2018

GROWTH DYNAMICS OF BLACK SPRUCE (PICEA MARIANA) ACROSS NORTHWESTERN NORTH AMERICA

Anastasia E. Sniderhan
Wilfrid Laurier University, snid3620@mylaurier.ca

Recommended Citation

Sniderhan, Anastasia E., "GROWTH DYNAMICS OF BLACK SPRUCE (PICEA MARIANA) ACROSS NORTHWESTERN NORTH AMERICA" (2018). *Theses and Dissertations (Comprehensive)*. 2006.
https://scholars.wlu.ca/etd/2006

GROWTH DYNAMICS OF BLACK SPRUCE (*PICEA MARIANA*) ACROSS NORTHWESTERN NORTH AMERICA

By:

Anastasia Elizabeth Sniderhan

B.Sc. Honours Ecology, University of Guelph, 2011

DISSERTATION

Submitted to the Department of Geography and Environmental Studies
in partial fulfillment of the requirements for
Doctor of Philosophy in Geography
Wilfrid Laurier University

Abstract

The impacts of climate change have been widely documented around the world. One of the most rapidly changing areas is the boreal forest of North America. The extent of change has been such that there have been shifts in long-standing climate-growth relationships in many boreal tree species; while the growth of many of these high-latitude forests were formerly limited by temperature, warming has increased the evapotranspirative demands such that there is widespread drought stress limiting productivity in the boreal forest. With the importance of the boreal forest as a global carbon sink, it is imperative to understand the extent of these changes, and to predict the resilience of the boreal forest in the face of continued climate change. One area of the boreal forest that has not been extensively studied, despite some of the most extreme warming, is northwestern Canada. Black spruce, the most widespread and dominant of North American boreal trees, is particularly under-studied in this region. In my doctoral research, I have sought to fill some of these knowledge gaps regarding black spruce growth dynamics across its latitudinal extent in northwestern Canada through addressing three main objectives: (1) Investigate the effects of permafrost thaw on the growth dynamics of black spruce in a discontinuous permafrost peatland; (2) Compare the productivity and main climatic drivers of black spruce growth across the latitudinal extent of the species in northwestern Canada; (3) Quantify the degree of plasticity vs. local adaptation in determining black spruce growth responses to resource availability in a common garden study. The results of this research highlight the variability in black spruce growth dynamics across this broad climate and permafrost gradient. While productivity has increased at the northern and southern margins of the boreal forest, the mid-latitude site in the discontinuous permafrost peatland has demonstrated dramatic declines in productivity. I demonstrate that this can be attributed to the negative impacts of permafrost thaw-induced drought stress, wherein the thickening of the active layer is reducing the capacity of shallow-rooted black spruce to access the water table. Thus, decreased growth at this site is an indirect effect of warming. At the northern margins of black spruce, growth is increasing as a result of warming, likely as it can drive longer growing seasons and increased nutrient mineralization. Growth at the southern margin does not appear to be driven by either temperature or precipitation alone, however growth patterns appear to be influenced by water balance at the site as well as CO_2 fertilization. The common garden study of seedlings from across the latitudinal extent of black spruce in northwestern Canada provided evidence for local adaptation in black spruce seedlings; the southern seedlings accumulated biomass rapidly at the cost of risking damage to new growth from the onset of harsh temperatures, while northern seedlings grew slowly and conservatively, reducing the risk of damage at the cost of lower growth rates than their southern counterparts. We did not see any significant effect of increased CO_2 concentrations on any of the seedling traits studied, however seedlings in the high nutrient treatment showed more pronounced signs of a competitive, fast-growth strategy, which ultimately led to extensive mortality of this treatment. Given this knowledge about black spruce growth dynamics in natural forests and under controlled environment conditions, I can conclude that while the mid-latitude population on a discontinuous permafrost peatland is likely to face substantial declines in productivity and forest cover loss, the northern and southern populations have the potential to remain highly productive provided evapotranspirative demands are met by precipitation, and that no major disturbances influence competitive interactions with this species.

Acknowledgements

First and foremost, my utmost gratitude goes to Dr. Jennifer Baltzer. Thank you so much for taking me on (even with the somewhat questionable parts of my undergrad transcripts), and then continuing to throw opportunity after opportunity my way. I'm grateful for every trip to the field, new project, tidbit of advice, or tough love that you put me through throughout these five years – and for tolerating my terrible "boring" jokes. I also cannot give enough thanks to the absolutely incredible team of people that Jenn manages to hire – the past and present crew of the Forest Ecology Research Group. You guys have been the most amazing lab family to spend my life as a grad student with – from productive lunchtime science talks, to impromptu potlucks, and all of the shared successes (and frustrations) that we've had, I'm so incredibly grateful to have gotten to know and work with all of you. And just because you guys don't get a name shout out doesn't mean you aren't exceptional and important in this journey – I would need a whole other thesis just to list you all!

Thanks also go out to my supervisory committee – Ze'ev Gedalof, Tom Lakusta, and Brent Wolfe – I know that parts of my project are somewhat tangential to your own research, but I appreciate your genuine interest throughout it all and your helpful guidance along the way! Also thanks to Tristan Long for serving on my MSc committee before I was whisked away into the PhD in Geography program.

Huge thanks to my friends outside of the lab, who have still stuck around even when I go MIA for extensive periods of time – especially Sarah, who somehow managed to keep regular contact and even in-person visits despite our different cities and different lifestyles.

My family has been absolutely exceptional support throughout this whole process. To Mom and Dad – thanks for always caring about what I'm doing, but knowing when to not ask the wrong questions about how things were progressing, for putting up with me coming home to "visit" for the weekend only to have me either sit around doing schoolwork or pass out for extensive naps, and especially for long-term care of my cats when I disappear to the field even though it creates chaos in your lives. To my siblings, Katy and Jon, who I've been closer with in the past few years than I've ever been, and provided many welcome breaks for adventures on hikes, to concerts, or just to hang around and play board games with. And last but not least, I could not have pulled this off without my other half, Cory. Kudos to you for putting up with me in the office, in the lab, in the field, and at home throughout the entirety of this – you've been the best sounding board, motivator, editor, and rational devil's advocate all along, and I'm lucky to have been able to spend it all with you.

Statement of Originality

I declare that the work presented here is original and the result of my own research, except as acknowledged, and has not been submitted, in part or whole, for a degree at this or any other university. Ideas taken from other sources have been properly cited to credit the original authors.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

1.1. Introduction

The boreal forest is one of the largest forest ecosystems in the world, spanning over 1066 million ha in the circumpolar north (Olson *et al.*, 1983). The productivity of this system has large implications for the forest industry, particularly in Canada where the >300 million ha of boreal forest contributes to 50% of forest products and sustains over 200 000 jobs (Weber & Stocks, 1998; Kurz *et al.*, 2013). In addition to these socioeconomic values, the boreal forest is central in the global carbon balance, serving as a carbon sink to approximately 1/3 of terrestrial carbon (Kasischke *et al.*, 2008). As atmospheric CO_2 continues to rise, the boreal forest and its capacity as a carbon sink is becoming increasingly important to global health – although there is concern that conditions are reaching a potential "tipping point" for boreal forest dieback (Lenton *et al.*, 2008).

The boreal forest is experiencing change that is threatening to compromise function in this widespread ecosystem. Climate change has resulted in rapid warming of many areas in the circumboreal region (Chapin *et al.*, 2005; Soja *et al.*, 2007) with widespread implications for boreal form and function. In the following sections, I describe several of the major impacts of climate change on boreal forests.

1.1.1. Impacts of Climate Change on the Boreal Forest

1.1.1.1. Direct effects of changing temperature and precipitation

As the northernmost forest ecosystem, productivity of the boreal forest has widely been assumed to be temperature-limited (Pojar, 1996). Based on this assumption, we would expect that increasing temperatures would result in increased productivity of boreal tree species. There is a substantial evidence that increased temperatures promote growth of many boreal tree species across a variety of latitudes in the boreal forest directly by improving conditions for growth through warmer temperatures (e.g., Lloyd & Bunn, 2007; Huang *et al.*, 2010; D'Orangeville *et al.*, 2016) or by increasing the length of the growing season (e.g., Hofgaard *et al.*, 1999; Huang *et al.*, 2010), with a large proportion of studies citing positive responses to increased temperature at the forest-tundra ecotone (e.g., Innes, 1991; Lescop-Sinclair & Payette, 1995; Suarez *et al.*, 1999; Driscoll *et al.*, 2005; Girardin *et al.*, 2005; Beck *et al.*, 2011; Lloyd *et al.*, 2011). However, these positive responses to warming are largely outnumbered by the reports of growth decline as temperatures have increased in the boreal region during the past century (e.g., Barber *et al.*, 2000; D'Arrigo *et al.*, 2004; Lloyd & Bunn, 2007; Huang *et al.*, 2010; Walker & Johnstone, 2014; Ols *et al.*, 2016). These negative responses to warming are often attributed to temperature-induced drought stress (e.g., Lloyd & Fastie, 2002; McGuire *et al.*, 2010; Ma *et al.*, 2012; Ohse *et al.*, 2012; Walker & Johnstone, 2014); warming without sufficient increases in precipitation is driving an imbalance between evapotranspiration and available moisture. Although there are many studies which demonstrate a positive relationship between increased precipitation and growth of boreal trees particularly in southern regions of the North American boreal forest (Dang & Lieffers, 1989; Brooks *et al.*, 1998; Hofgaard *et al.*, 1999; Girard *et al.*, 2011; Drobyshev *et al.*, 2013; D'Orangeville *et al.*, 2016), predictions for increases in precipitation are not as consistent, dramatic, or widespread as patterns of warming and cannot be expected to widely counteract the increased evapotranspirative demands from warming (Price *et al.*, 2013).

While treelines and northern margins of boreal species' distributions have demonstrated increased growth due to warming (Innes, 1991; Lescop-Sinclair & Payette, 1995; Suarez *et al.*, 1999; Driscoll *et al.*, 2005; Girardin *et al.*, 2005; Beck *et al.*, 2011; Lloyd *et al.*, 2011), and the southern limits of these species have shown indications of precipitation limiting growth (Dang & Lieffers, 1989; Brooks *et al.*, 1998; D'Orangeville *et al.*, 2016), mid-latitude populations are less consistent in their responses to climate. At mid-latitude sites in boreal species' distributions, there is a greater degree of climate insensitivity than at species' margins (e.g., Lloyd *et al.*, 2005, 2011), which has been attributed to the greater importance of local environmental conditions influencing growth than general climatic patterns (Wilmking & Myers-Smith, 2008).

1.1.1.2. Changes in fire regime

Changing climate also has proven to affect boreal forests through altering the fire regime. Warmer, drier temperatures are more conducive to the ignition of wildfire, which has been observed through an increase in area burned in Canada during the past century (Gillett *et al.*, 2004; Soja *et al.*, 2007). Aside from the obvious impact of wildfire resulting in widespread damage or mortality of trees (depending on the severity), fires play an important role in regeneration of some boreal tree species; jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) have serotinous and semi-serotinous cones (respectively), and store seed in their cones for long periods of time before the extreme heat from fire triggers their release (Lamont *et al.*, 1991).

Although fire is crucial to the regeneration of these serotinous species, changes in the fire regime may prove to be detrimental to this reproductive strategy. A shortened fire return interval can prevent serotinuous species from reaching reproductive maturity before exposure to fire, which hampers their ability to regenerate at the site post-fire (Johnstone & Chapin, 2006; Kasischke *et al.*, 2010; Brown & Johnstone, 2012). Such changes to the fire return interval may result in shifts in community composition if serotinous species cannot regenerate (Hogg, 1994;

Buma *et al.*, 2013). Additionally, changes in fire severity can alter substrates providing a competitive advantage to other species recolonizing after fire (Johnstone *et al.*, 2010).

1.1.1.3. Biotic disturbances

Warming climate has increased frequency and intensity of pest outbreaks with implications for forest productivity (Volney & Fleming, 2000; Logan *et al.*, 2003; Chapin *et al.*, 2010). This occurs primarily through reduced severity of winters; warmer winters increase the overwinter survival of many boreal forest pests such as spruce beetles, tent caterpillars, and the notorious pine beetles (Neuvonen *et al.*, 1999; Cooke & Roland, 2003; Berg *et al.*, 2006; Kurz *et al.*, 2008). Although insect outbreaks often do not result in complete defoliation and/or mortality of the host species across large regional extents, projected changes in outbreak frequency and severity are likely to increase forest mortality as climate warms (Price *et al.*, 2013). In addition, drought-stress, which is predicted to increase with continued climate change (Lenton *et al.*, 2008), generally results in greater susceptibility of trees to pest outbreaks (Price *et al.*, 2013).

Coupled closely with insect outbreaks is disease in boreal forests; not only can trees that have been attacked by pests be predisposed to infection, diseases can also make trees more susceptible to infestation by insects (Kliejunas *et al.*, 2009; Price *et al.*, 2013). Similar warming conditions that support infestation of pests are ideal for the outbreak of diseases affecting boreal trees as well, although large scale infection is often also dependent on either dry or wet conditions, depending on the disease (Woods *et al.*, 2005; Sturrock *et al.*, 2011). Overall, the boreal forest is expected to see reduced productivity as disease and intensity of outbreaks increases in this region, potentially triggering compositional changes when defoliation and mortality is extensive within a stand (Price *et al.*, 2013).

1.1.1.4. Impacts of permafrost thaw

Warming is also driving extensive permafrost thaw in the boreal, which in turn influences forest structure and function as much of the boreal region is underlain by permafrost (Tarnocai, 2006; Fig. 1.1). Although warming of permafrost results in increased nutrient availability through release of stored nutrients in the frozen permafrost and also the increased microbial activity due to warming soil (Bonan & Shugart, 1989; Bonan *et al.*, 1990; Keuper *et al.*, 2012), the effect of thawing permafrost on forest productivity has been largely negative (e.g., Baltzer *et al.*, 2014). Trees in the zone of discontinuous permafrost are particularly sensitive to thawing permafrost. The zone of discontinuous permafrost is degrading rapidly (Camill & Clark, 1998; Camill, 2005). In ice-rich soils, permafrost thaw results in subsidence of the ground (Jorgenson *et al.*, 2001; Hinzman *et al.*, 2005). These ice-rich landscapes tend to have tight correlations between forest cover and permafrost presence – as the permafrost thaws, forests lose the solid foundation upon which they have established, and extensive waterlogging as the encroaching wetlands drown out root systems (Camill & Clark, 1998; Osterkamp *et al.*, 2000; Camill, 2005). These permafrost thaw processes have led to loss of forest cover (Thie, 1974; Camill, 1999; Jorgenson *et al.*, 2001; Quinton *et al.*, 2011; Baltzer *et al.*, 2014), reductions in productivity (Wilmking & Myers-Smith, 2008), or in some cases transitions between forest types (Lara *et al.*, 2016). In contrast, in the Siberian boreal forest it has been shown that permafrost provides necessary moisture to larch trees (Zhang *et al.*, 2011).

1.1.1.5. Changes in competitive pressures

Although changes in interspecific competition as a result of shifting climate envelopes have been predicted based on differences in productivity between temperate and boreal tree species (Reich *et al.*, 2015), the effect of this competition is usually slow to emerge due to the challenges associated with invading and establishing in a mature forest, since competition between trees occurs primarily at the seedling and sapling stages (Loehle, 2003). Most cases at the southern limits of the boreal forest describe this potential for change, but there is little documentation of substantial northward migration of temperate species into the boreal region, or southern boreal ecotypes transitioning north in the present-day (e.g., Pastor & Post, 1988; Thompson *et al.*, 1998; Iverson & Prasad, 2001; Goldblum & Rigg, 2005; McKenney *et al.*, 2007; Messaoud *et al.*, 2007). At the northern limit of the boreal forest, the lack of arborescent competition in combination with more favourable climatic conditions for growth has allowed for northward movement of the boreal forest into the adjacent tundra in many areas (e.g., Lescop-Sinclair & Payette, 1995; Suarez *et al.*, 1999; Esper & Schweingruber, 2004).

Disturbances such as fire, pests, or landscape change due to permafrost thaw which result in loss of canopy cover can lead to faster compositional change in the boreal forest than competition solely due to shifting climate envelopes (Loehle, 2003; Price *et al.*, 2013). Such disturbance-based changes in boreal forest composition have been documented through the various mechanisms described in the previous sections (e.g., Camill, 1999; Johnstone *et al.*, 2010; Price *et al.*, 2013).

1.1.1.6. CO_2 fertilization

The main driver of climate change is the increase in greenhouse gases as a result of industrialization (Cubasch *et al.*, 2013). Although these greenhouse gases can lead to changes in climatic conditions which influence plant growth (described above), they can also directly impact productivity. CO_2 fertilization is the most common example of this whereby increased atmospheric CO_2 concentrations allow plants to reduce water loss through their stomata while maintaining CO_2 uptake, resulting in increased water use efficiency (WUE; Farquhar *et al.*, 1989; Bazzaz *et al.*, 1990). However, evidence of a CO_2 fertilization effect has been quite limited, particularly at large scales in natural systems (Gedalof & Berg, 2010; Silva *et al.*, 2010).

This lack of evidence for CO_2 fertilization is likely due to other limiting factors; it has been shown that nitrogen availability (Norby *et al.*, 2010) and soil moisture (Cole *et al.*, 2010; Lévesque *et al.*, 2014; Girardin *et al.*, 2015) limit the potential for CO_2 fertilization in trees. Across the boreal region, most studies investigating CO_2 fertilization of natural forests have not identified an increase in productivity attributable to increased atmospheric CO_2, and cite moisture limitation as the likely cause (Bond-Lamberty *et al.*, 2014; Girardin *et al.*, 2015; Dietrich *et al.*, 2016). However, positive growth trends driven by increased atmospheric CO_2 concentrations have been documented in boreal forests (e.g., Wang *et al.*, 2006; Cole *et al.*, 2010, with emphasis on the importance of sufficient soil moisture to detecting a CO_2 fertilization effect (Cole *et al.*, 2010). Thus, although not a widespread driver of productivity, CO_2 fertilization is still an important factor that may influence the impacts of climate change in the boreal forest.

1.2. The role of plasticity vs. local adaption in tolerance to climate change

Plasticity is the ability of an organism to express different phenotypes under different environments (Sultan, 1995; DeWitt *et al.*, 1998), which makes it an important component in assessing the tolerance of a species to rapid changes in their environment (Sultan, 2000; Aitken *et al.*, 2008; Nicotra *et al.*, 2010). On the other hand, individuals can exhibit locally-adapted traits, conferring a greater fitness to local populations in their given environment over populations of the same species from other locations (Savolainen *et al.*, 2007). Often, local adaptation is most pronounced at range margins due to limited gene flow and strong selective pressure by climate (Kreyling *et al.*, 2014). Although this strategy is beneficial under stable conditions, it may limit the capacity of a species to adjust to rapid changes (Aitken & Whitlock, 2013).

Under a changing climate, plants have three options to avoid facing loss of productivity: adjusting their range as their climate envelope shifts, adapting to new conditions through genetic changes, or through phenotypic plasticity permitting changes in their traits to optimize performance under new conditions (Aitken *et al.*, 2008). For trees, the rate that climate envelopes are shifting exceeds the migration rate that most species are capable of (Malcolm *et al.*, 2002; Aitken *et al.*, 2008). In addition, the long generation times of most trees will limit how effectively species will be able to adapt to a changing climate (Savolainen *et al.*, 2004; Jump & Peñuelas, 2005; Aitken *et al.*, 2008). As a consequence, the degree of plasticity of species across their ranges may be particularly important in understanding responses to climate change.

Generally, trees exhibit a high degree of plasticity in their traits in order to withstand a range of environmental conditions that they may experience over their long-lived, sessile existence (Alberto *et al.*, 2013). However, plasticity is costly making it difficult for a plant to maintain under low resource conditions (DeWitt *et al.*, 1998; Alpert & Simms, 2002). For example, a study on *Pinus sylvestris* (a Eurasian boreal tree species) found that growth cessation timing was less plastic in high latitude populations – likely a result of the lower resource availability and more severe conditions at the more northern sites (Savolainen *et al.*, 2004). This highlights that trait plasticity, as a trait in and of itself, is critical to population response to changing climate.

1.3. Black spruce: the arborescent icon of the boreal forest

One of the most dominant and widespread species within the boreal forest is black spruce (*Picea mariana* [BSP] Mill.). Black spruce tends to inhabit cold, wet, nutrient-poor soils– a niche which is often too stressful for other boreal trees to thrive (Viereck & Johnston, 1990). Thus, despite being a slow-growing species, black spruce-dominated forests can be found across the entire boreal region of North America (Fig. 1.2). Black spruce are characterized by a rugged appearance (Fig. 1.2), often with a dense spire-like crown, drooping branches, and reaching heights of up to 30 meters with diameter at breast height (DBH) up to 60 cm in the most productive sites, while maximum height and DBH at less productive sites are closer to 20 meters and 30 cm, respectively (Natural Resources Canada – Black spruce fact sheet, 2015). As mentioned in section 1.1.1.2., black spruce is a semi-serotinous species, relying on fire to trigger the mass release of seed (Viereck, 1983). However, being semi-serotinous, fire is not necessary for cones to open and release seed; indeed, after 5 – 15 years, cones will open without fire (Lamont *et al.*, 1991). In addition to this, black spruce can reproduce vegetatively through layering (Viereck & Johnston, 1990). Although black spruce takes an arborescent growth form across most of its range, at the northern and high-altitude margins of its distribution, black spruce will take krummholz forms, reproducing almost exclusively through layering since conditions are too severe for viable seed production (Viereck, 1983; Pereg & Payette, 1998; Sirois, 2000).

Black spruce has been studied extensively in eastern Canada (Drobyshev *et al.*, 2010; Girardin *et al.*, 2011; Huang *et al.*, 2013; Ols *et al.*, 2016). Within this region, some of the main climatic drivers of growth for this species include: previous summer precipitation (positive), current March and July precipitation (negative), current spring drought indices (positive), current spring temperature (positive), current winter temperature (positive), and current growing season temperature (positive) (Hofgaard *et al.*, 1999; Huang *et al.*, 2010; Drobyshev *et al.*, 2013) – just to list a few. Although there is a great deal of spatial variability in these responses, an analysis of an extensive network of black-spruce tree ring data across a large area of the Quebec boreal forest has identified a general trend in which southern black spruce respond positively to precipitation increases and negatively to increasing temperatures, while higher latitudes show an inverse relative to the southern sites (D'Orangeville *et al.* 2016). Analysis of black spruce growth dynamics at this magnitude have not been performed in northwestern Canada. Although not a highly productive species, the widespread nature of black spruce and its ability to regenerate after disturbances (particularly fire) have made it an important contributor to Canada's pulp industry (Lamhamedi & Bernier, 1994).

1.4. Research Objectives

Northwestern Canada has been a global hotspot of climate warming (Chapin *et al.,* 2005; Hartmann *et al.*, 2013), and is expected to continue to experience rapid change over the next century (Flato & Boer, 2001; Scinocca *et al.,* 2008). Given that much of the boreal forest in northwestern Canada is underlain by permafrost, the effects of warming on forest growth are two-fold: the direct influence of increased temperatures, and the indirect impacts of thawing permafrost on tree growth processes. Although not studied extensively, permafrost has been shown to be an important factor influencing function of trees Canada (Baltzer *et al.*, 2014; Patankar *et al.*, 2015; Warren, 2015). Despite how these characteristics of northwestern Canada's boreal forests make monitoring of growth patterns very prudent in the context of climate change, investigations of forest growth dynamics across this vast and rapidly changing landscape have been limited (see Wilmking & Myers-Smith, 2008; Walker & Johnstone, 2014; Walker *et al.*, 2015).

The conditions described above contrast considerably with the characteristics of boreal forests in eastern Canada, where black spruce has been studied quite extensively across its latitudinal gradients (e.g., Huang *et al.*, 2010; Drobyshev *et al.*, 2013; Girardin *et al.*, 2015; Ols *et al.*, 2016). Generally, these studies report increased growth of black spruce in response to cooler, wetter growing seasons. Relative to western Canada, the eastern boreal region has much higher water availability indices (D'Orangeville *et al.*, 2016), less permafrost (and consequently warmer soils; Brown & Péwé, 1973), and is largely underlain by the Canadian shield (Pojar, 1996). Given these differences, it is not feasible to speculate on historical patterns of black spruce growth dynamics in northwestern Canada based solely on trends in the eastern boreal forest.

In addition to establishing these historical records of growth responses, trait plasticity is important in allowing plants to tolerate climate change; this can be determined through provenance trials and common studies. Although such experiments have been performed with black spruce (e.g., Morgenstern, 1968a, 1968b; Khalil, 1984; Morgenstern & Mullin, 1990; Johnsen & Seiler, 1996; Johnsen *et al.*, 1996), few have addressed trait plasticity in populations from northwestern Canada. Given the differences in environmental conditions across the boreal forest in Canada, these northwestern populations may have developed different strategies and capacities to adjust to or tolerate the rapid change in this region. In order to begin to fill these knowledge gaps on black spruce growth dynamics and trait plasticity, there are three main objectives which I have addressed through my research:

(1) Investigate the effects of permafrost thaw on the growth dynamics of black spruce in a discontinuous permafrost peatland

(2) Compare the productivity and main climatic drivers of black spruce growth across the latitudinal extent of the species in northwestern Canada

(3) Quantify the importance of plasticity versus local adaptation in black spruce seedlings growth under two different resource treatments in a common garden study

1.5. Approaches and Techniques

In order to address the research objectives outlined above, I took two different approaches to understand how black spruce responds to changing environments: tree-ring studies to look at historical growth patterns, and a common garden study to investigate plasticity of seedlings. Background information and general details on how these techniques were applied in my research are described in the following sections. I have outlined the study sites used for this research on the map in Fig. 1.2.

1.5.1. Tree-Ring Studies

Tree-ring studies have long been used to understand the productivity of forests over time. In temperate systems, annual radial growth increments for a particular species at a site, measured as the distance between two consecutive growth rings, are standardized to ring width indices that take into account the reduction in growth increments as a tree ages (Speer, 2010). Using multiple tree-ring series from living and dead stems at a given site, the growth patterns in these standardized indices can be cross-dated to produce a "master chronology" that extends as far back in time as samples with distinguishable rings exist, and assigns a calendar year to each ring (Bortolot *et al.*, 2001). This master chronology serves as an archive for a site, possessing data about age structure and deviations from normal growth patterns for as much as thousands of years into the past. Subsequent samples taken at the site can then be dated against the master chronology, to confirm the accuracy of the dates that each ring is assigned and place dead stems into the appropriate temporal period based on common growth characteristics.

Traditionally within scientific fields, tree-rings have been utilized to reconstruct climate patterns extending centuries into the past by using chronologies (D'Arrigo & Jacoby, 1993), and the relationships between growth and climate have been used to predict the future of our forests (Williams *et al.*, 2010). The 'divergence effect' (decoupling of longstanding temperature-growth relationships; D'Arrigo *et al.*, 2007) has added challenges to this approach, and also complicated the use of chronologies to establish climatic drivers of growth because all trees in a site do not necessarily respond the same way. Indeed, examining only the chronology-level responses to climate may mask divergent climatic effects. Thus, in addition to investigating climate-growth responses with complete chronologies from each site, I performed individual tree climate-growth correlations in order to ensure that any variability in responses was captured.

1.5.2. $\delta^{13}C$ Analysis

A method of identifying physiological mechanisms underlying growth patterns in tree-ring records is through determining the carbon isotope composition of tree rings. The carbon isotope composition reflects balance between carbon fixation and water loss; low plant-to-atmosphere $^{13}C/^{12}C$ ratios (i.e. expressed as the $\delta^{13}C$ value – the ratio of ^{13}C to ^{12}C in a sample, relative to a known standard) reflects greater water loss compared to the rate carbon fixation, while high $\delta^{13}C$ occurs when carbon fixation is occurring at a greater rate than water is lost (McCarroll & Loader, 2004). This results from the preferential uptake of $^{12}CO_2$ over the larger $^{13}CO_2$ molecule. This isotopic signature is preserved in the wood, allowing historical reconstructions of water use efficiency (WUE) and assessment of how it relates to productivity under a changing climate (Silva *et al.*, 2010), thereby providing insights into the physiological drivers of tree growth responses.

Approaches for calculating WUE from $\delta^{13}C$ are under debate; WUE has traditionally been calculated using the ratio of C_i/C_a, which can be calculated from $\delta^{13}C$ where C_i represents the internal CO_2 concentration and C_a the atmospheric CO_2 concentration (McCarroll & Loader, 2004). However, it has been found that the calculation of WUE in this manner often overestimates plant response as a result of an inherent artifact of C_a increasing over time (Silva & Horwath, 2013). Due to this calculation bias, I have not presented actual values of WUE and instead make qualitative interpretations of WUE based on the assumption that when discrimination against ^{13}C is high, stomata are open and WUE efficiency is low due to stomatal water loss.

1.5.3. Common Garden Studies

Common garden studies are one of the most effective means of determining whether there are genetic differences among populations. When growing plants from different populations under the same conditions, a suite of traits can be compared (e.g., height, biomass, photosynthetic rate, etc.); if populations show no differences among these traits, we can assume that any phenotypic differences that are observed in situ can be attributed to plasticity. Conversely, if the plants exhibit differences in the traits studied, it can be concluded that the populations have some degree of inherent genetic differences. Thus, when making predictions about the dynamics of forest ecosystems under a changing climate, common garden studies provide key information about the variability of adaptive traits from different provenances of a single species (Saxe *et al.*, 2002; Aitken *et al.*, 2008).

1.6. Thesis Outline

1.6.1. Chapter 2:

Sniderhan AE and Baltzer JL (2016). Growth dynamics of black spruce (*Picea mariana*) in a rapidly-thawing discontinuous permafrost peatland. Journal of Geophysical Research – Biogeosciences, 121: 1288 - 3000.

We used tree-ring studies to document growth dynamics of black spruce, one of the most dominant boreal tree species, in a boreal peatland experiencing rapid permafrost thaw. In this chapter, we specifically examine how changing permafrost conditions influence growth. Growth of black spruce at this site has declined steadily since the mid-1900s and exhibited a shift from positive responses to temperature pre-1970 to predominantly negative responses in recent decades, despite precipitation increasing over time at this site. Our results show that there is no apparent effect of landscape position or rate of lateral permafrost thaw on growth trends in black spruce, despite gradients in soil moisture and active layer thickness across the mosaic of wetlands and comparatively drier permafrost plateaus at this site. These results support growing evidence that vertical permafrost thaw (i.e., active layer thickening) is causing drought stress in these slow-growing, shallow-rooted black spruce. To our knowledge, this study is the first to investigate permafrost as a driver of within-site variability in growth-climate responses, and we provide insight into the widespread growth declines and divergence of climate-growth relationships in high-latitude forests.

1.6.2. Chapter 3:

Sniderhan AE, Mamet SD, and Baltzer JL. An investigation of black spruce (*Picea mariana*) growth dynamics across its latitudinal extent in northwestern Canada. In preparation for Global Change Biology.

To determine the spatial and temporal variability in black spruce (*Picea mariana*) growth dynamics in northwestern Canada, we sampled tree rings from four sites spanning 15° of latitude – effectively encompassing the latitudinal extent of this widespread, dominant boreal tree. We investigated (1) the differences in growth patterns and magnitude of growth between sites, (2) the main climatic drivers of growth and how they change over time, and (3) trends in water use efficiency (WUE) among the sites (as indicated through stable carbon isotope compositions). In this study, we found that all sites showed a positive growth trend over time except the mid-latitude site, which demonstrated a decline in annual growth. Interestingly, while the magnitude of growth at our treeline site was, as expected, the lowest of all sites, our timberline site located only 50 km to the south of treeline achieved some of the highest annual growth increments in our study. The climatic drivers of these growth patterns varied among sites; the strongest growth responses at the northerly sites were with climatic variables which contributed to warmer, longer growing seasons, while growth at the southern sites was driven by climate conditions influencing drought stress of the trees. This was supported by carbon isotope compositions indicating increased WUE at the southern sites, with no significant trend at the northern sites. The results of this study suggest that continued warming will increase productivity of trees at the northern extent of black spruce, but southerly areas may begin to experience drought stress if precipitation does not continue to balance the increasing evapotranspirative demands from warming.

