture supply and, consequently, increased winter desiccation at treeline in northern Montana. Stems burdened by heavy snow loads are also vulnerable to physical damage through settling or creeping snow, or infection by various snow fungi (Holtmeier, 2009). Conversely, it has been suggested that a deeper snowpack reduces winter desiccation by burial of exposed stems (Grace, 1977). It is difficult to determine the effects of snowpack and soil temperatures on epidermal conductance around Churchill due to the limited timeframe of this study, and the potential for synergistic effects. Indeed, snowpack was deeper and soil temperatures 1.5°C warmer during 2009, compared with 2008, and the lowest values of g_{min} were observed during 2009. Therefore it is impossible to rule out potential interactions between environmental influences like snowpack, soil and air temperature. Observations of winter desiccation at a seasonal resolution, or the use of long-term monitoring (*sensu* Kullman, 2007) are necessary to evaluate synergistic environmental influences beyond conjecture.

Due to the short time frame of this study and the length of the winter season (~September through May), this study only revealed the extent of winter desiccation and water status up to the end of February/beginning of March. It is possible that desiccation as well as premature dehardening and freezing injury could happen during spring (Cannell, 1985). However, amounts of first-year needle death (derived by 100 – percent viability) of 1.7 to 7.0% over the duration of the study were comparable to those at other treelines in North America [e.g., 8.7% in Montana (Cairns, 2001) and 12% in Colorado (Weisberg & Baker, 1995)]. These data, combined with the lack of noticeable spring mortality observed at the sites sampled in this study, suggest that the possibility of increased spring mortality is likely low at treelines around Churchill. However, substantial winterkill has been observed at tree islands and krummholz stands proximal to the coast, and future sampling could include these sites that might be more susceptible to desiccation under spring conditions.

CONCLUSIONS

Though winter desiccation is widely believed to be a limitation of treeline position at some locations (Wardle, 1971; Tranquillini, 1979; Sowell *et al.*, 1982; Kullman, 2007), there is a growing body of evidence that argues against not only for the importance of winter desiccation in determination of treeline position, but against the causes of winter desiccation as well (Grace, 1990; Grace, 1993; Anfodillo *et al.*, 2002; Nakamoto *et al.*, 2011). The results of this study suggest that some winter desiccation does occur at diffuse treelines around Churchill, and that this desiccation is likely primarily related to temperature during the early growing season of the previous year, though with synergistic effects of snowpack and winter soil temperatures. Regardless of the origins for winter desiccation around Churchill, death of coniferous foliage appears to be low (< 10% of first year needles), and probably does not significantly influence regional tree growth (Mamet & Kershaw, 2011, accepted) and ongoing treeline advance in the area (Mamet & Kershaw, 2012). These results support the assertion that most diffuse treelines are not constrained by tissue dieback (Harsch & Bader, 2011). However, due to the occurrence of numerous tree islands and krummholz stands in the Churchill area and the presence of substantial winterkill during the spring, further research should focus on these patches of individuals in order to gain a better understanding of the regional framework for treeline dynamics around Churchill.

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CHAPTER FOUR

Multi-scale analysis of environmental conditions and conifer seedling distribution across the forest-tundra ecotone of northern Manitoba, Canada[3]

> "*A species microsite preference during the germination phase, structural facilitation from growth form modification, intraspecific and interspecific microsite facilitation, life history, and physiological tolerance probably dictate establishment success in the treeline ecotone,*"
>
> William K. Smith (2003)

INTRODUCTION

Growing season temperature is often considered to be the primary driver of changes in treeline position across the circumboreal (Hoch & Körner, 2003), though climate is only one facet of environmental variation (Holtmeier & Broll, 2005). As treeline heterogeneity increases from global to smaller scales, so does the influence of local biotic and abiotic factors on spatial variability of seedling establishment and survival, and therefore tree recruitment. Temporal scale is also an important factor in treeline sensitivity, as climate has been correlated with changes in treeline recruitment at decadal to centennial time-scales (Danby & Hik, 2007; Mamet & Kershaw, 2012), while annual to sub-seasonal establishment and recruitment dynamics of younger life stages are increasingly influenced by numerous factors, such as weather, edaphic characteristics, hospitable seedbed, viable seed production, microtopography, inter-specific facilitation, and mechanical stressors such as wind-blown snow abrasion, herbivory and granivory, among others (Holtmeier & Broll, 2007). As the factors controlling treeline

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position are strongly scale-dependent (Kupfer & Cairns, 1996), assessment of treeline response to changing climate at regional and finer scales requires a more comprehensive approach than at the circumboreal scale (cf. Körner & Paulsen, 2004). The form of treeline [i.e., diffuse, abrupt, tree island or krummholz *sensu* Harsch and Bader (2011)] should also be considered in treeline dynamics at the broad scale, though form effects can be mitigated by site-scale factors. In light of current and projected warming at numerous treeline sites, as well as the variable response of circumboreal treelines to recent warming (Harsch *et al.*, 2009), more multifaceted ecological reasoning is required to understand the nuances which drive treeline pattern and process from season-to-season at the site-scale.

Snowpack and microclimate

Soil and air temperatures across the forest-tundra transition, hereafter referred to as "treeline", vary considerably due to differences in surface energy balance and soil moisture (Rouse, 1984b). Albedo within forested areas near treeline can range from about 0.40 during the winter to 0.12 during summer, while tundra areas can change from about 0.87 to 0.16 (dry tundra) over the same period (Rouse, 1984a; Lafleur *et al.*, 1993). Furthermore, the change in albedo takes one month or longer in forested areas due to the persistence of snow within the trees, where mid-winter snowpack depth is significantly deeper (Kershaw & McCulloch, 2007). This late-lying snow causes wintertime net radiation to be larger than net radiation over the tundra due to albedo differences, resulting in substantially more energy available for heating the atmosphere above subarctic forest by sensible and latent heating (Lafleur *et al.*, 1993). Snow cover dynamics and net radiation differences between forest and tundra result in moist forest soils which are ~4°C warmer annually, and take about 2.5 months longer to freeze during early winter compared with dry tundra soils (Rouse, 1984b). Indeed, numerous treelines across the circumboreal occur within a narrow band of mean growing season soil temperatures between 5°C and 8°C (Körner & Paulsen, 2004)—just above the threshold temperature for tissue formation in plants (Körner, 2008). However, nutrient availability can also be low at treeline due to low microbial activity (Loomis *et al.*, 2006) and any increase in nutrients can alleviate growth limitations due to low soil temperatures (Weih & Karlsson, 1999).

Nutrient cycling

Differences in soil nutrient cycling have been observed across the treeline ecotone, commensurate with variation in seedbed, wind, snow depth and soil temperatures (Cairns, 1999; Hiemstra *et al.*, 2006). Liptzin and Seastedt (2009) found that nutrient availability, soil temperatures and snow depth were highly spatially variable across the ecotone, and extractable base cations, in particular, varied at the individual tree level due to differential snow deposition on the windward and leeward margins of trees. At a regional scale, Cairns (1999) found that soils across treeline differed only with regard to nitrogen and carbon, though greater differences in soil nutrients occurred at xeric treeline locations when studied at a finer scale. Moss-dominated seedbeds can also be moderately nutrient-enhanced relative to lichen seedbeds (Wheeler *et al.*, 2011). However, the presence of higher concentrations of nutrients such as calcium are likely due to the close proximity of litter leachates from birch (*Betula* spp.) growing within the moss (DeHayes *et al.*, 1999).

Seedbed and vegetation associations

Microtopography, seedbed, and neighbour effects have been shown to play a crucial role in seedling survival. Concavities in the landscape appear to mitigate the effects of wind blown snow abrasion and moisture stress on seedlings (Holtmeier & Broll, 1992), as long as waterlogging and frost hollows are not prevalent (Dy & Payette, 2007). Houle & Filion (2003) found that the presence of thick lichen mats (*Cladina* spp.) prevented seedling establishment. However, seedlings can germinate in desiccation cracks present in the mat (Cowles, 1982), and the inhibitory relationship becomes one of facilitation, after the early seedling stage, once saplings reach a height of >20 cm, due to increased moisture retention and nutrient leaching from decomposition of the lower part of the mat (Houle & Filion, 2003). Moist moss seedbeds have also been found to be preferred areas for seedling establishment (Black & Bliss, 1980; Wheeler *et al.*, 2011). The presence of ground cover appears to be crucial for survival of emergent seedlings as it can reduce sky exposure and low-temperature photo-inhibition (Germino *et al.*, 2002), and shrub shading of the ground can reduce growing season mid-day soil temperatures and make them more tolerable to new seedlings (Keyes & Maguire, 2008). However, while most studies suggest facilitation is the dominant mode of neighbor interactions in stressful environments like those found at treeline [following the Stress Gradient Hypothesis *sensu* Bertness & Callaway (1994)], some contradictions to this premise have been found (e.g., Forbis, 2009), which suggests a site-by-site evaluation of micro-environmental facilitation is warranted.

Churchill represents a relatively pristine and easily accessible forest-tundra landscape, and its diffuse treeline form (Harsch & Bader, 2011), could respond swiftly to current and anticipated warming (ACIA, 2004). While there have been a number of studies concerning population dynamics and spatial patterns of mature trees (Scott & Hansell, 2002; Harper *et al.*, 2011; Mamet & Kershaw, 2012), little research has been done into fine-scale biotic and abiotic influences on coniferous seedling establishment at treeline in the area. The objectives of this study were to: i) evaluate establishment and fecundity in forest and treeline sites; ii) characterize the micro-environment in which seedlings establish; and iii) determine which factors are most important in influencing seedling establishment.

MATERIALS AND METHODS

Study area

During February, July, and September 2008, field sampling was completed at three study sites southeast of Churchill, Manitoba (58°45′ N, 93°04′ W) (Fig. 4-1). Three zones at each site were sampled: forest, treeline and tundra. The area has a peak elevation of 39 m.a.s.l. Uplands are dominated by *Picea glauca* (Moench) Voss. with *Larix laricina* (Du Roi) K. Koch (tamarack) sub-dominant. Wetland environments are dominated by *Picea mariana* (Mill.) B.S.P. (black spruce) and *L. laricina* in fen and bog areas with *P. glauca* on hummocks. *Rhododedron groenlandicum* (Oeder) Kron & Judd (Labrador tea) and *Betula glandulosa* Michx. (dwarf birch) dominate the understory in treed environments across the region. Portions of the area lie on remnant beach ridges formed during isostatic rebound (Dredge, 1992), and the land is still rising at 11.4 mm year^{-1} (Wolf *et al.*, 2006). Mean January, July and annual temperatures are -26.7, 12.0 and -6.9°C, respectively (1971−2000 normal). An average of 562 mm of precipitation falls annually with 52% as snow (Environment Canada, 2012).

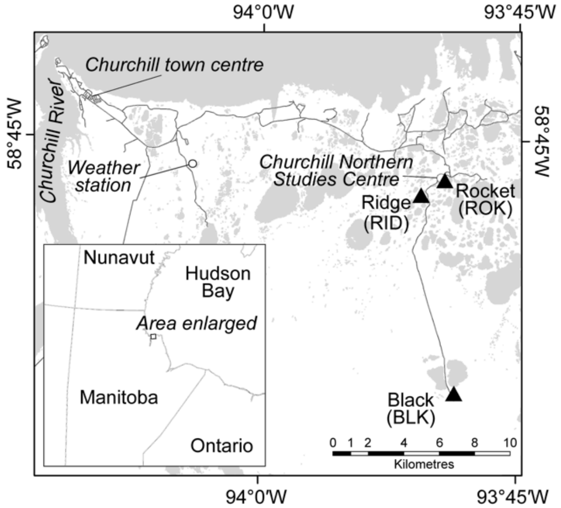

Figure 4-1. Location of the sampling sites near Churchill in northern Manitoba. The open circle indicates the location of the weather station from which air temperature was obtained (Environment Canada, 2011).

Field and laboratory methods

Snowpack

Mid-winter snowpack sampling was carried out from 28 February to 6 March 2008, and included snow pits and snow cores obtained using an Adirondack snow sampler (McClung & Schaerer, 2006), within the forest and at treeline at each site. Only the snow cores were analyzed for this study. Weight of the snow from the Adirondack sampler was determined in the field to calculate snow water equivalent (SWE). SWE was calculated from weight and depth using Pomeroy and Gray's equation for shallow snow (Pomeroy & Gray, 1995). Heat

Transfer Coefficient (HTC) was calculated following Kershaw (1991; 2001), in order to compare thermal properties of snow among sites.

Soil biotic and abiotic characteristics

To measure soil temperature at 10 cm depth, HOBO microloggers (HOBO H8 Pro, Onset Computer Corporation, Cape Cod, MA, USA; with a measuring range of –30 to +50°C and a resolution of 0.2°C) were deployed within the forest and at treeline. Loggers were initiated 22 June 2008, and data were downloaded during October and June each year. Due to logistical constraints, loggers were not deployed within the tundra zone at each site.

During July and September 2008, one soil pit per zone was excavated to describe horizons, and measure pH within the top 10 cm of the profile (one in forest and one at treeline, $n = 2$ per site). Ten "mini pits" were excavated to determine variability in organic matter depth following standardized protocols (Hofgaard & Rees, 2008). pH was determined in the field by mixing a ~50 g sample of each horizon with 50 mL of deionized water using a wooden stir stick, and immersing a Hanna HI-96301 DiST®1 pH tester (Hanna Instruments, Laval, Québec, Canada; 0.1 pH resolution). Mean pH for the top 10 cm of the profile was calculated. To determine rates of decomposition within the organic layer, a mesh bag containing five grams of *P. mariana* needles along with two white birch sticks were buried at 10 cm depth from 20 June 2008 to 25 June 2009 (several days after snow melt) (Hofgaard & Rees, 2008). This spruce needle-two stick grouping was replicated 10 times in each zone at each site (needle bags: $n = 30$, sticks: $n = 60$ per site).

Plant Root Simulator (PRS™) nutrient probes consisting of anion and cation exchange membranes embedded in plastic stakes (Western Ag Innovations, Inc., Saskatoon, Canada), were not deployed until 2009. It is apparent that soil nutrient supply rates are highly temporally variable (Huang & Schoenau, 1997), and because the probes were buried the year following all other field work, analyses focused on relative differences in nutrient supply rates among sites and zones. During two burials within each zone: 27 June to 22 August, and 22 August to 10 October, four probes for measuring cation exchange capacity and four probes measuring anion exchange capacity (replicated in each zone, cation: n = 24; anion: n = 24 per site), were inserted vertically into the organic soil horizon using a soil knife of the same dimension as the probes, to ensure complete contact between the soil and the resin membrane to ~10 cm depth. Probes were distributed randomly at each location, but at every spot one probe of each exchange capacity was put in the soil 2–5 cm apart. At the end of the burial period, the probes were washed and transferred to Ziploc® bags and shipped to the Western Ag Innovations Inc., laboratory in Saskatoon, Saskatchewan (Hangs *et al.*, 2004), where they were analyzed for numerous nutrients, though for the sake of simplicity, the focus of this study was on calcium, magnesium, nitrogen, phosphorous, and potassium.

Fecundity and reproduction

During early October 2008, at least ten cones were taken from five trees of each species present in each zone at a site, for a total of >100 cones per species, per site (no trees were present in the tundra zone). Cones were sampled from branches on all aspects of the tree when possible, and all cones except *L. laricina* were closed at the time of collection. Cones were preserved in paper bags and stored in a freezer at approximately −18°C until processing could begin. Cones were then left at room temperature (~20°C) for several months before seed extraction. It was determined that cones of *L. laricina* had already dehisced and so these samples were removed from further analysis. Cones of *P. mariana* are semi-serotinous, so were soaked in lukewarm water for two hours and then heated at 65°C for 9 h to facilitate opening following Leadem *et al*. (1997) and Sirois (2000). Extraction procedures for each species (*P. glauca* and *P. mariana*) were then as follows: each batch of cones was shaken in a closed 1-L plastic water flask for 30 s. The seeds were sorted and the batches shaken for another 30 s. This procedure was repeated once more, and then any remaining discernable seeds were extracted using forceps. Seeds were counted and cone scale debris removed. A random selection of 100 seeds was taken from each batch using the spoon method (Leadem *et al.*, 1997). The random selection was then set out on moistened Kimpak® within a transparent plastic germination box, and stratified at ~4°C for 14 days following species requirements outlined by the International Seed Testing Association (ISTA, 2009). Germination trials were carried out in environmental growth chambers, with a cycle of 25:18°C (day:night), 16 h light:8 h dark photoperiod for 30 days. No sterilization of seeds with peroxide was carried out in order to replicate natural growing conditions as closely as possible. Seeds were watered only as necessary in order to prevent mold growth. Germinants (radicle > 1 cm in length) were counted and subsequently removed daily to prevent duplicate counts. Seeds that failed to germinate after 30 days were dissected in order to determine the presence or absence of an embryo.

Seedling establishment and vegetation characteristics

During July and September 2008, three locations in each zone were sampled for seedling density using the point-centered quarter (PCQ) approach (Mitchell, 2007), and corrected for any missing quadrants (Warde & Petranka, 1981). As part of another study, seedlings were destructively sampled in the forest and at treeline in each of the three study sites for aging purposes (Mamet & Kershaw, 2012). In addition to seedling age, dominant plant cover (> 50% cover) within a 20 x 20 cm quadrat centered on each seedling was determined (Hofgaard & Rees, 2008). Dominant plants were stratified by height: < 5 cm, 5−15 cm, 15−199 cm, and > 2 m. Microtopography within each 20 x 20 cm quadrat was also characterized as flat, sloped, concave, or convex. Mean canopy openness was determined by taking hemispherical photographs at several locations in each zone, and openness was calculated using Gap Light Analyzer© (Frazer *et al.*, 1999).

Dominant plant composition of the landscape at each site, stratified by height, was determined along a 50 m transect within each zone. Each 50 m transect was divided into two meter intervals and dominant taxa (> 50% cover) intersecting each interval were assessed. While there are more vigorous methods for determination of plant composition, the methods used in this study were designed to be executed quickly in the field, as the objective was to sample several sites within a short window of time following IPY PPSA protocols (Hofgaard & Rees, 2008).

Data analyses

Differences in fecundity, reproduction and environmental characteristics were compared using either a one-way ANOVA, a Kruskal-Wallis one-way ANOVA on ranks, *t*-test, or a Mann-Whitney *U*-test, depending on normality and equality of variance (Legendre & Legendre, 1998). The analyses were repeated at two scales: intra-and inter-site. To isolate groups that differed from the others, a post hoc multiple comparisons procedure was performed. The type of post hoc test performed was dependent on sample variance or unequal sample sizes, and whether a parametric or non-parametric ANOVA was completed. Three multiple comparison procedures were used here: Dunn's pairwise, Holm-Sidak pairwise, and Tukey test. In order to determine habitat preference by seedlings, the habitat preference index (P_2) of Duncan (1983) was calculated using the vegetation survey and occurrence of seedlings aged one to seven years (cf. Germino *et al.*, 2002). The index is the percentage of an environmental attribute in the area occupied by seedlings, divided by the percentage of that attribute in the full area being considered, then transformed by adding one and calculating the logarithm. The resultant value provides an index of the importance of each plant category to the distribution of seedlings.

RESULTS

Physical environment

Canopy openness

Canopy openness was similar among like zones, though differed within a site, with values at forest/treeline of 64%/84%, 53%/83%, and 62%/80%, for three of the study sites (Ridge, Rocket, and Black, respectively) (One-way ANOVA followed by Holm-

Sidak multiple comparison procedure: $F_{5,48} = 27.669$, $P < 0.001$). The tundra of each site had no trees and so openness was assumed to be 100%.