1.6.3. Chapter 4:

Sniderhan AE, McNickle GG, and Baltzer JL. A common garden experiment reveals local adaptation in black spruce (*Picea mariana*) populations from across western Canada. In revision at AoB Plants.

In order to evaluate local adaptation vs. plasticity in black spruce, seeds from five provenances across the latitudinal extent of the species in northwestern Canada were planted in a common garden study in growth chambers. Two resource conditions were applied (low/high nutrient and ambient/elevated CO_2) in a fully factorial design. Several physiological and allocational traits, growth, and survival were measured over the course of the experiment. We found significant differences in several growth and biomass traits among populations (e.g., height, root length, leaf biomass), with southern populations producing the largest seedlings. However, we did not detect significant differences among nutrient or CO_2 treatments in any traits measured, and there were not population-level differences in physiological traits or allocational patterns. We found that there was greater winter mortality among the high nutrient treatments, which we attributed to a change in growth strategy which delayed hardening of needles before winter. Our study provides important insight into how black spruce might respond to the changing climate conditions predicted in this region.

1.6.4. Conclusions:

In this final chapter, I have integrated the findings from each of the three data chapters described above to summarize the effects of climate change on black spruce in recent decades and make projections regarding black spruce productivity and regeneration under future climate scenarios. I have applied temperature and precipitation projections from two IPCC climate model scenarios to estimate 2090 climatic conditions at each of my study sites in northwestern Canada. Using the known current climate responses of black spruce at these sites, I made the following predictions about future productivity of these forests: (1) warming in the Inuvik, NT region is likely to continue to promote growth of black spruce, and it is unlikely that extensive permafrost thaw at this site will result in negative effects on growth by 2090; (2) the discontinuous permafrost peatland site near Fort Simpson, NT is likely to continue to experience loss of permafrost and transition to wetlands during the next century, resulting in loss of forest cover and decreased productivity of any surviving black spruce by 2090; (3) productivity of trees at the southern edge of the boreal forest (near Prince Albert, SK) may continue to increase provided that the increase in precipitation meets increased evapotranspirative demands of warmer temperatures, but seasonality of precipitation and temperature increases will play an important role in determining water balance at this site. I predict that future regeneration success in the Inuvik region will be dependent on whether there is increased competition from faster-growing species, given the conservative strategy demonstrated by seedlings from the Inuvik region. In the discontinuous permafrost peatland site, regeneration is unlikely to be successful as a result of the low germination rates and survival of seedlings, suggesting a poor outlook for black spruce at this site. The strategy of seedlings in the Prince Albert, SK region may confer marginally greater competitive ability if temperate species extend northward. Overall, while the discontinuous permafrost peatland is expected to experience major successional changes, the northern and southern treeline sites that I investigated have the potential to remain very productive black spruce stands under projected climate conditions for the end of the 21st century.

1.7. References

Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, 44, 367–388.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.

Alberto FJ, Aitken SN, Alía R, González-Martínez SC, Hänninen H, Kremer A, Lefèvre F, Lenormand T, Teaman S, Whetten R, Savolainen O (2013) Potential for evolutionary responses to climate change - evidence from tree populations. *Global Change Biology*, 19, 1645–61.

Alpert P, Simms EL (2002) The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evolutionary Ecology*, 16, 285–297.

Baltzer JL, Veness T, Chasmer LE, Sniderhan AE, Quinton WL (2014) Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. *Global Change Biology*, 20, 824–834.

Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, 405, 668–673.

Bazzaz FA, Coleman J, Morse SR (1990) Growth responses of seven major co-occurring tree species of the northeastern United States to elevated CO_2. *Canadian Journal of Forest Research*, 20, 1479–1484.

Beck PS, Juday GP, Alix C, Barber VA, Winslow SE, Sousa EE, Heiser P, Herriges JD. Goetz SJ (2011) Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters*, 14, 373–379.

Berg EE, Henry JD, Fastie CL, De Volder AD, Matsuoka SM (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*, 227, 219–232.

Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, 20, 1–28.

Bonan GB, Shugart HH, Urban DL (1990) The sensitivity of some high-latitude boreal forests to climatic parameters. *Climatic Change*, 16, 9–29.

Bond-Lamberty B, Rocha AV, Calvin K, Holmes B, Wang C, Goulden ML (2014) Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest. *Global Change Biology*, 20, 216–227.

Bortolot ZJ, Copenheaver CA, Longe RL, Van Aardt JAN (2001) Development of a white oak chronology using live trees and post-Civil War cabin in south-central Virginia. *Tree-Ring Research*, 57, 197–203.

Brooks JR, Flanagan LB, Ehleringer JR (1998) Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. *Canadian Journal of Forest Research*, 28, 524–533.

Brown CD, Johnstone JF (2012) Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management*, 266, 34–41.

Brown RJE, Péwé TL (1973) Distribution of permafrost in North America and its relationship to the environment: a review, 1963 - 1973. In: *Permafrost: Proceedings of the Second International Conference (North American Contribution)*, pp. 71–100. National Academy of Sciences, Washington, DC.

Buma B, Brown CD, Donato DC, Fontaine JB, Johnstone JF (2013) The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience*, 63, 866–876.

Camill P (1999) Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany*, 77, 721–733.

Camill P (2005) Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. *Climatic Change*, 68, 135–152.

Camill P, Clark JS (1998) Climate change disequilibrium of boreal permafrost peatlands caused by local processes. *The American Naturalist*, 151, 207–222.

Chapin FS, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping C-L, Tape KD, Thompson CDC, Walker DA, Welker JM (2005) Role of land-surface changes in arctic summer warming. *Science (New York, N.Y.)*, 310, 657–60.

Chapin FS, McGuire AD, Ruess RW, Hollingsworth TN, Mack MC, Johnstone JF, Kasischke ES, Euskirchen ES, Jones JB, Jorgenson MT, Kielland K, Kofinas GP, Turetsky MR, Yarie J, Lloyd AH, Taylor DL (2010) Resilience of Alaska's boreal forest to climatic change. *Canadian Journal of Forest Research*, 40, 1360–1370.

Cole CT, Anderson JE, Lindroth RL, Waller DM (2010) Rising concentrations of atmospheric CO_2 have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Global*

Change Biology, 16, 2186–2197.

Cooke BJ, Roland J (2003) The effect of winter temperature on forest tent caterpillar (Lepidoptera: *Lasiocampidae*) egg survival and population dynamics in northern climates. *Environmental Entomology*, 32, 299–311.

Cubasch U, Wuebbles D, Chen D, Facchini MC, Frame D, Mahowald N, Winther J-G (2013) Introduction. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

D'Arrigo RD, Jacoby GC (1993) Secular trends in high northern latitude temperature reconstructions based on tree rings. *Climatic Change*, 25, 163–177.

D'Arrigo RD, Kaufmann RK, Davi N, Jacoby GC, Laskowski C, Myneni RB, Cherubini P (2004) Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles*, 18, GB3021.

D'Orangeville L, Duchesne L, Houle D, Kneeshaw D, Côté B, Pederson N (2016) Northeastern North America as a potential refugium for boreal forests in a warming climate. *Science*, 352, 1452–1455.

Dang QL, Lieffers VJ (1989) Climate and annual ring growth of black spruce in some Alberta peatlands. *Canadian Journal of Botany*, 67, 1885–1889.

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends in*

Ecology and Evolution, 13, 77–81.

Dietrich R, Bell FW, Silva LCR, Cecile A, Horwath WR, Anand M (2016) Climatic sensitivity, water-use efficiency, and growth decline in boreal jack pine (*Pinus banksiana*) forests in Northern Ontario. *Journal of Geophysical Research: Biogeosciences*, 121, 2761–2774.

Driscoll WW, Wiles GC, D'Arrigo RD, Wilmking M (2005) Divergent tree growth response to recent climatic warming, Lake Clark National Park and Preserve, Alaska. *Geophysical Research Letters*, 32, L20703.

Drobyshev I, Simard M, Bergeron Y, Hofgaard A (2010) Does soil organic layer thickness affect climate–growth relationships in the black spruce boreal ecosystem? *Ecosystems*, 13, 556–574.

Drobyshev I, Gewehr S, Berninger F, Bergeron Y (2013) Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change. *Journal of Ecology*, 101, 231–242.

Esper J, Schweingruber FH (2004) Large-scale treeline changes recorded in Siberia. *Geophysical Research Letters*, 31, L06202, doi:10.1029/2003GL019178.

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 503–537.

Flato GM, Boer GJ (2001) Warming asymmetry in climate change simulations. *Geophysical Research Letters*, 28, 195–198.

Gedalof Z, Berg AA (2010) Tree ring evidence for limited direct CO_2 fertilization of forests over the 20th century. *Global Biogeochemical Cycles*, 24, 2–7.

Gillett NP, Weaver AJ, Zwiers FW, Flannigan MD (2004) Detecting the effect of climate change on Canadian forest fires. *Geophysical Research Letters*, 31, L18211.

Girard F, Payette S, Gagnon R (2011) Dendroecological analysis of black spruce in lichen—spruce woodlands of the closed-crown forest zone in Eastern Canada. *Ecoscience*, 18, 279–294.

Girardin MP, Berglund E, Tardif JC, Monson K (2005) Radial growth of tamarack (*Larix laricina*) in the Churchill Area, Manitoba, Canada, in relation to climate and larch sawfly (*Pristiphora erichsonii*) herbivory. *Arctic, Antarctic, and Alpine Research*, 37, 206–217.

Girardin MP, Bernier PY, Raulier F, Tardif JC, Conciatori F, Guo XJ (2011) Testing for a CO_2 fertilization effect on growth of Canadian boreal forests. *Journal of Geophysical Research: Biogeosciences*, 116, 1–16.

Girardin MP, Hogg EH, Bernier PY, Kurz WA, Guo XJ, Cyr G (2015) Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. *Global Change Biology*, 22, 627–643.

Goldblum D, Rigg LS (2005) Tree growth response to climate change at the deciduous–boreal forest ecotone, Ontario, Canada. *Canadian Journal of Forest Research*, 35, 2709–2718.

Hartmann DL, Klein Tank AMG, Rusticucci M et al. (2013) Observations: Atmosphere and Surface. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Hinzman LD, Bettez ND, Bolton WR et al. (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, 72, 251–298.

Hofgaard A, Tardif J, Bergeron Y (1999) Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. *Canadian Journal of Forest Research*, 29, 1333–1346.

Hogg EH (1994) Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research*, 24, 1835–1845.

Huang J, Tardif JC, Bergeron Y, Denneler B, Berninger F, Girardin MP (2010) Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology*, 16, 711–731.

Huang J, Bergeron Y, Berninger F, Zhai L, Tardif JC, Denneler B (2013) Impact of future climate on radial growth of four major boreal tree species in the Eastern Canadian boreal forest. *PloS one*, 8, e56758, doi:10.1371/journal.pone.0056758.

Innes JL (1991) High-altitude and high-latitude tree growth in relation to past, present and future global climate change. *The Holocene*, 1, 168–173.

Iverson LR, Prasad AM (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems*, 4, 186–199.

Johnsen KH, Seiler JR (1996) Growth, shoot phenology and physiology of diverse seed sources of black spruce: I. Seedling responses to varied atmospheric CO_2 concentrations and photoperiods. *Tree Physiology*, 16, 367–373.

Johnsen KH, Seiler JR, Major JE (1996) Growth, shoot phenology and physiology of diverse seed sources of black spruce: II. 23-year-old field trees. *Tree Physiology*, 16, 375–380.

Johnstone JF, Chapin FS (2006) Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems*, 9, 14–31.

Johnstone JF, Hollingsworth TN, Chapin FS, Mack MC (2010) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, 16, 1281–1295.

Jorgenson MT, Racine CH, Walters JC, Osterkamp TE (2001) Permafrost degradation and ecological changes associated with a warming climate in Central Alaska. *Climatic Change*, 48, 551–579.

Jump AS, Peñuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, 8, 1010–1020.

Kasischke ES, Christensen NLJ, Stocks BJ (2008) Fire, global warming, and the carbon balance of boreal forests. *Ecological Applications*, 5, 437–451.

Kasischke ES, Verbyla DL, Rupp TS, McGuire AD, Murphy KA, Jandt R, Barnes JL, Hoy EE, Duffy PA, Calef M, Turetsky MR (2010) Alaska’s changing fire regime — implications for the vulnerability of its boreal forests. *Canadian Journal of Forest Research*, 40, 1313–1324.

Keuper F, van Bodegom PM, Dorrepaal E, Weedon JT, van Hal J, van Logtestijn RSP, Aerts R (2012) A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, 18, 1998–2007.

Khalil MAK (1984) All-range black spruce provenance study in Newfoundland: performance and genotypic stability of provenances. *Silvae Genetica*, 33, 63–71.

Kliejunas JT, Geils BW, Glaeser JM, Goheen EM, Hennon P, Kim M-S, Kope H, Stone J, Sturrock R, Frankel SJ (2009) *Review of literature on climate change and forest diseases of western North America*. 60 pp.

Kreyling J, Buhk C, Backhaus S, Hallinger M, Huber G, Huber L, Jentsch A, Konnert M, Thiel D, Wilmking M, Beierkuhnlein (2014) Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. *Ecology and Evolution*, 4, 594–605.

Kurz WA, Dymond CC, Stinson G et al. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, 452, 987–90.

Kurz WA, Shaw CH, Boisvenue C et al. (2013) Carbon in Canada's boreal forest — A synthesis. *Environmental Reviews*, 292, 260–292.

Lamhamedi M, Bernier P (1994) Ecophysiology and field performance of black spruce (*Picea mariana):* a review. *Annals of Forest Science*, 51, 529–551.

Lamont BB, Maitre DC, Cowling RM, Enright NJ (1991) Canopy seed storage in woody plants. *The Botanical Review*, 57, 277–317.

Lara MJ, Genet H, McGuire AD, Euskirchen ES, Zhang Y, Brown DRN, Jorgenson MT, Romanovsky V, Breen A, Bolton WR (2016) Thermokarst rates intensify due to climate change and forest fragmentation in an Alaskan boreal forest lowland. *Global Change Biology*, 22, 816–829.

Lenton TM, Held H, Kriegler E, Hall JW, Lucht W, Rahmstorf S, Schellnhuber HJ (2008) Tipping elements in the Earth's climate system. *Proceedings of the National Academy of*

Sciences, 105, 1786–1793.

Lescop-Sinclair K, Payette S (1995) Recent advance of the arctic treeline along the eastern coast of Hudson Bay. *Journal of Ecology*, 83, 929–936.

Lévesque M, Siegwolf R, Saurer M, Eilmann B, Rigling A (2014) Increased water-use efficiency does not lead to enhanced tree growth under xeric and mesic conditions. *New Phytologist*, 203, 94–109.

Lloyd AH, Bunn AG (2007) Responses of the circumpolar boreal forest to 20th century climate variability. *Environmental Research Letters*, 2, 45013.

Lloyd AH, Fastie CL (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, 52, 481–509.

Lloyd AH, Wilson AE, Fastie CL, Landis RM (2005) Population dynamics of black spruce and white spruce near the arctic tree line in the southern Brooks Range, Alaska. *Canadian Journal of Forest Research*, 35, 2073–2081.

Lloyd AH, Bunn AG, Berner L (2011) A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Change Biology*, 17, 1935–1945.

Loehle C (2003) Competitive displacement of trees in response to environmental change or introduction of exotics. *Environmental Management*, 32, 106–115.

Logan JA, Régnière J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, 1, 130–137.

Ma Z, Peng C, Zhu Q, Chen H, Yu G, Li W, Zhou X, Wang W, Zhang W (2012) Regional drought-induced reduction in the biomass carbon sink of Canada’s boreal forests. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 2423–2427.

Malcolm JR, Markham A, Neilson RP, Garaci M (2002) Estimated migration rates under scenarios of global climate change. *Journal of Biogeography*, 29, 835–849.

McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. *Quaternary Science Reviews*, 23, 771–801.

McGuire AD, Ruess RW, Lloyd A, Yarie J, Clein JS, Juday GP (2010) Vulnerability of white spruce tree growth in interior Alaska in response to climate variability: dendrochronological, demographic, and experimental perspectives. *Canadian Journal of Forest Research*, 40, 1197–1209.

McKenney D, Pedlar J, Lawrance K, Campbell K, Hutchinson M (2007) Potential impacts of climate change on the distribution of North American trees. *BioScience*, 57, 939–948.

Messaoud Y, Bergeron Y, Asselin H (2007) Reproductive potential of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Quebec. *American Journal of Botany*, 94, 746–754.

Morgenstern EK (1968a) Genetic variation in seedlings of *Picea mariana* (Mill.) BSP. I. Correlation with ecological factors. *Silvae Genetica*, 18, 151–161.

Morgenstern EK (1968b) Genetic variation in seedlings of *Picea mariana* (Mill.) BSP. II. Variation patterns. *Silvae Genetica*, 18, 161–167.

Morgenstern EK, Mullin TJ (1990) Growth and survival of black spruce in the range-wide provenance study. *Canadian Journal of Forest Research*, 20, 130–143.

Neuvonen S, Niemelä P, Virtanen T (1999) Climatic change and insect outbreaks in boreal forests: the role of winter temperatures. *Ecological Bulletins*, 47, 63–67.

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, 15, 684–92.

Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 19368–19373.

Ohse B, Jansen F, Wilmking M (2012) Do limiting factors at Alaskan treelines shift with climatic regimes? *Environmental Research Letters*, 7, 15505.

Ols C, Hofgaard A, Bergeron Y, Drobyshev I (2016) Previous growing season climate controls the occurrence of black spruce growth anomalies in boreal forests of Eastern Canada. *Canadian Journal of Forest Research*, 705, 1–35.

Olson JS, Watts JA, Allison LJ (1983) Carbon in live vegetation of major world ecosystems. *Oak Ridge National Laboratory*, 5862, 1–152.

Osterkamp TE, Viereck LA, Shur Y, Jorgenson MT, Racine CH, Doyle A, Boone RD (2000) Observations of thermokarst and its impact on boreal forests in Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research*, 32, 303–315.

Pastor J, Post WM (1988) Response of northern forests to CO_2-induced climate change. *Nature*, 334, 55–58.

Patankar R, Quinton WL, Hayashi M, Baltzer JL (2015) Sap flow responses to seasonal thaw and permafrost degradation in a subarctic boreal peatland. *Trees - Structure and Function*, 29, 129–142.

Pereg D, Payette S (1998) Development of black spruce growth forms at treeline. *Plant Ecology*, 138, 137–147.

Pojar J (1996) Environment and biogeography of the western boreal forest. *The Forestry Chronicle*, 72, 51–58.

Price DT, Alfaro RI, Brown KJ, Flannigan MD, Fleming RA, Hogg EH, Girardin MP, Lakusta T, Johnston M, McKenney DW, Pedlar JH, Stratton T, Sturrock RN, Thompson ID, Trofymow JA, Venier LA (2013) Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews*, 365, 322–365.

Quinton WL, Hayashi M, Chasmer LE (2011) Permafrost-thaw-induced land-cover change in the Canadian subarctic: implications for water resources. *Hydrological Processes*, 25, 152–158.

Reich PB, Sendall KM, Rice K, Rich RL, Stefanski A, Hobbie SE, Montgomery RA (2015) Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nature Climate Change*, 5, 148–152.

Savolainen O, Bokma F, García-Gil R, Komulainen P, Repo T (2004) Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of *Pinus sylvestris* to climatic changes. *Forest Ecology and Management*, 197, 79–89.

Savolainen O, Pyhäjärvi T, Knürr T (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, 38, 595–619.

Saxe H, Cannell MGR, Johnsen Ø, Ryan MG, Vourlitis G (2002) Tree and forest functioning in response to global warming. *New Phytologist*, 149, 369–399.

Scinocca JF, McFarlane NA, Lazare M, Li J, Plummer D (2008) Technical note: The CCCma third generation AGCM and its extension into the middle atmosphere. *Atmospheric Chemistry and Physics,* 8, 7055–7074.

Silva LCR, Horwath WR (2013) Explaining global increases in water use efficiency: why have we overestimated responses to rising atmospheric CO_2 in natural forest ecosystems? *PLoS ONE*, 8, 1–5.

Silva LCR, Anand M, Leithead MD (2010) Recent widespread tree growth decline despite increasing atmospheric CO_2. *PloS one,* 5, e11543.

Sirois L (2000) Spatiotemporal variation in black spruce cone and seed crops along a boreal forest - tree line transect. *Canadian Journal of Forest Research*, 30, 900–909.

Soja AJ, Tchebakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Parfenova EI, Chapin FS III, Stackhouse PW Jr. (2007) Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change*, 56, 274–296.

Speer JH (2010) *The Fundamentals of Tree-ring Research*. University of Arizona Press.

Sturrock RN, Frankel SJ, Brown AV, Hennon PE, Kliejunas JT, Lewis KJ, Worrall JJ, Woods AJ (2011) Climate change and forest diseases. *Plant Pathology*, 60, 133–149.

Suarez F, Binkley D, Kaye MW (1999) Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska. *Ecoscience,* 6, 465–470.

Sultan SE (1995) Phenotypic plasticity and plant adaptation. *Acta Botanica Neerlandica*, 44, 363–383.

Sultan SE (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, 5, 537–542.

Tarnocai C (2006) The effect of climate change on carbon in Canadian peatlands. *Global and Planetary Change*, 53, 222–232.

Thie J (1974) Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. *Arctic Institute of North America*, 27, 189–200.

Thompson ID, Flannigan MD, Wotton BM, Suffling R (1998) The effects of climate change on landscape diversity: an example in Ontario forests. *Environmental Monitoring and Assessment*, 49, 213–233.

Viereck LA (1983) The Effects of Fire in Black Spruce Ecosystems ofAlaska and Northern Canada. In: *The Role of Fire in Northern Circumpolar Ecosystems* (eds Wein RW, MacLean DA), pp. 201–220. Wiley, Chichester.

Viereck LA, Johnston WF (1990) *Picea mariana* (Mill.) B. S. P. Black Spruce. In: *Silvics of North America: vol. 1. Conifers* (eds Burns R, Honkala B), pp. 227–237. USDA Forest Service Agriculture Handbook, Washington, DC.

Volney WJA, Fleming RA (2000) Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems & Environment*, 82, 283–294.

Walker X, Johnstone JF (2014) Widespread negative correlations between black spruce growth and temperature across topographic moisture gradients in the boreal forest. *Environmental*

Research Letters, 9, 64016.

Walker XJ, Mack MC, Johnstone JF (2015) Stable carbon isotope analysis reveals widespread drought stress in boreal black spruce forests. *Global Change Biology*, 21, 3102–3113.

Wang GG, Chhin S, Bauerle WL (2006) Effect of natural atmospheric CO_2 fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology*, 12, 601–610.

Warren RK (2015) *Examining the spatial distribution of soil moisture and its relationship to vegetation and permafrost dynamics in a subarctic permafrost peatland*. University of Guelph, 53 pp.

Weber MG, Stocks BJ (1998) Forest fires and sustainability in the boreal forests of Canada. *Ambio*, 27, 545–550.

Wilmking M, Myers-Smith I (2008) Changing climate sensitivity of black spruce (*Picea mariana* Mill.) in a peatland–forest landscape in Interior Alaska. *Dendrochronologia*, 25, 167–175.

Woods A, Coates KD, Hamann A (2005) Is an unprecedented Dothistroma needle blight epidemic related to climate change? *BioScience*, 55, 761.

Zhang N, Yasunari T, Ohta T (2011) Dynamics of the larch taiga–permafrost coupled system in Siberia under climate change. *Environmental Research Letters*, 6, 24003.

1.8. Figures

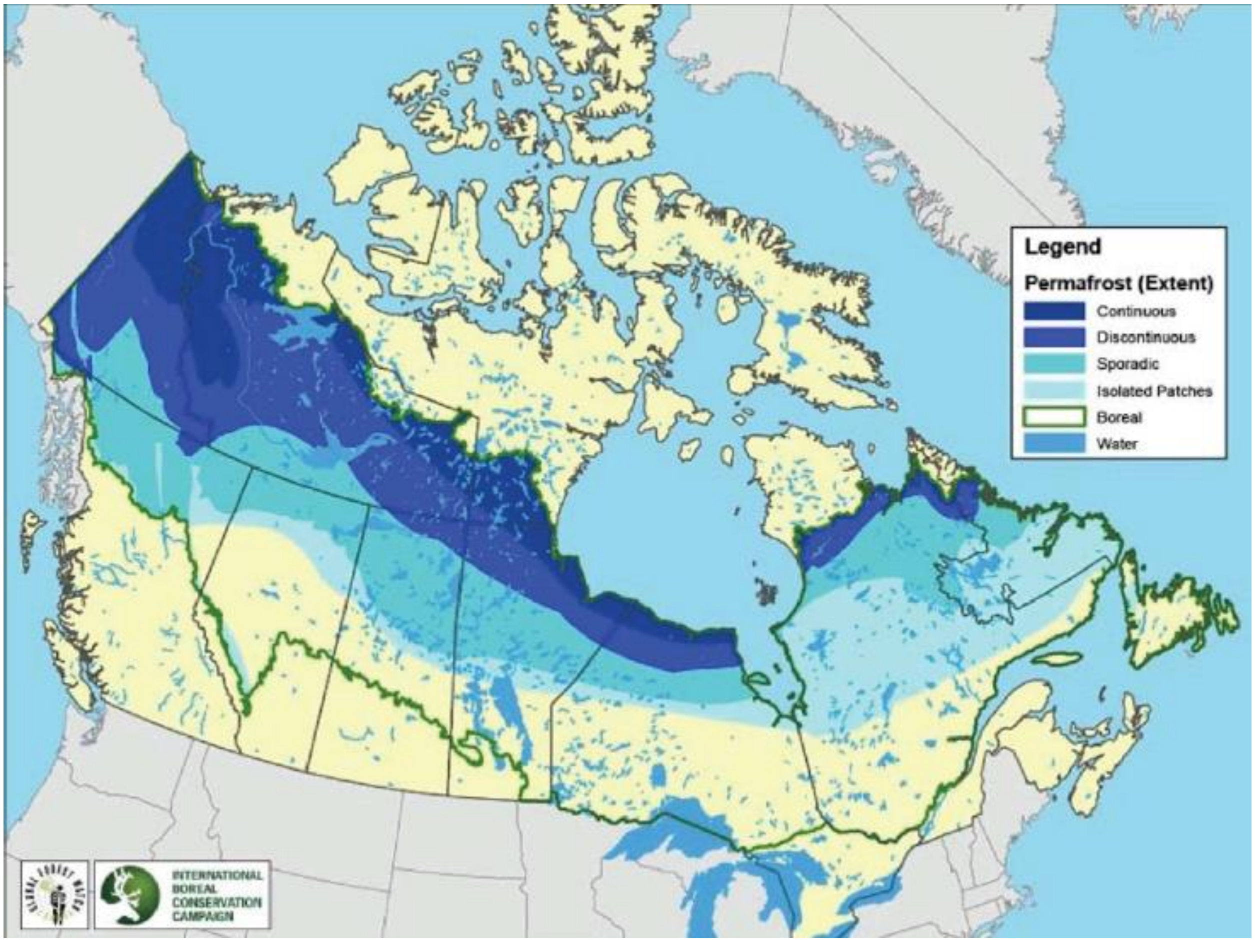

Fig. 1.1. A map of Canada outlining the boreal forest region, with the different permafrost zones within this region shown. Figure by Brown *et al.*, 2001.

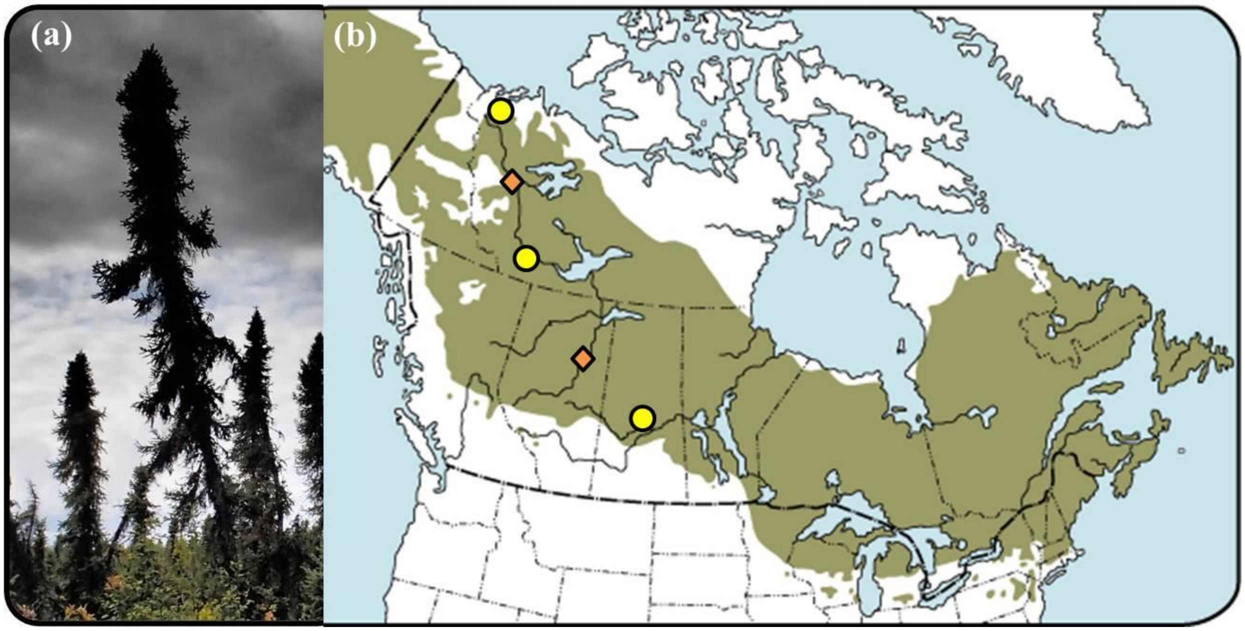

Fig. 1.2. (a) A typical black spruce, with drooping branches and a dense crown. Photo by A. Sniderhan (b) Distribution map of black spruce. Map from Natural Resources Canada black spruce fact sheet (https://tidcf.nrcan.gc.ca/en/trees/factsheet/39). Yellow circles show primary study areas where dendrochronological analyses were performed. Orange diamonds indicate sites where seed was collected and used for the common garden study in Chapter 4.

Chapter 2: Growth dynamics of black spruce (*Picea mariana*) in a rapidly-thawing discontinuous permafrost peatland

Anastasia E. Sniderhan and Jennifer L. Baltzer

Complete citation: Sniderhan AE and Baltzer JL (2016) Growth dynamics of black spruce (*Picea mariana*) in a rapidly-thawing discontinuous permafrost peatland. *Journal of Geophysical Research – Biogeosciences,* 121, 1288 - 3000.

Author roles: JB and AS developed the ideas for the project. AS collected all data, performed analysis, and wrote the manuscript. JB provided direction and editorial support throughout the analysis and writing process.

2.1. Abstract

We used tree-ring studies to document growth dynamics of black spruce, one of the most dominant boreal tree species, in a boreal peatland experiencing rapid permafrost thaw. In this chapter, we specifically examine how changing permafrost conditions influence growth. Growth of black spruce at this site has declined steadily since the mid-1900s and exhibited a shift from positive responses to temperature pre-1970 to predominantly negative responses in recent decades, despite precipitation increasing over time at this site. Our results show that there is no apparent effect of landscape position or rate of lateral permafrost thaw on growth trends in black spruce, despite gradients in soil moisture and active layer thickness across the mosaic of wetlands and comparatively drier permafrost plateaus at this site. These results support growing evidence that vertical permafrost thaw (i.e., active layer thickening) is causing drought stress in these slow-growing, shallow-rooted black spruce. To our knowledge, this study is the first to investigate permafrost as a driver of within-site variability in growth-climate responses, and we

provide insight into the widespread growth declines and divergence of climate-growth relationships in high-latitude forests.