Soil temperature

Soil temperature profiles were similar among sites, though mean values varied within-site (Fig. 4-2). Mean annual forest soil temperatures (22 June 2008 to 21 June 2009 / 2009−2010 as a longer term reference) were coolest at Rocket (-1.5°C/-1.2°C) and warmest at Ridge (-0.3°C/-0.5°C). Treeline soil temperatures were also warmest at Ridge (0.9°C/0.2°C), though warmer at Black from 2009 to 2010 (0.0°C/1.0°C) and coolest at Rocket (-1.5°C/-0.3°C). Soil temperatures for the complete record were comparable among similar zones between sites, though different across zones within-site (Kruskal-Wallis one-way ANOVA on ranks, Tukey test; $H_5 = 84.159$, $P < 0.001$). Regionally, soil temperatures in forest and at treeline were different when the first year of data was compared (Mann-Whitney U-test; $U_{2190} = 634961$, $P = 0.017$).

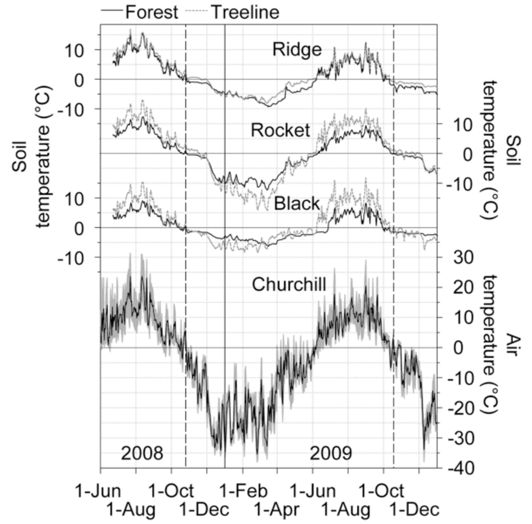

Figure 4-2. Mean soil temperatures at ~10 cm depth at each site 2008−2009. Values are a daily average of temperatures measured with one data logger, with two thermistors located in each zone (n = 4). The bottom time series represents air temperatures measured at 2 m height at the Churchill airport (Environment Canada, 2011). The shaded region shows the daily temperature range, and the solid black line represents mean daily temperatures. A horizontal black line indicates 0°C for each series. The vertical dashed line indicates when snow depth accumulated to 15 cm (23 October 2008 and 14 October 2009).

Growing season

The 2008 growing season [soil temperature at 10 cm ≥3.2°C (Körner & Paulsen, 2004)] started sometime before 22 June (no data were available before this time), and continued until between 13 and 28 September 2008, when compared among sites. The end of the growing season occurred later at treeline at all sites—Ridge: 16 September/28 September, Rocket: 16 September/28 September, and Black: 13 September/16 September (forest/treeline). When soil temperatures were averaged for each zone, the growing season ranged from June to 16 September 2008 within forest and from June until 27 September 2008 at treeline (Fig. 4-2). The spatial pattern of soil temperatures differed throughout the year. During the snow-covered season, soils remained within 1°C of the freezing point until the first week of December, and treeline soil temperatures remained within that temperature range from four to 11 days longer than forest soils (Fig. 4-2). However, forest soil temperatures were less variable over the 22 June 2008 to 21 June 2009 record, varying from -12.4°C to 15.7°C (28.1°C range), compared with a range of -19.3°C to 18.0°C (37.2°C) at treeline. Although soil temperature data were not available for February 2008, by February 2009 soil temperatures at treeline at all sites were significantly colder than within the forest (two-tailed t-test: t_{54}; $P < 0.01$). Air temperature ranged from -36.0°C to 31.4°C (67.4°C range) from June to September 2008 (Fig. 4-2) (Environment Canada, 2012).

Snowpack

Within a site, snow depth was typically similar within forest and at treeline, and significantly shallower within tundra ($H_2 = 191.867$, $P < 0.001$) (Fig. 4-3a).

SWE was either greatest at treeline, or similar within forest and treeline, and lowest SWE within a site was consistently found in tundra (H_2 = 197.574, P < 0.001) (Figs. 3b–3c). Thermal conductivity of snow (HTC) was consistently greatest within tundra, with some differences between forest and treeline (H_2 = 177.902, P < 0.001) (Fig. 4-3d).

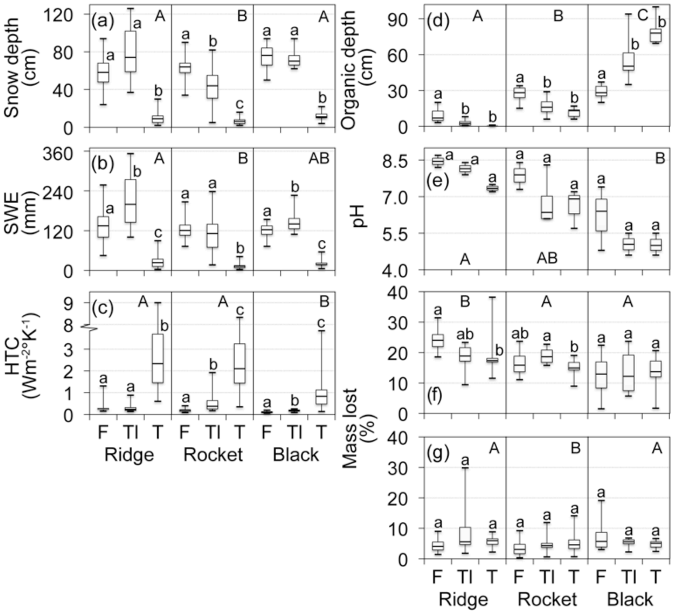

Figure 4-3. (a−d) Mid-winter snowpack (sampled February 2008) and (e−g) soil metrics (sampled July 2008) among sites along the forest-tundra transition near Churchill. (a) Snow depth. (b) Snow Water Equivalent (SWE). (c) Heat Transfer Coefficient (HTC) (Kershaw, 2001). (d) Soil organic matter (SOM) depth. (e) Soil pH in the top 10 cm of the soil profile. Percent mass loss for approximately: (f) five grams of *P. mariana* needles and (g) two grams of birch sticks from 20 June 2008 to 24 June 2009. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). Different lowercase letters at the top of each box stand for intra-site differences based on: (a−d) Kruskal-Wallis one-way ANOVA on ranks followed by a Tukey test (KW-TUK), and (e−g) the same test followed by a Dunn's pairwise multiple comparison procedure. Different uppercase letters represent differences among sites (KW-TUK). F = forest, Tl = treeline, and T = tundra. Statistical differences are significant at P < 0.05.

Soil organic thickness

There was no consistent pattern in organic layer thickness (SOM) evident among zones intra-site, though tundra SOM was typically less than in forest (H_2 = 11.090, P = 0.004), with the exception of the Black site. However, SOM was significantly different between sites (H_2 = 62.430, P < 0.001). While pH typically decreased from forest to tundra, no significant differences were evident, though there was some inter-site variability (Fig. 4-3f). There was no difference in percent mass lost from needles at Black (Fig. 4-3g) and from sticks at any site (Fig. 4-3h), though some variability among needle mass lost was evident at Ridge and Rocket.

Nutrient availability

Most nutrients were typically consistent within a given site, with the exception of N, K, and Ca at Ridge, and base cations at Black (Table 4-1). When averaged for each site, nutrient availability was significantly different at Black compared to the other two sites (Table 4-2).

Table 4-1. Mean nutrient supply rates within forest, treeline and tundra.

	Ridge				
Nutrient	Forest	Treeline	Tundra	*F*	Pr(>*F*)
N	16.2 (4.1)^{a}	28.1 (5.0)^{b}	13.8 (3.6)^{b}	6.46	**0.007**
P	3.9 (2.6)^{a}	1.8 (0.6)^{a}	0.5 (0.2)^{a}	1.58	0.230
K	177.4 (28.3)^{a}	126.0 (21.7)^{ab}	54.0 (25.0)^{b}	5.05	**0.016**
Ca	2323.6 (191.9)^{a}	3026.0 (314.0)^{ab}	1627.7 (454.4)^{b}	3.97	**0.034**
Mg	791.7 (63.0)^{a}	822.4 (51.7)^{a}	474.6 (102.4)^{a}	2.04	0.156
	Rocket				
N	15.8 (2.7)^{a}	17.3 (2.5)^{a}	9.5 (3.3)^{a}	0.74	0.489
P	1.7 (1.0)^{a}	3.1 (2.2)^{a}	0.8 (0.5)^{a}	0.64	0.537
K	126.4 (14.9)^{a}	144.5 (53.5)^{a}	53.9 (24.0)^{a}	0.42	0.663
Ca	2107.5 (436.0)^{a}	2618.6 (309.8)^{a}	1315.8 (266.2)^{a}	2.27	0.128
Mg	788.2 (178.1)^{a}	957.8 (86.6)^{a}	441.2 (79.8)^{a}	1.67	0.213
	Black				
N	34.8 (6.7)^{a}	32.0 (6.0)^{a}	16.8 (10.8)^{a}	0.21	0.815
P	2.5 (1.5)^{a}	3.9 (4.4)^{a}	0.8 (0.5)	0.11	0.895
K	195.9 (37.4)^{a}	170.5 (24.9)^{a}	108.8 (55.6)^{a}	0.41	0.671
Ca	296.7 (53.6)^{a}	358.1 (91.2)^{a}	474.1 (231.3)^{b}	15.51	**<0.001**
Mg	100.4 (21.2)^{a}	224.9 (65.6)^{b}	272.5 (128.0)^{c}	21.57	**<0.001**

Supply rates were measured as µg cm^{-2} 105 days^{-1}, between 27 June and 10 October 2009. Values in parentheses are one standard deviation. Different superscript letters indicate significant differences among zones (bold text; $P < 0.05$), determined by a one-way ANOVA followed by a Holm-Sidak multiple comparison procedure. Values were log-transformed in order to achieve normality and homoscedasticity *a priori* to statistical testing.

Table 4-2. Mean nutrient supply rates within three sites near Churchill.

Nutrient	Ridge	Rocket	Black	F	Pr(>F)
N	12.0 (5.0)^a	8.7 (2.8)^b	16.7 (7.8)^c	13.34	**<0.001**
P	1.1 (1.6)^a	1.1 (1.4)^a	1.3 (2.6)^a	0.12	0.885
K	68.6 (28.3)^a	63.1 (34.2)^a	97.3 (40.7)^b	17.80	**<0.001**
Ca	1434.2 (380.8)^a	1226.3 (352.4)^a	267.2 (205.4)^b	126.52	**<0.001**
Mg	427.2 (80.2)^a	438.1 (123.0)^a	145.0 (124.8)^b	53.11	**<0.001**

Supply rates were measured as µg cm^{-2} 105 days^{-1}, between 27 June and 10 October 2009. Values in parentheses are one standard deviation. Different superscript letters indicate significant differences among sites (bold text; $P < 0.05$), determined by a one-way ANOVA followed by a Holm-Sidak multiple comparison procedure. Values were log-transformed in order to achieve normality and homoscedasticity *a priori* to statistical testing.

Seed crop, fecundity, and seedling density characteristics

The mean number of seeds extracted per cone ranged from 20 to 60, and varied among ($F_{2,27} = 16.901$, $P < 0.001$) and within sites ($F_{5,24} = 8.282$, $P < 0.001$) (Fig. 4-4a). Percentage of filled seeds ranged from 18 to 50%, with no variation among or within sites ($F_{5,24} = 0.971$, $P = 0.455$) (Fig. 4-4b). Mean percentage of filled seeds that germinated was > 60% for all sites, and > 88% for all but the forest at Rocket (Fig. 4-4c). With the exception of Rocket forest, there was little variation in germination across the study area ($F_{5,24} = 10.304$, $P < 0.001$).

Total seedling density was relatively consistent between sites, though there was a disproportionate density of seedlings at treeline at Ridge, compared with other sites (Fig. 4-4d). Across the study area, there were more *L. laricina* (n = 187) seedlings found compared with *Picea* (*P. glauca*: n = 172; *P. mariana*: n = 9). The percentage of dead seedlings ranged from 0 to 20%, and was low for all species across all sites.

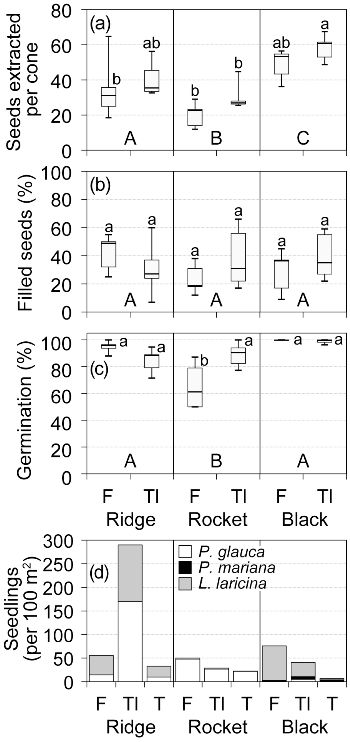

Figure 4-4. (a−c) Fecundity among *P. glauca* (Ridge and Rocket) and *P. mariana* (Black), and (d) seedling density (< 15 cm height) during 2008. (a) Number of seeds extracted per cone. (b) Percentage of filled seed as determined through dissection following germination trials. (c) Germination percentage of filled seeds. (a−c) Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). Different lowercase letters at the top of each box stand for differences based on a One-way ANOVA followed by a Holm-Sidak pairwise multiple comparison procedure. Different uppercase letters above the regional averages represent differences among sites. F = forest, Tl = treeline, and T = tundra. Statistical differences are significant at $P < 0.05$.

Seedling distribution, vegetation cover and microtopography

When habitat preference indices (P_2) were calculated for each vegetation category, seedlings were associated primarily with plants from the 0–5 cm layer (Fig. 4-5). Moss and litter was selected for both in forest and at treeline, while low shrubs and lichen were avoided in forest, but selected for at treeline (Fig. 4-5a). Seedlings were not associated with graminoids, tall shrubs and trees in both forest and at treeline (Fig. 4-5b–4-5d).

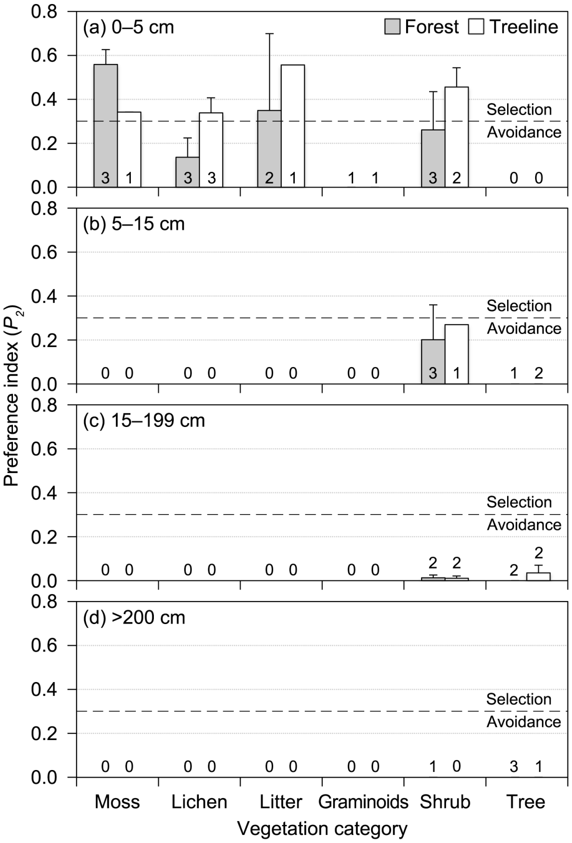

Figure 4-5. Seedling preference (P_2) for vegetation cover stratified by height of cover. Seedlings include individuals established since 2000. Bars indicate the mean preference value and error bars represent one standard error. Sample sizes (i.e., number of sites where the association was noted) are given at the base of each bar. P_2 provides an index of the importance of each category of vegetation to the distribution of seedlings on each vegetation category. Values less than 0.3 reflect a category that is under-represented which suggests avoidance, values close to 0.3 represent occurrence approximately in proportion to availability and is expected if use is random in relation to area of the category. Values in excess of 0.3 indicate over-representation and suggest a preference for that category of environmental variable.

Within the forest, most seedlings were found on sloped topography (44%), followed by concave (29%), flat (15%) and convex (12%). At treeline, seedlings were distributed equally among flat and sloped ground (both 35%), followed by convex (18%) and concave (12%).

DISCUSSION

Physical environment

Despite only surveying snowpack in one year, snow characteristics are related primarily to wind (Kershaw & McCulloch, 2007), and therefore snow characteristics are relatively insensitive to inter-annual fluctuations in precipitation (Hiemstra *et al.*, 2006). It could be expected that a decrease in snow depth would be observed from forest to treeline, due to a decrease in coniferous stem density and an increase in wind exposure (Liptzin & Seastedt, 2009) (however, see discussion on nutrient availability below). A decrease in snow depth from forest to tundra was observed in the Churchill region during 2002–2004 (Kershaw & McCulloch, 2007). For two of the three sites observed in our study this was indeed the case, however, the Ridge site was exceptional as significantly deeper snow was found at treeline (Fig. 4-3). This is due to the topography and aspect of the ridge on which treeline is situated. Because the environment changes from forest on the southwestern flank of a relict beach reach, oriented with its long axis in a northwest to southeast direction, to treeline near the crest of the ridge. The elevated position of treeline allows for greater exposure to the dominant northwesterly winds that redistribute snow into large snowdrifts within the trees. This results in significantly deeper snow at treeline, compared to the forest, as well as large values of SWE. Aspect also influences snowpack at the Rocket site, which grades from forest to treeline in a southerly direction, allowing for greater sun exposure and therefore greater melt-freeze metamorphism of treeline snow, which reduces the insulation capacity of the snow as reflected by elevated HTC values (Fig. 4-3).

The shallow snowpack at treeline at Rocket results in the greatest heat loss (i.e., greatest HTC), and the coldest winter soil temperatures observed among treed areas within the three sites (Fig. 4-2). Cold winter temperatures were partially offset at treeline at Ridge due to the insulation of the significantly deeper snow, resulting in little difference in forest and treeline soil temperatures during winter. The snow-covered season was typically shorter at treeline, compared with forest, which allowed for a longer period of soil exposure and therefore a longer growing season. Summer soil temperatures at treeline were usually higher than within the forest, with a greater diurnal variability—as has been found in other studies (Liptzin & Seastedt, 2009).

Nutrient availability and edaphic characteristics

Based on the Landscape Continuum Concept (LCC) of Seastedt *et al.* (2004), treeline should receive particularly high external inputs of snow and particulates, due to interception via increased aerodynamic roughness of trees. Indeed there was greater availability of nutrients at treeline, relative to forest, though the difference was not significant in most cases (Table 4-1). Moreover, it was beyond the scope of this study to determine if this greater availability of nutrients at treeline was due to increased interception or reduced biological uptake (Weih & Karlsson, 2002). While the LCC has only been applied in alpine environments (Seastedt *et al.*, 2004; Liptzin & Seastedt, 2010), the main premise that treeline (sink) can intercept nutrients from adjacent treeless areas (source) is likely relevant to treeline environments around Churchill due to the prevalence of windy conditions and related direct and indirect influences of wind-blown snow on vegetation (Scott *et al.*, 1993). Indeed there were often greater amounts of nitrogen, phosphorous, and calcium found at treeline relative to the other zones, and though the differences were not typically statistically significant (Table 4-1), there could be biological significance. Increased snow deposition results in increased deposition of inorganic nitrogen, as well as base cations like calcium in the Churchill area due to the ubiquitous nature of exposed gravels derived primarily from Silurian and Ordovician limestones and dolomites (Dredge, 1992). These nutrients are temporarily stored in the snow during the winter, and are frequently redistributed across the landscape by winds. Water and particulates contained within the snow are released during snowmelt and would be added to the soil *in situ*, unless the soil remained frozen and nutrients are transported elsewhere by flowing melt water without being processed on or within the soil (Seastedt *et al.*, 2004). Therefore, increased nutrients could benefit growth of seedlings in the area (Sullivan & Sveinbjörnsson, 2010), though study of such phenomena was beyond the scope of this study.