2.2. Introduction

High-latitude forests are facing radical changes to their growing conditions attributable to amplified warming in the north (Chapin *et al.*, 2005). Many studies have suggested that as temperatures and atmospheric carbon dioxide (CO_2) concentrations rise, widespread increases in tree growth and northward expansion of boreal forests would be expected as a result of more favourable growing temperatures, CO_2 fertilization, and warming soils leading to increased microbial activity and release of stored nutrients from permafrost (e.g., Bonan & Shugart, 1989; Keeling *et al.*, 1996; Myneni *et al.*, 1997; Schuur *et al.*, 2007). However, evidence from tree-ring studies refutes this idea with many boreal forests showing a negative growth response to the changing climate, particularly warming (Lloyd & Bunn, 2007; Wilmking & Myers-Smith, 2008 but see Wilmking *et al.*, 2004; Beck *et al.*, 2011 for examples of some positive growth responses).

In tree-ring studies, negative growth responses to warming have been widely attributed to higher incidences of drought stress as temperatures rise; without a corresponding increase in precipitation, higher evapotranspirative demands could drive declines in forest productivity and alter climate-growth relationships (e.g., Lloyd & Fastie, 2002; Driscoll *et al.*, 2005; Wilmking *et al.*, 2005; Walker & Johnstone, 2014). However, tree-ring studies have demonstrated substantial variability in these growth response patterns. Forest stands have often exhibited mixed responses to climate variables (primarily temperature) with some stands responding positively and others negatively (e.g., Lloyd & Bunn, 2007; Beck *et al.*, 2011; Porter & Pisaric, 2011). Within stands, individual trees have similarly shown contrasting growth responses to climate conditions (Wilmking *et al.*, 2004; Pisaric *et al.*, 2007; Walker & Johnstone, 2014).

One possible driver for increasingly negative growth responses or variable within-stand responses is changing permafrost conditions. Permafrost (ground that has remained below 0°C for two or more consecutive years; Muller, 1947) underlies much of the boreal forest. On discontinuous permafrost (30 to 80% areal extent; Heginbottom, 2002) which underlies much of the boreal forest (Tarnocai, 2006; Brandt, 2009), an in-depth examination of the potential role of changing permafrost conditions on tree growth responses has not been performed despite the dramatic changes associated with rapid permafrost thaw in discontinuous permafrost landscapes (e.g., Camill, 1999; Christensen *et al.*, 2004; Quinton *et al.*, 2011). In the lowland boreal forest of Alaska, thaw has led to the transition of birch forests to black spruce (*Picea mariana*) forest cover (Lara *et al.*, 2016). In Northwestern Canada, the most notable of these land cover changes has been the transition of black spruce-dominated permafrost plateaus to treeless bogs and fens in boreal peatlands (e.g., Thie, 1974; Camill, 1999; Quinton *et al.*, 2011; Baltzer *et al.*, 2014). In these boreal peatlands, permafrost thaw drives ground subsidence, which destabilizes the solid foundation upon which the black spruce-dominated forest is established (Quinton *et al.*, 2011). Furthermore, the encroaching wetlands cause waterlogging and tree death (Camill & Clark, 1998; Osterkamp *et al.*, 2000; Camill, 2005). Thus, permafrost thaw could be an important contributor to the spatial variability in individual and stand responses.

Boreal peatlands in the discontinuous permafrost zone consequently present a unique opportunity to test the drought stress hypothesis proposed in many of the studies of declining productivity in high-latitude forests, and to investigate the role of ground thaw processes as potential drivers of widespread boreal browning. The ample moisture available within this system, particularly where lateral thaw has occurred, could balance increasing evapotranspirative demands in trees as the climate warms. Our predictions are outlined in the schematic in Fig. 2.1.

We predict that growth response to warming will be mediated by access to moisture. Specifically, if precipitation is increasing at a similar rate as temperature, we should see positive growth responses – assuming that moisture availability at the site meets evapotranspirative demands of the trees. However, moisture availability is not purely determined by atmospherically-driven water shortages (i.e., PET > P); trees are also affected by soil processes including soil water holding capacity and root access to the water table.

In boreal peatlands, local variation in soil moisture associated with differential permafrost thaw may be important in dictating growth responses. Specifically, lateral thaw of permafrost reduces tree growth within the transition zone between permafrost plateaus and wetlands due to waterlogging of root systems (Baltzer *et al.*, 2014; Patankar *et al.*, 2015). Vertical thaw is also occurring in the system and can affect the growth of black spruce. A deeper active (seasonally thawed) layer could promote growth due to the warmer soils, increased nutrient availability, and greater rooting depth (Bonan & Shugart, 1989) if the trees are able to respond and take advantage of these changing conditions. Alternatively, vertical thaw may negatively impact growth through the drying of surface soils. Specifically, the water table is perched on the frost table thus vertical thaw results in the lowering of the water table and drying of upper soil layers (Quinton & Baltzer, 2013; Patankar *et al.*, 2015). The effect of disturbance from permafrost thaw may also influence growth-climate responses of these forests; extensive permafrost degradation results in an unstable foundation upon which trees have established. Increased negative growth responses may thus be expected at stands with high thaw rates for both physiological and physical reasons.

In this study, we used tree-ring analysis to address two main questions pertaining to growth dynamics of black spruce in discontinuous permafrost peatland landscapes: (1) Do trees demonstrate consistent growth patterns over time, and what climatic variables underlie these patterns?; (2) How does landscape position of a tree in relation to permafrost distribution and rate of lateral permafrost thaw within a stand influence the growth in black spruce?

This study provides an in-depth analysis of black spruce growth dynamics in a highly sensitive and rapidly changing peatland on discontinuous permafrost. We investigated possible mechanisms (outlined in Fig. 2.1) driving widespread growth declines in the boreal region, within-site variability in growth responses, and divergence of climate-growth relationships that have been documented in high-latitude forests. In particular, we provided a novel focus on the role of permafrost in the growth patterns observed in this landscape. As peatlands comprise 24% of the circumpolar boreal forest (Wieder *et al.*, 2006), identifying the drivers of growth patterns, particularly with respect to the rapidly-changing permafrost conditions in this region, is crucial to understanding variation in the long-term growth dynamics of boreal forests globally.

2.3. Methods

2.3.1. Study location

This study was conducted at Scotty Creek, in the lower Liard River Valley of the Northwest Territories (61°18’ N, 121°18’ W). Scotty Creek’s landscape is characterized by discontinuous permafrost. Areas underlain by permafrost (permafrost plateaus) form elevational relief of 0.5 to 1.5 meters (Fig. 2.2a; Baltzer *et al.*, 2014) due to the volumetric expansion of water in the soil as it freezes. These plateaus provide a solid, drained foundation, where black spruce-dominated forests establish. In addition, permafrost-free areas take the form of bogs and fens in which forests cannot establish (Fig. 2.2). Annual air temperature (1981 to 2010 climate normal) in neighbouring Fort Simpson is -2.8°C, while precipitation, of which nearly half falls in the form of snow (Quinton *et al.*, 2009), averages an annual total of 387.6 mm from 1981 to 2010 (Environment Canada). Scotty Creek has experienced extensive permafrost degradation since the mid-1900s (Quinton *et al.*, 2011). At one intensively studied permafrost plateau, vertical thaw (active layer thickening) has been 0.36 m between 1999 to 2010, and lateral thaw totaling 18.6 m over the same time (Quinton & Baltzer, 2013).

2.3.2. Field and laboratory methods

A total of seven forest stands within 2 km^2 were sampled in August 2012 and August 2013. These stands ranged in area, the ratio of edge to interior (quantified using remotely-sensed imagery), and rate of lateral thaw (see Table S2.1 and Fig. S2.1). Five of the stands had high edge to interior ratios, and the edges of the stands were generally well defined by the extent of the plateau (Fig. 2.2). In these five stands, a core sample was taken at breast height (1.3 meters) from all living and dead trees with a diameter at breast height (DBH) greater than or equal to 7 cm – the smallest DBH that we were able to core effectively. Due to the sensitivity of this system to disturbance, we did not take disc samples of smaller trees, as this would cause unnecessary disturbance to a highly sensitive landscape. The fairly uniform size distribution of the forests at the site permitted sampling of trees 7 cm DBH and greater without obvious bias towards dominant individuals (see Fig. S2.2). We also recorded the coordinates of each tree to facilitate mapping of individuals for analysis of landscape position (edge vs. interior of plateau) on growth dynamics. Two of the stands had low edge to interior ratios, and were without well-defined edges delineating the stand. In these two low-edge stands, cores were taken from a > 7 cm DBH tree nearest to every 20 m interval in a 100 × 100 m grid, totaling 36 trees per stand. Since these two low-edge stands did not have natural forest boundaries created by adjacent wetlands that we could use to delineate our sampling efforts, we required a different sampling strategy than at the high-edge stands. These low-edge trees were still treated the same way as trees from other stands in further analyses.

This sampling protocol resulted in a total of 445 trees (ranging from 22 to 171 trees per stand) that were successfully cross-dated and used in further analyses of this study. The core samples were mounted to boards and sanded with up to 800 grit sandpaper. Ring widths were measured in Coorecorder 7.6, and cross-dated visually and statistically using CDendro 7.6 (Cybis Elektronik & Data, AB 2012) and Cofecha (Holmes, 2000), respectively. Metadata on all individuals is provided in Dataset S2.1 in Supporting Information.

2.3.3. Characterization of permafrost conditions

Permafrost presence is tightly linked with forest cover at our study site (Fig. 2.2; Quinton *et al.*, 2011; Baltzer *et al.*, 2014). Because of this close relationship, we were able to use remotely-sensed imagery to determine the extent of permafrost in our seven stands for two time points with available imagery (1977 and 2010). The extent of permafrost at each stand was digitized in ArcMap10 using Worldview2 imagery (Digital Globe Corp.; taken August 31, 2010 at 1.4 meter pixel resolution) and two VIS panchromatic aerial photographs (taken on April 30, 1977 and June 12, 1977 at 0.53 meter pixel resolution; Chasmer *et al.*, 2010). These techniques have been shown to be highly robust, which in addition to the error associated with these approaches, is described in detail by Chasmer et al. (2010). We were then able to calculate the rate of lateral thaw of each stand (herein referred to as “thaw rate”) using the percent areal reduction in forest cover (forest die-off occurs as permafrost is entirely lost below the trees due to ground surface subsidence and waterlogging; Quinton *et al.*, 2011) between the 1977 and 2010 imagery described above (Fig. S2.3).

This imagery and the strong association between permafrost presence and forest cover gave us the ability to designate trees as being “edge” or “interior” within the permafrost plateau. Edge trees were within the 10 meter transition zone moving across the landscape between a plateau and wetland (e.g., soil moisture, active layer thickness differences associated with the proximity to edge penetrate approximately 10 m at this site; Baltzer *et al.*, 2014), while interior trees were greater than 10 meters from a wetland boundary. These groups were formed by mapping the coordinates of each tree onto the 2010 site imagery where permafrost edges were digitized, and applying a buffer using ArcMap10 to determine which trees were within the 10 m transition zone.

2.3.4. Analysis

All analyses described below were performed in the R statistical programming environment and unless otherwise noted, analysis was performed in the R base package (R Core Team, 2014).

2.3.4.1. Growth patterns and climate-growth relationships of black spruce

To characterize the growth trends of black spruce over time, we calculated annual basal area increments (BAI) of each tree. Under ideal, non-fluctuating conditions, the annual radial growth increments of a tree steadily decline as it ages; mathematically this trend is produced as a trivial result of a constant volume of wood being added to the girth of an ever-growing cylinder. The conversion of ring widths to annual BAI removes this mathematical artifact, and provides a robust means of representing growth changes over time (Biondi & Qeadan, 2008). BAI was then converted to indexed measures using the C-method (see Biondi & Qeadan, 2008) using the package dplR (Bunn *et al.*, 2016). The C-method of standardization maintains the biological growth trend of the individual series, and using area-based measurements provides a better representation of tree growth than ring width-based standardization methods (Biondi & Qeadan, 2008). Thus, we found it to be the most appropriate method to represent growth patterns over time.

While processing our individual tree-ring data, we noticed that there was variability in the growth trends of individuals over time – especially in the late 20th century growth patterns, which is contemporaneous with documentation of diverging growth-climate and/or growth patterns in several studies (e.g., Driscoll *et al.*, 2005; D'Arrigo *et al.*, 2007; Pisaric *et al.*, 2007). We grouped individual trees into one of three categories through fitting linear models to their C-BAI growth curve from 1970 to present. Trees with a significant positive slope over this time were categorized as increasing BAI trees, while those with a significant negative slope were designated as decreasing BAI trees. In addition, trees that did not exhibit a significant trend were designated as neutral trees.

Average annual temperature data was retrieved online from Environment Canada's historical climate data archives (Environment Canada – www.climate.weather.gc.ca), and precipitation records (total annual precipitation and total annual snowfall) were acquired from Environment Canada's second generation adjusted precipitation data (Mekis & Vincent, 2011) for the Fort Simpson, NT weather station (~50 km north of Scotty Creek). Missing climate data was infilled as described in Supporting Text S2.1. In addition to retrieving the average annual temperature, total annual precipitation, and total annual snowfall for the site, we calculated an annual climate-moisture index (CMI; after Hogg, 1997 and Text S2.2). CMI is calculated by subtracting potential evapotranspiration from total precipitation, resulting in negative values of CMI when a system is moisture-limited and positive values of CMI when there is ample or excess moisture in the system. Trends in annual average temperature, total annual precipitation, total annual snowfall, and annual CMI are shown in Fig. 2.3.

For the purposes of climate-growth analyses, all non-climatic growth trends were removed from individual tree growth series by detrending with a smoothing spline with a frequency of 0.5 and wavelength of 0.67 × n years. We used the package "gtools" (Warnes *et al.*, 2015a) to calculate the correlation coefficient for each individual series to our four climate variables (annual average temperature, total annual precipitation, total annual snowfall, annual CMI) in an early (1930 to 1970) and late (1971 to 2011) time period. We also performed climate-growth analyses with monthly climate variables, however we found no results that had different implications than our annual analyses. These results are shown in Fig. S2.4. Each period corresponds to half of the time series of continuous climate data available near our site, and is temporally consistent with when temperature and precipitation trends began to rise rapidly (Fig. 3). We compared the proportions of trees responding positively, negatively, and demonstrating no response to these variables using a Chi-Square test in the package "gmodels" (Warnes *et al.*, 2015b). This comparison allowed us to determine whether individual responses to climate variables have stayed consistent over time, or if there has been a shift in the directionality of climate responses that may be driving widespread growth declines. Post-hoc testing of significant differences between groups in our Chi-Square analyses was performed using the False Discovery Rate (FDR) method in the package "fifer" (Fife, 2014). We employed contingency table analyses using Fisher's Exact test in the package "gmodels" (Warnes *et al.*, 2015b) to compare the proportion of positive and negative growth responses to the four climate variables between trees exhibiting increasing BAI and decreasing BAI trends during the late (1971 – 2011) period. We confirmed that there was no stand-level variability introduced by pooling trees from different stands through creating semivariograms in the package “geoR” (Ribeiro and Diggle, 2016), which show that there is no increased autocorrelation between trees within a stand that between stands (Fig. S2.5).

2.3.4.2. Influence of permafrost change on growth dynamics

In order to determine the effects of lateral permafrost thaw (and consequently root waterlogging) on tree productivity, we compared two characteristics of growth dynamics between edge and interior trees. First, we investigated whether landscape position (edge vs. interior) affected growth trends of trees over time (i.e., increasing/decreasing BAI). The proportion of trees exhibiting increasing/decreasing BAI responses in the edge versus interior locations were compared using a Chi-Square test in the package “gmodels” (Warnes *et al.*, 2015b). To determine whether growth was higher in trees on the interior of plateaus compared to trees on degrading plateau edges, a Welch two-sample t-test was used to compare the 2010 BAI of edge and interior trees. We used only the 2010 BAI for this analysis to match the time period in which edge vs. interior classifications were made. Determining BAI over a longer period would mask the possible effect of edge conditions on BAI, simply because trees are not likely experiencing edge conditions over long time frames.

We determined the relationship between stand thaw rate and the proportion of increasing BAI/decreasing BAI trees using a multinomial logistic regression in the package “mlogit” (Croissant, 2013). We also investigated the relationship between thaw rate and the 2010 BAI of all trees within each stand using a weighted linear regression.

2.4. Results

2.4.1. Growth patterns and climate-growth relationships

The average annual BAI growth curve for black spruce showed a fairly consistent BAI from 1850 to 1900 before increasing until approximately 1950 (due to a period of rapid recruitment; Fig. S2.6), at which point BAI declined steadily (Fig. 2.4a). We also found that there was considerable divergence in this trend amongst individuals from 1950 to present – 69 trees demonstrated increasing BAI trends and 249 trees exhibited decreasing BAI, while 127 trees did not show any directional growth trend (Fig. 2.4).

The proportion of trees responding positively to annual average temperature decreased significantly between the early and late periods (Fig. 2.5, Table 2.1). While this shift occurred, there was a large increase in the proportion of trees demonstrating a negative growth response to temperature (Fig. 2.5, Table 2.1). There was also a significant difference in the proportions of trees exhibiting positive and negative growth responses to total annual precipitation, total annual snowfall, and annual CMI, with a reduction in the proportion of individuals demonstrating significant responses to these climate variables in the late time period (i.e., weakening relationships between growth and these three climate variables; Fig. 2.5, Table 2.1). In all cases reductions were attributable to decreases in positive responders, which was particularly marked in the relationship between growth and snowfall (Fig. 2.5). However, in these precipitation and CMI comparisons there was no directional change in the relative proportions of positive and negative responders between the early and late periods (Fig. 2.5).

We found a significant difference in the proportion of trees from the increasing and decreasing BAI groups responding to temperature; while there was little difference in the proportion of positive and negative temperature-growth relationships among the increasing BAI trees, the trees classified as decreasing BAI had a much greater proportion of negative temperature-growth responses (Fig. 2.6, Fisher’s Exact test, $p = 0.0050$). There were no significant differences found in the proportion of positive/negative climate-growth responses to the other three climate variables among the increasing BAI and decreasing BAI chronologies (prec – Fisher's Exact test, p = 0.54; snow – Fisher's Exact test, p = 0.16; CMI – Fisher's Exact test, p = 0.97).

2.4.2. Influence of permafrost change on growth dynamics

Of the trees that we sampled, 72% fell within the 10 m edge zone where permafrost plateaus transition into wetland features. The proportion of trees exhibiting an increasing BAI/decreasing BAI trend demonstrated significant differences between trees within edge zones versus on the interior parts of plateaus (Fig. 2.7; $X^2 = 8.74$, d.f. = 2, p = 0.013). There was no significant difference in 2010 BAI between edge and interior trees ($t_{260} = 0.647$, p = 0.52). Thaw rate did not influence the proportion of trees within the stand exhibiting increasing BAI or decreasing BAI trends (Log-Likelihood: -430.1, Likelihood ratio test: $X^2 = 4.83$, p = 0.089). There was also no significant relationship found between thaw rate and the 2010 BAI of trees within each stand (Fig. 2.8; $F_{1,5} = 2.372$, p = 0.184, Adjusted $R^2 = 0.186$).

2.5. Discussion

In this study, we investigated the growth patterns of black spruce and the potential climatic drivers behind these patterns, as well as how landscape position (edge vs. interior) and rate of lateral permafrost thaw influence growth patterns. We found that individual growth patterns have largely exhibited declining trends since the mid-1900s. These patterns coincide with a shift in the temperature-growth relationships of trees, which change from a predominantly positive response during the 1930 – 1970 time period to a predominantly negative response during the 1971 – 2011 time period. Neither precipitation nor climate moisture index (CMI) played a direct role in these changing responses, which undermines the idea that evapotranspirative drought stress is driving growth declines at this site.

We found that landscape position influenced the growth trends of individual trees, with trends towards more increasing BAI and less decreasing BAI patterns in trees on the interior of plateaus in comparison to those on the edge of plateau-wetland interfaces. Interestingly, we found no apparent effect of the rate of lateral permafrost thaw on the magnitude of black spruce growth despite rapid changes in permafrost conditions at this site. We suggest that warming-induced permafrost thaw leading to active layer thickening (vertical thaw) may be driving changes in soil moisture conditions that are directly impacting growth and productivity in boreal forests.

2.5.1. Growth patterns and climate-growth relationships

Our results show that black spruce has been experiencing growth declines since the mid-1900s, with over 50% of the 445 trees sampled exhibiting decreasing BAI trends (Fig. 2.4). The growth decline observed at this site is temporally consistent with the literature on boreal forest growth dynamics. Many studies of these high-latitude forests have shown a decline in annual tree growth occurring since the mid- to late- 1900s, particularly in spruce-dominated forests (e.g., Lloyd & Fastie, 2002; D'Arrigo *et al.*, 2004; Lloyd & Bunn, 2007; Girardin *et al.*, 2014). Furthermore, this is consistent with normalized difference vegetation index (NDVI) trends that have reported declining productivity across the boreal forest in Northwestern North America (e.g., Angert *et al.*, 2005; Bunn & Goetz, 2006; Beck *et al.*, 2011). Though a decline in annual BAI could be driven by tree senescence, productivity of black spruce forests on organic soils typically begins to decline at approximately 200 years (Viereck & Johnston, 1990). Because the longevity of this species is considerably higher than the average age of the trees in this study (mean age = 96.1 years ± 30.3 SD), the decline in average annual growth is not likely to be attributable to tree senescence and therefore it is more likely to be driven by other processes such as the changing climate regime. However, growth declines at such a large scale could also be driven by widespread disease or pest outbreaks, neither of which have been documented for black spruce in this region.

It is widely accepted that in the boreal region, "forest browning" (decreasing productivity) is a result of rising temperatures driving increases in evapotranspirative water loss and drought stress (e.g., Lloyd & Fastie, 2002; Driscoll *et al.*, 2005; Wilmking *et al.*, 2005). Similar to the widespread negative temperature-growth responses across the transition from the interior of a permafrost plateau to the wetland interface that we observed in this study, Walker and Johnstone (2014) found climate-growth relationships in black spruce were largely negative despite sampling across a regional moisture gradient in Alaska and the Yukon Territory. Carbon isotope analysis revealed widespread drought stress signals that are thought to be in part due to soil-based processes that influenced water availability to trees (Walker *et al.*, 2015). Similarly, we show that increases in precipitation, snowfall, and CMI over the late (1971-2011) time period have not promoted an increase in positive climate-growth responses despite our hypothesis that these could counteract effects of increased evapotranspirative water losses associated with warming temperatures.

Of the climatic variables examined, annual average temperature over the late 1900s is the strongest predictor of the decline in productivity. While early growth responses to annual average temperature were predominantly positive (i.e., warmer years promoted growth), there was a shift in the late period toward a much higher frequency of negative responses (Fig. 2.5). Such shifts from positive to negative responses have been documented in several studies of annual growth dynamics in boreal forests (e.g., Lloyd & Fastie, 2002; Porter & Pisaric, 2011). These have largely been attributed to evapotranspirative drought stress driven by warming temperatures that are not tracked by precipitation (atmospheric-driven evapotranspirative drought stress). Here, we propose that these late time period temperature-growth response trends are a result of warming-induced permafrost thaw and associated soil moisture stressors amplifying drought stress driven by a soil moisture deficit. At Scotty Creek and many boreal peatlands (e.g., Thie, 1974; Christensen *et al.*, 2004; Lara *et al.*, 2016), warming drives the thaw and loss of permafrost with dramatic implications for surficial hydrology. The widespread decreasing BAI trends and negative temperature-growth correlations without corresponding responses to precipitation or CMI support the hypothesis that changes to surface hydrology driven by active layer thickening (vertical permafrost thaw) may be playing a major role in influencing access by trees to soil water.

2.5.2. Influence of permafrost change on growth dynamics

The rapidly changing landscape within boreal peatlands on discontinuous permafrost drives heterogeneity in microsite conditions. Trees directly at permafrost plateau-wetland interfaces demonstrate reduced radial growth and sap flow compared to those on the interior of plateaus (>10 m from a wetland boundary; Baltzer *et al.*, 2014; Patankar *et al.*, 2015). Because the gradient in abiotic conditions (e.g., active layer thickness, soil moisture) penetrates as much as ~10 m from the plateau edge (Baltzer *et al.*, 2014), we expected to see growth trends reflect the edge conditions. We indeed found that there was a greater proportion of trees exhibiting increasing BAI trends within the interior grouping than the edge, and additionally more decreasing BAI in the edge than interior (Fig. 2.7). However, the proportion of trees with decreasing BAI trends was still overwhelmingly larger than increasing BAI in both edge and interior groups (Fig. 2.7) and there was no difference in the magnitude of growth in 2010 between edge and interior trees ($t_{260} = 0.647$, $p = 0.52$). This suggests that the part of the transition between permafrost plateaus and wetlands that drives documented physiological declines and associated reductions in tree growth is isolated to the immediate plateau-wetland interface. In other words, the penetration of the biotic edge effects of permafrost thaw may be much more limited than those of abiotic changes. We investigated whether there was a discernable continual pattern between growth and distance from edge, however we found no clear trend (Fig. S2.7). This is consistent with our proposed hypothesis that negative effects are constrained to the immediate edge.

The rate of land cover change (as quantified through lateral thaw rates) does not appear to be a driver of the growth dynamics (Fig. 2.8), despite the tight associations between permafrost presence and forest cover in this ecosystem (Quinton *et al.*, 2011). This result was unexpected as the stands sampled range from very stable with little change in areal permafrost extent since the 1970s to extensively degraded with little remaining permafrost. However, we only sampled seven stands and none of these fell within the mid-range of thaw rates, which may have restricted our ability to detect trends in the growth dynamics of these trees with respect to rate of thaw. Alternatively, our results may reflect the complex dynamics of permafrost thaw wherein both vertical and lateral thaw processes impact surface hydrology and tree growth processes (Quinton & Baltzer, 2013; Patankar *et al.*, 2015; Warren, 2015).

Given the high moisture availability in boreal peatlands on discontinuous permafrost (Zoltai, 1972) and the moisture gradient moving from edge to interior of a permafrost plateau (Baltzer *et al.*, 2014), it seemed improbable that these widespread negative growth responses at Scotty Creek could be driven by drought stress. There is already evidence for reduced root function (Baltzer *et al.*, 2013) and consequently sap flow of trees experiencing waterlogged conditions at the edges of degrading permafrost plateaus (Patankar *et al.*, 2015), which makes this site an unlikely candidate for experiencing drought. Though lateral permafrost thaw is most apparent in the discontinuous permafrost zone, it is coupled with vertical thaw (Quinton & Baltzer, 2013) which could be a major factor in the declining growth of black spruce at this site.

Patankar *et al.* (2015) and Warren (2015) linked a seasonal decline in black spruce sap flow at Scotty Creek with active layer thickening and surface soil drying. A conceptual diagram outlining the impacts of thaw processes on soil moisture with respect to the rooting zone and its implications for sap flow in black spruce is shown in Patankar *et al.* (2015). This clearly parallels the widespread negative temperature-growth relationships across regional moisture gradients as found by Walker & Johnstone (2014); despite large variability in moisture conditions, the shallow rooting structure of black spruce (~20 cm; Gale & Grigal, 1987) renders the species unable to access the water table as the active layer thickens.

In peat-dominated soils, water-holding capacity of the upper layer of soil is low and the water table perches upon the impenetrable frost table. As the active layer thickens and the depth to frost table increases, the depth to the water table also increases (Quinton & Baltzer, 2013). The current active layer thickness at Scotty Creek ranges from 35 to >150 cm at our forest stands (Fig. S2.8) meaning for black spruce, the deepening of the water table due to vertical thaw could lead to soil moisture deficits despite increases in precipitation and CMI. In other words, more precipitation is entering the system but because of warming-induced active layer thickening, less is available to the trees for growth. Indeed, Warren (2015) found that at this site, black spruce sap flow correlates most closely with soil moisture in the top 10 cm. Increasing snowfall may likewise amplify the effects of drought stress. As we observed in our climate-growth analysis, there were high proportions of positive growth responses to snowfall pre-1970, with many fewer positive responders in the post-1970 time period (Fig. 2.5), despite increasing snowfall (Fig. 2.3; Connon *et al.*, 2014). Snow serves an important role in the insulation of soils from cold temperatures over the winter months. With the increased snowfall at this site, the warmer soils would thaw earlier in the spring. We propose that this increasing snowfall in combination with the warming-induced permafrost thaw in the late 1900s is exacerbating active layer thaw and decreasing access to soil moisture for the black spruce forests at this site.

2.6. Conclusions

From this study, we have been able to conclude that climatically driven drought stress is not the mechanism behind the widespread growth declines in this boreal peatland system, as there have not been major shifts toward positive growth responses to either precipitation or CMI. However, there is evidence suggesting that the thickening of the active layer as warming continues in this region coupled with the low water holding capacity of peat is resulting in water limitations within the rooting zone of black spruce (Quinton & Baltzer, 2013; Patankar *et al.*, 2015; Warren, 2015). Such soil moisture deficits would be expected to contribute to the prevalence of negative growth – temperature relationships apparent in recent years in this thawing permafrost peatland as warming-induced active layer thickening may be affecting access to the water table for shallow-rooting black spruce. This mechanism is also influenced by the insulation of soils by the deeper snowpacks experienced in recent years; deeper snowpack can promote earlier soil thaw, active layer thickening, and further limit water availability within the rooting zone. This hypothesis is supported by our findings of reduced positive growth responses to snowfall in recent decades. Further investigation of rooting distribution and plasticity in light of the effects of thawing permafrost on the soil moisture profile will be required to understand

and predict responses of black spruce to warming. However, this study has provided notable additions to the ever-growing body of knowledge on the response of the boreal forest to climate change. As this study was one of the first to specifically test permafrost conditions as a mechanism driving individual growth patterns within a site, we have provided important insights into the underlying causes of growth patterns of black spruce in a landscape that has experienced, and is expected to continue to undergo dramatic change.

2.7. Acknowledgements

Funding for this research was provided by the Natural Sciences and Engineering Research Council, Wilfrid Laurier University, the Canadian Foundation for Climate and Atmospheric Science, the Northern Scientific Training Program for travel funding, and the Ontario Ministry of Research and Innovation Early Researcher Award program. AS was supported by Ontario Graduate Scholarships. We are grateful to M. Fafard, G. Lynch, and C. Wallace for field assistance. We gratefully acknowledge W. Quinton for the provision of imagery necessary for quantifying landscape change and for interesting discussions surrounding hydrological implications of active layer thickening. We are very grateful to L. Chasmer who processed the Worldview2 imagery data, and C. Hopkinson who derived the Lidar DEM in our figure. We thank G. McNickle for his comments on an earlier version of this manuscript and contribution to R code, and O. Sonnentag as well as everyone in the Forest Ecology Research Group for providing comments on this manuscript. We thank the Aurora Research Institute for their assistance in obtaining a research license (license number 15005). We thank the Denedeh Resources Committee, Dehcho First Nations, Fort Simpson Métis Local #52, Liidlii Kue First Nation and the Village of Fort Simpson for their support of ongoing research at Scotty Creek. We also gratefully acknowledge the Wilfrid Laurier University – Government of the NWT

Partnership Agreement for providing support for this study. Upon publication, data from this study will be available on the International Tree-Ring Data Bank.

2.8. References

Angert A, Biraud S, Bonfils C, Henning CC, Buermann W, Pinzon J, Tucker CJ, Fung I (2005) Drier summers cancel out the CO_2 uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 10823–10827.

Baltzer J, Patankar R, Downey A, Quinton W (2013) Impacts of seasonal thaw and permafrost degradation on *Picea mariana* root function in a subarctic boreal peatland. In: *Acta Horticulturae*, pp. 141–148.

Baltzer JL, Veness T, Chasmer LE, Sniderhan AE, Quinton WL (2014) Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. *Global Change Biology*, 20, 824–834.