The greater availability of base cations at sites with thin organic layers (Ridge, Rocket) resulted from the limestones and dolomites within a few cm of the surface. The influence of this calcareous substrate elevated pH levels in the top 10 cm of the soil profile (Fig. 4-3). Decomposition rates of coniferous litter (i.e., mass lost) across the region were comparable to those expected for cold oceanic or continental tundra environments (~20−30% per year; cf. Heal *et al.*, 1981), though no discernible pattern existed across the forest-tundra ecotone. Presumably decomposition would be greater in forested areas due to warmed winter temperatures and increased microbial activity, though the longer growing season at treeline could balance decomposition relative to forest. Further study is required to determine if this is indeed the case.

Reproduction

Except for seeds extracted per cone, there was little difference in fecundity metrics among sites, and there was no difference in seed production between forest and treeline (Fig. 4-4). The close proximity of forest and treeline zones at each site (~50−100 m) results in similar growth rates for adult trees in the region (Mamet & Kershaw, accepted), and presumably similar fecundity, though the connection between vitality and fecundity is tenuous (Holtmeier & Broll, 2007). Vertebrate and insect predation of seeds from cones was not assessed in this study (Prévost, 1986), though predation was assumed to be low as cones were closed at time of collection. Contrast to seed crop, there was little inter- and intra-site difference in percentage of filled seeds and germination. These indices of reproductive potential are not influenced by predation or extraction factors, as is the case for seed crops. Empty seeds in spruce are typically caused by incomplete growth of the gametophyte due to selfing or pollination failure (Owens & Blake, 1985), though canopy openness was probably not great enough in either zone to increase incidence of self-pollination (Smith *et al.*, 1988).

Although cone collection of *L. laricina* did not prove fruitful (most seeds had already dehisced), reproduction is probably not a bottleneck to establishment given the numerous seedlings found across the region (Fig. 4-4). Moreover, *L. laricina* seedlings of all ages were found, which suggests annual production of filled seeds, and successful germination and survival is an ongoing phenomenon. In contrast with *L. laricina*, *P. mariana* seedlings were only found at the Black site, though this was probably due to edaphic conditions, rather than reproduction. The Black site is ~10 km further inland compared to Ridge and Rocket, and is approximately 15 m higher in terms of elevation, which means that the area emerged from Hudson Bay ~1300 years before the other two sites, based on a rate of isostatic rebound of 11.4 mm yr^{-1} (Wolf *et al.*, 2006). Thus Black has accumulated peat for a longer period of time and is subject to ongoing paludification (cf. Fenton *et al.*, 2005), resulting in environments better suited for *P. mariana* establishment (Dredge, 1992). Frequency of occurrence of *P. mariana* trees, and therefore seed source, becomes increasingly rare towards the coast of Hudson Bay, so the lack of *P. mariana* seedlings at the Ridge and Rocket sites was expected.

Seedling density

It was expected that seedling density would decrease from forest to tundra, which was seen at two of three sites, though the notable increase in density of seedlings found at treeline at the Ridge site was exceptional. Though it is tenuous to link multi-age seedling density to the environmental variables measured in this study due to sampling methodology, it seems likely that topography or snowpack, or some combination of these and/or other factors results in the seedling density patterns observed at Ridge. Based on a deep treeline mid-winter snowpack between 50 and 150 cm (cf. Hättenschwiler & Smith, 1999), with the greatest SWE observed there, and notable nutrient availability, we can speculate that conditions are conducive to not only seedling establishment, but also to growth and survival. The occurrence of treeline on a raised beach ridge at the Ridge site would likely result in enhanced snow and nutrient accumulation (as discussed previously). A deeper snowpack has been found to facilitate seedling establishment by providing shelter from climatic injury, and a moisture supply to possible seedlings (Holtmeier & Broll, 1992). However, persistence of snow drifts lingering late into spring or early summer can have negative effects, as they promote parasitic snow fungi and shortening of the growing season, which could impair successful seedling establishment (Holtmeier, 2009). Though little evidence of snow fungi infestation has been observed at Ridge during field studies, further research into other factors such as seed rain, and multiple seasons of recorded seedling demographics are necessary to conclusively determine the origins of seedling density patterns observed within forested and treeline environments around Churchill.

Seedling occurrence and ground cover

Seedlings were found disproportionately on moss ground cover, relative to the availability of this seedbed on the landscape (Fig. 4-5). Moss seedbeds have been found to facilitate seedling establishment and survival in climatically stressed habitats such as those at treeline (Wheeler *et al.*, 2011). Relative to bare seedbeds, or those dominated by *Cladonia* spp., feathermoss seedbeds (*Pleurozium* spp.) have been found to enhance seedling emergence, height growth, and reduce first-winter mortality, seed predation and herbivory (Wheeler *et al.*, 2011). Some studies have found moss seedbeds to compete with seedlings (Charron & Greene, 2002), though under the environmentally stressful conditions around treeline, the interaction probably shifts from competition to facilitation (Wheeler *et al.*, 2011). At present, it appears that moss seedbeds promote successful seedling establishment and survival, however, anticipated warming could alter this relationship via increased moisture stress if these seedbeds dry out and seedling roots have not reached moist soil beneath these mats (Hille & den Ouden, 2004).

The presence of low shrubs appeared to favor seedling establishment at treeline, though not in forest (Fig. 4-6). Shrubs could provide shelter from strong winds and excessive solar radiation within the more exposed treeline sites (Germino *et al.*, 2002). However, within the forest, shading of the ground by shrubs can reduce soil temperatures and light intensity to an extent that establishment and growth of shade-intolerant species could be impaired (Johnson *et al.*, 2004). Thus the facilitative effects of shrubs on seedlings likely increases from forest to treeline.

The relationship between seedlings and lichens is difficult to interpret. Surveys of the ground cover surrounding seedlings did not differentiate between seedlings found on lichen mats, or within desiccation cracks present within the mat. Seedlings frequently die following establishment on top of lichen mats due to physiological and mechanical stressors (Houle & Filion, 2003). However, seeds that germinate in cracks within the mat, or at the margins of lichen polygons can benefit from better seed retention, higher seed protection from predators, and increased soil moisture relative to larger surfaces devoid of lichens (Sirois, 1993), due to increased microtopographical roughness (Holtmeier & Broll, 2010). The sampling methodology employed in this study cannot explicitly describe the nature of the relationship between lichens and seedlings. However, based on our field observations and the work of others (e.g., Cowles, 1982; Sirois, 1993; Houle & Filion, 2003), perhaps it is reasonable to speculate that lichen mats can provide some microtopographic facilitation to seedling establishment and growth within the treeline ecotone, though further research is required to evaluate this hypothesis for the Churchill area.

CONCLUSIONS

As temperatures warm, circumboreal treeline will likely move up elevation and towards more northerly positions. It is however, much more difficult to predict regional and site-specific variations and dynamics of treeline, due to the increasing relevance of factors other than climate (Holtmeier & Broll, 2010). The results of this study show that biotic and abiotic factors can vary significantly not just between sites, but within a site as well. Soil temperature, snowpack, soil organic depth, soil nutrient availability, and seedling density all varied noticeably intra-site.

The results of this study suggest that microsite competition in the forest changed to facilitation in the tundra. Seedlings were not associated with lichens and low shrubs in forests, but preferred these habitats at treeline. Moss and litter facilitated seedlings in both forest and at treeline, while shrubs and trees greater than 5 cm in height inhibited establishment. Low seedling mortality and the presence of all ages of seedlings suggests that seedling establishment and survival is an ongoing phenomena, which is facilitated by protection from the elements via association with other plant cover types.

The short temporal window used in this study certainly warrants careful and conservative interpretation of the results. However, findings were comparable to other research. Numerous other studies have found the benefits of growing in proximity to neighboring plants outweigh the effects of competition and inhibition in environmentally stressful habitats (Maestre *et al.*, 2009). Furthermore, facilitative effects are more important than competition and inhibition during the early seedling stage (Brooker *et al.*, 2008). As well, snowpack plays an important role in treeline dynamics by providing protection from the elements in winter and contributing to growing season soil moisture (Holtmeier & Broll, 1992).

Future research should include continuous monitoring of forest-tundra population dynamics, as well as biotic and abiotic environmental variables. Still the results obtained here certainly reinforce the notion that patterns and processes controlling demographics of treeline species are strongly scale and site-dependent. Further regional and local studies are needed to determine if current relationships between treeline and biotic and abiotic factors will continue in a generally warmer climate.

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CHAPTER FIVE

Recent seedling establishment within subarctic forested wetland and upland environments, northern Manitoba

“*The development and maintenance of lichen woodlands of northern Canada reflect a delicate interdependence between the lichen ground cover and the ecology of spruce trees.*”

Kenneth Kershaw (1978)

INTRODUCTION

The arctic forest-tundra ecotone is an important phytogeographical boundary between boreal forest to the south and tundra to the north. There are a myriad of potential climate-related feedbacks if the physical structure of the ecotone were to change, such as: reduction of snow-covered land and albedo-induced warming (Bonan *et al.*, 1995); alteration of the carbon budget by modified sequestration and release of carbon (Kasischke & Stocks, 2000); change in radiation budget through increased aerosols from fire emissions (Dale *et al.*, 2001); and by modification of the moisture balance (Tinner *et al.*, 2008). Accordingly, the forest-tundra has been a prime location for research on biotic and abiotic pattern and process as it relates to climate change (e.g., Danby & Hik, 2007; Batllori *et al.*, 2009; Mamet & Kershaw, 2012).

Mean growing season temperature is the primary factor limiting tree growth within the forest-tundra (Mamet & Kershaw, 2011) and radial growth of mature trees has been responding favorably, in many cases, to increased temperatures (D'Arrigo *et al.*, 2008). However, it is the successful germination and survival of tree seedlings rather than increasing growth of mature trees, which are likely the most crucial processes in treeline advance poleward and to higher elevations with climate warming (Holtmeier & Broll, 2007). Local treeline positions can also be modified by frost damage, winter desiccation and wind-blown snow abrasion, seedling inhibitive ground cover (Houle & Filion, 2003), and combinations of these and other factors (Körner, 1998). Thus while radial growth of mature trees responds more rapidly to increases in temperature (Holtmeier & Broll, 2005), it is the establishment of individuals in the forest-tundra and pertinent environmental factors which must be assessed in order to evaluate spatial forest cover dynamics (Smith *et al.*, 2009).

There have been numerous studies of the forest-tundra around Churchill, Manitoba including dendroclimatic investigation (D'Arrigo & Jacoby, 1993a, 1993b; Mamet & Kershaw, 2011, accepted), tree-ring isotopes (Tardif *et al.*, 2008), fire history (Monson, 2003), insect herbivory (Girardin *et al.*, 2005), tree morphology (Scott *et al.*, 1987b), wind and snow effects on forest-tundra trees (Scott *et al.*, 1993) and historical establishment of *Picea glauca* (Moench) Voss. (white spruce) (Scott *et al.*, 1987a). But to our knowledge there have been no studies specifically on recent local seedling establishment. The Churchill region is predicted to warm significantly during the next 100 years (Gagnon & Gough, 2005) and the potential for treeline movement and feedbacks with climate (MacDonald *et al.*, 1998) makes the area a prime location for investigation of forest cover dynamics. Uplands around Churchill are often dominated by a lichen mat, which could inhibit establishment (Houle & Filion, 2003). In contrast, mosses and sedges dominate wetland environments in the area, which could be more suitable to successful establishment of seedlings (Black & Bliss, 1980). Thus seedbed must be taken into consideration when evaluating local seedling establishment. The objective of this study was to examine: (1) which environmental variables most influence seed-based regeneration and (2) compare recent history of seedling establishment between wetland and upland sites within the forest-tundra near Churchill.

MATERIALS AND METHODS

Study area and site description

A *Picea mariana* (Mill.) B.S.P. (black spruce) wetland and a *P. glauca* upland open forest near subarctic Churchill, Manitoba were studied (Fig. 5-1). The mean annual temperature at Churchill is -6.9°C and monthly means vary between -26.7°C in January and 12.0°C in July (1971-2000 normal) (Environment Canada, 2012). The frost-free season extends from mid-June to mid-September and 562 mm of precipitation falls annually with 52% as snow. Mean annual temperatures have increased by 1.9°C since 1929 (start of the instrumental record), with most of that warming occurring during the last 20 years (Environment Canada, 2012).

The upland site (39 m a.s.l.) was dominated by *P. glauca* with some *Larix laricina* (Du Roi) K. Koch (tamarack), and a closed ground cover of lichen (primarily *Cetraria* spp., *Cladina* spp. and *Cladonia* spp.) beneath a sparse cover of *Ledum groenlandicum* (Labrador tea). The wetland site (23 m a.s.l.) consisted of an open forest dominated by *P. mariana* and subdominant *L. laricina* with a closed ground cover of moss (*Sphagnum*, *Hylocomium* and *Pleurozium* spp.) beneath sparse *L. groenlandicum*, *Salix* spp. (willow), and *Betula glandulosa* (dwarf birch). There is no record of fire or major disturbance at either site for at least 200 years (Monson, 2003), indicating stand development has occurred since at least the early 19th century.

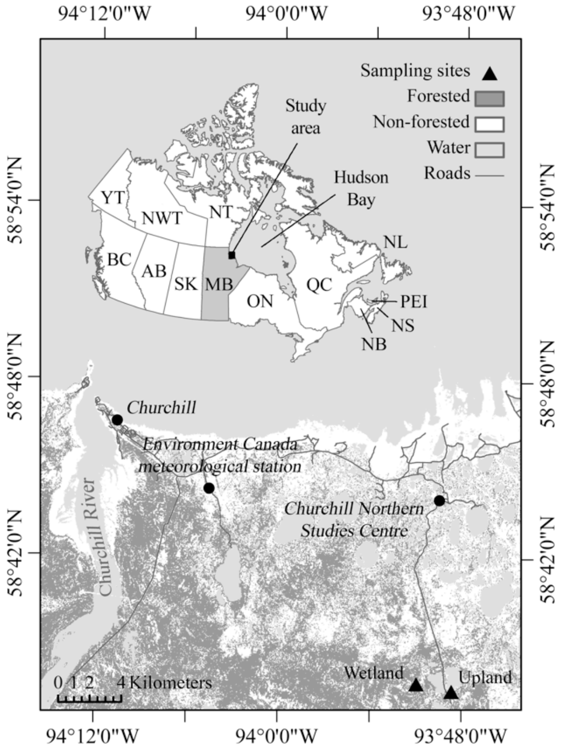

Figure 5-1. Location of the wetland and upland sampling sites. Forested and non-forested areas were derived from the landcover map of Brook & Kenkel (2002).

Field and laboratory techniques

During October 2007, samples were taken from three randomly selected five x five meter plots at each site. Following standardized protocols (Hofgaard & Rees, 2008), all seedlings (up to 0.15 m) and saplings (0.15 m to 2 m) were destructively sampled for age determination. The dominant ground cover (>50% cover) around each stem was visually assessed within a 0.2 m radius. Our objective was to sample an additional three plots, though an early season snowfall on 11 October 2007 prevented further seedling/sapling surveys that year. However, surveys were repeated at each site during 2009 and 2010 with the exception that whorl counts replaced destructive sampling and ground cover was not recorded. Moreover, plot sizes were 1.3 x 1.3 m in 2009 and 1 x 2 m in 2010, and replicated 16 times. The different plot sizes were an attempt to better sample in an environment where seedlings could be missed due to using a square plot where there is microtopographical variation. Therefore the area sampled was 27 m^2 and 32 m^2 in 2009 and 2010, respectively. In order to have similar-sized plots to make inter-year comparisons, the smaller 2009 and 2010 plots were combined in each year. Thus, the total area sampled was 134 m^2 at each site.

All samples taken during 2007 were dried at 25°C for at least 24 hours. Seedlings and saplings were sectioned at the root crown for age determination. Samples were sanded (Stokes & Smiley, 1996) and rings were counted under a stereo microscope. Samples were cross-dated by comparison of narrow rings (Yamaguchi, 1991). Individuals surveyed during 2009 and 2010 were aged by counting branch whorls and bud scars (cf. Daniels & Veblen, 2004). Age determinations were checked using regression equations derived from plots of height *versus* ring counts from the 2007 data, and adjusted if necessary.

Ring-width chronologies were created for each species using breast-height tree cores taken from the area during 2006–2011 (Mamet & Kershaw, 2008; Mamet & Kershaw, accepted), and standardized using the Regional Curve Standardization (RCS) method (Cook & Kairiukstis, 1990). This method has been found to be useful for retention of low-frequency climatic trends in tree growth (Esper *et al.*, 2003), and visualization of these trends was necessary for graphical comparison with establishment data. RCS chronologies were generated by aligning the rings of samples by cambial age and calculating the mean of these age-aligned time series. If the pith of the sample was missing, the number of missing rings was visually estimated and the age-alignment of the sample in question was adjusted accordingly (Melvin *et al.*, 2007). Since there is usually some degree of noise in the mean of the age-aligned series resulting from inter-sample variability, the mean series was then smoothed using a spline that preserved 50% of the variance at wavelengths of 32 years to create the ‘regional curve’ (RC). The wavelength and variance values were chosen in order to best characterize the low-frequency variability in the mean age-aligned series (Grissino-Mayer, 2001). The RC was assumed to represent only the overall, age-related growth trend of a given species at a given site (Esper *et al.*, 2003). When the raw data in each age-aligned year were divided by the RC, the resultant ring-width indices were interpreted to be related to climate or some other non-biological forcing (Briffa *et al.*, 1996). The index of each individual was then re-aligned by calendar year and averaged to form the master chronology. In order to avoid potential bias in the ring-width chronologies due to age-dependent growth responses of younger trees (Szeicz & MacDonald, 1994), series from each species were subsampled such that only series that originated before 1940 were included in the chronologies. This resulted in chronologies with homogenous sample depth throughout the period of comparison with establishment and climate data (see below).

Data analyses

Data from each sampling plot from each site were analyzed both separately and combined in order to examine plot- and site-level variability. Ring-width statistics for the RCS chronologies were calculated using COFECHA following Fritts (2001). Seedling and sapling densities *per* hectare were determined and age structures were grouped into five-year classes in order to diminish any error in establishment date determination. Preliminary analyses of the static age structures indicated that seedling frequency typically declined with age, but the curves were not smooth. Variability in static age distributions could be due to variation in establishment, survival or mortality, which make interpretations of demographic processes from age distributions difficult (Johnson *et al.*, 1994). The decline in seedling frequency was accounted for by fitting two theoretical distributions, the exponential and power functions, to the age structures (Hett & Loucks, 1976). The distribution with the best fit, as determined by highest values of r^2, was selected for further analysis. The difference between the theoretical and observed age distribution provided a time series of residuals from the smooth depletion curve, and these residuals were a relative measure for the number of seedlings that established and survived up to the year of sampling.