Beck PS, Juday GP, Alix C, Barber VA, Winslow SE, Sousa EE, Heiser P, Herriges JD. Goetz SJ (2011) Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters*, 14, 373–379.

Biondi F, Qeadan F (2008) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research*, 64, 81–96.

Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, 20, 1–28.

Brandt JP (2009) The extent of the North American boreal zone. *Environmental Reviews*, 17, 101–161.

Bunn, AG, Korpela M, Biondi F, Campelo F, Mérian F, Qeadan F, Zang C (2016) dplR: Dendrochronology Program Library in R. R package version 1.6.4. https://CRAN.R-project.org/package=dplR

Bunn AG, Goetz SJ (2006) Trends in satellite-observed circumpolar photosynthetic activity from 1982 to 2003: the influence of seasonality, cover type, and vegetation density. *Earth Interactions,* 10, 1–19.

Camill P (1999) Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany*, 77, 721–733.

Camill P (2005) Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. *Climatic Change*, 68, 135–152.

Camill P, Clark JS (1998) Climate change disequilibrium of boreal permafrost peatlands caused by local processes. *The American Naturalist*, 151, 207–222.

Chapin FS, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping C-L, Tape KD, Thompson CDC, Walker DA, Welker JM (2005) Role of land-surface changes in arctic summer warming. *Science (New York, N.Y.)*, 310, 657–60.

Chasmer L, Hopkinson C, Quinton W (2010) Quantifying errors in discontinuous permafrost plateau change from optical data, Northwest Territories, Canada : 1947 – 2008. *Canadian Journal of Remote Sensing*, 36, S211–S223.

Christensen TR, Johansson T, Åkerman HJ, Mastepanov M, Malmer N, Friborg T, Crill P, Svensson BH (2004) Thawing sub-arctic permafrost: Effects on vegetation and methane emissions. *Geophysical Research Letters,* 31, L04501.

Connon RF, Quinton WL, Craig JR, Hayashi M (2014) Changing hydrologic connectivity due to permafrost thaw in the lower Liard River valley, NWT, Canada. *Hydrological Processes,* 28, 4163–4178.

Croissant Y (2013) mlogit: multinomial logit model. R package version 0.2-4. https://CRAN.R-project.org/package=mlogit

D'Arrigo RD, Kaufmann RK, Davi N, Jacoby GC, Laskowski C, Myneni RB, Cherubini P (2004) Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles*, 18, GB3021.

D'Arrigo R, Wilson R, Liepert B, Cherubini P (2007) On the "Divergence Problem" in Northern Forests: A review of the tree-ring evidence and possible causes. *Global and Planetary Change*, 60, 289–305.

Driscoll WW, Wiles GC, D'Arrigo RD, Wilmking M (2005) Divergent tree growth response to recent climatic warming, Lake Clark National Park and Preserve, Alaska. *Geophysical Research Letters*, 32, L20703.

Fife D (2014). fifer: A collection of miscellaneous functions. R package version 1.0. https://CRAN.R-project.org/package=fifer

Gale MR, Grigal DF (1987) Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research,* 17, 829–834.

Girardin MP, Guo XJ, De Jong R, Kinnard C, Bernier P, Raulier F (2014) Unusual forest growth decline in boreal North America covaries with the retreat of Arctic sea ice. *Global Change Biology*, 20, 851–866.

Heginbottom JA (2002) Permafrost mapping: a review. *Progress in Physical Geography*, 26, 623–642.

Hogg EH (1997) Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology*, 84, 115–122.

Holmes RL (2000) The Dendrochronological Program Library.

Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature*, 382, 146–149.

Lara MJ, Genet H, McGuire AD, Euskirchen ES, Zhang Y, Brown DRN, Jorgenson MT, Romanovsky V, Breen A, Bolton WR (2016) Thermokarst rates intensify due to climate change and forest fragmentation in an Alaskan boreal forest lowland. *Global Change Biology*, 22, 816–829.

Lloyd AH, Bunn AG (2007) Responses of the circumpolar boreal forest to 20th century climate variability. *Environmental Research Letters*, 2, 45013.

Lloyd AH, Fastie CL (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, 52, 481–509.

Mekis É, Vincent LA (2011) An overview of the second generation adjusted daily precipitation dataset for trend analysis in Canada. *Atmosphere-Ocean*, 49, 163–177.

Muller SW (1947) *Permafrost or permanently frozen ground and related engineering problems*. Ann Arbor, Michigan, 231 pp.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, 386, 698–702.

Osterkamp TE, Viereck LA, Shur Y, Jorgenson MT, Racine CH, Doyle A, Boone RD (2000) Observations of thermokarst and its impact on boreal forests in Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research*, 32, 303–315.

Patankar R, Quinton WL, Hayashi M, Baltzer JL (2015) Sap flow responses to seasonal thaw and permafrost degradation in a subarctic boreal peatland. *Trees - Structure and Function*, 29, 129–142.

Pisaric MFJ, Carey SK, Kokelj SV, Youngblut D (2007) Anomalous 20th century tree growth, Mackenzie Delta, Northwest Territories, Canada. *Geophysical Research Letters*, 34, L05714.

Porter TJ, Pisaric MFJ (2011) Temperature-growth divergence in white spruce forests of Old Crow Flats, Yukon Territory, and adjacent regions of northwestern North America. *Global Change Biology*, 17, 3418–3430.

Quinton WL, Baltzer JL (2013) The active-layer hydrology of a peat plateau with thawing permafrost (Scotty Creek, Canada). *Hydrogeology Journal*, 21, 201–220.

Quinton WL, Hayashi M, Chasmer LE (2009) Peatland hydrology of discontinuous permafrost in the Northwest Territories: Overview and synthesis. *Canadian Water Resources Journal*, 34, 311–328.

Quinton WL, Hayashi M, Chasmer LE (2011) Permafrost-thaw-induced land-cover change in the Canadian subarctic: implications for water resources. *Hydrological Processes*, 25, 152–158.

Ribeiro PJ Jr, Diggle PJ (2016) geoR: Analysis of Geostatistical Data. R package version 1.7-5.2. https://CRAN.R-project.org/package=geoR

Schuur EAG, Crummer KG, Vogel JG, Mack MC (2007) Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. *Ecosystems*, 10, 280–292.

Tarnocai C (2006) The effect of climate change on carbon in Canadian peatlands. *Global and Planetary Change*, 53, 222–232.

Thie J (1974) Distribution and thawing of permafrost in the southern part of the discontinuous permafrost zone in Manitoba. *Arctic Institute of North America*, 27, 189–200.

Viereck LA, Johnston WF (1990) *Picea mariana* (Mill.) B. S. P. Black Spruce. In: *Silvics of North America: vol. 1. Conifers* (eds Burns R, Honkala B), pp. 227–237. USDA Forest Service Agriculture Handbook, Washington, DC.

Walker X, Johnstone JF (2014) Widespread negative correlations between black spruce growth and temperature across topographic moisture gradients in the boreal forest. *Environmental Research Letters*, 9, 64016.

Walker XJ, Mack MC, Johnstone JF (2015) Stable carbon isotope analysis reveals widespread drought stress in boreal black spruce forests. *Global Change Biology*, 21, 3102–3113.

Warnes GR, Bolker B, Lumley T (2015a) gtools: Various R Programming Tools. R package version 3.5.0. https://CRAN.R-project.org/package=gtools

Warnes GR, Bolker B, Lumley T, Johnson RC (2015b) gmodels: Various R Programming Tools for Model Fitting. R package version 2.16.2. https://CRAN.R-project.org/package=gmodels

Warren RK (2015) *Examining the spatial distribution of soil moisture and its relationship to vegetation and permafrost dynamics in a subarctic permafrost peatland*. University of Guelph, 53 pp.

Wieder K, Vitt DH, Benscoter BW (2006) Peatlands and the Boreal Forest. In: *Boreal Peatland Ecosystems*, Vol. 188 (eds Wieder RK, Vitt DH), pp. 1–8. Springer, Berlin; New York.

Wilmking M, Myers-Smith I (2008) Changing climate sensitivity of black spruce (*Picea mariana* Mill.) in a peatland–forest landscape in Interior Alaska. *Dendrochronologia*, 25, 167–175.

Wilmking M, Juday GP, Barber VA, Zald HSJ (2004) Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology*, 10, 1724–1736.

Wilmking M, D'Arrigo RD, Jacoby GC, Juday GP (2005) Increased temperature sensitivity and divergent growth trends in circumpolar boreal forests. *Geophysical Research Letters*, 32, L15715.

Zoltai SC (1972) Palsas and peat plateaus in Central Manitoba and Saskatchewan. *Canadian Journal of Forest Research*, 2, 291–302.

2.9. Tables

Table 2.1. Results of Chi-Square tests comparing the proportion of trees responding positively and negatively to each of the four annual climate variables in an early (1930-1970) and late (1971-2011) time period.

Climate Variable	**X^2**	**d.f.**	**p-value**
Temperature	65.7	2	$p < 0.0001$
Precipitation	7.02	2	$p = 0.029$
Snow	25.2	2	$p < 0.0001$
CMI	19.2	2	$p < 0.0001$

2.9. Figures

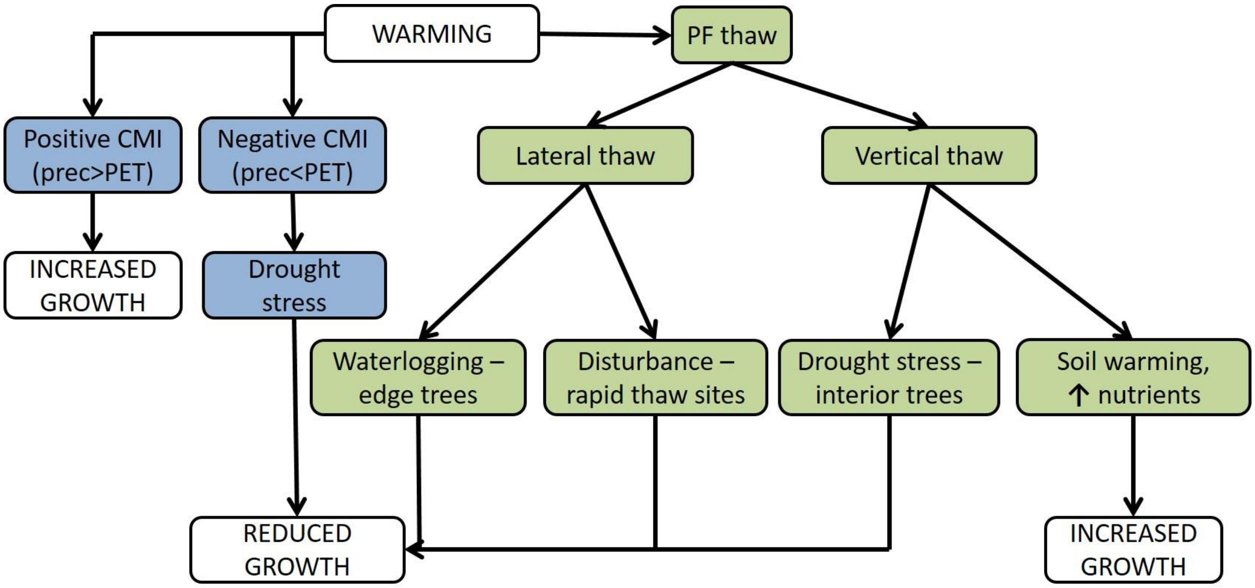

Fig. 2.1. Predictions for possible effects of climate warming on black spruce growth dynamics, through both direct effects of warming and indirectly through permafrost thaw. Atmospheric processes are shown in blue boxes, while soil-driven processes are in green boxes. Abbreviations: CMI – Climate Moisture Index (measure of drought stress in a system), prec – precipitation, PET – potential evapotranspiration, PF – permafrost.

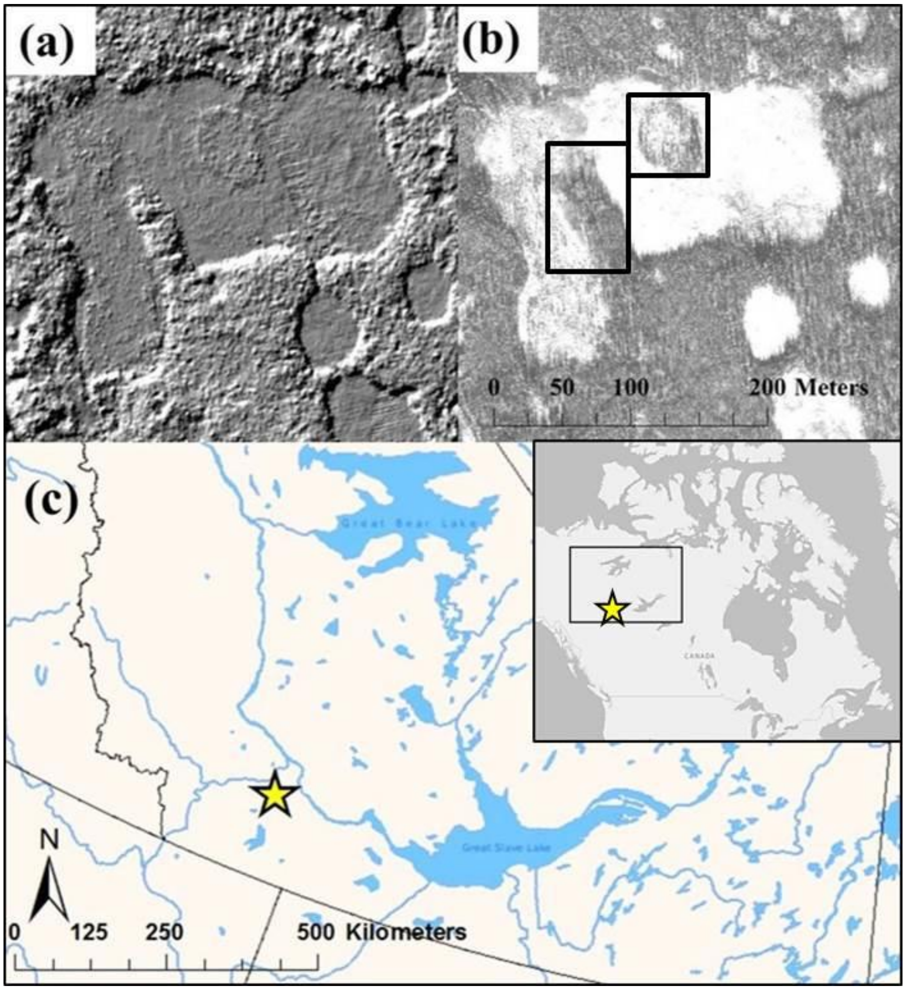

Fig. 2.2. (a) Lidar-based shaded relief digital elevation model showing permafrost extent across the landscape (derived by Dr. C. Hopkinson) and (b) Worldview2 (© Digital Globe Corp, All Rights Reserved – acquired by Dr. W. Quinton) imagery showing the heterogeneous landscape of forests and bogs at Scotty Creek, NT (light/white areas are bogs) for the same area. In panel (a), the gradient in elevation extends 102 cm, where black is the lowest elevation and white is the highest. As seen from these images, the forest extent is closely related to the extent of permafrost. The two boxes in panel (b) indicate examples of stands sampled where the stand is defined by the edge of the plateau. The scale on panel (b) applies to panel (a) as well. Panel (c), a map of the southern part of the Northwest Territories, Canada, shows the location of the study site, depicted by a star. Colour base map from panel (c) used with permission from NWT Centre

for Geomatics, ENR-ITI Shared Services, Government of the Northwest Territories, 2015 – 2016. Map inset acquired on ArcMap 10.3, ESRI, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors and the GIS user community.

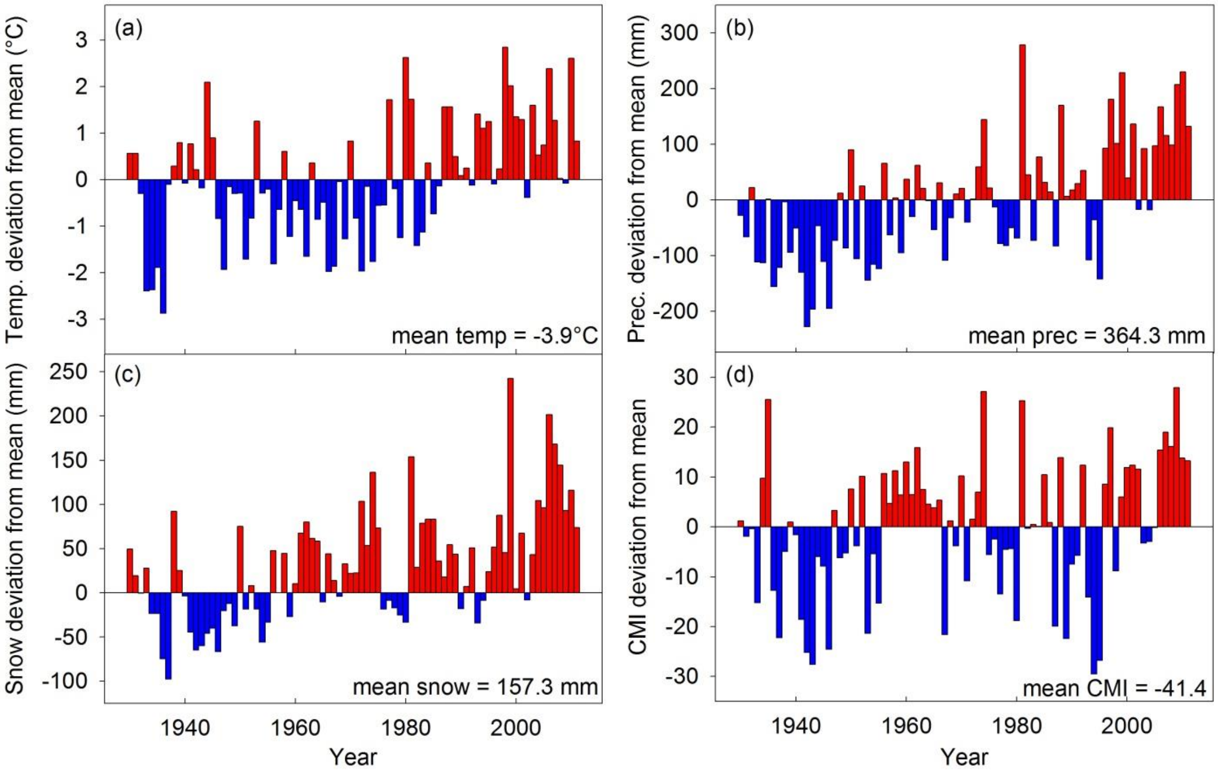

Fig. 2.3. Trends in (a) average annual temperature (Temp), (b) total annual precipitation (Prec), (c) total annual snowfall (Snow), and (d) annual climate-moisture index (CMI) for Fort Simpson NT (www.climate.weather.gc.ca; Mekis & Vincent, 2011). The annual deviations from mean values over the early (1930 to 1970) time period are shown in each panel, where positive values indicate higher-than-mean conditions.

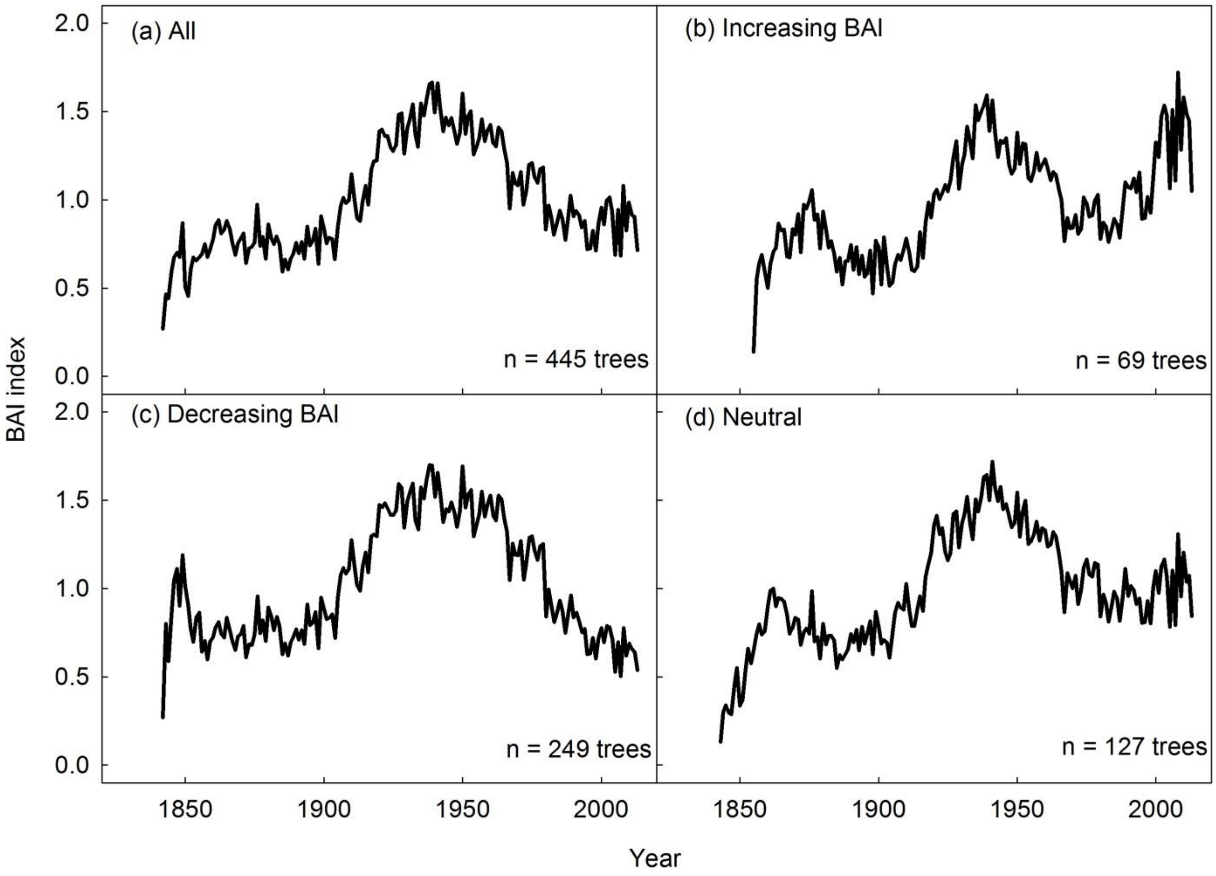

Fig. 2.4. Average annual basal area index (BAI; calculated using the C-method) for black spruce at Scotty Creek NT. Panel (a) shows the master chronology. Panels (b)-(d) show the chronologies for the individuals demonstrating increasing BAI/decreasing BAI/neutral trends. A table comparing the slopes of these four chronologies pre-1970 and post-1970 is shown in Table S2.

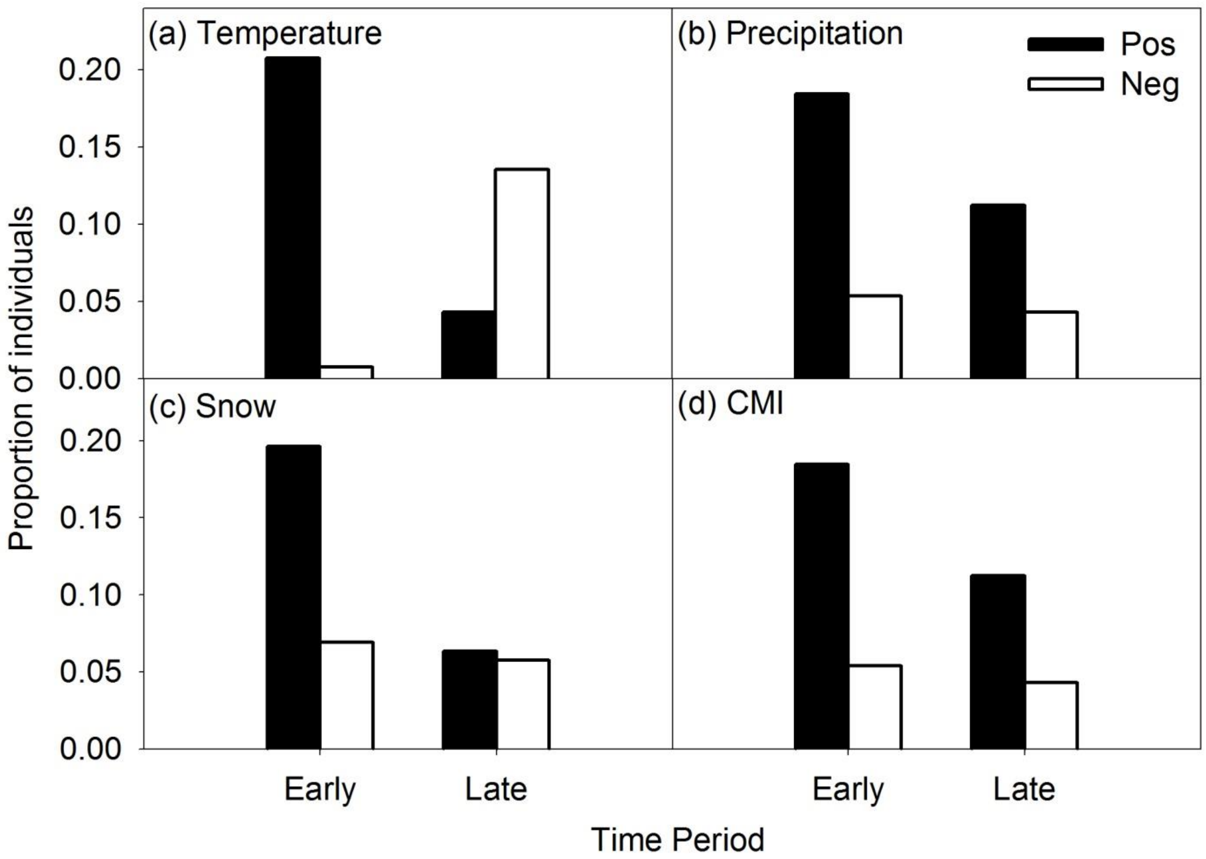

Fig. 2.5. Proportion of trees responding to (a) average annual temperature, (b) total annual precipitation, (c) annual snowfall, and (d) annual climate-moisture index (CMI) in an early (1930-1970) and late (1971-2011) time period. Pos (Positive) and Neg (Negative) indicate the series' correlation to the given climate variables. There were significant changes in the number of responders to each variable over the two time periods. Only positive and negative responders are shown, but the proportions sum to unity with the remainder being neutral responders. All pairwise comparisons of both early/late and positive/negative results were significant ($p<0.05$), with the exception of precipitation positive vs. negative populations ($p=0.67$).

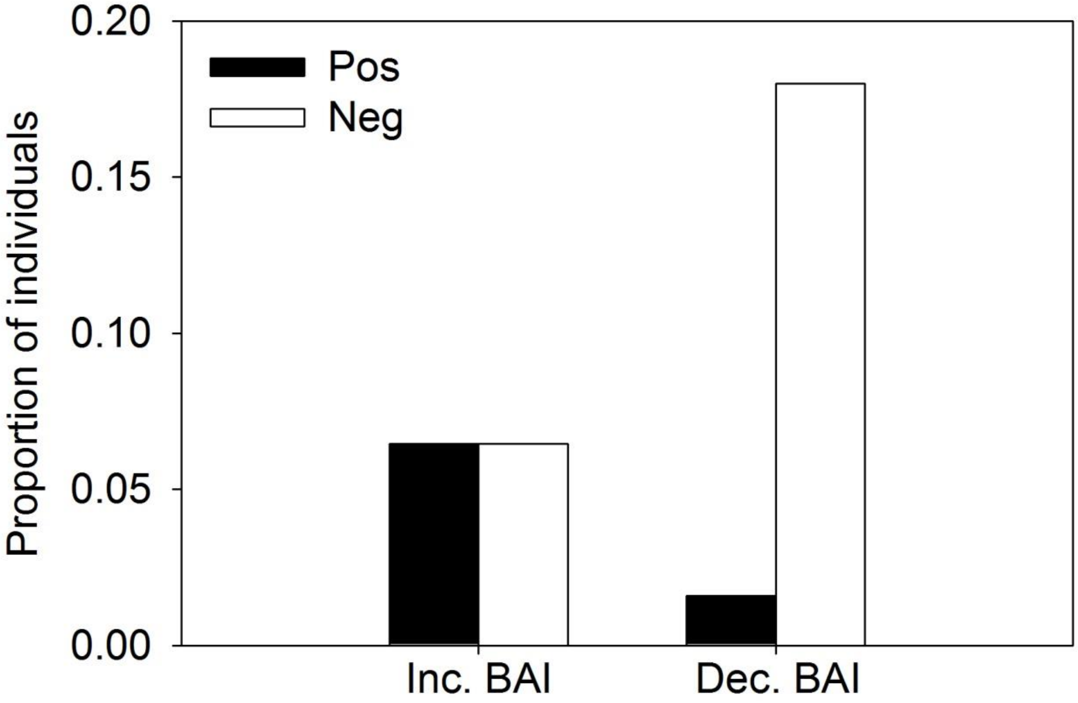

Fig. 2.6: Proportions of individual trees demonstrating a positive (pos) and negative (neg) growth response to annual average temperature within the increasing BAI (Inc.BAI) and decreasing BAI (Dec.BAI) chronologies (Fisher's Exact test, p = 0.0050).

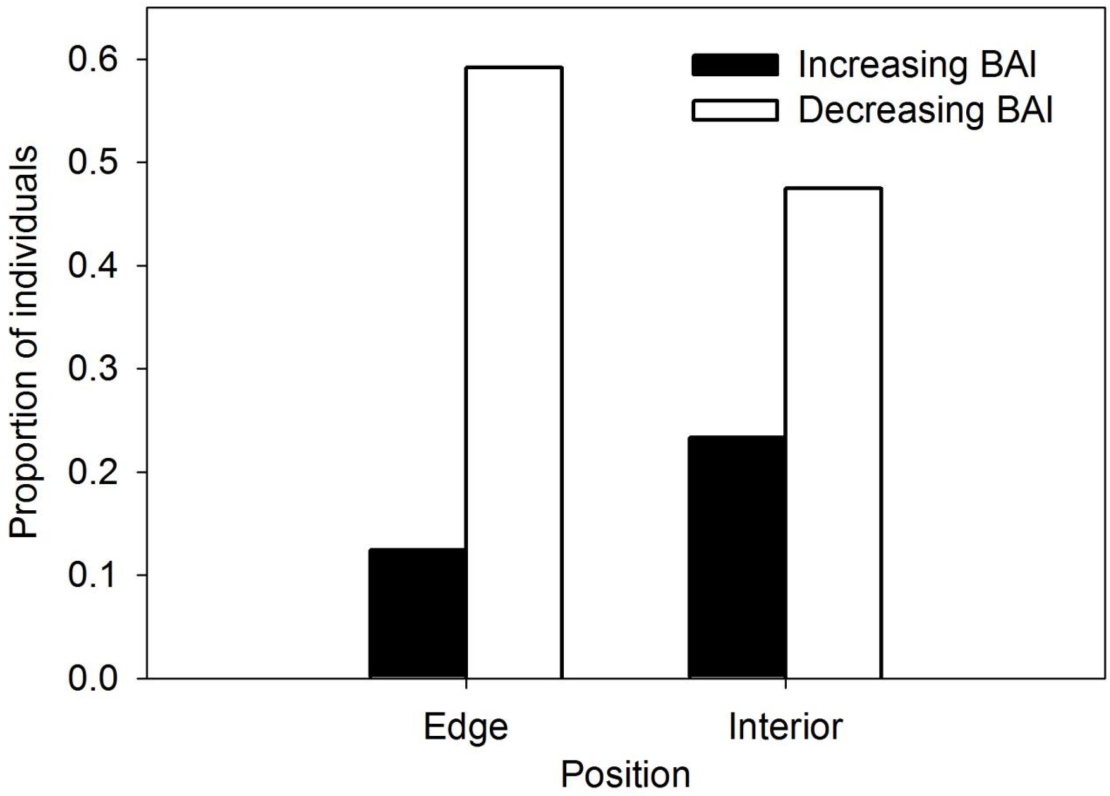

Fig. 2.7. Proportions of trees exhibiting increasing BAI/decreasing BAI trends on the edge of plateaus (within 10 m of permafrost plateau-wetland interface) vs. interior of plateaus ($X^2 = 8.74$, d.f. = 2, p = 0.013).