Seedling residuals were compared to five-year means of mean monthly temperature and monthly precipitation sums (Environment Canada, 2012) using simple Pearson correlations. Graphical patterns of establishment were visually compared to June–September temperature and precipitation, and the RCS chronologies (cf. Esper & Schweingruber, 2004). The June-September period was chosen based on the growing season duration for each species. Peak germination occurs when daily minimum temperatures stay above 5°C and maximum daily temperatures range between ~10°C and 24°C (Johnston, 1990; Nienstaedt &

Zasada, 1990), which typically occurs between June and September around Churchill (Environment Canada, 2012).

RESULTS

A total of 270 seedlings and saplings were sampled from the study area (Table 5-1). Only one seedling was found at the upland site during the three sampling years and there was a greater density of individuals at the wetland site—up to an order of magnitude larger for height class totals.

Table 5-1. Number of samples and stem densities in wetland and upland sites near Churchill.

		Wetland				Upland			
Year	Height class	*Pg*[a]	*Pm*	*Ll*	Total	*Pg*	*Pg*	*Ll*	Total
2007	Seedling	–	12 (0.16)[b]	110 (1.47)	122 (1.63)	–	–	–	–
	Sapling	–	30 (0.40)	62 (0.83)	92 (1.23)	10 (0.13)	–	1 (0.01)	11 (0.15)
	Total	–	42 (0.56)	172 (2.29)	214 (2.85)	10 (0.13)	–	1 (0.01)	11 (0.15)
2009	Seedling	1 (0.04)	2 (0.07)	13 (0.48)	16 (0.59)	–	–	–	–
	Sapling	9 (0.33)	2 (0.07)	6 (0.22)	17 (0.62)	–	–	–	–
	Total	10 (0.37)	2 (0.14)	19 (0.70)	31 (1.21)	–	–	–	–
2010	Seedling	–	–	11 (0.34)	11 (0.34)	1 (0.03)	–	–	1 (0.03)
	Sapling	–	–	2 (0.06)	2 (0.06)	–	–	–	–
	Total	–	–	13 (0.40)	13 (0.40)	1 (0.03)	–	–	1 (0.03)

[a] *Pg* = *P. glauca*, *Pm* = *P. mariana*, *Ll* = *L. laricina*

[b] Values are number of samples and values in parentheses are samples per m^2.

Age structure

Despite an overstory dominated by *P. mariana* within the wetland site, most seedlings and saplings were *L. laricina* (Table 5-1), with ages ranging from 0 (establishment during the year of sampling) to 167 years, and a mean of 14.1 and standard deviation of 23.5 years (Fig. 5-2). Ages of *L. laricina* were not significantly different between plots (one-way ANOVA followed by a Holm-Sidak comparison: $F_{4,184} = 1.456$, $P = 0.217$). Ages of wetland *P. mariana* ranged from 0 to 151 years (mean of 47.0 ± 46.5 years), establishment was relatively uniform over time, and ages were not significantly different among plots ($F_{3,38}$ = 2.376, $P = 0.085$) (Fig. 5-3). The mean age of wetland *P. glauca* was somewhat younger than that of the other species from the wetland site (18.3 ± 15.5 years), and with a less variable age range from 7 to 49 years—though *P. glauca* individuals were only found in one plot (Fig. 5-3). At the upland site, ages of *P. glauca* ranged from 3 to 107 years (53.8 ± 27.9 years), and individuals were significantly younger within the 2009 plot ($F_{3,19}$ = 8.572, $P < 0.001$). There was little evidence of recent mortality at the study sites with 0%, 11.9% ($n = 5$), and 1.1% ($n = 2$) of *P. glauca*, *P. mariana*, and *L. laricina* stems dead, respectively. No dead individuals were found at the upland site.

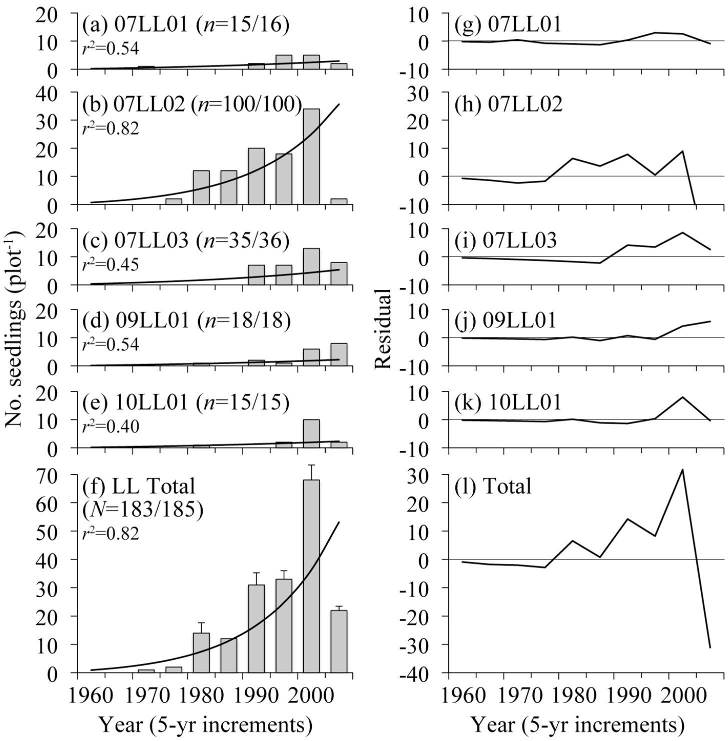

Figure 5-2. (a–f) Age distributions of wetland *L. laricina* and (g–l) residuals determined from exponential or power models fit to each age distribution. Note the change in scale of the y-axis between sites and species. Plot labels represent year, species and plot number (e.g., 07LL01 corresponds to 2007, *L. laricina*, plot one). Low establishment since 2005 is partly related to sampling, which likely excluded very young individuals. Sample sizes are expressed as the number of individuals established since 1960 over the total number of samples.

Ring-width chronologies

All chronologies had mean correlations among series greater than or near to the generally acceptable value of 0.5 when comparing 50 year portions of series lagged by 25 years at each time step (Grissino-Mayer, 2001) (Table 5-2). Sensitivity and standard deviation of *P. mariana* was lowest of the three species, likely indicating a less climate-sensitive ring-width series which would reduce the correlation among individual series and resulted in a low, but statistically significant mean correlation ($r = 0.48$, $P < 0.01$). Nonetheless, the growth of most species was graphically similar (Fig. 5-4), particularly during the last 50 years. Each species had the following general patterns of growth during the last ~50 years: (1) enhanced growth (index > 1) until around 1970; (2) a local minima in growth around 1975; (3) near average growth until the early 1990s; and (4) increasing growth from the early 2000s onward—though growth of *P. mariana* was notably reduced relative to the other species during the 21st century (Fig. 5-4). The greatest *P. glauca* growth since the 1960s was during 2008 (Fig. 5-2). Growth of *L. laricina* during 2008 was the greatest on record. A brief plateau interrupted the increase in *L. laricina* growth following the 1990s during the early 2000s followed after 2004 by increased growth.

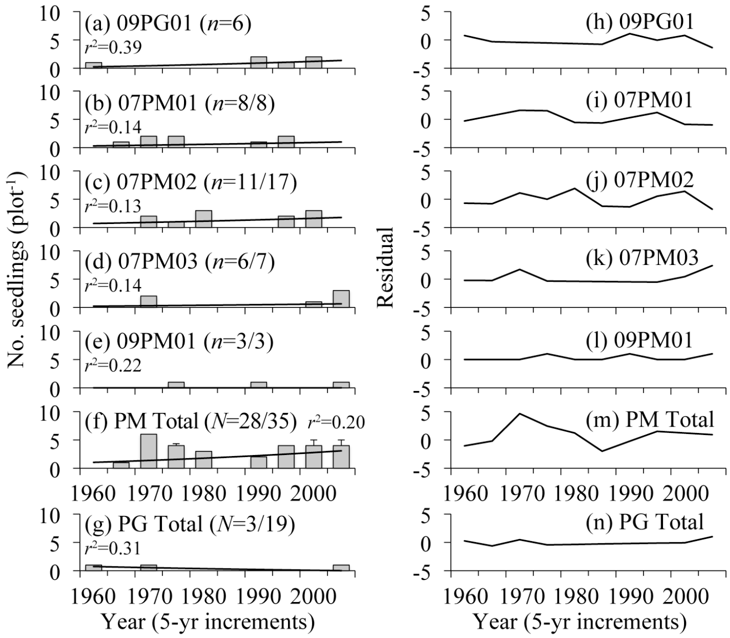

Figure 5-3. Age distributions of wetland (a) *P. glauca* and (b–f) *P. mariana*, and (g) upland *P. glauca*. Residuals determined from exponential or power models fit to each age distribution: wetland (h) *P. glauca* and (i–m) *P. mariana*, and (n) upland *P. glauca*. Plot labels are as in fig. 5-2. (g) Only three individuals were found within the upland after 1960, and these were distributed over three plots (one in each), so only the total number found is shown for simplicity. Sample sizes are expressed as the number of individuals established since 1960 over the total number of samples.

Table 5-2. Statistical characteristics of combined wetland and upland ring-width indices derived from COFECHA

	Picea glauca	*Picea mariana*	*Larix laricina*
Chronology length	1600–2011	1716–2011	1744–2008
No. years	412	296	265
No. trees	257	89	80
No. radii	448	140	159
Mean ring width (mm)	0.52	0.32	0.45
Mean sensitivity	0.20	0.20	0.27
Standard deviation[a]	0.24	0.16	0.22
First order autocorrelation[b]	0.79	0.83	0.71
Mean series correlation[c]	0.55	0.48	0.54

[a] Calculated from standard chronology (Grissino-Mayer, 2001)

[b] Removed to form whitened chronology

[c] To master series (50-year segments)

Environmental influences on growth and establishment

Within the wetland, 10 of the *P. mariana* (83% of the 2007 samples) and three of the *L. laricina* (3%) seedlings were found on a lichen substrate, with the remaining on moss (2007 data). All saplings within the wetland, and five (50%) of the *P. glauca* saplings within the upland were found on moss.

Establishment residuals for wetland *L. laricina* at the plot level were significantly correlated with each other (7/10 comparisons), and no significant correlations were found among wetland *Picea* conspecifics (Table 5-3). A paucity of upland samples post-1945 precluded the use of statistics for plot-level comparisons. When all individuals at both sites were combined into species-specific age distributions, no significant correlations were observed with conspecific growth indices, even when lagged ±5 years. Residuals of *P. glauca* were positively correlated with temperature during June–September, July and September during the five years prior to establishment (*t*-5), and negatively correlated with temperature during May, and precipitation during October five years after establishment (*t*+5) (Fig. 5-5). *L. laricina* residuals were positively correlated with temperature during June (*t*), July (*t*-5, *t*+5), August (*t*, *t*+5), September (*t*+5), and June–September (*t*-5, *t+5*) (Fig. 5-5). Precipitation during August (*t*-5, *t*+5), September (*t*), and June–September (*t*) were also positively correlated with residuals. Establishment residuals of *P. mariana* were not associated with temperature or precipitation (Fig. 5-5).

Table 5-3. Correlation matrix between plot-level establishment residuals for each species in upland and wetland sites for the 1945–2000 period. Plot labels represent year, species and plot number (e.g., 07LL1 corresponds to 2007, *L. laricina*, plot one). Only plots in which samples were found are shown. Correlations in bold are significant at $P < 0.05$ and asterisks indicate $P < 0.01$ significance.

Plot	1	2	3	4	5	6	7	8	9	10
1 07LL1	1									
2 07LL2	0.209	1								
3 07LL3	**0.831***	**0.598**	1							
4 09LL1	0.541	**0.676**	**0.844***	1						
5 10LL1	**0.618**	0.500	**0.766***	**0.922***	1					
6 07PM1	0.129	**-0.609**	-0.197	-0.469	-0.404	1				
7 07PM2	0.304	0.104	0.186	0.351	0.458	-0.042	1			
8 07PM3	0.187	-0.212	0.057	0.197	0.248	0.292	0.398	1		
9 09PM1	-0.161	0.152	0.089	-0.046	-0.264	0.385	-0.358	-0.254	1	
10 09PG1	0.489	0.430	**0.741***	**0.606**	0.386	-0.249	-0.184	-0.048	0.236	1

When residuals were visually compared with June–September temperatures and tree growth, several patterns were observed since the mid-1980s: (1) all three species had increased establishment since 1985, with peaks around 1995 (with the exception of *P. mariana*), (2) establishment up to 2000 was the highest for *P. glauca* and *L. laricina*—*P. mariana* peaked during the early 1970s, and (3) 5-year averages of tree growth, temperature and precipitation were the highest or second highest during the early 2000s (*P. mariana* was the exception), mirroring patterns in establishment, though there appears to be an offset in establishment by approximately five years (i.e., correlations with temperature during t+5 appear most frequently). Therefore, visual correspondence between the various metrics of population demographics and climate appear commensurate with statistical correlations observed between the time series (Fig. 5-4).

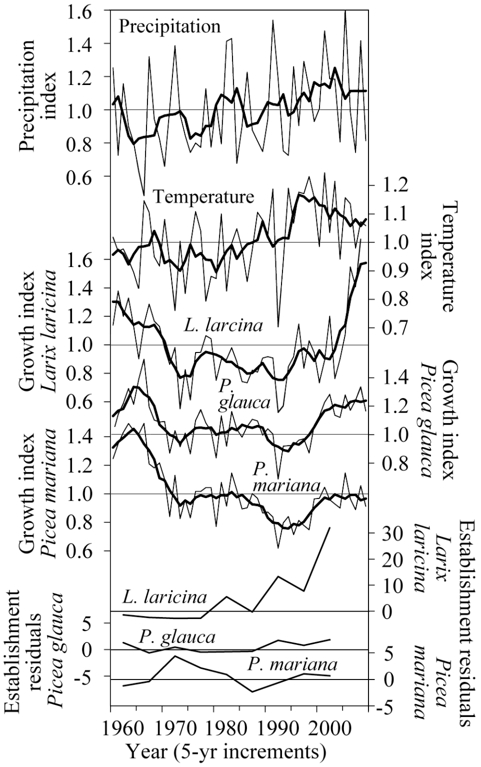

Figure 5-4. Mean Churchill June-September temperature and precipitation departures from the 1971-2000 mean, RCS growth indices (see text for explanation) and the timing of seedling and sapling establishment (five-year classes) combined from the wetland and upland sites. Thick black lines are five-year running means. Note the change in scale for the y-axis of *L. laricina* residuals. The most recent age class (2005) was removed as it was likely incomplete and not indicative of seedling frequency during that period (see discussion).

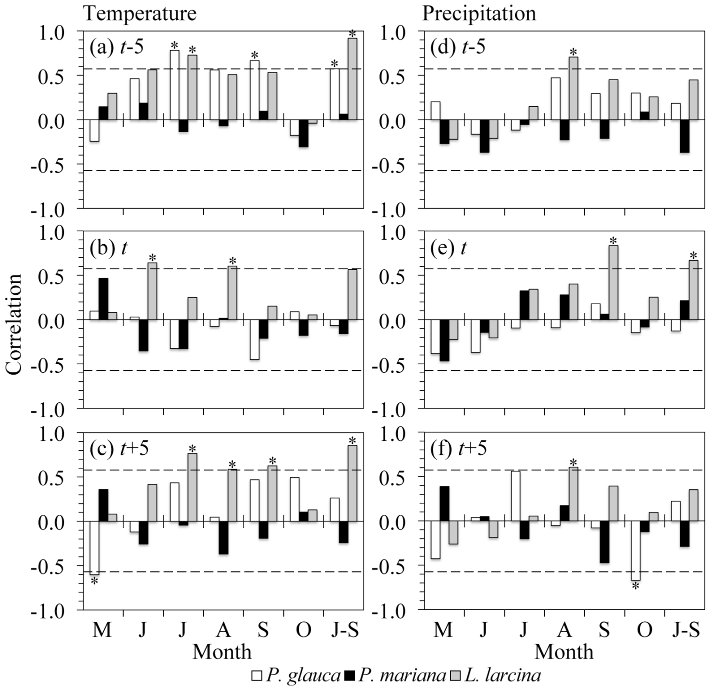

Figure 5-5. Correlation functions showing the effect of monthly (a–c) temperature and (d–f) precipitation on combined seedling establishment at the upland and wetland sites from 1940–2005. Coefficients are for seedling age residuals against monthly climate variables. J-S represents mean temperature and sum of precipitation during the growing season (June–September). *t*-5 = comparison between residuals and climate of the preceding five years, *t* = comparison between the current five years, and *t*+5 = comparison with the following five years. Asterisks indicate statistically significant correlations at $P < 0.05$.

DISCUSSION

Environmental influences on seedling establishment

Climate during the growing season was important for the successful survival of conifer seedlings and saplings. Precipitation during September was particularly important for *L. laricina*. September is when snow accumulation typically starts around Churchill (Environment Canada, 2012), and could act to insulate seedlings against daily minimum air temperatures below 0°C which occur during autumn (Germino *et al.*, 2002). Temperatures during June and September are particularly important for a deciduous species such as *L. laricina*, as seasonal growth initiation and conclusion are largely temperature-dependent (Johnston, 1990). Thus a warmer spring could allow growth to commence sooner and a warm September can allow growth to extend longer, resulting in enhanced winter hardiness. Several factors should be considered when interpreting the correlations between establishment and climate: (1) Sample size: the paucity of samples found at the upland site precludes the use of statistics to objectively assess relationships between variables—however, such a small number of seedlings found in an area that has a viable seed source and germinated seedlings (see Chapter 4), suggests a superseding influence on seedling establishment (see below); (2) Effective sample size: grouping establishment dates and climate data into five-year bins—while necessary—reduced the effective sample size for data being analyzed; and (3) Seedling and sapling samples: sampling of recent age classes provides a shorter timeframe in which to observe establishment and indeed only a single recruitment period was found within the data. Despite these limitations, statistically significant relationships were observed between *P. glauca* and *L. laricina* establishment and climate.

The upland site was characterized by a continuous mat of lichen, which can prevent seedling roots from reaching the soil if they germinate on or within the mat (Houle & Filion, 2003), or adversely affect seedlings via allelopathy (Dayan & Romagi, 2001). In the absence of a continuous plant cover dominated by a fruticose lichen mat, seedlings can successfully colonize upland sites (Houle & Filion, 2003).

Establishment patterns of *P. mariana* were not commensurate to the other species, and were not correlated with climate. These results contribute to a growing body of evidence that suggests another factor is limiting growth and natality of *P. mariana* around Churchill (Mamet & Kershaw, 2011; Mamet & Kershaw, 2012; Mamet & Kershaw, accepted). Since *P. mariana* is restricted primarily to wetland bog areas around Churchill, establishment could be limited by edaphic characteristics, as bog soils tend to be wetter, cooler and more acidic than well-drained upland soils (Fenton *et al.*, 2005). Therefore, while air temperatures could be adequate for tree growth and establishment, regeneration could be limited by the development of peat (Crawford *et al.*, 2003). Indeed, forest-tundra was replaced with bogs on the eastern side of Hudson Bay during the mid-Holocene (Payette, 1984). Paludification could be an important factor in limiting *P. mariana* regeneration in wetland areas around Churchill (cf. Mamet & Kershaw, 2012). However, further research is necessary to determine the main influences limiting regeneration of *P. mariana* around Churchill.

Besides the direct effect of climate in seedling establishment, there are numerous other factors, which could be climate-controlled and can influence the observed patterns of establishment around Churchill. These factors can include seed production, soil moisture and surface temperature, ice-melt and permafrost conditions, late and early frosts, and a combination of these or other factors (Holtmeier & Broll, 2007; Graae *et al.*, 2009). While specific ecological explanation of the linkages between climate and establishment is uncertain, significant statistical relationships as well as visual correspondence between climate during ecologically important months and establishment were found. This suggests that local climate does exert an influence on seedling establishment (cf.