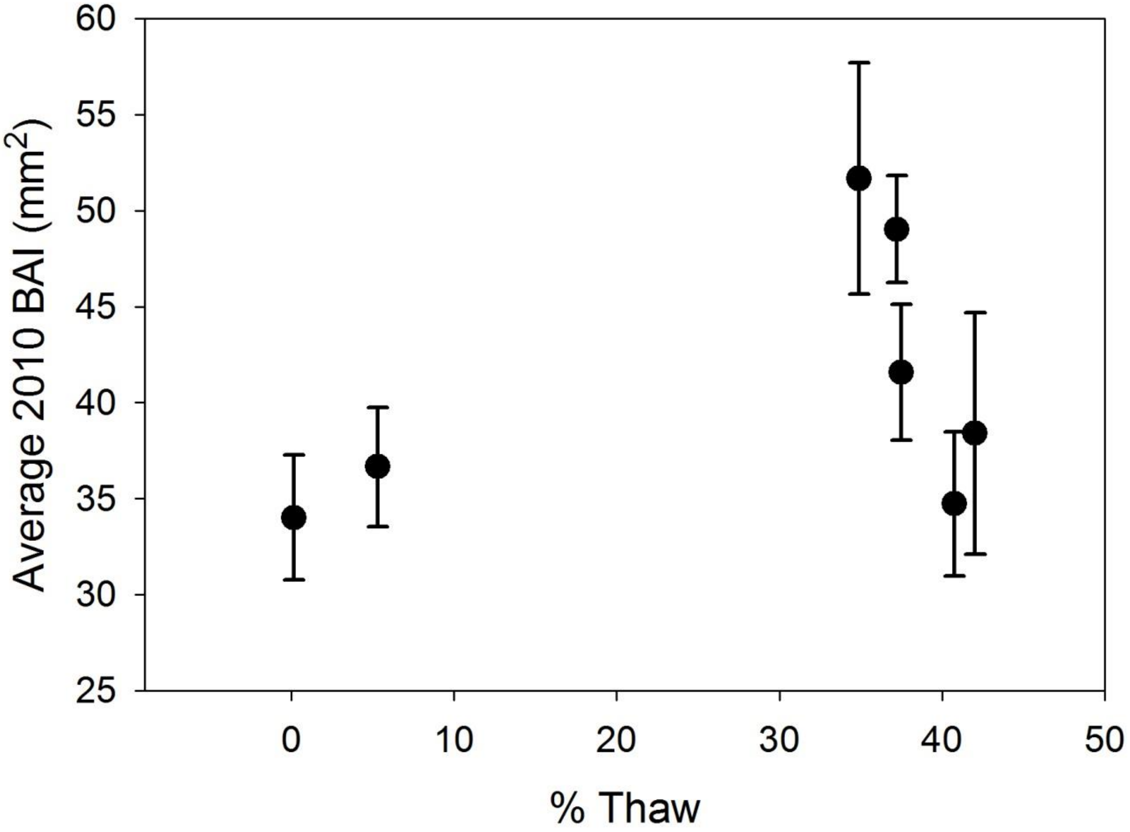

Fig. 2.8. Relationship between the thaw rate of stands (calculated as % lateral permafrost thaw between 1977 and 2010) and averaged 2010 total basal area increment (BAI) for individuals at each site ($F_{1,5} = 2.372$, $p = 0.184$, Adjusted $R^2 = 0.186$). Error bars represent the standard error of average 2010 BAI of all trees at each site.

2.10. Supplementary Information

Text S2.1. Climate Data Infilling

Total monthly precipitation and total monthly snowfall were not available for four of the 984 months (i.e. 0.4% of time periods) during the period of study (May 1934, May 1935, October 1979, November 1979). Because of the rarity of these events we simply gap-filled these four missing data points by averaging the observations for the precipitation in the year before and after the missing value. This step was necessary to create a complete set of annual precipitation measurements as required for further analysis.

Text S2.2. CMI Calculations

Climate-Moisture Index (CMI) is a metric of drought stress potential of a system. This is a variation of the Penman-Monteith Equation, and was originally described by Hogg (1997). Below are the equations for calculating monthly CMI. Annual CMI is then calculated by taking the sum of the monthly moisture indices.

$$CMI = Precipitation - Potential\ Evapotranspiration$$

Potential evapotranspiration (PET) is calculated through the following equations, where VPD is the vapour pressure deficit (measured in kPa), K_t is a cold temperature modifier.

$$PET = 93 \times VPD \times K_t \times e^{\left(\frac{elevation}{9300}\right)}$$

Where VPD is the vapour pressure deficit (measured in kPa), calculated as:

$$VPD = 0.5 \times (e_{Tmax} + e_{Tmin}) - e_{Tdew}$$

Where e_{Tmax}, e_{Tmin}, and e_{Tdew} are the vapour pressures at given temperatures:

$$e_{Tmax} = 0.61078 \times e^{\left(\frac{17.269 \times T_{max}}{273.3 + T_{max}}\right)}$$

$$e_{Tmin} = 0.61078 \times e^{\left(\frac{17.269 \times T_{min}}{273.3 + T_{min}}\right)}$$

$$e_{Tdew} = 0.61078 \times e^{\left[\frac{17.269 \times (T_{min} - 2.5)}{273.3 + (T_{min} - 2.5)}\right]}$$

And K_t is a cold temperature modifier (described in Hogg *et al.* 2013):

$$K_t = MAX\left[MIN\left(\frac{T_{mean} + 5}{15}, 1\right), 0\right]$$

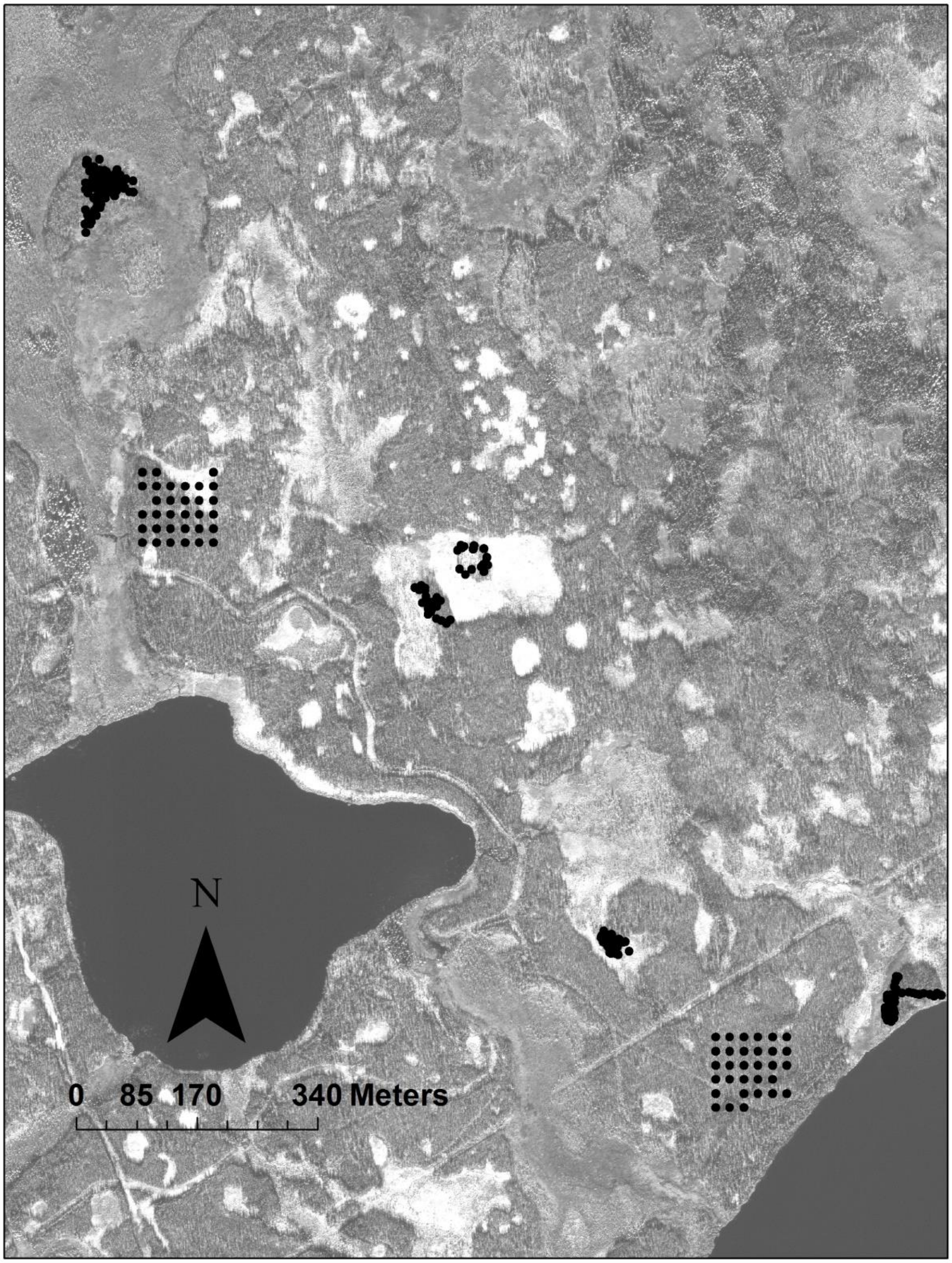

Fig. S2.1. Locations of stands sampled and tree locations (shown by black dots) across the landscape. Background imagery from Worldview2 (Digital Globe Corp – acquired by Dr. W. Quinton).

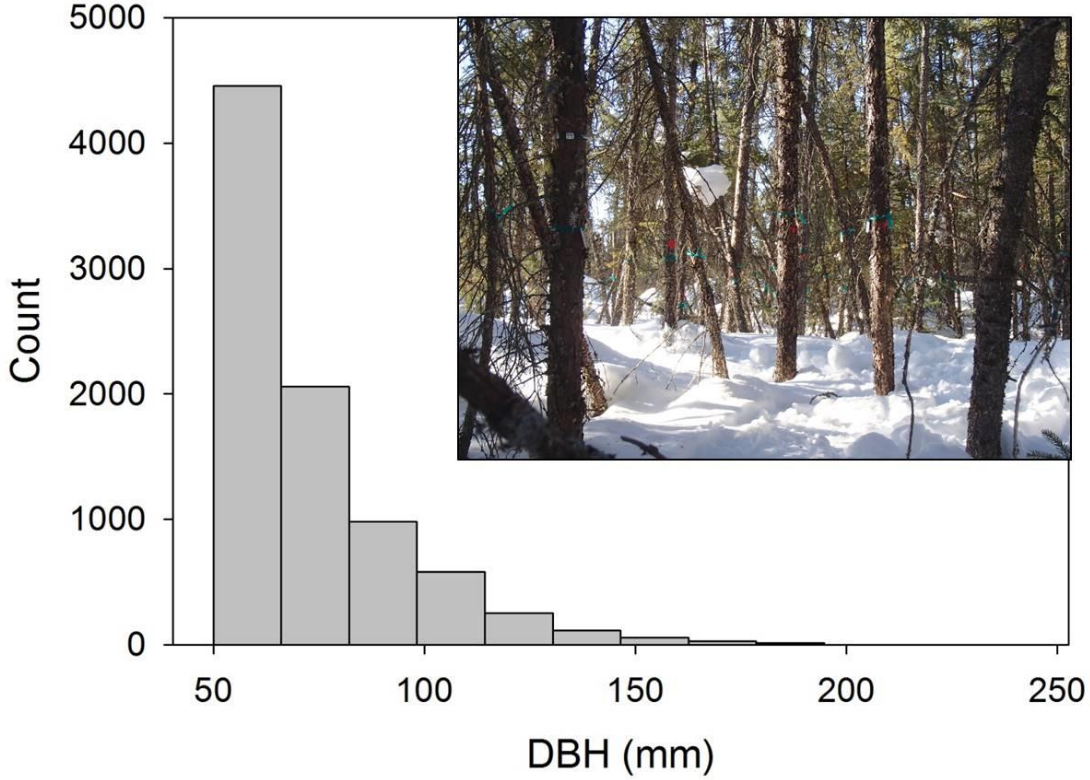

Fig. S2.2. Histogram showing the size distribution of black spruce trees from plots nearby (<1 km) our sampling stands. Trees 7 cm DBH and above comprise nearly half of the total black spruce at this site. Photo inset depicts the relatively uniform size of trees found in most areas at Scotty Creek.

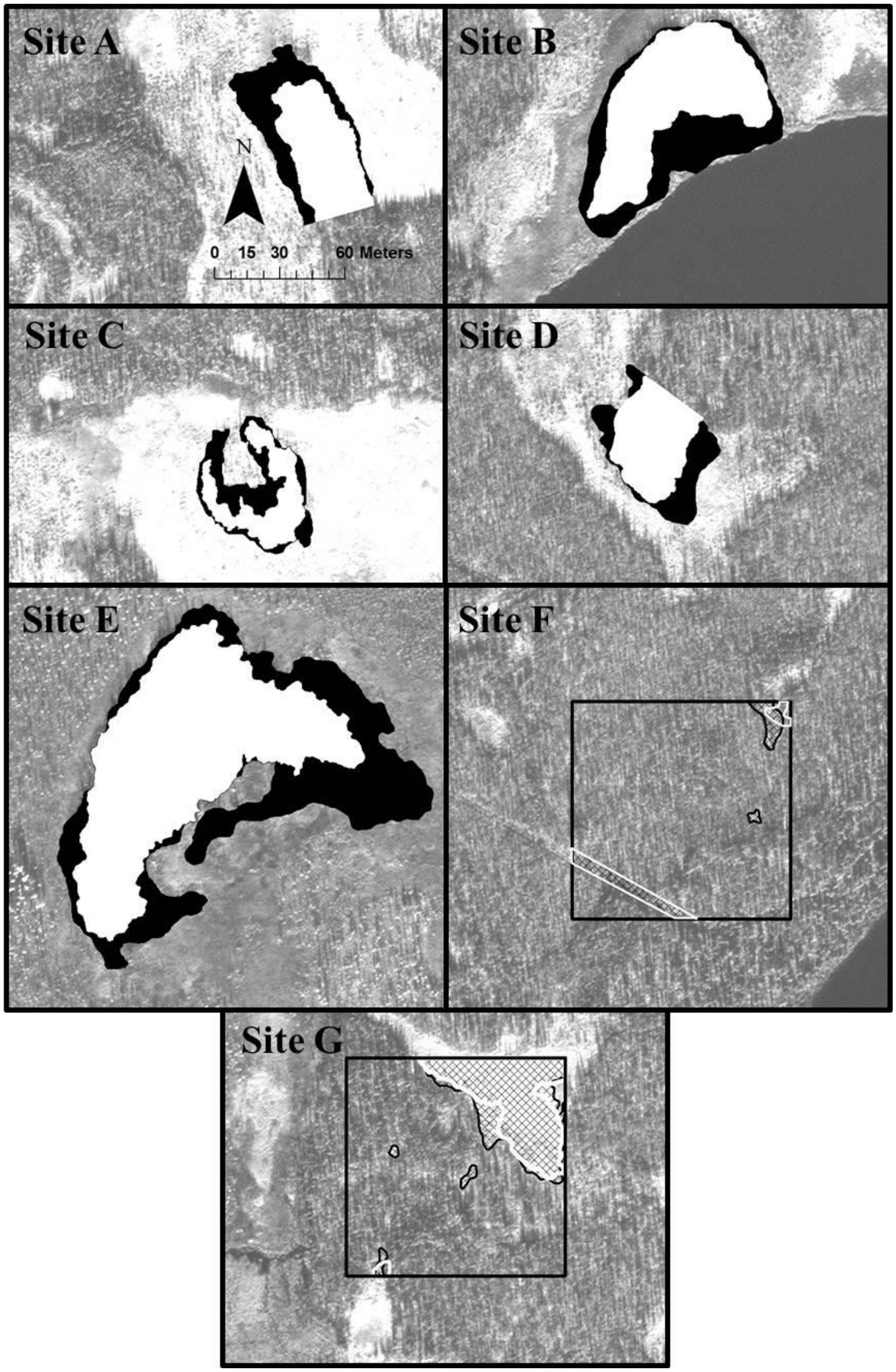

Fig. S2.3. Comparison of permafrost extent at each site between 1977 (black) and 2010 (white). For sites F and G, cross-hatched areas outlined in black represent permafrost-free areas in 2010, while white outlines show 1977 extent. Background imagery from Worldview2 (Digital Globe Corp – acquired by Dr. W. Quinton). Scale bar in the Site A panel applies to all panels.

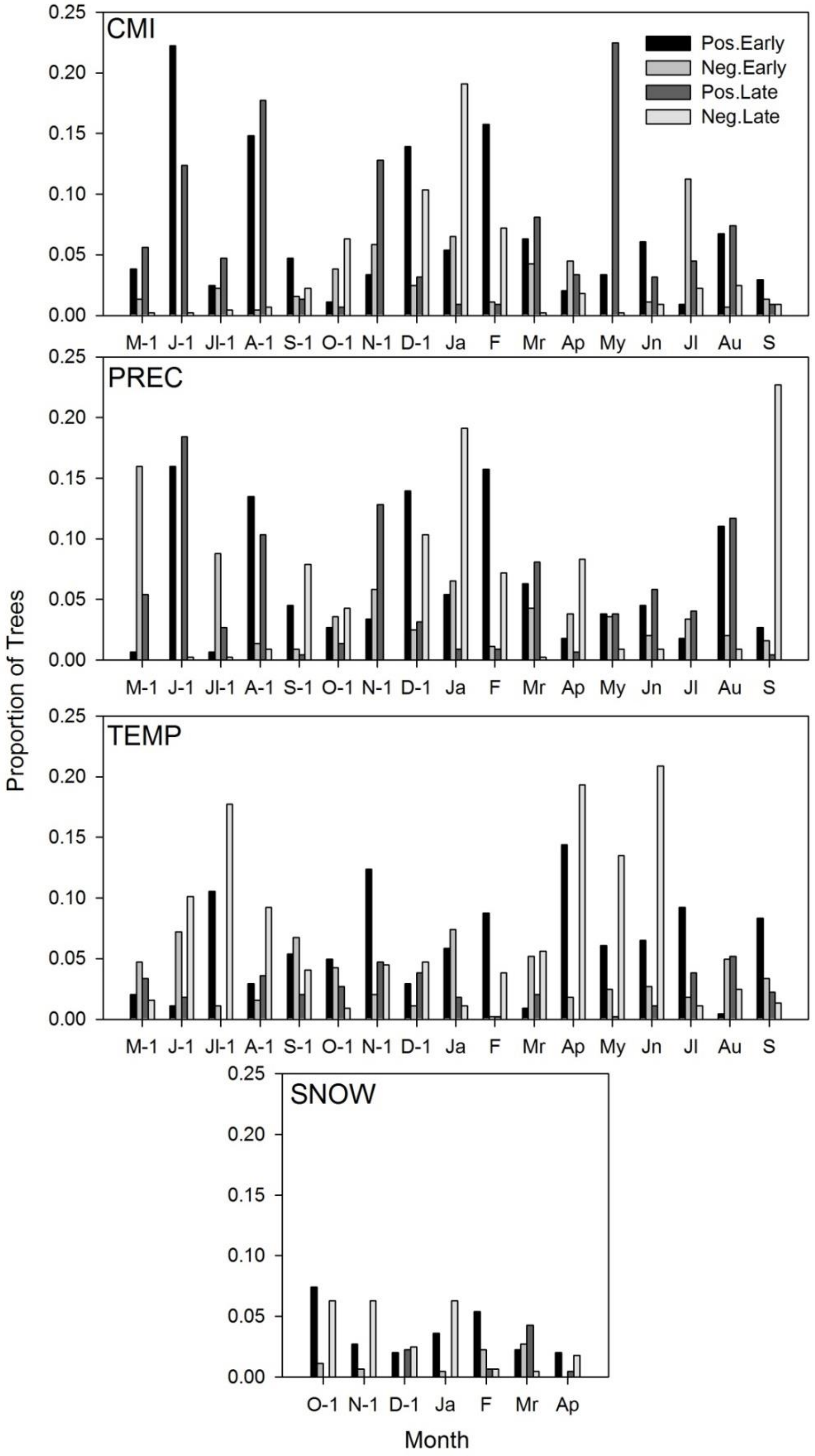

Fig. S2.4: Monthly climate-growth correlations from March (year n-1) to September (year n).

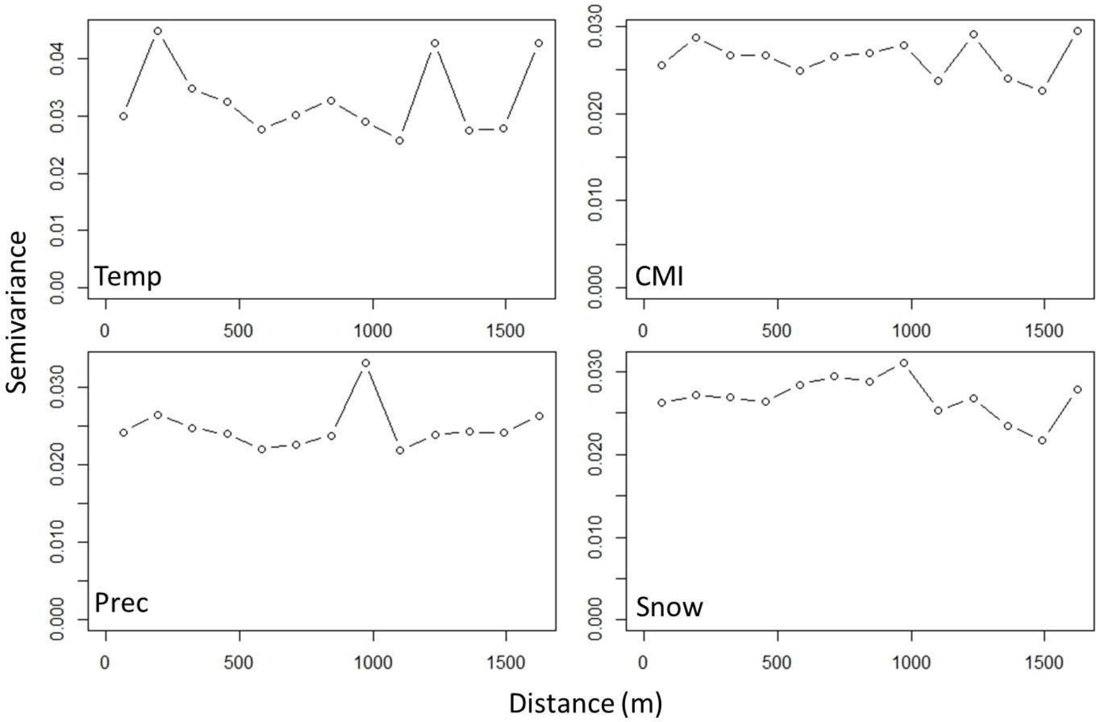

Fig. S2.5: Semivariogram of autocorrelation of climate-growth correlations between all trees across the site. Semivariance does not increase as distance increases, indicating that autocorrelation is no different at the site level than stand level.

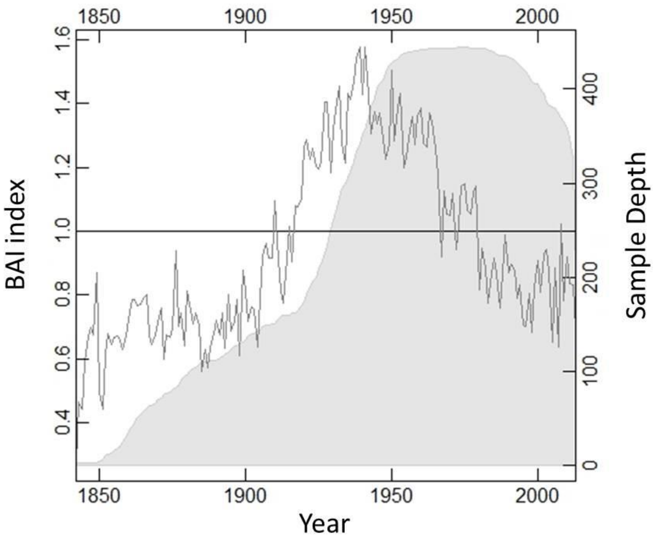

Fig. S2.6. Sample depth and basal area increment index (C-BAI) of the entire chronology from Scotty Creek. Graph produced in R using the package dplR.

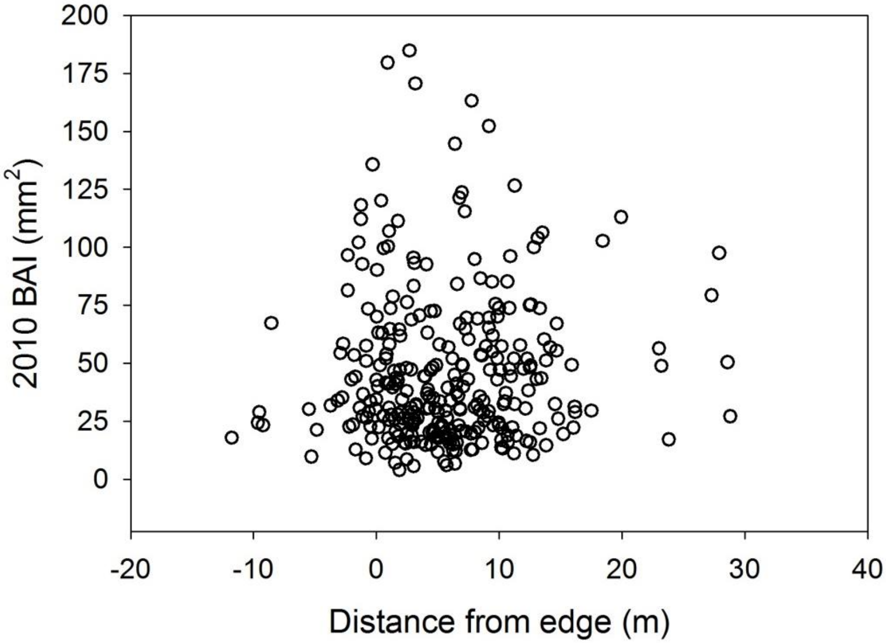

Fig. S2.7. Graph showing the relationship between the distance from each tree to the nearest wetland interface and 2010 basal area increment (BAI). Negative distances indicate that the tree was in the wetland ($F_{1,293} = 0.966$, p-value = 0.326, $R^2 = 0.0033$).

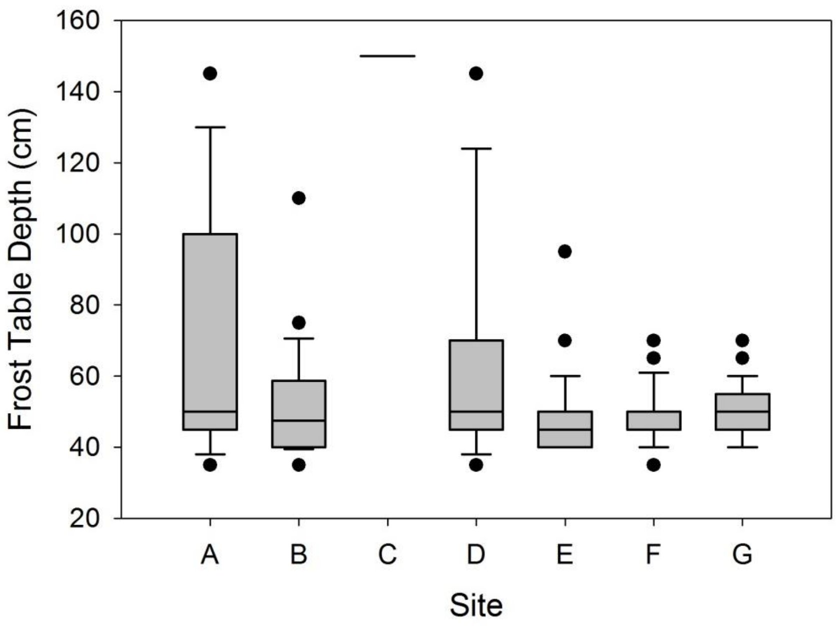

Fig. S2.8. End of summer frost table depth across the permafrost plateaus supporting the forest stands sampled from. For sites A – E, frost table depth was taken every 5 meters along a north-south and east-west transect intersecting the plateau. For site F and G, frost table depth was taken at each grid point. Site C was heavily degraded and the frost table depth was greater than the 1.5 meter frost probe. All measurements were taken in August 2013.

Table S2.1. Metadata of all stands sampled.

Site	# trees sampled	2010 area (m^2)	1977 area (m^2)	Coordinates
A	23	1742	2941	10V 591003 6798343 (centre)
B	64	3415	5462	10V 591657 6797784 (NE corner)
C	18	1077	1858	10V 591062 6798393 (centre)
D	45	1520	2335	10V 591260 6797852 (centre)
E	136	8039	12805	10V 590512 6798931 (centre west)
F	32	7806	8244	10V 590595 6798421 (SW corner)
G	32	9594	9608	10V 590595 6798421 (NW corner)

Table S2.2. Slopes from data presented in Fig. 4 to demonstrate the trends in the four curves presented. The 1950 – present slopes shown for comparisons between different time scales only; this time period is not used for analysis within the manuscript.

Response	**Pre – 1970**	**1950 – present**	**1970 – present**
All	0.007819966***	-0.01052296***	-0.006040324**
Increasing BAI	0.006190456***	0.003108285*	0.01478587***
Decreasing BAI	0.007646777***	-0.01674502***	-0.01532175***
Neutral	0.007912767***	-0.006172605***	-5.62086e-05 (n.s.)

***$p<0.0001$ **$p<0.001$ *$p<0.05$

Data Set S2.1. Individual tree metadata. Trees with IDs beginning with SCF and SCG do not have exact coordinates (the coordinates in grey are the location of the closest grid point). Those with no “Grouping” listed were sampled nearest a grid point that could have resulted in the tree being sampled on either the edge or interior, therefore these trees were not included in any analyses where landscape position was considered. Excel file available online at: http://onlinelibrary.wiley.com/doi/10.1002/2016JG003528/full

Chapter 3: Black spruce growth dynamics in northwestern Canada: contrasting trends and climatic drivers from treeline to treeline

Anastasia E. Sniderhan, Steven D. Mamet, Jennifer L. Baltzer

In preparation for Global Change Biology.

Author roles: JB and AS developed the ideas for the project. AS and SM collected and processed the samples. AS performed the analysis and wrote the manuscript. SM provided advisement and code for statistical analysis procedures. JB and SM provided direction and editorial support throughout the analysis and writing process.

3.1. Abstract

To determine the spatial and temporal variability in black spruce (*Picea mariana*) growth dynamics in northwestern Canada, we sampled tree rings from four sites spanning 15° of latitude – effectively encompassing the latitudinal extent of this widespread, dominant boreal tree. We investigated (1) the differences in growth patterns and magnitude of growth between sites, (2) the main climatic drivers of growth and how they change over time, and (3) trends in water use efficiency (WUE) among the sites (as indicated through stable carbon isotope compositions). In this study, we found that all sites showed a positive growth trend over time except the mid-latitude site, which demonstrated a decline in annual growth. Interestingly, while the magnitude of growth at our treeline site was, as expected, the lowest of all sites, our timberline site located only 50 km to the south of treeline achieved some of the highest annual growth increments in our study. The climatic drivers of these growth patterns varied among sites; the strongest growth responses at the northerly sites were with climatic variables which contributed to warmer, longer growing seasons, while growth at the southern sites was driven by climate conditions influencing

drought stress of the trees. This was supported by carbon isotope compositions indicating increased WUE at the southern sites, with no significant trend at the northern sites. The results of this study suggest that continued warming will increase productivity of trees at the northern extent of black spruce, but southerly areas may begin to experience drought stress if precipitation does not continue to balance the increasing evapotranspirative demands from warming.