Germino *et al.*, 2002) though the exact mechanism of that influence has yet to be investigated.

Methodological considerations

Several factors should be taken into consideration when interpreting these results. There is seedling detectability error, which is particularly pronounced for the most recent year of seedling establishment as well as with increasing time before present. Current-year seedlings are extremely difficult to find, as they are quite small and at such a young age are hard to differentiate from other plants such as *Polytrichum* spp., *Juniperus communis* and *Empetrum nigrum*. Thus the most recent age classes would have fewer individuals than those of two or three years old. During this study, one square meter at a time was surveyed for seedlings and surveying was completed very slowly and carefully to mitigate detection issues. So while some error was expected for the most recent two or three years, it is likely minimal and age structures should be considered representative of recent establishment. A small sampling area of 134 m^2 might not accurately represent historical establishment rates, as it is probable that decomposition removed evidence of earlier unsuccessful establishment. Accordingly, as recent age classes were the focus of this study and were adequately represented, any interpretation of establishment beyond several decades before present should be treated cautiously.

Due to the limited time frame of this study, facilitation of establishment by vegetation or topography was not included in the analyses, though it has been found to be important by regulation of direct sunlight, cold-induced photo-inhibition, winter desiccation and other factors (Smith *et al.*, 2003; Batllori *et al.*, 2009; Keyes *et al.*, 2009). Additionally, air temperature might not be indicative of the micro-environmental conditions to which seedlings are exposed (Körner, 2004). This study does not empirically test the hypothesis that a high density of lichens limits seedling establishment within the upland site. In order to test this hypothesis, seedling establishment on comparable plots at the upland site with lower lichen densities or where lichens were removed should be compared with lichen-dominated plots. Future sampling should also include vegetation structure stratified by species and height, soil analyses, microtopography and microclimate, animal browsing, damping-off fungi, and should be extended to include older age classes. Increased sample sizes and monitoring survival of seedlings at the beginning and end of the growing season would provide assessment of mortality at a seasonal resolution (sensu Batllori *et al.*, 2009).

CONCLUSIONS

While it is not a revelation that seedling establishment was related to growing season conditions, it is noteworthy that an increasing number of studies suggest that conditions not only during establishment, but also years preceding and following are important metrics in forest-tundra population dynamics (Szeicz & MacDonald, 1995; Lloyd & Fastie, 2003; Danby & Hik, 2007; Mamet & Kershaw, 2012). However, local environmental effects can overwhelm climatic forcing influences on seedling establishment. Seedling establishment within wetland environments was controlled to some extent by climate, though *P. mariana* could be responding more to edaphic influences. Whereas upland establishment could be limited more by ground cover if extensive lichen mats are present. If environmental conditions change with predicted climate change, forest-cover dynamics around Churchill can be expected to change as well. Thus continued species-specific monitoring of establishment and survival of forest-tundra individuals within northern Manitoba is warranted.

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CHAPTER SIX

Subarctic and alpine treeline dynamics during the last 400 years in northwestern and central Canada[1]

"*The position of a treeline is a balance between a slow tendency to advance upslope (or poleward) and more dramatic retreats due to infrequent disturbances. If this is correct, treeline will provide opportunities to study the processes controlling vegetation change in relation to climate change.*"

Ralph Slatyer and Ian Noble (1992)

INTRODUCTION

Vegetation change at the boundary between boreal forest and arctic and alpine tundra ecosystems, henceforth referred to as the 'treeline', has demonstrated marked linkages with climatic change during the Holocene (Leitner & Gajewski, 2004; Jiménez-Moreno *et al*., 2008). Recent evidence supports the prediction that future climatic warming and feedbacks will be greatest in arctic and subarctic regions (ACIA, 2004; Chapin *et al*., 2005), and the limits of the boreal forest are widely expected to extend northwards in subarctic regions and upslope in mountainous regions (Kaplan *et al*., 2003; ACIA, 2004). This advance could result in further warming through various mechanisms such as: (1) alteration of the solar radiation budget through increased emissions from fire and decreased albedo (Harden *et al*., 2000; Chapin *et al*., 2005); (2) modification of the moisture balance (Tinner *et al*., 2008); and (3) alteration of the global carbon budget with current sinks becoming sources (Kasischke & Stocks, 2000), among others. Therefore, knowledge of the current response of subarctic and alpine treelines to

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climatic change is essential in forecasting the treeline response to the anticipated future warming trend.

There have been numerous studies of treeline responses to climate change during the last several centuries. In some regions, the treeline has advanced (Kullman, 2002; Lloyd & Fastie, 2003). Other studies have found increases in stand density without advance of the treeline (Payette & Filion, 1985; Szeicz & MacDonald, 1995a). Some studies suggest that the treeline cannot advance without disturbances such as fire (Johnstone & Chapin III, 2006) or thermokarst (Lloyd *et al*., 2003), or that treeline position is moderated by disturbances such as herbivory (Cairns *et al*., 2007) and granivory (Castro *et al*., 1999). In some regions, there could be a change in the dominant treeline species from coniferous to deciduous (Landhäusser *et al*., 2010). In other areas, there could be a change from stunted individuals (krummholz) to upright growth forms (Lescop-Sinclair & Payette, 1995; Vallée & Payette, 2004). The treeline has receded in some areas (Payette, 2007), remained unchanged in others (Butler *et al*., 1994) and in some regions, is thought not to be in equilibrium with the present climate (Hofgaard & Wilmann, 2002; Johnstone & Chapin, 2003). Such treeline variability is mediated by species-specific and environmental controls at a range of scales (Holtmeier & Broll, 2007). Further research is necessary to determine these controls and to improve understanding of feedbacks between climate and treeline dynamics with potential warming of subarctic and alpine regions.

The objectives of this study were to: (1) identify episodes and rates of establishment and mortality of treeline individuals across the forest–tundra transition at several sites at the alpine treeline in the western Northwest Territories and the latitudinal treeline in northern Manitoba; (2) infer changes in the structure and location of the treeline from these data; (3) examine any relationship between these changes and climate; and (4) investigate causes of variability between sampling sites and study areas.

MATERIALS AND METHODS

Study areas

The study area incorporates the western edge of the Mackenzie Mountains in the Northwest Territories and the northwestern Hudson Bay lowlands near Churchill in northern Manitoba (Fig. 6-1). Study sites within the Mackenzie Mountains were located along the Canol Heritage Trail, which runs about 370 km from Macmillan Pass at the eastern edge of the Yukon, northeast to Norman Wells. The trail follows a derelict service road, built to service the Canol Pipeline during the early 1940s (Barry, 1992). Prior to the CANOL project, few people of European descent other than a handful of surveyors for the Geological Survey of Canada had travelled to the area, and the region was essentially unexplored by anyone except for a few native people (Kershaw & Kershaw, 1982; Kershaw, 1983). This area was chosen for this study due to its relative ease of access and, in spite of the development during the 1940s, represents relatively pristine forest–tundra. The Churchill area was also chosen based on its accessibility and relatively unspoiled forest–tundra. In addition, large natural disturbances, such as insect infestations, slope failure and winter avalanches, have been infrequent or non-existent at all study sites. Most notably perhaps, is that wildfire occurrence is rare in both study sites (as indicated by a lack of fire scars in the tree ring record), and is not predicted to increase appreciably during the next 100 years, despite projected increases for most of boreal Canada (Monson, 2003; Kochtubajda *et al.*, 2006; Wotton *et al.*, 2010). Therefore, population changes detected in stand reconstructions are more likely to be related to changes in climate than to other factors.

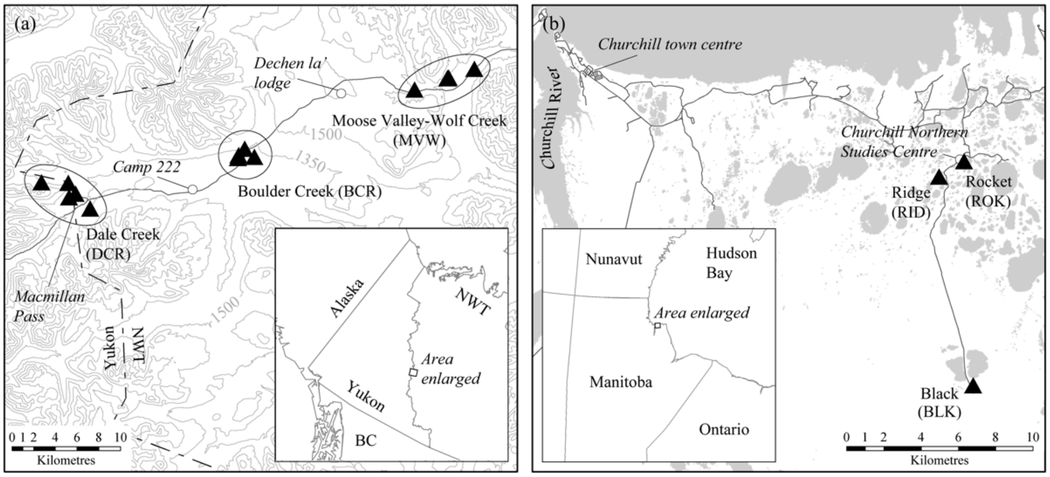

Figure 6-1. Location of the (a) western Mackenzie Mountains and (b) northern Manitoba study areas (inset) and the sampling sites in each region. The solid grey line in panel (a), which runs from southwest to northeast, is the Canol Heritage Trail. The contour interval in panel (a) is 150 m.

The Mackenzie Mountains reach elevations of around 2000 m a.s.l., and the forest–tundra ecotone generally occurs at elevations between 800 and 1200 m a.s.l., depending on aspect and edaphic characteristics (Szeicz & MacDonald, 1995a). There is a transition from open forest dominated by *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir) with some *Picea glauca* (Moench) Voss. (white spruce) in the Yukon about 20 km south-west of Macmillan Pass, to scattered tree islands of *A. lasiocarpa* near the border in the Northwest Territories. Along the Canol Heritage Trail, *P. glauca* occurs primarily as prostrate individuals and small tree islands in the tundra east of Dechen la' Lodge (Fig. 6-1). Deciduous shrubs cover the entire length of the ecotone, with *Betula glandulosa* (dwarf birch) as the dominant species, often forming a dense layer over 1 m in height. At Macmillan Pass (63.2°N, 130.0°W), at an elevation of 1380 m a.s.l., the mean January, July and annual temperatures from 1971 to 2000 were –26.2, 10.0 and –8.3°C, respectively. Mean annual sum of precipitation is 339 mm, with about 50% falling as snow (New *et al.*, 2000).

The Churchill area has a peak elevation of approximately 39 m a.s.l. Uplands around Churchill are dominated by *P. glauca* with some *Larix laricina* (Du Roi) K. Koch (tamarack). Wetland environments further south are dominated by *Picea mariana* (Mill.) B.S.P. (black spruce) and *L. laricina* in bog areas, and *P. glauca* on hummocks. An understory of *Rhododedron groenlandicum* (Labrador tea) and *B. glandulosa* occurs in treed environments across the region. Much of the ecotone lies on remnant beach ridges formed during isostatic rebound (Dredge, 1992), and the land is still rising at approximately 11.4 mm year^{-1} (Wolf *et al.*, 2006). Mean January, July and annual temperatures are –26.7, 12.0 and –6.9°C, respectively. Approximately 562 mm of precipitation falls annually with 52% as snow (New *et al.*, 2000; Environment Canada, 2011).

Field methods

Trees, saplings and seedlings were sampled from 11 tree islands in the western Mackenzie Mountains and three sites southeast of Churchill (Fig. 6-1). The 11 tree islands in the mountains were grouped into three study sites based on similar exposure and elevation. Study plots were established at each site in order to sample a minimum of 30 stems of each species present at each study area, in each of the following height categories: trees (> 2 m height), saplings (between 2 and 0.15 m) and seedlings (< 0.15 m) (Hofgaard & Rees, 2008). In the mountains, elliptical plots of a known length and width were set up to sample as many stems as possible within the tree islands, while rectangular plots were arranged at random points within the open forest and ecotone near Churchill. One plot was established per zone, and plot areas differed due to the objective of including at least 30 individuals of each species and size class. All living and dead individuals (fallen and standing) were sampled within each plot. Live trees were bored as near to ground as possible (Canol in the Mackenzie Mountains: n = 266, Churchill, Manitoba: n = 282) and dead trees were sectioned at the root collar (n = 37, n = 47). Saplings (n = 40, n = 341) and seedlings (n = 0, n = 299) were removed from the ground and later sectioned at the root collar for age determination. Stem height, diameter at breast height (dbh), diameter at boring height, number of cones and dominant plant cover was recorded for each sample where applicable.

Laboratory methods

All samples were dried at 20 to 30 °C and then the cores were mounted on wooden blocks. Both cores and cross-sections were sanded until individual xylem cells were visible (Stokes & Smiley, 1996). Samples were dated using a stereomicroscope and Velmex slide stage micrometre with a digital encoder (Velmex Inc., Bloomfield, NY, USA). Crossdating was completed using light rings (Yamaguchi, 1991) and narrow marker years (Fritts, 2001). Crossdating was statistically verified using the program cofecha (Grissino-Mayer, 2001).

Two adjustments were made to inner ring dates of cores following crossdating in order to account for instances of missed pith and boring height (cf. Lloyd & Fastie, 2003). First, the number of rings to the pith was estimated either from the curvature of the inner ring or from the tree's diameter at boring height. Secondly, the number of years required for a tree to reach the height at which it was bored was estimated using height-growth rates determined by sectioning saplings at root collar and 10 cm height, and ageing each section. Height corrections ranged from nine to 24 years for Churchill samples and from five to 11 years for Canol samples. The error introduced was assumed to be minimal as age structures were grouped into decadal classes prior to analysis.

For all dead stems, the outer ring was adjusted to account for loss due to weathering. Crossdating indicated that death for most individuals occurred during the last two decades and that at least some bark persisted on most dead stems. For all other individuals, an attrition rate of one ring per decade after death was used to correct mortality dates (Szeicz & MacDonald, 1995a). Error due to this adjustment was assumed to be minimal because of the 10-year age grouping described previously.

Data analyses

Two broad approaches were used to identify any changes in the treeline location at each site. For the first approach, age-structures of living individuals were constructed and then age characteristics across the ecotone were compared using four statistical tests (Danby & Hik, 2007a): (1) age distributions were compared using a Kolmogorov–Smirnoff test; (2) median age of each species in each plot was compared using a Mann–Whitney *U*-test; (3) establishment dates of each species in a plot was compared using a Mann–Whitney *U*-test; and (4) mean age of the five oldest living individuals was compared by means of a Student's *t*-test. For parametric statistical comparisons, the data were log-transformed to achieve normality and homoscedasticity. Additionally, to account for the decreased presence of individuals with increasing time before present, two theoretical distributions – the exponential and power functions (Hett & Loucks, 1976) – were fitted to the static age structures grouped for each species at each site. The distribution with the best fit, determined by statistical significance at $P < 0.05$ and high values of r^2, was selected for further analysis of age structure. The difference between the theoretical age distribution (expected) and the observed age structure provided recruitment/survival residuals, which can reflect changing patterns of recruitment/survival over time (Szeicz & MacDonald, 1995a; Daniels & Veblen, 2004).

For the second approach, establishment and mortality dates were used to estimate the density of live trees for each decade. Additionally, the decade in which stand densities reached 50 stems ha^{-1} [approximate density of adult trees at the treeline (Danby & Hik, 2007a)] was calculated and compared across the ecotone. An advance of treeline should be indicated by a more recent onset of establishment in ecotone plots compared to forest plots at each site. Thus, reconstructions of stand density provide information on changes in stem structure at a given location and may provide a basis for inferences about movement of the treeline. The caveat to this method is that, compared to trees, decomposition of seedlings and saplings is quite rapid, which means that underestimation of tree density increases with increasing years before present. Without a long record of continuous monitoring, understanding of temporal dynamics of seedling establishment and survival is severely limited. Therefore, any estimates of tree density beyond the last 30 years should be considered the density of trees that lived to adulthood.

Any approximation of stand mortality rates is likely to be an underestimation due to the vanishing record of dead seedlings. Therefore, in order to have an estimate of instantaneous mortality rates, the abundance of dead seedlings at the time of sampling was assessed. This estimate of instantaneous mortality is somewhat crude due to the difficulty in differentiating dead seedlings from the surrounding vegetation. However, these estimates provide some insight into the plausibility that a high density of seedlings relative to adult trees could be evidence of stand infilling, as opposed to a high mortality of young age classes and stand stability.

Pearson's correlation analysis was used to evaluate the relationship between recruitment/survival residuals and climate at treeline. Residuals during each decade were quantified and compared to: (1) mean June–July temperature for 1638–1988 in north-western Canada (Canol sites) (Szeicz & MacDonald, 1995b) and annual temperature for Churchill from 1671 to 1973 (Jacoby & D'Arrigo, 1989); (2) summer-weighted arctic temperature anomalies from 1600 to 1990 (Overpeck *et al.*, 1997); and (3) June–August Palmer drought severity index (PDSI) for the western Northwest Territories and north-central Manitoba from 1599 to 2003 (Cook *et al.*, 2004). Because successful recruitment can be related to climate during several decades after establishment, residuals were also compared to climate averages over 20-, 30-, 40- and 50-year periods (Szeicz & MacDonald, 1995a; Danby & Hik, 2007a). Therefore, the 50-year forward mean temperature for the 1900–1909 decade represents the average temperature for the 1900–1949 period, the 1910–1919 decade represents the average temperature for the 1910–1959 period, and so on.

RESULTS

Stand age structure

Throughout the Churchill region and considering all species, trees were older in the forest compared with the ecotone (*t*-test: $t_{58} = 1.966$, $P = 0.027$, all sites and species) (Fig. 6-2a–l; Table 6-1). *Picea glauca* was older in the forest ($t_{28} = 5.709$, $P<0.001$, all sites) while *P. mariana* was older in the ecotone [$t_8 = -2.190$, $P = 0.033$, site Black (BLK)], and ages of *Larix* were similar across the region [$t_{18} = 0.505$, $P = 0.310$, sites Ridge (RID) and BLK]. Additionally, recruitment of *Picea* occurred earlier than *Larix* across the region. At the site level near Churchill, most recent recruitment occurred in the ecotone, although *L. laricina* established concurrently across zones (Table 6-2). In the western Mackenzie Mountains, there was no difference in the age of the oldest individuals of *A. lasiocarpa* and *P. glauca* (one-way ANOVA: $F_{2,14} = 0.551$, $P = 0.590$). Despite the visual similarity in age structures from the Mackenzie Mountains (Fig. 6-2m–o), there were statistically significant differences between populations, which suggest that recruitment of individuals in the mountains occurred synchronously at lower elevations, and *A. lasiocarpa* established more recently at higher elevations (Table 6-2).