3.2. Introduction

Anthropogenic climate forcing due to increased atmospheric CO_2 and other greenhouse gases has resulted in an unprecedented rate of warming, with particularly rapid increases in temperature occurring since the mid-1900s (Hartmann *et al.*, 2013). Although climate warming is a global phenomenon, northwestern North America has experienced some of the largest increases in temperature worldwide (Hartmann *et al.*, 2013). A large part of this region is the boreal forest - one of the largest biomes in the world and a key player in global carbon budgets and energy balance (Bonan & Shugart, 1989; Denman *et al.*, 2007; Ciais *et al.*, 2013; Kurz *et al.*, 2013).

Climate is a major driver of the productivity of boreal forests - an area characterized by short growing seasons, harsh winters, and generally low nutrient availability due to the cold, wet soils (Bonan & Van Cleve, 1992). Thus, warming can elicit considerable changes in the growth dynamics of trees in the boreal region. Warmer temperatures can promote greater soil microbial activity and nutrient mineralization (Bonan & Shugart, 1989; Bonan *et al.*, 1990), while earlier snowmelt contributes to earlier warming of the soils and consequently a longer growing season (Vaganov *et al.*, 1999). However, climate-induced changes in growth dynamics are not uniform across the broad boreal forest.

At the northern limits of the boreal forest, increased growing season temperatures and earlier snowmelt have both been shown to enhance growth of conifers globally (Siberian taiga: Vaganov *et al.* 1999; Kirdyanov *et al.* 2003; Lloyd *et al.* 2011; Fennoscandia: Mäkinen *et al.*, 2002; North American boreal: Hofgaard *et al.*, 1999; Girard *et al.*, 2011). Conversely, there have been reports of forests at latitudinal treelines in North America experiencing decreased growth as a result of temperature-induced drought stress (Lloyd & Fastie, 2002; Wilmking *et al.*, 2004). At the southern margins of the boreal forest, results from many studies have reported increased sensitivity to precipitation and/or soil water availability, and widespread negative responses to warming (Dang & Lieffers, 1989; Huang *et al.*, 2010; Girard *et al.*, 2011; Girardin *et al.*, 2015; D'Orangeville *et al.*, 2016) – all of which are indicative of evapotranspirative drought stress as warming occurs without a corresponding increase in precipitation. While drought stress is likely to be temperature-driven in the southern boreal forest, mid-latitude sites in the boreal forest may experience permafrost-driven water stress (Sniderhan & Baltzer, 2016). Where permafrost is discontinuous, warming is driving permafrost thaw and active layer thickening or complete loss of permafrost, both of which have implications for water table positions and soil moisture. These belowground changes have been found to induce drought stress and growth decline in shallow-rooted species such as black spruce that cannot access the deepening water table (Baltzer *et al.*, 2013; Walker & Johnstone, 2014; Sniderhan & Baltzer, 2016) and waterlogging stress in places where thaw leads to subsidence and wetting (Baltzer *et al.* 2014; Patankar *et al.* 2015).

Although correlations between past growth and climatic conditions can be quantified through basic tree-ring measurements, this does not provide mechanistic information about physiological responses of the tree. We can further understand physiological change over time, particularly changes in stomatal conductance and photosynthesis, through the use of stable carbon isotope analysis of tree rings (McCarroll & Loader, 2004). CO_2 molecules containing the ^{12}C isotope are preferentially utilized during photosynthesis, but when stomata are closed, ^{13}C concentrations increase proportionally inside the leaf resulting in increased fixation of ^{13}C (McCarroll & Loader, 2004). Thus, lower values of plant discrimination against ^{13}C (commonly reported as '$\Delta^{13}C$') are associated with two conditions: periods of drought stress, or CO_2 fertilization wherein high levels of atmospheric CO_2 allow for plants to reduce water loss through stomatal closure while maintaining CO_2 uptake (increased water use efficiency (WUE) - Farquhar *et al.*, 1989; Bazzaz, 1990).

For black spruce, (*Picea mariana* [Mill.] B.S.P.), the most widespread and dominant tree species in the boreal forest of North America (Viereck & Johnston, 1990), the effects of climate warming are not uniform across its broad latitudinal range; there is variability in the main climatic drivers of growth and the directionality of responses both locally (Wilmking & Myers-Smith, 2008; Sniderhan & Baltzer, 2016) and at a regional scale (Hofgaard *et al.*, 1999; Huang *et al.*, 2010; D'Orangeville *et al.*, 2016). The majority of studies on black spruce growth dynamics have occurred in eastern Canada, where both climatic drivers and carbon isotope compositions have been investigated across extensive latitudinal gradients (e.g., Hofgaard *et al.*, 1999; Huang *et al.*, 2010; Silva *et al.*, 2010; D'Orangeville *et al.*, 2016; Ols *et al.*, 2016). However, the western boreal forest differs in its warming trends (Chapin *et al.*, 2005; Hartmann *et al.*, 2013), drought potential (D'Orangeville *et al.*, 2016), and edaphic conditions (Brown & Péwé, 1973; Pojar, 1996), making studies of black spruce growth dynamics in this distinct ecosystem to be prudent.

In this study, we sought to address three main questions: (1) What are the differences in growth patterns across the latitudinal extent of black spruce in western Canada? We predict a latitudinal gradient in productivity with greatest productivity in the most southerly sites. (2) What are the main climatic drivers of these differences, and do they change over time? We predict that southerly sites will be precipitation limited whereas northerly sites will be temperature limited. (3) Do trends in carbon isotope signals of water use efficiency (WUE) differ among sites? We predict that more southerly sites will show evidence of physiological drought stress in the tree ring carbon isotope record. To address these questions, we have obtained tree-ring samples from four sites that capture the latitudinal extent of black spruce across 15° of latitude in northwestern Canada (Fig. 3.1) – effectively enabling us to quantify black spruce growth responses from treeline to treeline. This study will greatly enhance our understanding of the potential responses of western Canadian boreal forests to ongoing rapid climate warming, thereby enhancing our predictive capacity for this region.

3.3. Methods

3.3.1. Study Sites

We selected four sites for this study that encompass the latitudinal extent of black spruce forests in western Canada, spanning 2250 km from the southern reaches of the boreal forest in Saskatchewan to the arctic treeline in the Northwest Territories (Fig. 3.1). Southern Old Black Spruce (SOBS) represents the southern boreal forest, a permafrost-free site where black spruce is the dominant tree species with smaller stands of tamarack (*Larix laricina* [du Roi] Koch) and jack pine (*Pinus banksiana* Lamb.) in wet and mesic areas, respectively (Gower *et al.*, 1997). Scotty Creek is our mid-latitude forest site, 50 km south of Fort Simpson, NT. Here, the forest cover is almost exclusively (95%) black spruce (Baltzer, unpublished data). Scotty Creek typifies a discontinuous permafrost peatland, where black spruce forest stands underlain by permafrost are interspersed with permafrost-free wetland features. The northern timberline (continuous forest) black spruce site that we sampled is approximately 20 km south of Inuvik, NT. Permafrost is continuous, and the forests are mixed black spruce and white spruce (*Picea glauca* [Moench.] Voss) stands, with white spruce dominating drier upland sites while black spruce is more common in low-lying, wet soils. We also took black spruce samples from Trail Valley Creek (TVC) – our treeline site. Although Trail Valley is predominantly a shrubby tundra landscape, distinct patches of arborescent and krummholz black spruce and white spruce trees are present.

3.3.2. Sampling and processing

Sampling design varied as a result of the differences between the landscapes, tree density, and opportunistic overlap with other dendroecology projects at some of the sites. At SOBS, black spruce trees were sampled extensively (all stems >1 cm DBH – diameter at breast height, 1.3 m) from three 10 × 10 m plots and two 5 × 5 m plots in 2012, totaling 159 trees. Variable plot sizes were used to achieve similar sample size amongst plots with differing stem densities. However, for this study we only used trees with DBH greater than 5 cm to maintain similar size classes to our other sites, resulting in a total of 121 trees. An additional 38 trees were sampled from two sets of transects in 2015, where a core sample was taken from the nearest tree with DBH greater than 7 cm every 5 m along two parallel 45 m transects, 25 m apart. At Scotty Creek, we sampled mature living and dead trees from seven stands within a 2 km^2 area, taking core samples from trees with greater than 7 cm DBH. Further details of this sampling strategy can be found in Sniderhan & Baltzer (2016). In Inuvik, four stands were sampled within a 7 km^2 area in 2013. At each site, we took core samples from the nearest black spruce (with DBH greater than ~5 cm to ensure we could still take a non-destructive core sample) every 10 m along three parallel 90 meter transects, spaced 25 m apart – a total of 10 trees per transect. Where there were not trees present within a 5 m radius of a sampling point, the transect was extended by an additional 10 m until 10 trees were sampled. Due to the sparse forest cover at TVC, samples were taken arbitrarily across a 4 km^2 area in 2013, wherever arborescent or >4 cm DBH krummholz leaders were found; this provided a representative sample of mature black spruce across this landscape as sampling was nearly exhaustive.

All core samples were taken at breast height using an increment borer where possible, and stem discs when core samples could not be taken. Core samples were mounted to boards and sanded with progressively finer grit sandpaper until all rings were visible. Ring width measurements for samples from TVC, Inuvik, Scotty Creek, and the 2015 SOBS samples were performed using Coorecorder 7.8 and visually cross-dated using CDendro 7.8 (Cybis Elektronik & Data, AB). Ring width measurements from the 2012 SOBS samples were performed using WinDendro (Regent Instruments Inc.). Each chronology was cross-dated statistically using Cofecha (Holmes, 2000); successful cross-dating resulted in chronologies composed of 159 trees at SOBS, 445 trees at Scotty Creek, 119 trees from Inuvik, and 18 trees from TVC. The sample size from TVC is low relative to our other sites because we were limited by the sparse tree cover and few trees large enough to acquire core samples from (we did not want to take disk samples due to the destructive nature of this sampling).

To ensure that the chronologies are representative of the whole population we calculated the expressed population signal (EPS) using dplR (Bunn *et al*, 2014), where a value of 1 would be a perfect representation of the population chronology and 0 would be not at all representative (Cook & Pederson, 2011). All chronologies were above the recommended threshold of 0.85 (Wigley *et al.*, 1984) except for TVC, which had an EPS of 0.80. Given the sampling restrictions at TVC, we believe that this chronology is still a reasonable representation of the population.

Average basal annual area increment (BAI) was calculated for each chronology to provide robust growth records that can be compared among sites. The raw ring widths were converted to BAI using the package dplR (Bunn *et al*, 2014). In order to perform climate-growth correlations, we also produced ring-width index (RWI) chronologies by detrending with a flexible smoothing spline with a frequency of 0.5 and a wavelength of 0.67 x n years in the package dplR (Bunn *et al*, 2014).

A subset of cores from each site was used for $\delta^{13}C$ analysis: six cores from each of the three southernmost sites, and three cores from TVC due to the low sample size overall. Despite being a small proportion of the overall number of samples taken, this subset of three to six of trees from each site has been shown to be effective at representing the stand-level isotopic variation (Livingston & Spittlehouse, 1993; Silva *et al.*, 2009; Bégin *et al.*, 2015). All trees selected were required to encompass the entire period of 1947-2006 to correspond with the period of complete climate data availability. Due to the extremely narrow ring widths of many of the black spruce sampled, we were unable to acquire enough material for isotopic analysis at an annual resolution. Instead, we sectioned five-year blocks over the 1947-2006 period, and homogenized approximately 1 mg of whole wood from these sections into fine particles using a razor blade (Brienen *et al.*, 2011). Although alpha-cellulose wood is traditionally used in isotopic analysis of wood samples, several studies have shown that there are not significant differences in the carbon isotope composition of different wood components in various tree species (Leavitt & Long, 1982; Loader *et al.*, 2003; Harlow *et al.*, 2006) including black spruce (Walker *et al.*, 2015). The samples were weighed, placed in tin capsules and sent to the University of California, Davis Stable Isotope Facility (UC-Davis SIF) for analysis. The ratio of $^{13}C/^{12}C$ was determined using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Results are reported using a δ-notation in units per mil (‰) relative to the Vienna PeeDee Belemnite standard, and the results from this method at the UC-Davis SIF have a standard deviation of 0.2‰.

To correct for the effect of changing atmospheric $\delta^{13}C$ that the trees were exposed to over time, we calculated $\Delta^{13}C$ (discrimination in the plant against ^{13}C) as

$$\Delta^{13}C = \frac{\delta^{13}C_a - \delta^{13}C_p}{1 - \frac{\delta^{13}C_p}{1000}} \qquad (1)$$

where $\delta^{13}C_a$ is the carbon isotope ratio of the air (from McCarroll & Loader, 2004) and $\delta^{13}C_p$ is the carbon isotope ratio of the plant. To account for the changes in plant physiology as atmospheric CO_2 increases, we provide a further correction to these raw $\Delta^{13}C$ values (herein referred to as $\Delta^{13}C_{raw}$) as described by Schubert and Jahren (2012):

$$\Delta^{13}C_{corr} = \Delta^{13}C_{raw} - \left\{\frac{[(A)(B)(pCO_{2(t)}+C)]}{[A+(B)(pCO_{2(t)}+C)]} - \frac{[(A)(B)(pCO_{2\,(t=0)}+C)]}{[A+(B)(pCO_{2\,(t=0)}+C)]}\right\} \qquad (2)$$

where A = 28.26, B = 0.22, and C = 23.9 are constants described in Schubert & Jahren (2015), $pCO_{2(t=0)}$ is the pre-industrial atmospheric CO_2 level (285 ppm), and $pCO_{2(t)}$ is the average atmospheric CO_2 concentration for each time period (from McCarroll & Loader, 2004).

3.3.3. Statistical analysis

All statistical analyses were performed in R version 3.3.1 (R Core Development Team 2016). We compared the magnitude of growth between sites using a linear mixed effects model in the package "lme4" (Bates *et al.* 2015). An interaction between site and year was included as the fixed effect, BAI as the response variable (log-transformed), and individual as the random effect. To determine the growth trend over time, we used a Mann-Kendall trend test of the average annual BAI at each site using the package "Kendall" (McLeod 2011). Trends in $\Delta^{13}C_{corr}$ over time were also determined using a Mann-Kendall trend test. Pearson's Product-Moment Correlation was used to test the association between $\Delta^{13}C_{corr}$ and BAI (averaged to correspond with the same five-year blocks over the 1947-2006 period used for $\Delta^{13}C_{corr}$ analysis).

To determine the key climatic drivers of growth patterns (RWI; ring width indices), we first assessed correlations between seasonal temperature and precipitation with the ring width RWI from each individual tree series that had a complete growth records over the time frame analyzed (1945 – 2006). Seasons were defined as summer (June – August), fall (September – October), Winter (November – March), and Spring (April – May) which are typical season definitions in northern dendroecological studies (Lloyd *et al.*, 2013; D'Orangeville *et al.*, 2016). These correlations were performed for each season from summer of the previous year (year n-1) to summer of the current growing season (year n), for an early (1945 – 1975) and late (1976 – 2006) time period. The start of the late time period corresponds with the mid-1970 inflection points in the rate of warming and growth change (Fig. 3.2, 3.3). Performing correlations with previous year growing season conditions is important because black spruce is a determinate species, so optimal conditions for bud formation in the previous growing season result in enhanced growth in the following year due to greater production of new foliage (Jacoby & D'Arrigo, 1989). All temperature data were acquired online from the Environment Canada Climate Weather Archives (Environment Canada – www.climate.weather.gc.ca) and precipitation data from Environment Canada's Second Generation Adjusted Precipitation Data (Mekis & Vincent, 2011; stations used shown in Table S3.1).

We used hierarchical cluster analysis (HCA) and redundancy analysis (RDA) in the package "vegan" (Oksanen *et al.* 2016) to determine significant climatic drivers of growth within each site, in both early (1945 – 1975) and late (1976 – 2006) periods. The HCA was used to group trees within each site that exhibit similar responses based on their seasonal climate-growth correlations using Euclidean distances and Ward's linkage method (dendrograms shown in Fig. S3.1). We determined the optimal number of clusters within each site by selecting the highest Mantel correlation coefficient (correlation between the original distance matrix and binary matrices representing different possible partitions of clustering; Borcard *et al.* 2011). This approach for selecting clusters thus resulted in variability in the optimal number of clusters for each site. We then employed RDA, which uses multivariate multiple linear regression to determine which combinations of the predictor variables best explain the response variables (Borcard *et al.* 2011). The RWIs of individuals within each group were incorporated into the RDA as response variables, while the seasonal climate variables used in the original climate-growth correlations were tested as the explanatory variables. Using forward-step model selection, the RDA identified the primary climatic drivers of growth for each group. We then performed traditional climate-growth correlations between RWI chronologies created for each group and the climate variables that were identified as significant climatic drivers of growth.

3.4. Results

We found that the magnitude of growth differed considerably among the four study populations, particularly in the late time period (Fig. 3.3a-d, Table 3.1). As expected, the northernmost site, TVC, had the lowest annual BAI. Surprisingly, trees in Inuvik had some of the largest average annual growth in the late 1900s and early 2000s relative to all other sites studied, which was not apparent in the early time period. Growth rates were moderate at SOBS and Scotty Creek, while TVC had the lowest annual growth increments in both early and late time periods.

Scotty Creek had a negative growth trend over time (Fig. 3.3b; $\tau = -0.588$, $p < 0.001$). All other sites demonstrated a significant positive growth trend, which is most apparent after 1975 (Fig. 3.3a,c-d; SOBS: $\tau = 0.373$, $p < 0.01$; INVK: $\tau = 0.250$, $p < 0.01$; TVC: $\tau = 0.387$, $p < 0.001$). There was less variability in the isotopic trends among sites. Scotty Creek and SOBS had significant negative trends in $\Delta^{13}C_{corr}$ over time (Fig. 3.3ef; SOBS: $\tau = -0.788$, $p < 0.001$; SC: $\tau = -0.606$, $p=0.007$), while Inuvik and TVC sites did not exhibit a significant trend (Fig. 3.3gh; INVK: $\tau = -0.394$, $p = 0.086$; TVC: $\tau = -0.273$, $p = 0.244$). Within SOBS, there was a significant negative correlation between $\Delta^{13}C_{corr}$ and BAI (Fig. 3.4a; $r = -0.588$, $p = 0.044$), while SC demonstrated a positive correlation (Fig. 3.4b; $r = 0.630$, $p = 0.028$). Neither INVK nor TVC exhibited a significant trend in the relationship between $\Delta^{13}C_{corr}$ and BAI (Fig. 3.4cd; INVK: $r = -0.446$, $p > 0.10$; TVC: $r = -0.363$, $p > 0.20$).

The climatic drivers of growth varied among sites mostly as we expected based on their latitudinal positions (Table 3.2). At the southernmost site (SOBS), we found that a large proportion of the trees demonstrated a positive response to greater spring precipitation during the early period. In the late period, the entirety of trees sampled at SOBS became climate insensitive. At Scotty Creek, during the late period, many of the trees began responding positively to high summer precipitation (both current and previous growing season) and negatively to previous growing season summer temperatures.

The suite of climatic drivers at the two northernmost sites contrast sharply with climatic drivers in either of the more southern sites. In the early period, growth of Inuvik trees was positively related to warmer wintertime temperatures, in addition to positive responses to greater spring precipitation and negative responses to warmer summertime temperatures in the previous growing season. In the late period, there was a large increase in climate insensitive individuals at the Inuvik site, while many trees maintain the positive growth response to warming winter temperatures. Additionally, some Inuvik trees exhibit a positive growth response to spring temperature coupled with a trend toward negative responses to winter precipitation. During the early period, the majority of trees at TVC were climate insensitive, with a few trees showing positive growth responses to winter temperature and summer temperature in the previous growing season, and negative responses to increased winter precipitation. In the late period, growth of trees at TVC was driven by either years of low winter precipitation or warm summer temperatures.

3.5. Discussion

In this study we found that there were different growth patterns across the latitudinal extent of black spruce forests in western Canada. Our investigation of the drivers of these growth patterns revealed that there were considerable differences in the suite of significant climate variables among the sites, which largely aligned with our predictions; growth patterns at Scotty Creek was most strongly related to climatic conditions that would ameliorate permafrost-driven drought stress at Scotty Creek (e.g., Walker & Johnstone, 2014; Sniderhan & Baltzer, 2016), while growth at the northern sites was driven by climate variables which contributed to the development of longer, warmer growing seasons. Climatic drivers of growth at SOBS did not follow our predictions; rather than demonstrating an increased positive correlation to greater precipitation, we instead observed an increase in climate insensitivity. Our predictions about how the isotopic trends would differ among sites were supported: there was a significant negative trend in $\Delta^{13}C_{corr}$ over time at SOBS and Scotty Creek indicating decreased discrimination against ^{13}C and increased stomatal closure of the plant, while Inuvik and TVC did not exhibit significant trends.

Although our prediction that the northernmost site, TVC, would have the lowest annual BAI values relative to other sites was supported, we were surprised to find that overall annual growth was quite comparable among the other three sites. In fact, average annual BAI was greater in Inuvik during the late 20th and early 21st century than the peak growth of any other site (Fig. 3.3). This trend does not seem to be out of the ordinary for black spruce; Silva *et al.* (2010) compared annual average BAI of black spruce across a 9° latitudinal gradient in Ontario, and though there were trends in the growth patterns over time, there was no apparent latitudinal trend in the magnitude of growth among the sites. Due to the generally cold, nutrient-poor organic soils on which black spruce establishes, productivity of this species is constrained by nutrient availability (Van Cleve *et al.*, 1983; Viereck *et al.*, 1983). This would indicate that nutrient availability may be quite variable among our sites. Indeed, we do find that the depth of organic soil is variable among our sites, with the shallowest average organic layer at the Inuvik sites (Fig. S3.2), which also had the highest annual BAI (Fig. 3.3).

While the magnitude of growth at most sites may be driven by nutrient availability, the growth trends that we see within each site are driven by different suites of climate variables. In addition, the climatic drivers at each site are not necessarily consistent drivers of growth over time. At SOBS, we found that trees had significant positive growth-climate relationships with spring precipitation during the early period. In the late time period, climate sensitivity decreased and we found that neither temperature nor precipitation were a significant driver of growth. This result was surprising, as we expected growth to become increasingly limited by precipitation as warming continued, in order to meet the increasing evapotranspirative demand. However, we do find that despite warming temperatures and relatively stable levels of precipitation, the climate moisture index for this site is increasing in this area (Fig. S3.2) – an indication that there are lower occurrences of climate-driven drought stress. The reduction in drought conditions is likely contributing to the increase in annual growth of SOBS trees (Fig. 3.3).

Consistent with previous work (Sniderhan & Baltzer, 2016), recent climate-growth relationships at Scotty Creek suggest that summer drought stress is occurring at this site. Here trees have become sensitive to precipitation in the late time period, but we see that both temperature and precipitation are increasing over time (Fig. 3.2), which makes it unlikely that recent trends toward drought stress are directly driven by climate – especially given that the climate-moisture index (the difference between precipitation and potential evapotranspiration) does not suggest that the system is becoming more moisture-limited over time (Fig. S3.2; Sniderhan & Baltzer, 2016). Since summer precipitation has a positive influence on the growth of many trees and summer temperature in the previous growing season elicits a negative growth response, we believe that drought stress is occurring but driven by changing permafrost conditions. Over the course of the summer, the water table in permafrost peatland landscapes gets deeper due to seasonal thaw; specifically, the water table follows the frost table. Years of high summer precipitation contribute to enhanced moisture in the upper profile of the soil and elevation of the water table which is perched on the impenetrable frost table (Quinton & Baltzer, 2013). Similarly, high temperatures in the previous summer growing season contribute to drying surface soils, a more rapidly thickening active layer, and consequently a deeper water table and earlier drying of surface soils. Black spruce have very shallow rooting systems (Gale & Grigal, 1987), which makes them particularly sensitive to drought stress when the surface soils are dry as they access water from such shallow depths (Patankar *et al.*, 2015; Warren, 2015). The determinate nature of black spruce growth (wherein previous year carbon gains have major impacts on current growth) causes these drought stressed conditions in the previous growing season to influence current year growth.

At the Inuvik site, the warming temperatures are benefitting the trees in two ways – first, by creating a longer, warmer growing season which ameliorates conditions for growth in this cold limited part of the species' range, but also indirectly through the deeper thaw and warmer soils, which have been shown to increase nutrient mineralization (Bonan & Shugart, 1989; Bonan *et al.*, 1990). Although this may be occurring at Scotty Creek, the negative effects of the deeper water table (as described above) appear to be outweighing such benefits. At both Inuvik and TVC, there are many trees exhibiting negative responses to increased winter precipitation. This trend is common for trees at their northern range margins; Vaganov *et al.* (1999) found that conifers in the forest-tundra zone across the Siberian subarctic showed strong negative growth responses to snow accumulation. Timing of snowmelt is a major constraint on growth at the northern forest limits due to the already limited growing season. High snow accumulation leads to later snowmelt and later initiation of ground thaw with negative impacts on growth (Kirdyanov *et al.* 2003); we suggest that similar processes are at play in Inuvik and TVC.

We found that while Scotty Creek and TVC both moved towards a lower proportion of climate-insensitive trees in the late (1976 – 2006) period, Inuvik (as well as SOBS, discussed above) showed a large increase in trees that did not have significant climatic drivers (Table 3.2). The decrease in climate sensitivity at this site is likely as a result of capturing a period wherein the trees are experiencing a shift in their growth-limiting factor (D'Arrigo *et al.*, 2007). At Scotty Creek, the shift toward greater climate sensitivity that we have observed is likely driven by warming causing a transition from fairly optimal climatic conditions to a threshold at which the trees are more sensitive to water balance (Wilmking *et al.*, 2005).

Our isotopic data supports our climate-growth analyses results. There was no significant trend in $\Delta^{13}C_{corr}$ at TVC and Inuvik (Fig. 3.4), which means that the trees have not significantly changed their patterns in stomatal conductance through time. At the two southerly sites, $\Delta^{13}C_{corr}$ has shown a significant decrease over time. At Scotty Creek, the decrease in $\Delta^{13}C_{corr}$ corresponds with decreasing BAI over time (Fig. 3.4). This relationship provides further evidence that growth trends at this site are driven by drought stress; increased occurrences of water stress are causing stomatal closure, and that this is driving reduced productivity. However, this is not the case at SOBS. Rather than seeing reduced growth as $\Delta^{13}C_{corr}$ declines, productivity at SOBS is increasing over time (Fig. 3.4) which is evidence that there may be CO_2 fertilization occurring at this site (Silva & Anand, 2013) – especially since drought conditions are becoming less frequent at this site (Fig. S3.2). At SOBS, we expect that the effect of CO_2 fertilization is more likely to decline if temperatures continue to increase and induce evapotranspirative drought stress – a scenario that models have predicted for much of the boreal region (Girardin *et al.*, 2015).

The variability in growth trends and climatic responses that we have found in this study correspond with the diversity of climate-growth relationships that have been found in other studies of black spruce. Similar to our findings at Scotty Creek, warm, dry summer temperatures are often detrimental to growth of black spruce, both in eastern and western Canada (Dang & Lieffers, 1989; Girardin & Tardif, 2005; Lloyd & Bunn, 2007; Drobyshev *et al.*, 2013; Walker & Johnstone, 2014). In addition, research across the boreal region confirms that climate insensitivity is also not an uncommon dendroclimatic response of black spruce, both at mid-latitude sites (Lloyd *et al.*, 2005; Lloyd & Bunn, 2007; Wilmking & Myers-Smith, 2008) and even at range margins (Dufour-Tremblay *et al.*, 2012; Mamet & Kershaw, 2013). Climate insensitivity of trees is attributed to a greater importance of other influences of growth, such as disturbance, competition, topography, and edaphic conditions (Wilmking & Myers-Smith, 2008; Mamet & Kershaw, 2013).

Other studies have also found that factors that contribute to an earlier start to the growing season, such as reduced snow accumulation and warm winter and spring conditions, can contribute to increased growth in black spruce (Hofgaard *et al.*, 1999; Huang *et al.*, 2010; Drobyshev *et al.*, 2013). However, unlike in our study, these examples of sites with sensitivity to snow and spring temperatures are not restricted to the northern margins of the species' extent. Interestingly, the sensitivity of trees at SOBS to spring moisture conditions (as seen in the early time period) has not been demonstrated in other studies of black spruce, although increased precipitation over summer months has been show to positively influence growth in many sites across the boreal region (Dang & Lieffers, 1989; Brooks *et al.*, 1998; Hofgaard *et al.*, 1999; Drobyshev *et al.*, 2013). Conversely, sites in Quebec have shown a negative growth response to increased precipitation (D'Orangeville *et al.*, 2016), where both too much precipitation and effect of light limitation due to overcast conditions may be driving this negative response (e.g., Bergeron *et al.*, 2007).

In this study, we identified non-uniformity in the growth dynamics of black spruce across its latitudinal extent in western Canada, an area in which growth dynamics of black spruce has not been widely studied despite the extreme nature of warming that has occurred. We coupled traditional tree-ring studies with carbon isotope analysis across 15 degrees of latitude to link physiological mechanisms with growth responses, allowing us to identify both drought stress and possibly carbon fertilization signals at sites within this study. From the results of our study, it is clear that there are challenges to making generalizations about the growth dynamics across the widespread range of black spruce. Not only is there variability across the species' latitudinal extent and differences in growth responses to changing climate between our study in western Canada and previous work across latitudinal gradients in eastern Canada, there is also variability in growth responses within sites. Although there are inherent difficulties in increasing the spatial resolution of sampling in the expansive and largely remote areas of the western boreal forest, using remote-sensing techniques to identify areas with high potential for variability in local growth responses will aid in targeting sites that may not be well-represented by large-scale generalizations. Making such efforts to increase the resolution of studies of black spruce growth dynamics in the expansive western boreal region of Canada, where warming is expected to continue at a rapid rate, is integral to anticipate the effects of these changes on not just black spruce, but the flora, fauna, and communities treeline to treeline that rely on its resources.

3.6. References

Baltzer J, Patankar R, Downey A, Quinton W (2013) Impacts of seasonal thaw and permafrost degradation on *Picea mariana* root function in a subarctic boreal peatland. In: *Acta Horticulturae*, pp. 141–148.

Baltzer JL, Veness T, Chasmer LE, Sniderhan AE, Quinton WL (2014) Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. *Global Change Biology,* 20, 824–834.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bazzaz FA (1990) The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology and Systematics*, 21, 167–196.

Bégin C, Gingras M, Savard MM, Marion J, Nicault A, Bégin Y (2015) Assessing tree-ring carbon and oxygen stable isotopes for climate reconstruction in the Canadian northeastern boreal forest. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 423, 91–101.

Bergeron O, Margolis HA, Black TA, Coursolle C, Dunn AL, Barr AG, Wofsy SC (2007) Comparison of carbon dioxide fluxes over three boreal black spruce forests in Canada. *Global Change Biology,* 13, 89–107.

Bonan GB, Van Cleve K (1992) Soil temperature, nitrogen mineralization, and carbon source-sink relationships in boreal forests. *Canadian Journal of Forest Research,* 22, 629–639.

Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, 20, 1–28.

Bonan GB, Shugart HH, Urban DL (1990) The sensitivity of some high-latitude boreal forests to climatic parameters. *Climatic Change*, 16, 9–29.

Borcard D, Gillet F, Legendre P (2011) *Numerical Ecology with R*. New York, NY: Springer New York.

Brienen RJW, Wanek W, Hietz P (2011) Stable carbon isotopes in tree rings indicate improved water use efficiency and drought responses of a tropical dry forest tree species. *Trees*, 25, 103–113.

Brooks JR, Flanagan LB, Ehleringer JR (1998) Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. *Canadian Journal of Forest Research*, 28, 524–533.