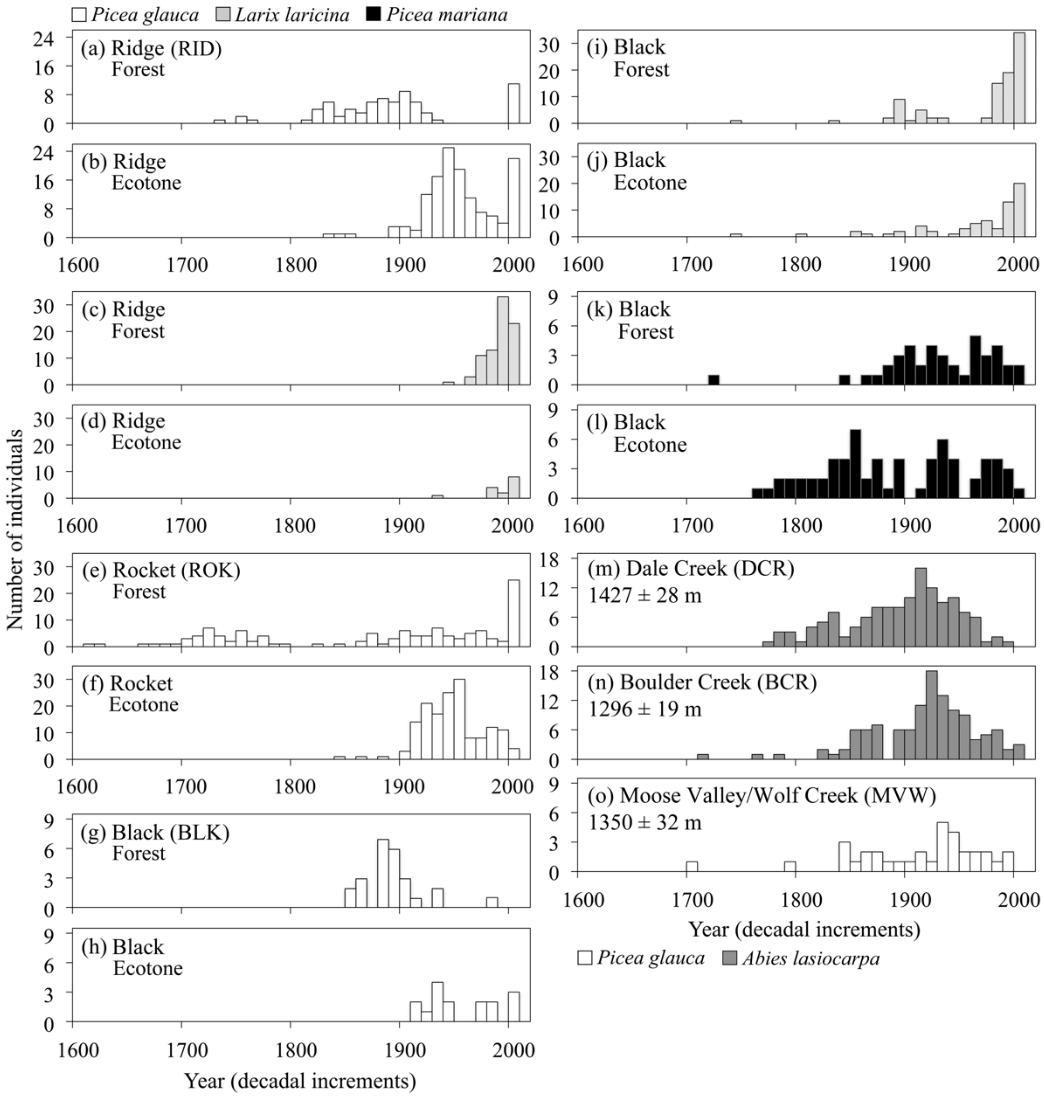

Figure 6-2. Age distributions of living individuals of *Picea glauca*, *P. mariana* and *Larix laricina* sampled near Churchill, Manitoba (a–l), and of *P. glauca* and *Abies lasiocarpa* sampled in the western Mackenzie Mountains (m–o), divided into decadal age classes. The mean and standard error of the sampling area elevation within the Mackenzie Mountains is shown. Note the change in scale of the y-axis between sites and species.

Stem recruitment and mortality

Most sampling plots near Churchill exhibited a recruitment pulse during the early 20th century; particularly ecotone plots where 60% of all individuals established 1920–1950 (Fig. 6-2a–l). Peak establishment occurred from 1890 to 1920 in forest plots with 28% of individuals establishing during that time. In the Mackenzie Mountains, 39% of all stems established from 1910 to 1940 (Fig. 6-2m–o). There were periods of mortality apparent at each site, though most occurred during the last 30 years (Fig. 6-3h,i). There was some synchronicity in mortality among Churchill sites, but no pattern was evident among the Mackenzie Mountain sites.

Stem density

For all species combined across the Churchill region, the date at which a threshold of 50 stems ha^{-1} was reached did not differ between the forest and ecotone ($t_8 = -1.425$, $P = 0.096$) (Fig. 6-3a–e). However, *P. glauca* reached the 50 stems ha^{-1} threshold in the forest 163 ± 114 years (mean age difference ± 1σ) before the ecotone ($t_4 = -2.420$, $P = 0.037$, all three sites) and *P. mariana* (70 years) and *L. laricina* (40 years) reached the threshold in the ecotone before the forest (site BLK). In addition, there were significantly more individuals established in the ecotone than the forest from 1900 to 1950 (paired *t*-test: $t_5 = -2.765$, $P = 0.020$), compared to recent decades (i.e. 1960 to 2000) ($t_5 = 1.064$, $P = 0.168$). With the exception of *P. glauca* at site Rocket (ROK), forest density increased dramatically during the late 1800s (Fig. 6-3a–e). Ecotone tree density at sites RID, ROK and BLK nearly tripled as a result of the recruitment pulse during the first half of the 20th century. Recruitment of *P. glauca* at the BLK site was noteworthy as all forest individuals were established after 1850 and all ecotone individuals were established after 1900. Lower elevation sites in the western Mackenzie Mountains reached 50 stems ha^{-1} earlier [Boulder Creek (BCR): 1790, Moose Valley/Wolf Creek (MVW): 1710] than the highest elevation site [Dale Creek (DCR): 1800)] (Fig. 6-3f,g). Additionally, recruitment of *A. lasiocarpa* was gradual throughout the record, whereas density of *P. glauca* nearly doubled due to the 1910 to 1940 cohort.

Table 6-1. Characteristics of sites sampled in the western Mackenzie Mountains, Northwest Territories (NWT), and the Churchill region, Manitoba (MB).

	Western Mackenzie Mountains, NWT			Churchill region, MB											
Site	DCR	BCR	MVW	RID				ROK		BLK					
Zone	TI	TI	TI	F		E		F	E	F			E		
Elevation (m a.s.l.)	1449	1347	1377	22		21		16	17	38			36		
Quadrat size (m^2):															
Tree (> 2 m)	855	557	79	699		204		750	1200	300			345		
Sapling (0.15–2 m)	0	0	0	150		660		460	100	175			115		
Seedling (< 0.15 m)	0	0	0	90		30		100	135	75			120		
Species	*Al*	*Al*	*Pg*	*Pg*	*Ll*	*Pg*	*Ll*	*Pg*	*Pg*	*Pg*	*Pm*	*Ll*	*Pg*	*Pm*	*Ll*
n (> 0.15 m)	134	120	34	63	50	95	6	75	122	31	36	41	10	61	18
n (> 2 m)	128	88	29	62	4	48	1	42	54	21	17	23	2	35	9
Oldest tree (establishment date)	1771	1719	1707	1735	1948	1833	1937	1578	1850	1856	1723	1746	1919	1769	1743
Density of stems > 2 m (ha^{-1})	1333	1652	3656	887	72	2451	49	667	467	767	600	767	58	1043	261
Decade when 50 stems ha^{-1} reached	1800	1790	1710	1770		1900		1630	1920	1860	1850	1840	1930	1780	1800
Maximum height (m)	9.0	5.7	8.2	7.6	6.3	5.1	6.7	11.9	5.4	9.2	8.8	9.6	2.8	8.0	5.4
Maximum diameter (cm)	33.0	16.4	41.8	33.7	23.1	15.0	6.7	46.0	28.0	28.5	20.0	23.4	7.3	24.0	23.5

BCR = Boulder Creek; BLK = Black; DCR = Dale Creek; MVW = Moose Valley/Wolf Creek; RID = Ridge; ROK = Rocket.

E = ecotone; F = forest; TI = tree island.

Al = *Abies lasiocarpa*; *Ll* = *Larix laricina*; *Pg* = *Picea glauca*; *Pm* = *Picea mariana*.

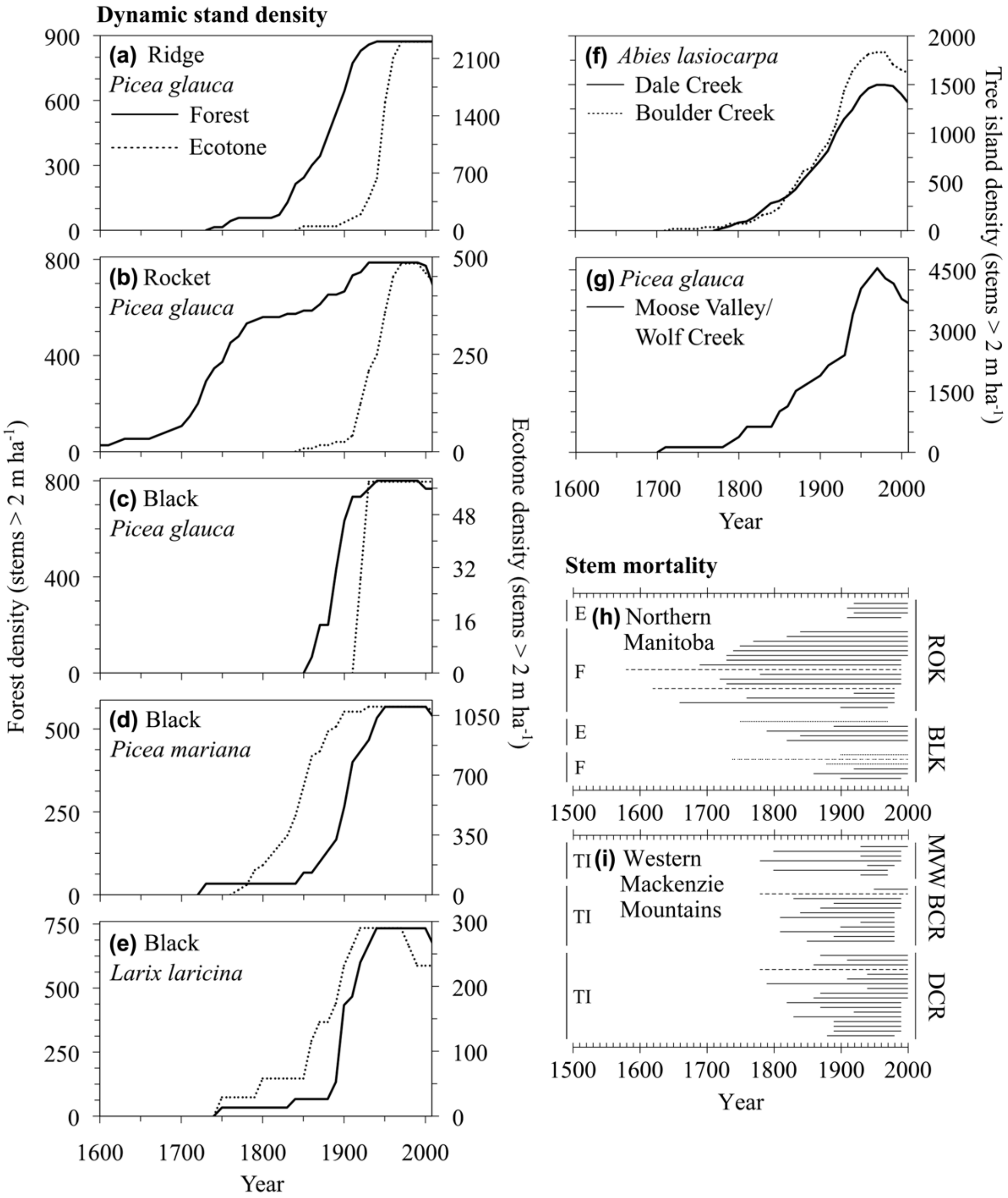

Figure 6-3. Tree density reconstructions for individuals ≥ 2 m sampled from the year 1600 to 2000 at (a–e) Churchill, Manitoba, and (f, g) the western Mackenzie Mountains. Data points represent density in the first year of a given decade based on changes in recruitment and mortality during the preceding decade. Life spans of dead stems in each sampling plot near (h) Churchill and (i) the western Mackenzie Mountains are also shown. Solid horizontal lines represent life spans of individual trees. Dashed horizontal lines indicate uncertainty in dating due to core rot. F = forest, E = ecotone, TI = tree island. Species include: *Picea glauca* [Moose Valley (MVW), Rocket (ROK) F and E, Black (BLK) F], *Picea mariana* (BLK E), *Abies lasiocarpa* [Boulder Creek (BCR) and Dale Creek (DCR)] and *Larix laricina* (grey). No dead stems were located in plots at Ridge (RID).

Table 6-2. Results of age structure statistical comparisons of the four treeline species in forest (F) and ecotone (E) plots using a Kolmogorov–Smirnoff (K-S) test and a Mann–Whitney (M-W) *U*-test. Bold text represents comparisons that were statistically different at $P < 0.05$.

Comparison	Age distribution (K-S test)	Median age (M-W test)	Establishment date (M-W test)
		Churchill	
ROK: F-*Pg* × E-*Pg*	**$P < 0.001$**	**$P < 0.001$**	**$P = 0.002$**
RID: F-*Pg* × E-*Pg*	**$P < 0.001$**	**$P < 0.001$**	**$P = 0.002$**
RID: F-*Ll* × E-*Ll*	—	$P = 0.956$	$P = 0.065$
BLK: F-*Pg* × E-*Pg*	**$P < 0.001$**	**$P < 0.001$**	**$P = 0.002$**
BLK: F-*Pm* × E-*Pm*	**$P < 0.001$**	**$P < 0.001$**	$P = 0.065$
BLK: F-*Ll* × E-*Ll*	**$P < 0.001$**	**$P = 0.027$**	$P = 0.065$
		Western Mackenzie Mountains	
DCR × BCR	**$P = 0.003$**	**$P = 0.002$**	**$P = 0.005$**
DCR × MVW	**$P = 0.002$**	**$P = 0.039$**	$P = 0.158$
BCR × MVW	$P = 0.889$	$P = 0.951$	$P = 0.970$

BCR = Boulder Creek; BLK = Black; DCR = Dale Creek; MVW = Moose Valley/Wolf Creek; RID = Ridge; ROK = Rocket.
Al = Abies lasiocarpa; *Ll = Larix laricina*; *Pg = Picea glauca*; *Pm = Picea mariana.*

Seedling establishment and mortality

There were a similar number of seedlings found in the forest and ecotone near Churchill (paired *t*-test: $t_{12} = 2.447$, $P = 0.590$), and no seedlings were found in the western Mackenzie Mountains (Fig. 6-4). The relative abundance of dead seedlings in the Churchill region ranged from 0 to 20% and did not differ significantly between forest and ecotone ($t_{12} = -1.348$, $P = 0.202$).

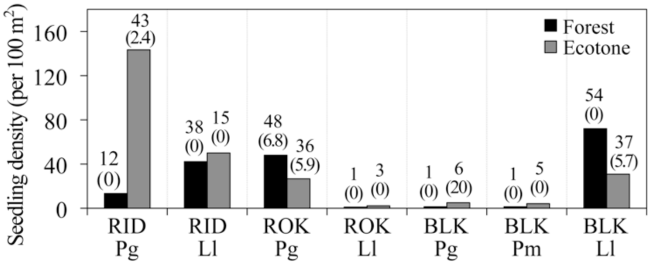

Figure 6-4. Density of seedlings within the forest and ecotone at each site in Churchill, Manitoba (see Fig. 1 for site locations). Values represent the number of seedlings and numbers in parentheses show the percentage of all seedlings that were dead at the time of sampling. No seedlings were found at sites in the western Mackenzie Mountains. Pg = *Picea glauca*; Pm = *Picea mariana* and Ll = *Larix laricina*.

Recruitment–climate relationships

Recruitment/survival residuals were positively correlated with temperature anomalies in the western Mackenzie Mountains and near Churchill (Fig. 6-5; Table 6-3), with the exception of BLK individuals (negatively correlated). PDSI correlations were positive for all Churchill sites except BLK and were either negative or not significant in the Mackenzie Mountains. No one particular window of climate averaging consistently performed best in terms of correlations, although most correlations were with 50-year forward means.

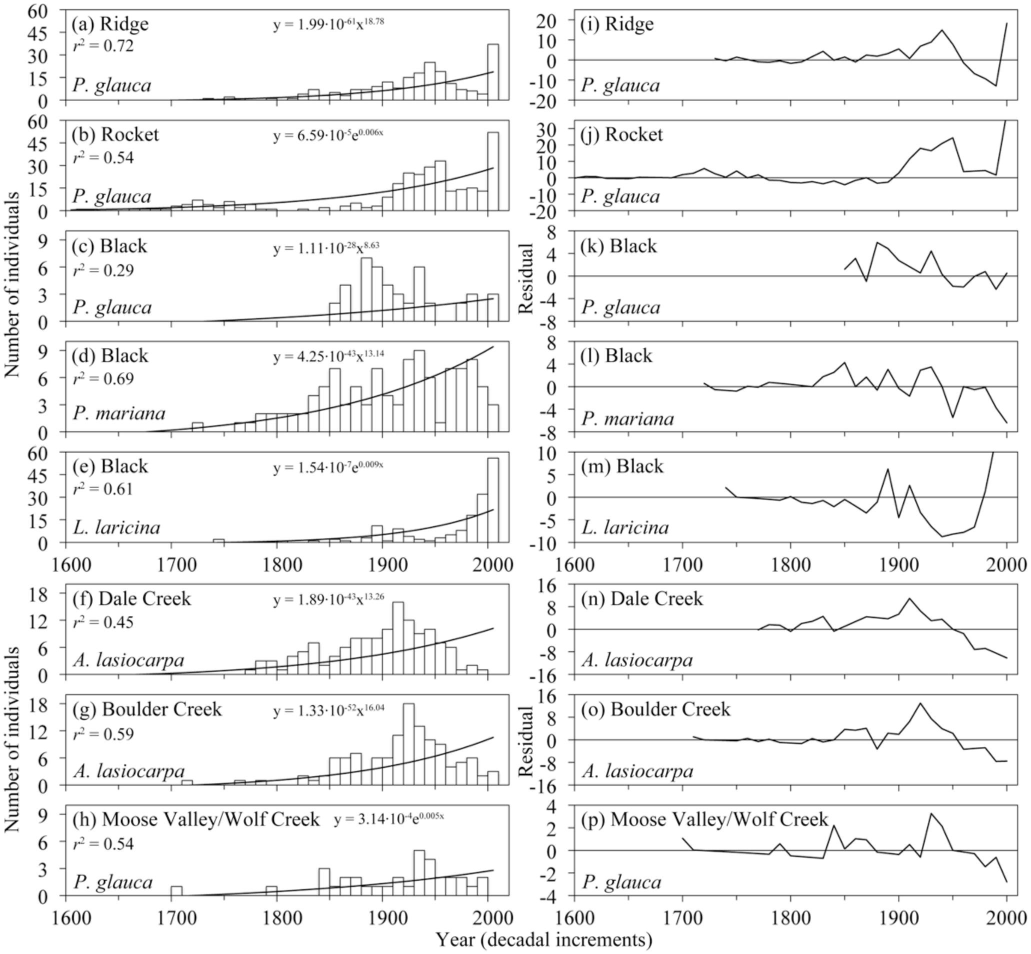

Figure 6-5. (a–h) Age distributions of living individuals of the four treeline species grouped at each study site (see Fig. 1 for site locations), and (i–p) residuals determined from exponential or power models fit to each age distribution. The line superimposed on each age distribution is the relative frequency predicted by the exponential or power model. Note the change in scale of the y-axis between sites and species.