Brown RJE, Péwé TL (1973) Distribution of permafrost in North America and its relationship to the environment: a review, 1963 - 1973. In: *Permafrost: Proceedings of the Second International Conference (North American Contribution),* pp. 71–100. National Academy of Sciences, Washington, DC.

Bunn A, Korpela M, Biondi F, Campelo F, Mérian P, Qeadan F, Zang C (2014) dplR: Dendrochronology Program Library in R. R package version 1.6.4. https://CRAN.R-project.org/package=dplR

Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, Canadell J, Chhabra A, DeFries R, Galloway J, Heimann M, Jones C, Le Quéré C, Myneni RB, Piao S, Thornton P (2013) Carbon and Other Biogeochemical Cycles. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate*

Change. (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), pp. 465–570. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Chapin FS, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping C-L, Tape KD, Thompson CDC, Walker DA, Welker JM (2005) Role of land-surface changes in arctic summer warming. *Science* (New York, N.Y.), 310, 657–60.

Cook ER, Pederson N (2011) Uncertainty, Emergence, and Statistics in Dendrochronology. In: *Dendroclimatology, Developments in Paleoenvironmental Research*, Vol. 11 (eds Hughes MK, Swetnam TW, Diaz HF), pp. 77–112. Springer Netherlands, Dordrecht.

D’Arrigo R, Wilson R, Liepert B, Cherubini P (2007) On the “Divergence Problem” in Northern Forests: A review of the tree-ring evidence and possible causes. *Global and Planetary Change*, 60, 289–305.

D’Orangeville L, Duchesne L, Houle D, Kneeshaw D, Côté B, Pederson N (2016) Northeastern North America as a potential refugium for boreal forests in a warming climate. *Science*, 352, 1452–1455.

Dang QL, Lieffers VJ (1989) Climate and annual ring growth of black spruce in some Alberta peatlands. *Canadian Journal of Botany*, 67, 1885–1889.

Denman K, Brasseur G, Chidthiasong A, Ciais P, Cox PM, Dickinson RE, Hauglustaine D, Heinze C, Holland E, Jacob D, Lohmann U, Ramachandran S, da Silva Dias PL, Wofsy SC, Zhang X (2007) Couplings Between Changes in the Climate System and Biogeochemistry. In:

Climate Change 2007: The Physical Science Basis (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt K, Tignor M, Miller H), pp. 499–587. Cambridge University Press, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Drobyshev I, Gewehr S, Berninger F, Bergeron Y (2013) Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change (ed McGlone M). *Journal of Ecology*, 101, 231–242.

Dufour-Tremblay G, Lévesque E, Boudreau S (2012) Dynamics at the treeline: differential responses of *Picea mariana* and *Larix laricina* to climate change in eastern subarctic Québec. *Environmental Research Letters*, 7, 44038.

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 503–537.

Gale MR, Grigal DF (1987) Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research*, 17, 829–834.

Girard F, Payette S, Gagnon R (2011) Dendroecological analysis of black spruce in lichen—spruce woodlands of the closed-crown forest zone in Eastern Canada. *Ecoscience*, 18, 279–294.

Girardin M-P, Tardif J (2005) Sensitivity of tree growth to the atmospheric vertical profile in the Boreal Plain of Manitoba. *Canadian Journal of Forest Research*, 35, 48–64.

Girardin MP, Hogg EH, Bernier PY, Kurz WA, Guo XJ, Cyr G (2015) Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. *Global Change Biology*, 22, 627–643.

Gower ST, Vogel JG, Norman M, Kucharik CJ, Steele SJ (1997) Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *Journal of Geophysical Research*, 102, 29029–29041.

Harlow B, Marshall J, Robinson A (2006) A multi-species comparison of ^{13}C from whole wood, extractive-free wood and holocellulose. *Tree Physiology*, 26, 767–774.

Hartmann DL, Klein Tank AMG, Rusticucci M, Alexander LV, Brönnimann S, Charabi Y, Dentener FJ, Dlugokencky EJ, Easterling DR, Kaplan A, Soden BJ, Thorne PW, Wild M, Zhai PM (2013) Observations: Atmosphere and Surface. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Hofgaard A, Tardif J, Bergeron Y (1999) Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. *Canadian Journal of Forest Research*, 29, 1333–1346.

Hogg EH (1997) Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology*, 84, 115–122.

Holmes RL (2000) The Dendrochronological Program Library, Laboratory of Tree-Ring Research, University of Arizona, Tuscan, Arizona, U.S.A.

Huang J, Tardif JC, Bergeron Y, Denneler B, Berninger F, Girardin MP (2010) Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology*, 16, 711–731.

Jacoby GC, D'Arrigo RD (1989) Reconstructed northern hemisphere annual temperature since 1671 based on high-latitude tree-ring data from North America. *Climatic Change*, 14, 39–59.

Kirdyanov A, Hughes M, Vaganov E, Schweingruber F, Silkin P (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees*, 17, 61–69.

Kurz WA, Shaw CH, Boisvenue C, Stinson G, Metsaranta J, Leckie D, Dyk A, Smyth C, Neilson ET (2013) Carbon in Canada's boreal forest — A synthesis. *Environmental Reviews*, 292, 260–292.

Leavitt SW, Long A (1982) Stable carbon isotopes as a potential supplemental tool in dendrochronology. *Tree-Ring Bulletin*, 42, 49–55.

Livingston NJ, Spittlehouse DL (1993) Carbon isotope fractionation in tree rings in relation to the growing season water balance. *Stable isotopes and plant carbon-water relations*, 141–153.

Lloyd AH, Bunn AG (2007) Responses of the circumpolar boreal forest to 20th century climate variability. *Environmental Research Letters*, 2, 45013.

Lloyd AH, Fastie CL (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, 52, 481–509.

Lloyd AH, Wilson AE, Fastie CL, Landis RM (2005) Population dynamics of black spruce and white spruce near the arctic tree line in the southern Brooks Range, Alaska. *Canadian Journal of Forest Research*, 35, 2073–2081.

Lloyd AH, Bunn AG, Berner L (2011) A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Change Biology*, 17, 1935–1945.

Lloyd AH, Duffy PA, Mann DH (2013) Nonlinear responses of white spruce growth to climate variability in interior Alaska. *Canadian Journal of Forest Research*, 43, 331–343.

Loader NJ, Robertson I, McCarroll D (2003) Comparison of stable carbon isotope ratios in the whole wood, cellulose and lignin of oak tree-rings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 196, 395–407.

Mäkinen H, Nöjd P, Kahle H-P, Neumann U, Tveite B, Mielikäinen K, Röhle H, Spiecker H (2002) Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. *Forest Ecology and Management*, 171, 243–259.

Mamet SD, Kershaw GP (2013) Age-dependency, climate, and environmental controls of recent tree growth trends at subarctic and alpine treelines. *Dendrochronologia*, 31, 75–87.

McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. *Quaternary Science Reviews*, 23, 771–801.

McLeod AI (2011) Kendall: Kendall rank correlation and Mann-Kendall trend test. R package version 2.2. https://CRAN.R-project.org/package=Kendall

Mekis É, Vincent LA (2011) An overview of the second generation adjusted daily precipitation dataset for trend analysis in Canada. *Atmosphere-Ocean*, 49, 163–177.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016) vegan: Community Ecology Package. R package version 2.4-0. https://CRAN.R-project.org/package=vegan

Ols C, Hofgaard A, Bergeron Y, Drobyshev I (2016) Previous growing season climate controls the occurrence of black spruce growth anomalies in boreal forests of Eastern Canada. *Canadian Journal of Forest Research*, 705, 1–35.

Patankar R, Quinton WL, Hayashi M, Baltzer JL (2015) Sap flow responses to seasonal thaw and permafrost degradation in a subarctic boreal peatland. *Trees - Structure and Function*, 29, 129–142.

Pojar J (1996) Environment and biogeography of the western boreal forest. *The Forestry Chronicle*, 72, 51–58.

Quinton WL, Baltzer JL (2013) The active-layer hydrology of a peat plateau with thawing permafrost (Scotty Creek, Canada). *Hydrogeology Journal*, 21, 201–220.

Schubert BA, Jahren AH (2012) The effect of atmospheric CO_2 concentration on carbon isotope fractionation in C3 land plants. *Geochimica et Cosmochimica Acta*, 96, 29–43.

Schubert BA, Jahren AH (2015) Global increase in plant carbon isotope fractionation following the last glacial maximum caused by increase in atmospheric pCO_2. *Geology*, 43, 435–438.

Silva LCR, Anand M (2013) Probing for the influence of atmospheric CO_2 and climate change on forest ecosystems across biomes. *Global Ecology and Biogeography*, 22, 83–92.

Silva LCR, Anand M, Oliveira JM, Pillar VD (2009) Past century changes in *Araucaria angustifolia* (Bertol.) Kuntze water use efficiency and growth in forest and grassland ecosystems of southern Brazil: Implications for forest expansion. *Global Change Biology*, 15, 2387–2396.

Silva LCR, Anand M, Leithead MD (2010) Recent widespread tree growth decline despite increasing atmospheric CO_2. *PloS one*, 5, e11543.

Sniderhan AE, Baltzer JL (2016) Growth dynamics of black spruce (*Picea mariana*) in a rapidly thawing discontinuous permafrost peatland. *Journal of Geophysical Research: Biogeosciences*, 121, 2988–3000.

Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, 400, 149–151.

Van Cleve K, Oliver L, Schlentner R, Viereck LA, Dyrness CT (1983) Productivity and nutrient cycling in taiga forest ecosystems. *Canadian Journal of Forest Research*, 13, 747–766.

Viereck LA, Johnston WF (1990) *Picea mariana* (Mill.) B. S. P. Black Spruce. In: *Silvics of North America: vol. 1. Conifers* (eds Burns R, Honkala B), pp. 227–237. USDA Forest Service Agriculture Handbook, Washington, DC.

Viereck LA, Dyrness CT, Van Cleve K, Foote MJ (1983) Vegetation, soils, and forest productivity in selected forest types in interior Alaska. *Canadian Journal of Forest Research*, 13, 703–720.

Walker X, Johnstone JF (2014) Widespread negative correlations between black spruce growth and temperature across topographic moisture gradients in the boreal forest. *Environmental Research Letters*, 9, 64016.

Walker XJ, Mack MC, Johnstone JF (2015) Stable carbon isotope analysis reveals widespread drought stress in boreal black spruce forests. *Global Change Biology*, 21, 3102–3113.

Warren RK (2015) *Examining the spatial distribution of soil moisture and its relationship to vegetation and permafrost dynamics in a subarctic permafrost peatland*. University of Guelph, 53 pp.

Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, 23, 201–213.

Wilmking M, Myers-Smith I (2008) Changing climate sensitivity of black spruce (*Picea mariana* Mill.) in a peatland–forest landscape in Interior Alaska. *Dendrochronologia*, 25, 167–175.

Wilmking M, Juday GP, Barber VA, Zald HSJ (2004) Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology*, 10, 1724–1736.

Wilmking M, D’Arrigo RD, Jacoby GC, Juday GP (2005) Increased temperature sensitivity and divergent growth trends in circumpolar boreal forests. *Geophysical Research Letters,* 32, L15715.

3.7. Tables

Table 3.1. ANOVA table for the linear mixed effects model of black spruce basal area increment (BAI) for individual annual growth from SOBS, SC, INVK, and TVC over time. Individual was included as a random effect. Denominator degrees of freedom was calculated using a Satterthwaite approximation.

	Sum of squares	**Mean squares**	**Numerator DF**	**Denominator DF**	**F-value**	**p-value**
Site	494.3	164.8	3	70028	213.8	<0.0001
Year	3360.2	3360.2	1	75729	6379.6	<0.0001
Site*Year	485.9	162.0	3	73476	307.5	<0.0001

Table 3.2. Results of climate-growth correlations between clusters from each site and climate variables identified as important drivers within each cluster, for both an early (1945 – 1975) and late (1976 – 2006) time period. The "Clust." column lists the cluster from the HCA, and "n" is the number of individuals in that cluster. "Clim. Var." shows the climatic variables identified as important through the RDA; T is average seasonal temperature, P is total seasonal precipitation, and a subscript n-1 indicates a climatic driver from the previous year. Climate n.s. is shown where there were not any significant climatic drivers within the group, indicating climate insensitivity. +/- shows the direction of the correlation. Clusters were created based off of similarities in climate-growth relationships of individual trees.

	EARLY					**LATE**				
Site	**Clust.**	**n**	**Clim. Var.**	**+/-**	**p-value**	**Clust.**	**n**	**Clim. Var.**	**+/-**	**p-value**
SOBS	G1	100	Climate n.s.			G1	159	Climate n.s.		
	G2	57	Spring_P	+	<0.001					
SC	G1	400	Climate n.s.			G1	188	Climate n.s.		
						G2	59	Summer_P_{n-1}	+	0.023
								Summer_P	+	0.017
						G3	133	Summer_T_{n-1}	-	<0.01
INVK	G1	49	Winter_T	+	<0.01	G1	71	Climate n.s.		
	G2	21	Spring_P	+	<0.01	G2	34	Winter_T	+	0.033
			Summer_T_{n-1}	-	<0.01					
						G3	5	Spring_T	+	0.031
								Winter_P	-	0.058
TVC	G1	8	Climate n.s.			G1	11	Summer_T	+	<0.01
	G2	1	Winter_T	+	<0.01	G2	8	Winter_P	-	0.037
			Winter_P	-	0.014					
	G3	2	Summer_T_{n-1}	+	0.044					

3.8. Figures

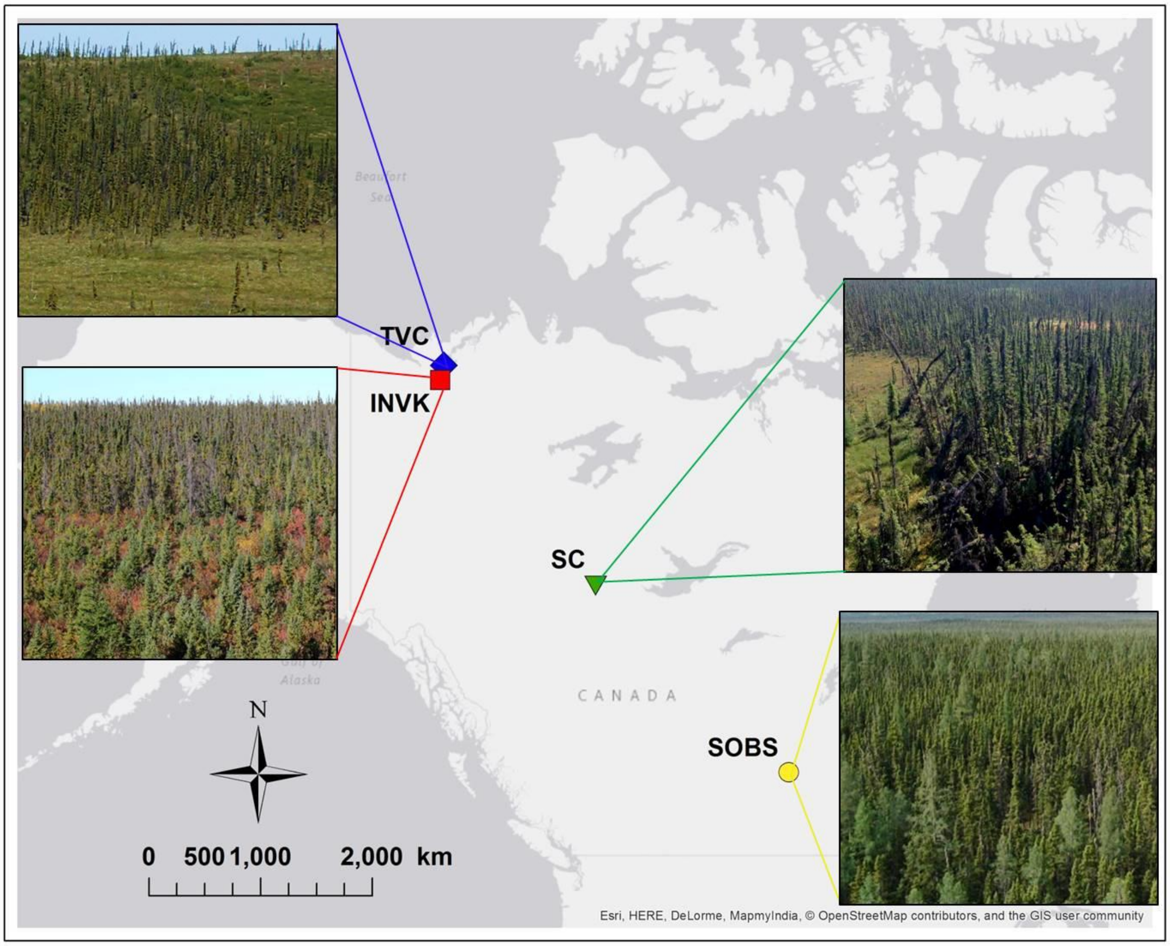

Fig. 3.1. Map showing sampling sites and photographs of each site. SOBS – Southern Old Black Spruce, SK. SC – Scotty Creek, NT. INVK – Inuvik, NT. TVC – Trail Valley Creek, NT. Photos by A. Sniderhan (TVC, INVK, SOBS) and R. Warren (SC). Map image acquired on ArcMap 10.3, ESRI, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors and the GIS user community.

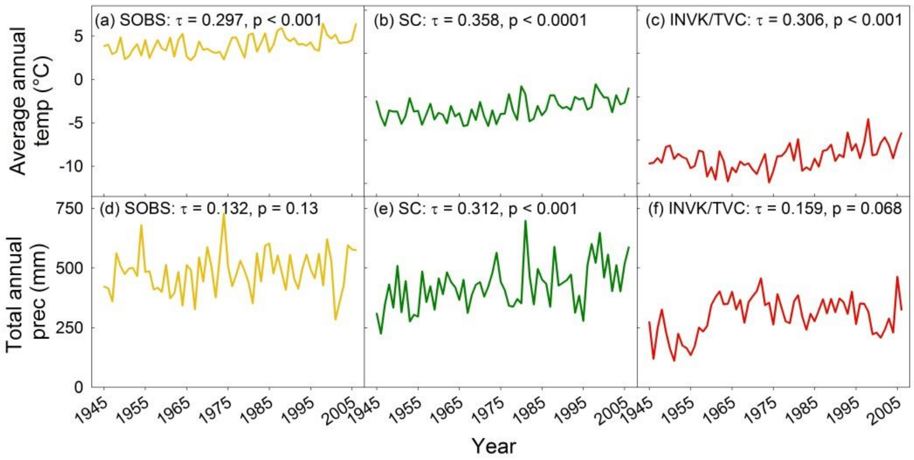

Fig. 3.2. Temperature and precipitation trends over time at nearest weather station to each study site. Southern Old Black Spruce (SOBS) – Prince Albert A Station (53°12'N, 105°40'W); Scotty Creek (SC) – Fort Simpson A Station (61°45'N, 121°14'W); Inuvik (INVK) and Trail Valley Creek (TVC) – Inuvik A Station (68°18'N, 133°28'W) with infilling from the Aklavik A Station (68°13'N, 135°00'W) from 1945 – 1957 prior to the establishment of Inuvik. Temperature and precipitation at these two stations was well correlated from 1957 – 2006 ($R^2 = 0.99$ and $R^2 = 0.39$, respectively). Climate data from Mekis & Vincent (2011) and Environment Canada – www.climate.weather.gc.ca.

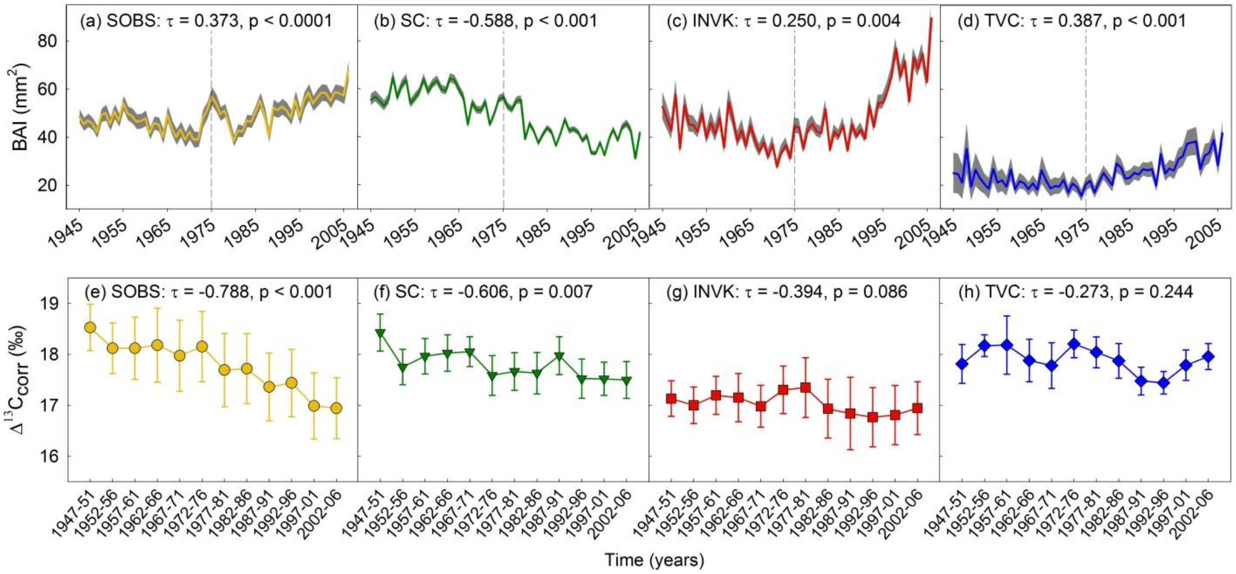

Fig. 3.3. (a-d) Annual average basal area increment (BAI) for all trees sampled at Southern Old Black Spruce (SOBS – n=159), Scotty Creek (SC – n=445), Inuvik (INVK – n=119), and Trail Valley Creek (TVC – n=18) over time. Vertical dashed lines show the transition point from the early (1945 – 1975) to late (1976 – 2006) period. These time periods were selected based off of approximate inflection points in the rate of growth and warming. Grey shading represents the standard error around the mean; (e-h) trends in $\Delta^{13}C_{corr}$ over time for each of the sites mentioned above. $\Delta^{13}C_{corr}$ was analyzed over 5 year blocks, and error bars represent the standard error of the mean for the trees subsampled from each site (n=6 at SOBS, SC, INVK; n=3 at TVC). Results of linear Mann-Kendall trend tests are shown on each panel.

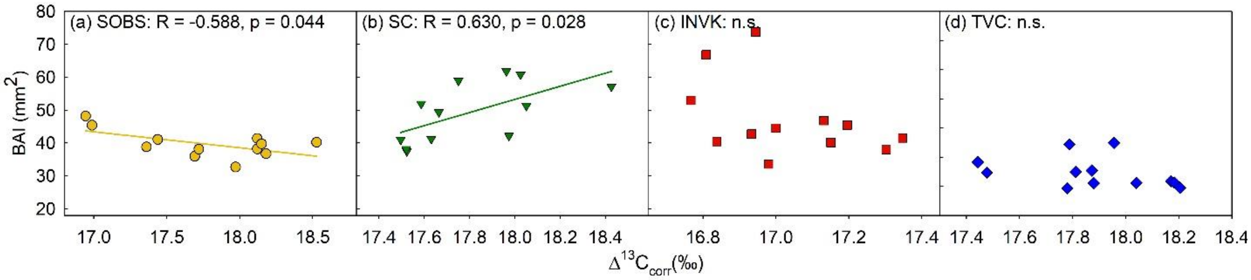

Fig. 3.4. (a-d) Correlations between average BAI and $\Delta^{13}C_{corr}$ for Southern Old Black Spruce (SOBS), Scotty Creek (SC), Inuvik (INVK), and Trail Valley Creek (TVC). BAI was averaged across averaged to correspond with the same five-year blocks over the 1947-2006 period used for $\Delta^{13}C_{corr}$ analysis. Results of significant Pearson Product-Moment Correlation tests are shown on each panel.

3.9. Supplementary Information

Table S3.1: Climate metadata from weather stations used for each site. The same weather station (Inuvik A) was used for both Inuvik and Trail Valley Creek due to their close proximity. The Inuvik station was not established until 1957, so climate data predating this time (and missing data throughout the rest of the series) was infilled directly using data from the Aklavik. The temperature and precipitation data from these stations were strongly correlated over the 1957-2006 time (Pearson's R = 0.99 and 0.63 respectively).

Site	Station Name	Location	Distance from site	MAT 1977-2006 (°C)	MAP 1977-2006 (mm)
SOBS	Prince Albert A	53.22, -105.67	92 km	1.30	492.86
SC	Fort Simpson A	61.8, -121.2	55 km	-2.68	456.11
INVK	Inuvik A	68.3, -133.48	2 km	-8.21	311.98
TVC	Inuvik A	68.3, -133.48	50 km	-8.21	311.98

Text S3.1: Infilling of climate data

Climate data from the Prince Albert and Fort Simpson stations were infilled by averaging the year prior to and after the missing data. The following data were infilled using this method:

Prince Albert: Temperature - March 2004, May 2004

Fort Simpson: Precipitation - October 1979, November 1979

At the Inuvik station, we infilled missing data using additional stations in or around Inuvik. The following data was infilled from the respective stations:

Aklavik: Precipitation – January 1945 to February 1957, June to August 1957, October 1958, June 1995, June 2000, June 2001 to September 2001

Temperature - January 1945 to February 1957, November 1959, July 1995 to December 1996,

Inuvik UA: Precipitation – July 1995 to December 1996, July 1999 to September 1999, May 2000, July 2000 to September 2000, April 2001 to May 2001, May 2002 to September 2002, August 2003

Inuvik Climate: Temperature – January 2006 to December 2006

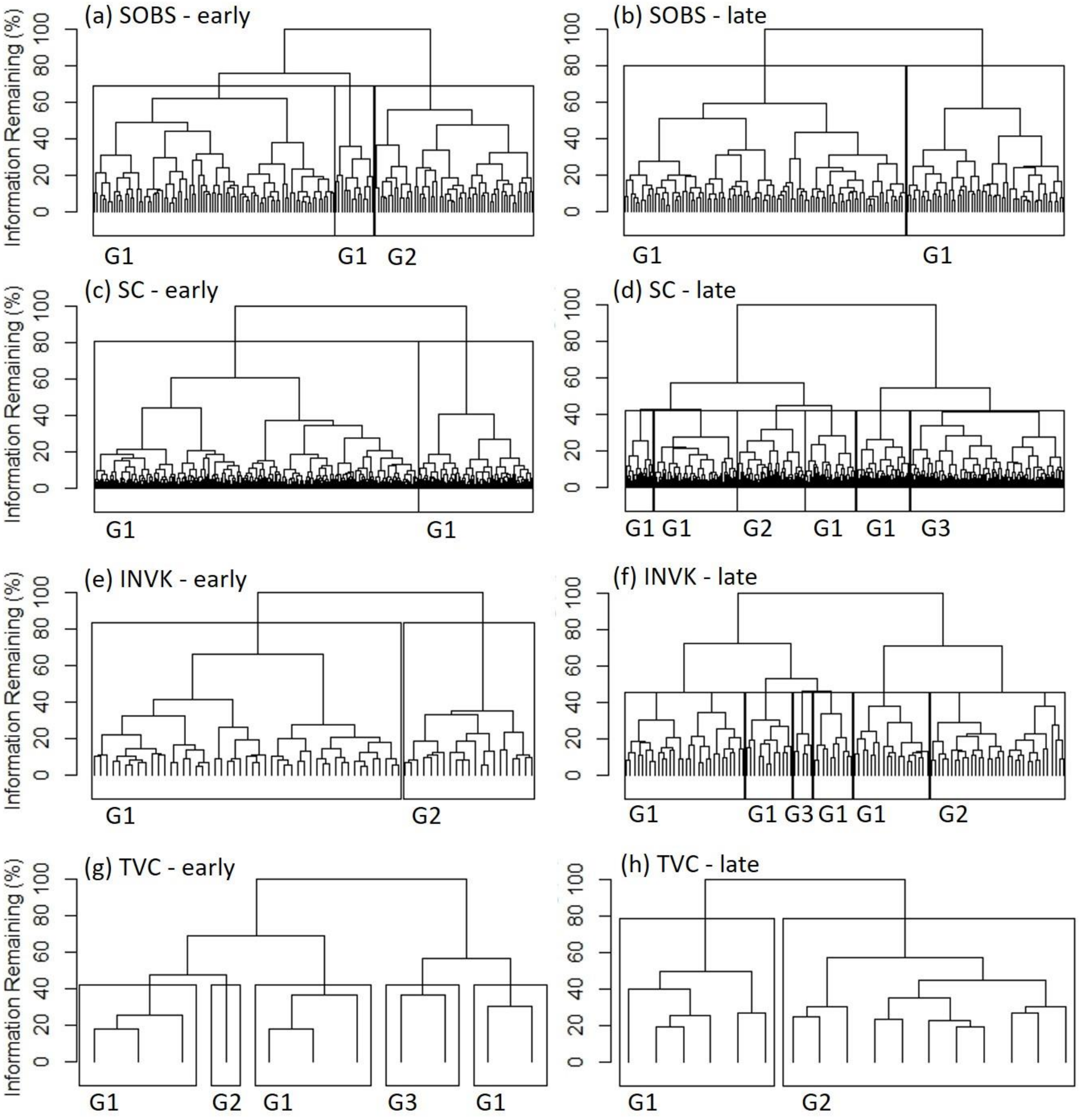

Fig. S3.1: Hierarchical agglomerative cluster analysis (HCA) dendrograms of clusters from each site, for the early (1945 – 1975) and late (1976 – 2006) time periods. Similarities are based off climate-growth correlations of individual trees at each site, calculated using Euclidean distances with Ward's linkage method. The optimal number of clusters within each site was determined by selecting the highest Mantel correlation coefficient (correlation between the original distance matrix and binary matrices representing different possible partitions of clustering; Borcard *et al.*

2011). This approach for selecting clusters thus resulted in variability in the optimal number of clusters for each site. Group labels below each cluster correspond to the results in Table 3.2; all “G1” labels are climate insensitive clusters.

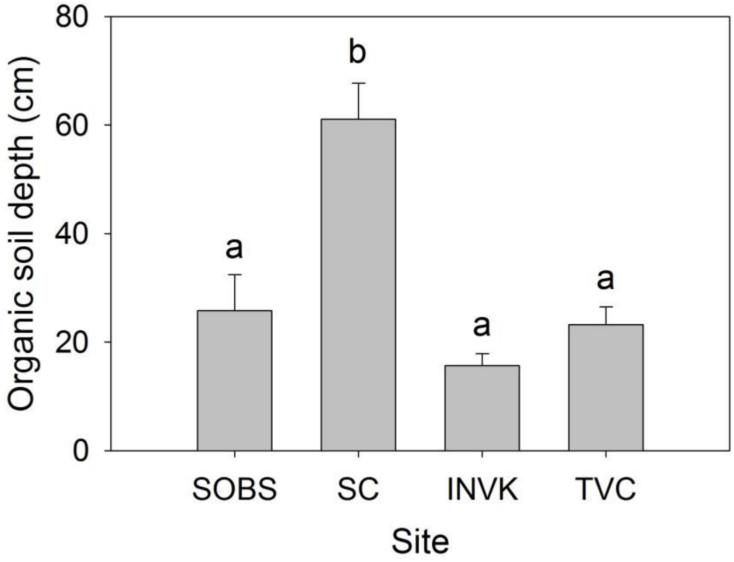

Fig. S3.2: Average depth of organic soil at each of the sites. Depth of organic soil was measured at least once within each stand sampled. SOBS: n = 10, SC: n = 16, INVK: n = 12, TVC: n = 15. Error bars shown represent standard error. Treatments showing significant differences (ANOVA, Tukey HSD, $p<0.05$) are indicated by different letter codes.