Table 6-3. Correlations between recruitment/survival residuals of the four treeline species from exponential models and reconstructed climate from 1800 to 2000. Cell values are the Pearson correlation coefficients. See Fig. 1 for site locations.

		Temperature			
Site	Species	Churchill[a]	Arctic[b]	PDSI[c]	*n*[d]
ROK[e]	*P. glauca*	**0.944* (50 years)**[f]	**0.920* (40 years)**	**0.617* (50 years)**	21
RID	*P. glauca*	**0.792* (50 years)**	**0.761* (40 years)**	**0.733* (40 years)**	21
BLK	*P. glauca*	**-0.673* (10 years)**	**-0.604* (10 years)**	—	16
	P. mariana	**-0.499 (20 years)**	-0.404 (20 years)	**-0.506* (10 years)**	21
	L. laricina	-0.370 (30 years)	—	—	21
		NW Canada[g]	Arctic	PDSI	
DCR	*A. lasiocarpa*	**0.538 (50 years)**	**0.589* (50 years)**	-0.302 (10 years)	21
BCR	*A. lasiocarpa*	**0.760* (50 years)**	**0.721* (50 years)**	—	21
MVW	*P. glauca*	**0.510 (40 years)**	0.364 (50 years)	—	21

[a] Churchill annual temperature (Jacoby & D'Arrigo 1989).

[b] Arctic summer-weighted temperature (Overpeck *et al*., 1997).

[c] PDSI, Palmer drought severity index (Cook *et al*., 2004).

[d] *n*, sample size is a function of the age of the stand at each site.

[e] BCR = Boulder Creek; BLK = Black; DCR = Dale Creek; MVW = Moose Valley/Wolf Creek; RID = Ridge; ROK = Rocket.

[f] Correlations are followed by the length of the forward average (in years yielding the best correlation for each variable). Only values significant at $P < 0.20$ are shown; $P < 0.05$ for bold and $P < 0.01$ for values marked with an asterisk.

[g] Northwestern Canada, June–July average (Szeicz & MacDonald, 1995a).

Patterns of *Picea* recruitment were similar to trends in June through September temperatures at Churchill until the mid-20th century, when the records diverge (Fig. 6-6). A dramatic increase in *L. laricina* establishment occurred after *c*. 1975, and continued until the mid-1990s when approximately 25% of all sampled *Larix* stems were established. Recruitment of *A. lasiocarpa* in the Mackenzie Mountains peaked in the mid-1920s, and decreased steadily until the 1990s. Similarly, *Picea* recruitment peaked during the 1930s and decreased until the 1990s, and the records of recruitment of both *P. glauca* and *A. lasiocarpa* appear to diverge from May through September temperature during the last few decades.

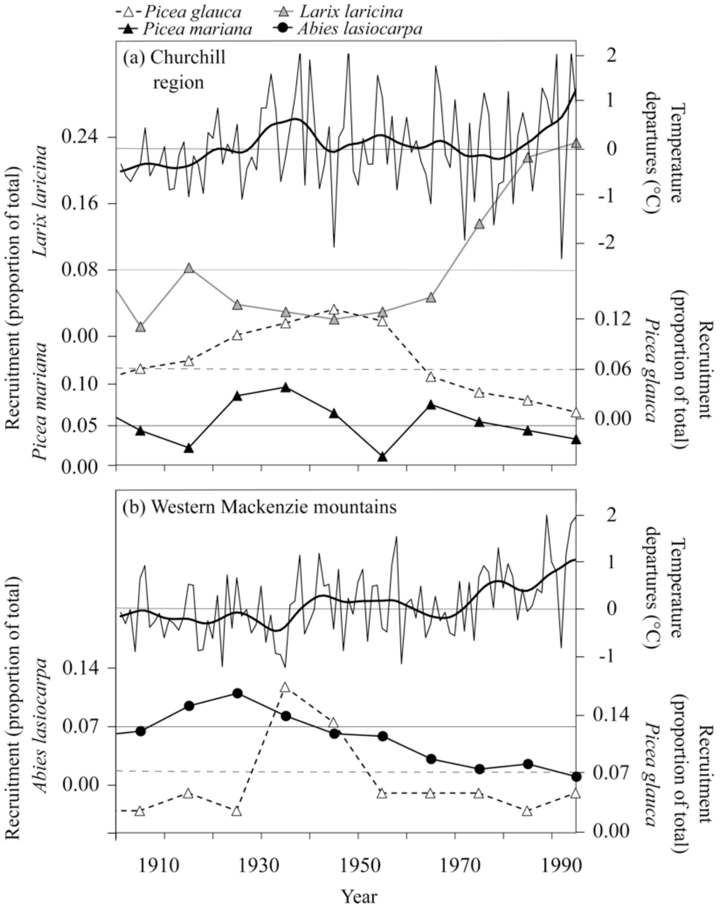

Figure 6-6. Relationship between forest–tundra dynamics and climatic change during the 20th century around Churchill, Manitoba, and the western Mackenzie Mountains. (a) Mean June–September temperatures for the region bounded by 58° N, 94° W and 59° N, 93° W, and (b) mean May–September temperatures for the region bounded by 63° N, 130° W and 64° N, 129° W, from New *et al*. (2000). The thin line is temperature departures relative to the 1971–2000 mean and the thick line is the same data fitted with a cubic smoothing spline. (b) Proportion of the total number of stems sampled in this study that established in the noted decade up to the 1990s. Horizontal solid and dashed lines represent the mean proportion of each corresponding species established during the 20th century.

DISCUSSION

20th century population dynamics

Advance of the treeline would generate a pattern of declining stand age with distance past the forest limit at Churchill and with increasing elevation in the western Mackenzie Mountains. It could be hypothesized that younger populations of individuals beyond the forest limit at Churchill (i.e. in the ecotone plots) and younger tree islands at higher elevations in the western Mackenzie Mountains would be expected if there had been an advance of the treeline at both sites. Evidence of advance was found in both regions, although with some differences at both species and site levels. At Churchill, advance of *P. glauca* was ubiquitous across the three study sites as suggested by absolute oldest establishment and mean oldest establishment dates across the forest–tundra transition (i.e. more recent establishment in ecotone plots). In addition, a density of 50 *P. glauca* stems ha^{-1} was achieved earlier in forest plots compared to ecotone plots. Conversely, while the oldest *P. mariana* individual sampled in BLK forest plots pre-dated the oldest individual in ecotone plots by *c*. 40 years, the mean establishment dates were older and 50 stems ha^{-1} was reached earlier in ecotone plots, suggesting advance of the 'treeline' from ecotone to forest. Similarly, *L. laricina* reached the threshold of 50 stems ha^{-1} in the ecotone earlier, but there was not a considerable difference in absolute or mean oldest establishment dates at the RID and BLK sites, although current stem densities were higher in forest plots. Within the BLK site, the seedbed changes from upland in the forest to *Sphagnum* bog in the ecotone, which suggests an edaphic influence on the magnitude and direction of treeline advance within BLK (Fenton *et al*., 2007). However, further study is needed to refine this hypothesis.

In the western Mackenzie Mountains, despite the visual similarities between age structures, absolute and mean oldest establishment dates of stems were younger at higher elevations (DCR), which suggests past advance of the treeline upslope. Furthermore, higher elevation stands reached a density of 50 stems ha^{-1} more recently than lower elevation stands (however, see climate discussion below). Although there was not a higher elevation stand of *P. glauca*, the age distribution and mean establishment dates of *Picea* was statistically similar to that of *Abies*, which suggests that inception of stand development for both species was synchronous in the area.

Another potential explanation for a pattern of relatively young individuals beyond the forest limit could be that mortality rates were higher, resulting in a quick turnover and therefore few to no old trees. If mortality rates have been high, then one would expect dead trees and seedlings to be common past the forest limit among the sampling sites. However, high mortality rates were not apparent, as relatively few dead trees compared to live trees were found in either region. One caveat to this line of reasoning is that most dead trees found had died in recent years and there was little evidence of older mortality at the sites. It is possible that decomposition and/or inundation by moss and understory vegetation is relatively quick and dead trees that fall are swiftly decomposed or buried by organic material. This suggests that the mortality record is incomplete. Therefore, it is still unknown as to whether or not recent mortality resulted from a discrete event, or has occurred continuously during the last several centuries. Accordingly, reconstructed mortality rates might not be reliable beyond the last two or three decades and should be interpreted cautiously. However, mortality of seedlings was low and did not differ significantly across the forest–tundra transition, which implies that high mortality past the forest limit is an unlikely explanation for the younger age structures observed in ecotone plots. High densities of live seedlings, considerable increase in stand density over time, and low abundance of dead seedlings in plots past the forest limit suggest more recent establishment of trees beyond the forest limit is the result of treeline advance. Further research should include continuous monitoring of demographics of these treeline study sites, including establishment and survival, winter desiccation, mortality, seed viability and microclimate. Such studies are invaluable to the development of treeline theory as they can monitor treeline dynamics at a seasonal time scale and would be expected to reinforce the results obtained in this study. Continuous monitoring of treeline metrics in Sweden has shown ubiquitous treeline advance over the same time period (Kullman, 2007; Kullman & Öberg, 2009; and see discussion below), which adds support to the premise that circumboreal treeline advance with projected warming may be an ecological reality and, pending increased disturbances such as wildfire or unusually cold winters, could continue (Kullman, 2002; Harsch *et al.*, 2009).

Forest–tundra dynamics and climate change

The start of considerable recruitment in the western Mackenzie Mountains (when density of stems reached 50 ha^{-1}), coincided with a warm period in western Canada from the 1740s to 1810s (Szeicz & MacDonald, 1995b). The presence of this cohort implies a connection between warming and recruitment, which is reflected in the significant correlations with climate on a regional and synoptic scale (Table 6-3). However, this relationship appears to have broken down in recent decades as temperatures have increased by approximately 1.6 °C since 1901—most of that warming occurring during the last 30 years (New *et al.*, 2000), yet no seedlings were found in the western Mackenzie Mountains. A number of possible reasons could account for this phenomenon such as an inhospitable seedbed (Houle & Filion, 2003), moisture stress (Malanson *et al.*, 2007), decreased reproductive potential (Sirois, 2000), herbivory and granivory (Castro *et al.*, 1999; Cairns & Moen, 2004), or a combination of these and other factors. Little to no ovulate and pollen cones have been observed on sampled stands since a mast year occurred in the Mackenzie Mountains during 2006, implying a direct limitation of reproduction. Similarly, germination trials of seeds of *A. lasiocarpa* from a small sample of cones collected in 2009 yielded no successful germinants (S.D. Mamet & G.P. Kershaw, unpublished data). The region has also experienced a higher frequency of drier than normal summers (relative to the 1961–1990 mean) from the mid-1970s to the late-1990s coincident with warmer temperatures (New *et al.*, 2000), which may be related to an extended positive phase of the Pacific Decadal Oscillation (PDO) (Alftine *et al.*, 2003; Malanson *et al.*, 2007). Therefore, it is possible that recent moisture availability has resulted in a decrease in fecundity of the high temperature-intolerant *A. lasiocarpa* (Alexander *et al.*, 1990) and in seedling establishment (Black & Bliss, 1980) in this region. This may also partially explain the low, albeit significant, negative correlation between DCR recruitment residuals and PDSI, although further research is necessary to properly evaluate this working hypothesis.

Multi-decade windows of forward temperature averaging yielded the highest correlations with recruitment residuals, and significant correlations with the PDSI were observed at both study areas (Churchill: $P < 0.05$, western

Mackenzie Mountains: $P < 0.20$). These connections reinforce the notion that temperature influences recruitment as much as establishment, and that establishment is greatest when relatively warm and dry environmental conditions prevail—although with sufficient soil moisture availability as indicated by the responses of *P. mariana* and *A. lasiocarpa.* Low temperatures slow the growth of seedlings and saplings, thereby extending the time between germination and maturation and increasing the risk of seedling mortality (Danby & Hik, 2007b). Therefore, favourable temperature and moisture regimes at both the time of establishment and throughout the early life stages are crucial for successful recruitment.

Along the east coast of Hudson Bay in northern Québec, establishment of *L. laricina* has increased dramatically in recent years (Peñalba & Payette, 1997). Similarly, in the Rocky Mountains of southern Alberta, a pulse of *Larix* recruitment has occurred since the 1980s (Roush, 2009). This recent phenomenon of *Larix* establishment is not just restricted to North America. Similar patterns have been observed in Sweden (Kullman, 1998), Switzerland (although with a confounding human influence) (Heiri *et al*., 2006), Russia (MacDonald *et al*., 2008), Mongolia (Treter, 2000) and China (Baker & Moseley, 2007), which suggests this has been a circumboreal event. A caution to interpretation of the recent *L. laricina* infilling of both forest and ecotone plots is that the age classes consist primarily of seedlings and saplings that, as mentioned previously, are quick to decompose following death. Thus, from these data it is impossible to determine whether the abundance of the early life stages of *L. laricina* is a recent phenomenon, or whether the majority of established individuals only survive to saplings, then die before becoming mature trees. Perhaps this is related to a ‘nursery’ effect of the surrounding shrubs (Maher *et al*., 2005) and mosses (Wheeler *et al*., 2011), which facilitate growth of saplings until they extend above the shrub canopy where they can be subjected to frigid, desiccating air and winter blown snow abrasion. Continued monitoring of seedling and sapling survival is necessary to determine the fate of the recent *L. laricina* cohort around Churchill. Nonetheless, the recent dramatic increase in *Larix* establishment illustrates the importance of species-specific responses to climate change, and highlights the complexity of treeline dynamics in a changing environment.

CONCLUSIONS

There was a period of rapid infilling and treeline advance around Churchill and in the western Mackenzie Mountains during the first half of the 20th century. Periods of heightened recruitment and rapid advance have been observed at subarctic treelines in other locales over the same period (Scott *et al*., 1987; Szeicz & MacDonald, 1995a; Lloyd & Fastie, 2003; Danby & Hik, 2007a). As in other studies, recruitment at and beyond the forest limit was correlated with periods of warm summer temperatures at various scales (Lloyd & Fastie, 2003; Danby & Hik, 2007a), which contributes to the growing body of evidence that treeline advance with warming may be a circumboreal rule, rather than an exception.

An abundance of seedlings and low mortality suggest stand infilling and the advance of the treeline around Churchill will continue, while in the western Mackenzie Mountains the current treeline has stagnated, due to the lack of sexual reproduction. The slight differences in timing of recruitment and advance between sites (particularly for *L. laricina*) and study areas can be indicative of a certain amount of inertia, or a slow gradual change followed by rapid change in response to changing temperature regimes. This type of change has been hypothesized (Lloyd, 2005) and confirmed by empirical evidence (Danby & Hik, 2007a). In addition, the results of this study demonstrate that population-level responses can vary dramatically at several scales and might not be static through time. While temperature changes can be the primary forcing behind treeline dynamics, actual responses could be contingent on existing vegetation, edaphic characteristics, species-specific traits and terrain variability.

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CHAPTER SEVEN

Synthesis and conclusion

> "*It is not helpful for an understanding of the treeline phenomenon to state that* 'everything matters'*, that all climatic factors must be considered, that climatic means cannot be used etc. and, instead of carefully applying available data, providing verbose elaborates which do not bring us any nearer to solving the problem.*"
>
> Christian Körner (2003)

INTRODUCTION

Attempts have been made to find a functional explanation for treeline position at a global scale. Körner (2003) suggested separating regional-scale modulative drivers from global-scale fundamental drivers (i.e., temperature). Irrespective of scale, Körner identified five groups of partly interrelated mechanisms:

(i) Stress hypothesis: repeated damage by freezing, frost-desiccation, or phototoxic effects which impair tree growth;

(ii) Disturbance hypothesis: mechanical damage by wind, ice-blasting, snow break, avalanches, or herbivory and fungal pathogens may remove more biomass or meristems than can be replaced by growth and development;

(iii) Reproduction hypothesis: pollination, seed development, seed dispersal, germination, and seedling establishment may be limited and prevent tree recruitment at high latitudes/altitudes;

(iv) Carbon balance hypothesis: either carbon uptake or balance between uptake and loss are insufficient to support maintenance and minimum growth of trees;

(v) Growth limitation hypothesis: synthetic processes which lead from sugars and amino acids to the complex plant body might not match the minimum rates required for growth and tissue removal independently of the supply of raw materials (i.e., photosimilates).

Recently Harsch and Bader (2011) categorized treelines as one of four types based on physiognomy: diffuse, abrupt, tree island, and krummholz. Similar to Körner, they suggested that there were dominant mechanisms that controlled treeline dynamics—albeit dependent on treeline form—which they categorized into three levels of influence in order of decreasing influence: tree performance, stress and neighbour effects (Fig. 7-1). Thus while Körner's (2003) list of mechanisms is useful at broad-scales, it becomes more problematic at increasingly finer scales. The distinction of treeline form by Harsch and Bader (2011) helps to mitigate some of the problems associated with ascribing a universal explanation for treeline, though since it is impossible to study everything—even though everything does matter—the complexity of fine-scale influences on treeline dynamics must be organized in a comprehensible and relevant way.

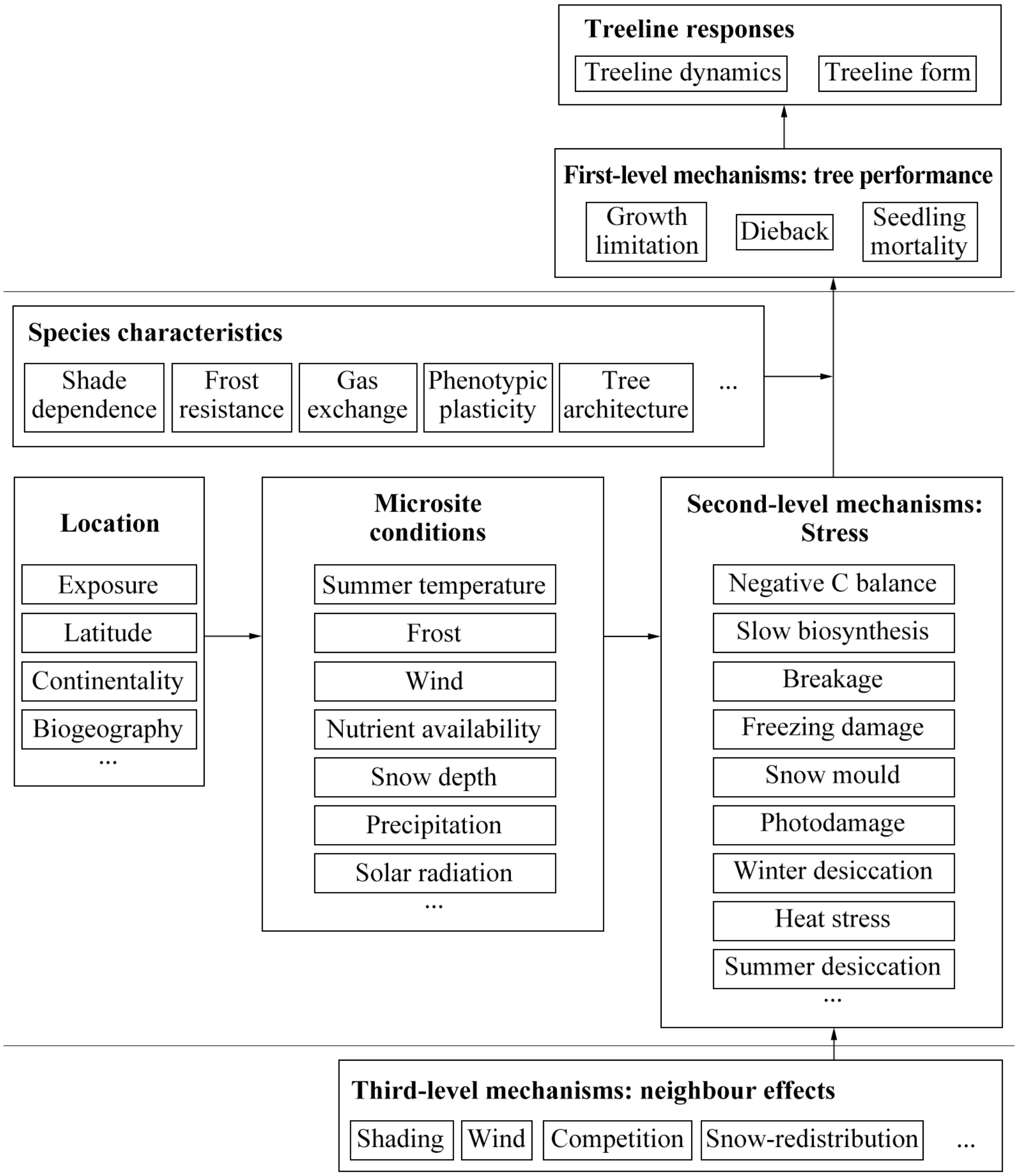

Figure 7-1. Outline of a framework for understanding treeline dynamics, showing three levels of control mechanisms and the factors and conditions that determine how these mechanisms operate. Ellipses indicate that the listing of mechanisms is not exhaustive. Reproduced from Harsch and Bader (2011).

Treeline form and dynamics

Low-temperature-induced growth limitation is the most general phenomenon at all treelines worldwide—that is, in the absence of all other limiting factors, the treeline would most likely occur beyond the current position in the event of warming (Holtmeier & Broll, 2005). Therefore, the observed treeline forms and positions are the result of interactions between growth limitation and stresses that influence mortality and dieback (Fig. 7-1). At diffuse treelines, such as is observed in the Churchill area, tree height and density tend to gradually decline with proximity to the treeline (Fig. 7-2a). Harsch and Bader (2011) hypothesized that diffuse treelines are formed and maintained primarily by growth limitation—the primary stressor being low growing season temperature. Harsch and Bader expected that warming should increase growth rates and seedling survival, resulting in more rapid recruitment past treeline and, indeed, at 86 treeline sites worldwide, 80% of diffuse treelines advanced recently with mean annual warming (Harsch *et al.*, 2009).

Island treelines occur as patches of upright trees or krummholz growing above a continuous forest line—as is the case in the western Mackenzie Mountains in the Northwest Territories (Fig. 7-2b). The direction, size, and shape of tree islands are thought to be controlled primarily by seedling mortality and dieback, but can also be influenced by microtopography (Holtmeier & Broll, 1992; Bekker *et al.*, 2009). Reproduction in islands is primarily by layering, the direction of which is determined by dieback. Dieback typically occurs at the windward sides of islands and in shoots extending above the snowpack (Bekker, 2005). Island genesis typically starts where small topographic features (such as boulders) modify conditions—which improve survival in localized patches—with subsequent modification of conditions by existing trees through positive feedbacks (Alftine & Malanson, 2004). The importance of this positive feedback, inferred from the degree of clumping of trees, typically increases with environmental severity (Bekker & Malanson, 2008; Harper *et al.*, 2011). Tree islands typically occur in very extreme environments and, accordingly, less than 10% of tree island treelines worldwide are advancing (Harsch *et al.*, 2009). Moreover, in the case of stable island treelines, directional growth (i.e., layering) can allow for slow migration of individual islands (Holtmeier & Broll, 1992), but in order for the ecotone to advance as a whole, there needs to be amelioration of the climatic conditions limiting survival (Bekker, 2005).

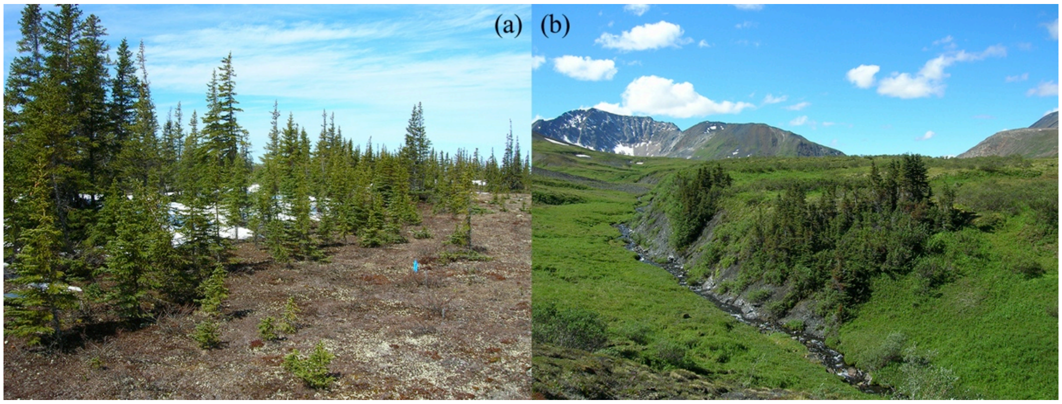

Figure 7-2. Examples of treeline forms observed in this study. (a) Diffuse treeline of *Picea glauca* southeast of Churchill, Manitoba (30 June 2009, photo S.D. Mamet). (b) *Abies lasiocarpa* tree island treeline east of Macmillan Pass, Northwest Territories (28 July 2008; photo S.D. Mamet).

SUMMARY OF RESULTS

The following sections provide a synthesis of the five main investigations that encompassed this research. Results from each chapter are briefly précised and opportunities for future research are identified. The results of these investigations, along with personal experience obtained while completing the research, are then used as conceptual tools for considering potential responses of subarctic and alpine treelines to anticipated climate change (ACIA, 2004; Gagnon & Gough, 2005). Lastly, the results of this study are integrated in the context of treeline ecological theory, and extant frameworks for considering treeline dynamics in this scientific study are evaluated.

Growth limitation and climate at treeline

Spatial and temporal variability in growth and climate response of trees at and near treeline was investigated in the western Mackenzie Mountains, Northwest Territories, and the Hudson Bay Lowlands of northern Manitoba. Residual ring width chronologies were constructed using cores extracted from 108 trees in the mountains and 170 from the lowlands, and compared to historical climate data. Growth of most trees exhibited significant correlations with summer and autumn temperatures, and the growth-climate relationship did not differ noticeably between trees at and distal to treeline.

Most mountain trees had significant positive growth trends from 1851−2006 that corresponded with warming over the same period, while growth trends varied among sites and species in the lowlands. Regionally, growth of all species responded positively to warming during the 20th century with the exception of lowland *Picea mariana*, which exhibited little response. Growth response for most trees was age-dependent, with trees established after 1920 demonstrating improved growth and sensitivity to temperature than older individuals, and growth of most species since the 1990s was greater than any time during the last 250 years, particularly for lowland *Larix laricina*.

This study suggests that site factors and tree age can be more important drivers of local-scale growth trends than regional climate at arctic treelines where temperature is often assumed to be the main constraint on tree growth. Thus spatial scale of study is an important consideration for further research.

Future monitoring of treeline populations is crucial due to the age-dependent and interspecific nature of growth response to climate, and should consider detrending end-effects in any further dendroclimatological research. It is curious that long-term trends of tree growth at a regional scale reproduce long-term trends in temperature (recall table 2-5), though short-term (i.e., annual) fluctuations in growth can be opposite of air temperature variations (Fig. 2-8). Recent evidence suggests that treeline trees can acquire a sufficient provision of photosynthates, though there persists a direct or indirect low-temperature-induced limitation of tissue formation at otherwise sufficient carbon acquisition by photosynthesis [growth limitation hypothesis (*sensu* Körner, 1998)] to growing tissue (Hoch & Körner, 2009; 2012). Given that xylogenesis typically occurs between 4–14°C in treeline trees (Rossi *et al.*, 2008), and the suggestion that soil moisture could become limiting in a warming environment (Barber *et al.*, 2000), seasonal monitoring of soil moisture at treeline should be paramount, and used to help to decipher the actual mechanisms that control tissue formation at treeline.

Needle health and biomass dieback

Growing season air temperatures around Churchill were significantly cooler in 2009, resulting in the development of significantly shorter needles sampled during mid-winter of 2010. Minimum epidermal conductance ($g_{\min}$) varied little with height on the tree or orientation to the wind. Most notably perhaps is that the highest values of $g_{\min}$ (4.6×10^{-5} m s^{-1}) were observed in 2010, when temperatures during the previous June were 3.7°C; 2.9°C cooler than normal. Conversely, the lowest g_{min} of 2.8×10^{-5} m s^{-1} occurred during 2009 when the previous June was 7.8°C; 1.2°C warmer than normal. There were few correlations between needle viability and water content, and little consistency in correlations from year to year. However, significant correlations were observed during all three years in northwestern-facing needles within the ecotone zone, which suggests that treeline trees could be the most susceptible to water loss and dieback, relative to forest and tundra individuals.

These results indicate that there is some evidence for winter desiccation at diffuse treelines in the western Hudson Bay Lowlands, though the magnitude of that influence on treeline dynamics is debatable. Winter desiccation is widely believed to be a limitation of treeline position at some locations (Wardle, 1971; Tranquillini, 1979; Sowell *et al.*, 1982; Kullman, 2007). However, my observations of little winterkill at diffuse treelines within the western Hudson Bay Lowlands, though abundant winterkill at tree islands and krummholz stands further towards the most exposed Hudson Bay coast, suggests that the scale of study could impact the magnitude of winter desiccation observed at treeline. For example, had I run a transect from areas of open forest and woodlands, grading through the diffuse treelines and into tree and krummholz islands further towards the coast, I speculate that the dichotomy between desiccation and water loss at each end of the transect would be much more pronounced. Therefore, further research should focus on tree and krummholz islands within the western Hudson Bay Lowlands, similar to the investigation undertaken by Cairns (2001) in Glacier National Park, Montana. As well, sampling should be completed throughout the annual cycle of needle development and exposure (i.e., during the the autumn, winter and spring following development) in order to evaluate needle desiccation and dieback with greater temporal resolution.

Seedling establishment, environment, and plant interactions

Growing season—as it related to the 3.2°C soil temperature threshold at 10 cm depth (*sensu* Körner & Paulsen, 2004)—was longer at treeline relative to forest at Churchill. Snowpack depth was similar within forest and treeline, though much more shallow and heat conducting within tundra. Soil organic matter (SOM) thickness and pH typically decreased from forest to tundra, and decomposition rates were similar across the ecotone. Soil nutrient supply rates were typically consistent within a site, though varied between sites. Many *Picea* seeds were produced within the region, with typically high germination (> 88%) of filled seeds. Many seedlings were found within forest and at treeline, and there were more *L. laricina* (n = 187) seedlings found compared with *Picea* (*P. glauca*: n = 172; *P. mariana*: n = 9). The percentage of dead seedlings ranged from 0 to 20%, and was low for all species across all sites. Seedlings appeared to preferentially establish in moss and duff, and the influence of low shrubs and lichen seemed to change from competition in forest to facilitation at treeline.

One of the conclusions of Hobbie and Chapin (1998) was that treeline is in part a consequence of an inability of trees to establish in tundra. The results of this study and my personal observations of numerous seedlings, saplings and stunted individuals past the tree limit within the Hudson Bay Lowlands, suggest that establishment is possible in tundra nearer to treeline, though this might not be applicable to areas well beyond the distributional limit of *Picea* and *Larix*. Indeed there appears to be sufficient seed source, germination success, and survival to imply that reproduction is not a limitation to treeline advance around Churchill. However, future advance will be contingent on suitable seedbed and facilitative effects of low stature vegetation.

Long-term investigations like that of Kullman (2007) in the Swedish Scandes would be the ideal avenue for future work of treeline dynamics anywhere—where establishment, recruitment and advance are observed over many years and are explicit. In the absence of long-term monitoring, I would suggest extending the vegetation and seedling survey techniques applied here to include tundra individuals in order to examine potential facilitative effects in exposed areas. As well, population censuses at a seasonal resolution, would allow annual assessment of mortality rates of the various life stages of trees, in order to elucidate the low mortality rates speculated by this study.

Seedling establishment, recruitment and climate

During 2007, 2008 and 2009, from a plot-based survey of seedlings and saplings, a greater density of seedlings—in fact an order of magnitude more—was found at a wetland site (a combination of sedge-rich fen and sphagnum spruce bog micro-environments), compared to an upland site (lichen-spruce forest). Of the 270 individuals found in this study, 205 (76%) were *L. laricina*, and all but one were found in the wetland site. Seedling establishment was low and virtually non-existent in some years, in the nearly continuous *Cladina* lichen mat of the upland forest. Residuals from models fit to seedling/sapling age structures were not correlated with standardized growth indices of extant trees, though had significant correlations with growing season (June–September) temperatures—particularly *L. laricina*. Temperature five years following establishment appeared to be the most important driver of population dynamics, though the conspicuous absence of seedlings in the upland site, suggests a superseding influence, which I speculated was the lichen-dominated seedbed. Establishment of wetland *P. mariana* was not related to climate, and could be responding more to edaphic influences.

It is no secret that seedling establishment can be limited by extensive lichen mats via uprooting, desiccation and allelopathy (Allen, 1929; Kershaw, 1978; Houle & Filion, 2003). However, due to the conflicting results of the investigations presented in chapters four and five, further research is necessary. While the surface of *Cladina* lichen mats can be extremely dry, the lichens themselves impede water loss from the ground below so that soils beneath a thick mat can remain at field capacity (Fraser, 1956). Thus if seedlings can germinate within desiccation cracks or at the margins of mats, they could be shielded from excessive solar radiation and low-temperature photoinhibition, and have an adequate moisture supply for growth and survival (Houle & Filion, 2003). Further research should include assessment of moisture dynamics beneath lichen mats, as well as a more detailed assessment of the nature and longevity of seedling establishment within lichens (e.g., within cracks, lichen margins, etc.).

Contrasting responses of subarctic and alpine treelines to warming

Results of the dendroecological stand analyses indicate that treeline position and stand density increased in the western Mackenzie Mountains and western Hudson Bay Lowlands appreciably during the early-mid-20th century. Increases in tree recruitment were strongly correlated with reconstructed summer temperatures. The period of rapid change in the second quarter of the 20th century coincided with a 30-year period of above average temperatures, from ~1920 to 1950. The highest correlations were obtained using a 30-50 year window of forward averaging—comparable to other studies (Szeicz & MacDonald, 1995; Danby & Hik, 2007). This supports what was found in analyses of seedling/sapling age structure: that treeline dynamics are controlled more by conditions that influence recruitment (e.g., survival to 0.15 to ~2 m in height), rather than solely establishment.

An abundance of seedlings and low mortality suggest stand infilling and the advance of the treeline around Churchill will continue, while in the western Mackenzie Mountains the current treeline has stagnated, due to the lack of sexual reproduction. While reproduction deficits appear to be the limiting factor for treeline advance within the mountains, it is yet unknown why there are few cones and no viable seeds produced there. It is possible that recent moisture availability has resulted in a decrease in fecundity of the high temperature-intolerant *A. lasiocarpa* (Alexander *et al.*, 1990) and in seedling establishment (Black & Bliss, 1980) in this region. Future research should include analysis of edaphic characteristics and monitoring of fecundity and reproduction (*sensu* Krebs *et al.*, 2012) at these tree islands.

The conspicuous increase in recruitment of *Larix* in the western Hudson Bay Lowlands is extraordinary. This recruitment is mirrored by abundant establishment of *L. laricina* seedlings in forest and at treeline across the study area (see chapters four and five), as well as a dramatic increase in growth of both old (established prior to 1920) and young (established following 1920) trees, which is reiterated throughout the circumboreal treeline (Peñalba & Payette, 1997; Kullman, 1998; Treter, 2000; Heiri *et al.*, 2006; Baker & Moseley, 2007; MacDonald *et al.*, 2008; Roush, 2009). However, due to the young nature of many of the *L. laricina* stems (i.e., most are seedlings and saplings), continued monitoring of these cohorts (*sensu* Kullman, 2007) is warranted to determine if the momentum of this population dynamic will continue into the 21st century.

TREELINES IN THE WESTERN MACKENZIE MOUNTAINS AND WESTERN HUDSON BAY LOWLANDS: HOW DO THEY FIT INTO EXISTING TREELINE THEORY?

Recent advances in general treeline theory have provided a framework within which to evaluate the treeline phenomenon in the context of a changing climate. Based on the proposed ecophysiological process and physiognomic pattern at treeline (Körner, 1998; Harsch & Bader, 2011), island treeline within the western Mackenzie Mountains should be limited primarily by reproduction and dieback, while diffuse treeline around Churchill should be limited primarily by growth limitation due to low growing season temperatures.

Growth of trees at both locales has maintained a positive response to growing season temperature throughout the 20th century (chapter two), while recruitment at both treelines responded positively to warm temperatures during the early, but not late, 20th century—with Churchill as the exception (chapter six). Indeed site-scale growth at Churchill has typically remained positive for the last two decades, significant correlations between growth and growing season temperature were observed, viable seeds have been produced (chapter four), and treeline has advanced and continued to advance. Conversely, growth within the mountains has remained positive, though become uncorrelated with growing season temperatures in recent decades, no seedlings were found, and few cones and little, if any, viable seeds have been produced. Consequently, treeline has remained stable in recent decades, in spite of warming temperatures (New *et al.*, 2000), though does not appear to be limited by dieback or seedling mortality as predicted by Harsch and Bader (2011).

The results of this research beg the question: was treeline theory helpful in these investigations? In the western Hudson Bay Lowlands the answer is yes. Both the application of treeline form and regional-scale drivers was useful in evaluating treeline dynamics in that area. However, the question is more difficult to answer within the western Mackenzie Mountains. The lack of sexual reproduction supports the reproduction hypothesis of Körner (1998), though precludes the hypothesis of Harsch and Bader (2011) that seedling mortality and dieback limit treeline islands.

Nonetheless, my time in the field around the Mackenzie Mountains was truncated compared with Churchill, and therefore observation of dieback during the spring was not possible. Therefore I would suggest that applying existing treeline theory was predominantly useful here. Although classifying a continuum of treeline forms into discrete classes based on several characteristics creates ambiguous cases, it is necessary and helpful to clarify general patterns (Harsch & Bader, 2011). There will always be exceptions to the rule, and therefore site, scale, and species-specific responses warrant careful consideration and impartiality when employing these paradigms. Because what is expected (e.g., warming equates to treeline advance) might not be observed, and what is observed, might not be expected.

CONCLUSIONS

The research presented here is the first multi-site, in-depth study of treeline pattern and process in the western Mackenzie Mountains and the western Hudson Bay Lowlands. The basic methods employed in each investigation have been used elsewhere, but by integrating them within a single study I have been able to elucidate influences on pattern and process across the forest-tundra ecotone. This included a rapid increase in radial growth increments and regeneration number, stand densification, treeline shift, and vegetative facilitation variations across treeline.

Based on this study it can be concluded that in the absence of increased natural or anthropogenic disturbances and/or moisture stress, treeline shall continue to advance around Churchill, potentially with a change from *Picea* to *Larix*-dominated communities. Despite significantly increased growth rates during the last several decades, no seedlings were found within the western Mackenzie Mountains since at least 2006, and reproduction has been exclusively asexual. The disparity in response between the two treelines highlights the need for consideration, not just of climate, but also of treeline form, vegetation interactions, and autecology in treeline dynamics.

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