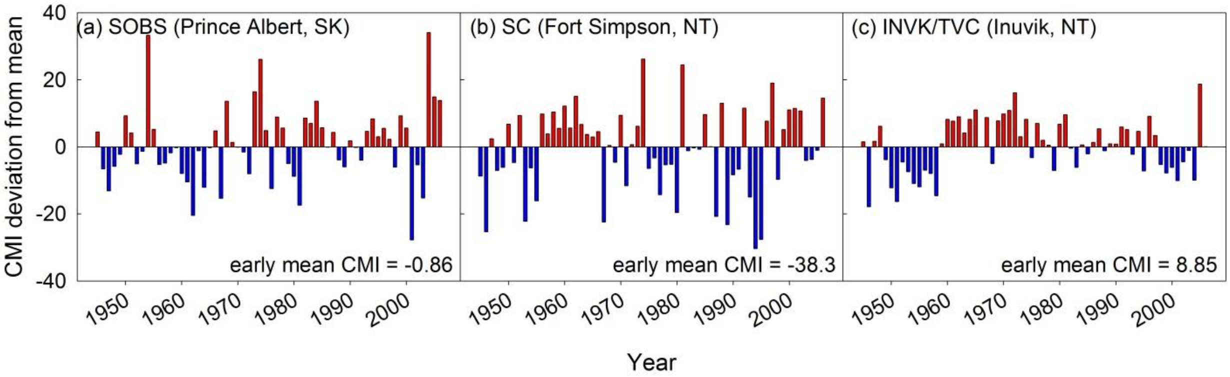

Fig. S3.2: Climate Moisture Index (CMI) trends at each site over time to show drought conditions, calculated as the difference between precipitation and potential evapotranspiration (described in Hogg 1997; Sniderhan and Baltzer 2016). A negative CMI value indicates drought stressed conditions. Shown in the figure are deviations from the mean CMI over the early time period in the study (1945 – 1975). Mann-Kendall trend tests showed no significant change in CMI over time, although there was a notable trend toward higher CMI at SOBS (τ=0.148, p=0.09). Precipitation data acquired from the following stations: Southern Old Black Spruce (SOBS) – Prince Albert A Station (53°12’N, 105°40’W); Scotty Creek (SC) – Fort Simpson A Station (61°45’N, 121°14’W); Inuvik (INVK) and Trail Valley Creek (TVC) – Inuvik A Station (68°18’N, 133°28’W) with infilling from the Aklavik A Station (68°13’N, 135°00’W) from 1945 – 1957 prior to the establishment of Inuvik. Climate provided by Mekis & Vincent (2011) and Environment Canada – www.climate.weather.gc.ca.

Chapter 4: Assessing local adaptation vs. plasticity under different resource conditions in seedlings of a dominant boreal tree species

Anastasia E. Sniderhan, Gordon G. McNickle, Jennifer L. Baltzer

In review at AoB Plants.

Author roles: JB and GM developed the ideas for the project. AS and GM set up the experiment and collected measurements throughout the experimental period. AS performed all data collection at the end of the experiment, performed the analysis, and wrote the manuscript. JB and GM provided direction and editorial support throughout the analysis and writing process.

4.1. Abstract

In order to evaluate local adaptation vs. plasticity in black spruce, seeds from five provenances across the latitudinal extent of the species in northwestern Canada were planted in a common garden study in growth chambers. Two resource conditions were applied (low/high nutrient and ambient/elevated CO_2) in a fully factorial design. Several physiological and allocational traits, growth, and survival were measured over the course of the experiment. We found significant differences in several growth and biomass traits among populations (e.g., height, root length, leaf biomass), with southern populations producing the largest seedlings. However, we did not detect significant differences among nutrient or CO_2 treatments in any traits measured, and there were not population-level differences in physiological traits or allocational patterns. We found that there was greater winter mortality among the high nutrient treatments, which we attributed to a change in growth strategy which delayed hardening of needles before winter. Our study provides important insight into how black spruce might respond to the changing climate conditions predicted in this region.

4.2. Introduction

Recent changes in global climate patterns have led to shifts in modern climate envelopes, that is, the set of climatological characteristics that delineate the extent of a species' range (Walther *et al.*, 2002). These shifts in climate present organisms with a limited set of options: migrate at the same rate as the climate is shifting, adapt to the new conditions through genetic change, or tolerate the new conditions through plasticity in their functional traits (Aitken *et al.*, 2008). Trees are particularly vulnerable to changes in climatic conditions that influence survival and reproduction. Unlike animals which are mobile and able to shift their range quickly to follow their climatic envelopes within a generation, or short-lived plants which may have the capacity to adapt to changing conditions over their short generation times, most trees are long-lived and their migration or genetic adaption may not keep pace with changing climate conditions (Jump & Peñuelas, 2005).

The capacity of individual trees to exhibit trait plasticity (i.e., the ability to express different phenotypes under different environments; e.g., Sultan, 1995) thus becomes an important tool for trees to tolerate environmental variability. As a response to the rapidly changing climate, plasticity is a means of acclimating to the effects of these changes (Sultan, 2000). For example, phenology of several European tree species has tracked warmer spring temperatures, resulting in earlier bud burst events (Menzel *et al.*, 2006). Alternatively, trees with fixed traits that are no longer compatible with current conditions may be simply doomed to mortality (Aitken *et al.*, 2008; Allen *et al.*, 2015). However, the degree of plasticity vs. fixed traits is not necessarily consistent within a given tree species. There have been observations of variability in the presence or degree of trait plasticity among populations (e.g., Benito Garzón *et al.*, 2011). For example, a study on *Pinus sylvestris* demonstrated latitudinal differentiation in plasticity of the timing of growth cessation under variable climate conditions (Savolainen *et al.*, 2004) – likely as a result of the high cost of maintaining plasticity in the face of resource limitations at some sites (DeWitt *et al.*, 1998).

The boreal region of northwestern North America has experienced some of the world's most dramatic changes in climate. Since the late-1800s, the mean annual temperature in this region has increased 1.5 – 3.4°C, and it is predicted to warm an additional 2-4°C by the end of the 21st century (Canadian Centre for Climate Modelling and Analysis, Canadian Global Circulation Model 3 – www. http://climate-modelling.canada.ca). This warming can provide favourable growth conditions for trees through greater plant-available nutrients (due to increased soil microbial activity and in some areas permafrost thaw) as well as increased atmospheric CO_2 concentrations which can provide a fertilization effect (e.g., Bonan & Shugart 1989, Keeling *et al.*, 1996).

Overall in this study, we aim to address one main question: do populations across the extent of black spruce (*Picea mariana* [Mill.] BSP) forests in northwestern Canada exhibit plasticity in key physiological traits and patterns of growth and allocation, are there fixed differences driven by local adaptation at each site, or are all black spruce created equal? To begin to understand the relative importance of local adaptation vs. plasticity in the warming boreal forests of northwestern Canada, we performed a common garden experiment using black spruce seeds from five sites across a 2250 km transect (Fig. 4.1). This transect essentially captures the latitudinal extent of black spruce, the most dominant tree species in northwestern Canada and thus an important subject to study in order to understand widespread boreal forest dynamics. We compared a range of traits (physiological, growth, and allocational) to assess similarities among populations grown under four conditions of resource availability (high/low nutrient and elevated/ambient CO_2 in a factorial design).

We hypothesize that the responses to resource addition will be more pronounced and variable in the southern populations than the northern populations. This follows the basic understanding of plant economics in the trade-offs between productivity and stress tolerance in plants, particularly with respect to "slow" and "fast" trait strategies (Reich, 2014); plants with slow trait strategies maintain low rates of resource acquisition and expenditure, whereas those with fast trait strategies require high rates of resource uptake and use. There is evidence that this fast-slow continuum corresponds with the degree of plasticity that species can maintain; organisms with greater resources show greater plasticity in their traits than resource-limited individuals, which take a slow and steady approach that does not support plasticity. This is pattern is seen in studies along elevational gradients that have found that plasticity of some tree seedlings is lower at higher altitudes (e.g., Green, 2005; Vitasse *et al.*, 2013).

For the northern trees in our study, which must withstand very harsh conditions at the extreme limit of the species, we expect a slow trait strategy. A fast trait strategy would be maladaptive in these resource poor environments, as pulses of high resource availability are likely short-lived making strong responses to changing conditions a risky approach (e.g., DeWitt *et al.*, 1998). We expect greater plasticity to variable resource conditions from southern populations coming from more productive, lower latitude environments than northern populations within the four experimental treatments. In addition, we hypothesize that southern populations will exhibit higher physiological rates and thus greater growth (e.g., biomass production, height growth) than northern populations under the ideal conditions of a controlled growth chamber experiment. We anticipate that enhanced access to a given resource will amplify these differences through strategic shifts in biomass allocation and changes in physiological rates (e.g., Oleksyn *et al.*, 1998; Green, 2005).

4.3. Methods

4.3.1. Germination and Planting

Black spruce seed was acquired from five locations across the latitudinal extent of the species in western Canada (Fig. 4.1). The 14-month long experiment began in July 2014. After a period of cold stratification, the non-viable seeds were removed by performing a float in 70% ethanol, which also served to surface-sterilize the seeds. Seeds were then plated by population in 60 x 15 mm petri dishes of 1% agar and 0.2 g L^{-1} of liquid fertilizer (Miracle-Gro 24-8-16 Water Soluble All Purpose Plant Food, Miracle-Gro Lawn Products, Inc., Marysville, Ohio, USA), with approximately 20 seeds per plate. The plated seeds were maintained in growth chambers (Bigfoot models LTCB-19 and TPC-19; BioChambers Inc., Winnipeg, Manitoba, Canada) at a 16/8 hour dark/light cycle at 20°C.

After two weeks, 60 germinants each from the Prince Albert, Fort McMurray, and Inuvik populations were individually transplanted into 1L Treepots (5×5×30 cm, Stuewe & Sons, Inc., Tangent, Oregon, USA) containing a mixture of 50% potting soil (0.18-0.1-0.1 Miracle-Gro Moisture Control Potting Mix, Miracle-Gro Lawn Products, Inc., Marysville, Ohio, USA; equivalent to 465.77 g N m^{-2}) and 50% Turface (Turface Athletics MVP, Profile Products LLC, Buffalo Grove, Illinois, USA) with 3 mL of mycorrhizal inoculum (MYKE PRO LANDSCAPE, Premier Tech Ltd., Rivière-du-Loup, Québec, Canada) surrounding the seed to aid in successful establishment of these seedlings (Lamhamedi & Bernier, 1994). Poor germination of the Fort Simpson and Norman Wells populations led to only 24 and 19 germinated seeds being planted, respectively. These populations were excluded from the remainder of the experiment due to insufficient replication.

4.3.2. Experimental Design

Our experiment consisted of four treatments in a fully factorial design: elevated CO_2 (EC), ambient CO_2 (AC), high nutrient (NPK; HN), and low nutrient (LN). Plants with assigned HN treatments were given 3 mL of slow release fertilizer mixed throughout the upper 15 cm of the soil column in the pot (equivalent to an additional 8.57 g N m^{-2} greater than the potting soil; Miracle-Gro Multi-Purpose Shake N Feed 10-10-10, Miracle-Gro Lawn Products, Inc., Marysville, Ohio, USA). The magnitude of fertilizer applied was based on the application instructions for the fertilizer; we were simply interested in increasing resource availability at a moderate rate rather than emulating natural conditions.

4.3.2.1. Growing Conditions

All plants were kept at ambient CO_2 (~400 ppm) for the first four months of the experiment to allow seedlings to establish. At the end of this period, surviving plants were randomly assigned to eight blocks (using a random number generator) within two CO_2 chambers. All AC seedlings were grown in a growth chamber at ambient CO_2 conditions (average 400 ppm), while EC plants were kept in a growth chamber where the CO_2 concentration was maintained at an average of 750 ppm (the projected atmospheric CO_2 concentrations for 2100 in models presented by the IPCC - www.ipcc-data.org/observ/ddc_co2) using Sentinel PPM controller (CPPM-4) and CO_2 regulator (Sentinel Global Product Solutions, Inc., Santa Rosa CA, USA). The CO_2 was scrubbed using a potassium permanganate scrubber as described in Morison & Gifford (1984) to remove any potential organic contaminates such as ethylene that might influence growth. Although we recognize that it is not ideal to restrict all EC plants to one growth chamber while maintaining AC plants in one separate chamber, it is an accepted standard given the logistical constraints of elevating CO_2 in an experimental setting with extensive replication (e.g., Bazzaz *et al.*, 1990; Tjoelker *et al.*, 1998; Way *et al.*, 2010): it simply isn't practical or possible to have each replicate in its own chamber.

Following the seedling establishment period, the elevated CO_2 treatment began and the experiment included a growing season and a dormant period. During the growing season, the growth chambers were kept at a 16 hour light cycle, with 22°C/18°C day/night temperatures. These conditions were maintained for three month blocks before initiating a "winter" cycle, during which temperatures and hours of light were gradually reduced over the course of 17 days to bring the chambers down to 4°C and complete darkness. This 4°C dark period lasted for three weeks, at which point the temperature and light were gradually increased over 17 days back to the conditions of the growing period. These artificial seasonal shifts have been proven successful in black spruce experiments from across latitudinal ranges (Johnsen & Seiler, 1996; Bigras & Bertrand, 2006), and our 38 day period is sufficient to induce dormancy and growth reactivation for boreal trees (Mcleod, 2001); this was confirmed through observing post-winter cycle bud burst of all seedlings. However, the intention was not to emulate a natural cycle. We repeated this every three months, resulting in a total of three growth cycles over the course of the experiment. The growth chamber conditions chosen were not designed to emulate natural environmental conditions, rather they were to provide non-stressful conditions for plant growth. During the growing period, trees were watered twice weekly until water was observed to drain out the bottom of the pots, and 1.5 mL of slow release fertilizer (equivalent to 60 g N m^{-2}; Miracle Gro Multi-Purpose Shake N Feed, 10-10-10) was added to all HN plants after each winter cycle to maintain the high nutrient conditions. We added 0.5 mL of slow release fertilizer (equivalent to 20 g N m^{-2}; Miracle-Gro Multi-Purpose Shake N Feed, 10-10-10) to the LN seedlings after the second winter because we began to notice signs of nutrient limitation.

4.3.2.2. Monthly Measurements

Each month of the growing period, we took measurements of seedling height and visible root length. Height was measured as the distance from the soil surface to the apical shoot tip. Root lengths were measured using by tracing visible roots in 5×15 cm windows cut into the front of each pot (Fig. S4.1). The tracings were scanned and root lengths were measured using IJ_Rhizo (Pierret *et al.*, 2013), an image analysis macro in ImageJ (version 1.50b).

4.3.2.3. Gas Exchange Measurements

At the end of the 14 month experiment, we took a series of gas exchange measurements on four randomly selected seedlings from each population and CO_2 treatment using a LI-6400 XT (LI-COR Environmental, Lincoln NB, USA). We used the lighted conifer chamber when seedlings were large enough for a signal to be detected in this chamber. The seedlings were clamped into the chamber so as to fit as much of the plant from the apical meristem down, on fully expanded leaf tissue. For seedlings too small for the conifer chamber, a 2×3 chamber with a light source was used, placing the plant into the chamber using the same approach as above with all parameters maintained between the two chambers. Light response curves were created by measuring gas exchange (CO_2 assimilation rate - $\mu mol \cdot m^{-2} \cdot s^{-1}$) at increasing light levels (0, 20, 50, 100, 400, 600, 800, 1200, 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) with sufficient time for all readings to stabilize. These measurements were taken at CO_2 concentrations of both 400 ppm and 750 ppm to emulate the CO_2 conditions experienced under the two experimental CO_2 treatments. The gas exchange data were post-corrected for actual fresh leaf area. We fit modified Michaelis-Menten models to the PAR vs. CO_2 assimilation rate data using the following equation:

$$A = \frac{A_{max} \times PAR}{(K_m + PAR)} \qquad (1)$$

Where A is the photosynthetic rate, A_{max} is the maximum photosynthetic rate, PAR is the intensity of photosynthetically active radiation (µmol m^{-2} s^{-1}), and K_m is the Michaelis-Menten constant. These were implemented with the nls() function in R (R Core Team, 2014), which allowed us to solve for the dark respiration rate (R_d - µmol m^{-2} s^{-1}; A where PAR is equal to 0), maximum photosynthetic rate (A_{max}; µmol m^{-2} s^{-1}), and leaf-level light compensation point (LCP - µmol m^{-2} s^{-1}; PAR where A is equal to 0) under both 400 ppm and 750 ppm CO_2 concentration (indicated by subscripts 400 and 750, respectively).

4.3.2.4. Post-Harvest Measurements

After all gas exchange measurements were made, the seedlings were harvested. We measured dry root biomass ($Biomass_{root}$), dry leaf biomass ($Biomass_{leaf}$), dry stem biomass ($Biomass_{stem}$), dry total biomass ($Biomass_{total}$), total root length (TRL; using WinRhizo version 2012b, Regent Instruments Inc., Quebec QC, Canada), and total leaf area (TLA; using WinSeedle version 2004a, Regent Instruments Inc., Quebec QC, Canada). Total root length and total leaf area were measured on fresh tissue. We also investigated allocation patterns in the seedlings by calculating specific leaf area (SLA; fresh leaf area divided by dry leaf mass), specific root length (SRL; fresh root length divided by dry root mass), root/shoot ratio (R:S), root/mass ratio (RMR), leaf/mass ratio (LMR), and stem/mass ratio (SMR). These abbreviations are defined in Table S4.1, for reference throughout the article.

4.3.3. Statistical Analyses

All statistical analyses were performed in R version 3.1.2 (R Core Development Team 2014). Root length and seedling height from treatments over time were compared by fitting generalized linear mixed effect models using lmer() in the package lme4 (Bates *et al.,* 2015), with population, CO_2 treatment, and time as fixed effects, height or root length as the response, and individual nested in block as the random effect term. Plant height and root length were log-transformed in order to meet assumptions of normality, and the data were homoscedastic. The package "lmerTest" (Kuznetsova *et al.,* 2016) was used to calculate Satterthwaite approximations of the denominator degrees of freedom in order to perform analysis of variance (ANOVA), and post-hoc pairwise comparisons were performed where necessary for interpretation using the package "lsmeans" (Lenth, 2016). We explored interaction effects of population, CO_2 treatment, and time in both the height and root length models. Gas exchange and post-harvest measurements were compared using two-way ANOVAs with CO_2 treatment, population, and block as factors. Log-transformations were applied to LCP_{750}, LCP_{400}, $Biomass_{root}$, $Biomass_{leaf}$, $Biomass_{stem}$, $Biomass_{above}$, $Biomass_{total}$, TRL, TLA, and SMR in order to meet assumptions of normality, and data met assumptions of homoscedasticity. Tukey HSD tests were used to test for significant differences between populations and CO_2 treatments.

Due to extensive mortality of the HN seedlings early on in the experiment, this treatment was excluded from all of the above analyses. However, the HN treatment was included in survival analysis of the seedlings. Survival analysis was performed using Kaplan-Meier survival estimates in the "survival" package in R (Therneau, 2015). To determine differences in cumulative survival of each treatment, we implemented a log-rank test using the function survdiff().

4.4. Results

4.4.1. Monthly Measurements

Over the course of the experiment, we found an interaction between population and time, driven by the fact that southern populations grew at a faster rate than northern populations (Fig. 4.2, Table 4.1). Although we found a significant interaction between CO_2 treatment and time in our model, post-hoc testing of EC vs. AC height within each time period did not identify significant contrasts. The patterns we observed reflect the latitudinal gradient captured by the study; the seedlings from Inuvik were consistently the shortest, while tallest seedlings were found in the Prince Albert population (Fig. 4.2a; Table 4.1). In contrast, we found no effect of population or treatment on root length (from our monthly root windows) throughout the experiment – the only significant term in our model was time ($F_{1,225}$=203.34, p<0.0001), which simply demonstrates root growth over time (Fig. 4.2b).

4.4.2. Gas Exchange Measurements

Physiological rates were surprisingly invariable in our study; we found no significant effect of either population or CO_2 treatment on R_d (at 400 ppm or 750 ppm), LCP (at 400 or 750 ppm), or A_{max} (at 400 ppm). However, we found a marginally significant interaction between population and CO_2 treatment on A_{max} at 750 ppm, despite no overall effect of these variables (Fig. 4.3; $F_{2,10}$ = 4.396, p=0.0427). However, post-hoc analysis (Tukey HSD) could not detect significant differences in any of the combinations of CO_2 treatment and population. ANOVA tables are listed in Table S4.2.

4.4.3. Post-Harvest Measurements

There were many population-level differences in the physical traits measured post-harvest, however the CO_2 treatment had no effect on the outcomes of these traits. Leaf area, leaf biomass, and total biomass were significantly greater in the Prince Albert population compared to either Fort McMurray or Inuvik (Fig. 4.4; TLA – $F_{2,20}$ = 13.081, p<0.001; $Biomass_{leaf}$ - $F_{2,20}$ =

11.736, $p<0.001$; $\text{Biomass}_{\text{total}}$ – $F_{2,20} = 10.140$, $p<0.001$). There was a significantly greater total root length, root biomass, and stem biomass in the Prince Albert population compared to the Inuvik population (Fig. 4.4; TRL – $F_{2,20} = 6.622$, $p<0.01$; $\text{Biomass}_{\text{root}}$ – $F_{2,20} = 6.127$, $p<0.01$; $\text{Biomass}_{\text{stem}}$ – $F_{2,20} = 11.574$, $p<0.001$). However, despite these aforementioned population-level differences, we found no treatment effect on SLA, SRL, R:S, RMR, LMR, and SMR (definitions in Table S4.1; Table S4.3, Fig. S4.2; $p>0.05$).

4.4.4. Survival Analysis

We found that there was a significant difference in survival between treatments – HN seedlings had consistently lower survival than their LN counterparts (Fig. 4.5, $X^2= 38.7$, d.f. = 11, p= <0.0001).

4.5. Discussion

The results of this experiment provide support for fixed (non-plastic) growth-related traits among the populations of black spruce studied. There were distinct differences in growth among populations, while within a population there was limited response to variation in resource availability. Specifically, the southernmost population exhibited significantly greater height growth and biomass production than the mid- and northern-latitude populations (Fig. 4.2a). Although biomass, total root length, and leaf area differed among populations (Fig. 4.3), allocational traits were consistent across all three populations; SRL, SLA, R:S, RMR, LMR, and SMR were likewise consistent among populations (Fig. S4.2 and Table S4.3).

Consistent with our hypotheses, we found that the southernmost population (Prince Albert) had greater height and biomass production, leaf area, and root length than the more northerly populations (Fig. 4.4). At the southernmost extent of black spruce, these trees are competing for resources with many faster-growing tree species than at northern sites (e.g. Bell et al 2000). The parent trees of these seedlings would also have been accustomed to longer, fairer growing seasons than northern populations, making them likely candidates to exhibit a fast trait strategy. In situ, we would thus expect these southern populations to be able to take advantage of increasing resource availability in a changing climate. At a species' northernmost extent, growth is constrained to a very limited frost-free growing season. For northern populations, a conservative slow trait strategy in which individuals produce new biomass early, harden new growth, and set bud before severe weather strikes should facilitate persistence under the extreme conditions at these northernmost extents of forest (e.g., DeWitt *et al.,* 1998). Although we found contrasting results in root length between the monthly and end of experiment analyses, this is likely as a result of the lack of differentiation between populations during the first few months of the experiment. During this time, there were few roots visible in the root windows – the differences in root length between populations by month became more evident at the end of the experiment, and it is reflected in the total root length measurements post-harvest.

Similar to our findings, many studies on black spruce from various age classes, provenances, and types of experiments support our result that black spruce is not very plastic in many traits including phenology, biomass, height, gas exchange, and wood anatomy (Morgenstern & Mullin, 1990; Parker *et al.*, 1994; Johnsen & Seiler, 1996; Johnsen *et al.*, 1996; Beaulieu *et al.*, 2004; Bigras & Bertrand, 2006; Balducci *et al.*, 2014). In contrast to our finding that R:S (and other allometric relationships) were not significantly different among populations and treatments, Johnsen & Seiler (1996) observed greater R:S in northern provenances of black spruce. This could be as a result of the longer (20 hour) photoperiod implemented by Johnsen & Seiler (2006) that allowed for seedlings to develop more pronounced differences in their allocation patterns. Experiments with similar CO_2 treatments to our study found that black spruce responded to the elevated CO_2 conditions through increases in height growth, shoot mass, and nonstructural carbohydrates as well as decreases in stomatal conductance, leaf nitrogen content, and SLA (Tjoelker *et al.*, 1998; Bigras & Bertrand, 2006). However, it should be noted that these experiments did not indicate that the CO_2 used to elevate the experimental CO_2 conditions had been scrubbed of ethylene. Ethylene is a plant growth hormone that can result in effects such as increased shoot elongation and diameter (Abeles, 1971), and it is a known contaminant in CO_2 cylinders (Morison & Gifford, 1984). More work is needed to determine whether our results contrast with previous studies because of the ethylene scrubber on our CO_2 treatment. There is also evidence to support no effect of CO_2 on physiological and morphological traits (Johnsen & Seiler, 1996). The different responses observed could be due to differences between eastern provenances and those used in our study, or acclimation to increased CO_2 conditions over the course of the experiment as observed by Johnsen & Seiler (1996).

In the present study, physiological traits were largely invariable. There was no effect of CO_2 treatment on LCP, A_{max}, or R_d, nor was there a latitudinal trend or consistent response of physiological traits among populations (Fig. 4.3). The conditions under which the seedlings are grown has previously been shown to have a significant influence on similar physiological traits – temperature and CO_2 treatments have been shown to affect gas exchange in several experiments with black spruce (Tjoelker *et al.*, 1998; Bigras & Bertrand, 2006; Way & Sage, 2008). Differences in photosynthetic rates between a northern and southern provenance of black spruce in Quebec have also been previously reported (Bigras & Bertrand, 2006). We found that the magnitude of maximum photosynthetic rates observed in our experiment ($0.88 – 4.23\ \mu mol \cdot m^{-2} \cdot s^{-1}$) were overlapping but lower than other studies of black spruce, which ranged from 2.5 – 25

$\mu mol \cdot m^{-2} \cdot s^{-1}$ (Tjoelker *et al.*, 1998; Bigras & Bertrand, 2006; Way & Sage, 2008). However, the seed stock for these experiments were all sourced from provenances in Ontario, Quebec, and Minnesota – all of which are considerably southeast of our study region. Differences between the large-scale climate patterns and environmental pressures (e.g., competition) between the western and eastern boreal forests may drive different strategies that could have led to this contrasting result.

Although we attempted to characterize plastic vs. fixed traits under different nutrient treatments, poor survival of the high nutrient treatment after our first "winter" prevented further inclusion of this treatment. However, we found that our high nutrient treatment had significantly lower survival than seedlings under low nutrient treatments (Fig. 4.5). We interpret the poor survival of our HN seedlings not as nutrient toxicity (N toxicity in black spruce seedlings occurs at 2000 mg N L^{-1} soil (Salifu & Timmer, 2003) in comparison to our 905 mg N L^{-1}), but instead as support for some degree of plasticity in the strategies of seedlings. During the experiment, the greatest deaths occurred during the first "winter" cycle (Fig. 4.5b). We observed that the majority of the HN seedlings continued to grow new shoots throughout the three month "summer" cycle and had not hardened these new needles or set bud prior to the transition to the first "winter". Over this time, we found that the HN treatment promoted height growth in comparison to the LN treatment (Fig. S4.3). However, these HN seedlings suffered severe damage over winter, and ultimately led to the widespread mortality recorded in the HN plants. This trend was most apparent in the HN × EC treatment, and in the two southerly populations (Fig. 4.5a). Several studies have shown that nutrient additions have significant impacts on tree phenology, particularly with respect to bud set. The effects of nutrient additions to black spruce bud set have only been demonstrated at low levels of fertilization, and it was found that increasing fertilizer from deficient to low levels decreased the proportion of seedlings that had set bud (Bigras *et al.*, 1996). Our high nutrient treatments are higher than those in Bigras *et al.* (1996), but they identify that the concentrations of nutrient additions in their experiment are likely just shy of the optimum range, and higher concentrations could further impair the ability for seedlings to effectively set bud in preparation for fall and winter. Thus, we believe the mortality we observed to be part of the plastic response of black spruce in growth and bud set strategies.

Experiments with other tree species support the hypothesis that high nutrient treatments may induce growth strategies leading to higher risk of mortality. In both Sitka spruce (*Picea sitchensis*) and black cottonwood (*Populus trichocarpa*), high nutrient treatments delayed bud set, especially in seedlings that were also undergoing elevated CO_2 treatments (Murray *et al.*, 1994; Sigurdsson, 2001). In particular, high levels of nitrogen fertilization are known to reduce cold hardiness over winter and delay bud set (van den Driessche, 1991). These results support our interpretation of the survival patterns that we observed in nutrient and CO_2 treatments with black spruce. This implies that if warming increases plant-available nutrients bud set could be delayed. Depending on future climate patterns, this could benefit black spruce by allowing it to take advantage of lengthening growing season. Alternatively, if there is greater variability in weather patterns (particularly in autumn), delayed bud set may lead to increased risk of frost damage and reduced productivity. Unfortunately, we did not anticipate this result, and so our experiment was not designed to examine these effects in detail. However, this hypothesis has important implications for the future of the boreal forest – particularly those on permafrost where thaw is expected to increase nutrient availability – and should be explored in future experiments.

In order to more effectively discern whether or not local adaptation is present among the populations that we studied, a reciprocal transplant experiment should be performed (e.g., Sultan 2000). The photoperiod and temperature cues that we implemented in this study are much more similar to conditions at the southern population than the north. Although we expect major changes to climate trends and atmospheric CO_2 concentrations (Hartmann *et al.*, 2013), which all play crucial roles in determining plant growth, photoperiodic cues for phenological events will remain the same. Photoperiod is one of the most important cues to bud break and bud set in black spruce (Johnsen *et al.*, 1996). For the northern population, which experiences photoperiods of up to 24 hours of daylight, the 16 hour light cycle may have been enough to trigger early season bud set and hamper its growth and responses to treatments. Although several reciprocal transfer or common garden studies have been performed on black spruce over the years (e.g., Khalil, 1984; Park & Fowler, 1988; Bigras & Bertrand, 2006), few capture northern provenances (but see Morgenstern & Mullin, 1990; Johnsen *et al.*, 1996) and none have performed reciprocal transplants at the northern extent of this species in western Canada. Trait plasticity has the potential to provide greater tolerance changing conditions. Thus, filling these gaps and determining the potential for populations of this dominant boreal tree species to demonstrate plastic responses to variable resource conditions is crucial to predicting how black spruce forests will withstand ongoing climate change in the boreal region.

4.6. Conclusions

In this study, we found evidence of local adaptation among the populations, as there were significant trends in growth rates and many of the morphological traits measured in this experiment. These differences were not reflected in the allocation traits or among most of the physiological traits. Our unexpected survival data generated a novel hypothesis that under enhanced resource conditions, black spruce seedlings may delay bud set, putting them at greater risk of winter damage. Because we cannot confirm or deny the extent of plasticity through the results of this experiment, reciprocal transplant studies are required to be able to make predictions about the future of the boreal forest as climate change continues. In addition, there are known differences in the responses between ontogenetic stages of trees (Chung *et al.*, 2013; Camarero *et al.*, 2015), so although we did not find evidence for plasticity at the seedling stage, mature trees may still have capacity for trait plasticity. However, this study has examined an extensive suite of morphological, allocation, and physiological traits across an area of the boreal forest where black spruce traits have remained largely understudied. The results of this experiment provide an important first look at populations in this area and how they may respond to the extreme warming that is predicted for northwestern Canada.

4.7. References

Abeles F (1971) *The role of ethylene in plant growth and development*. Frederick, Maryland, Department of the Army, 1-21 pp.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.

Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6, 129.

Balducci L, Deslauriers A, Giovannelli A, Beaulieu M, Delzon S, Rossi S, Rathgeber CBK (2014) How do drought and warming influence survival and wood traits of *Picea mariana* saplings? *Journal of Experimental Botany*, doi: 10.1093/jxb/eru431.

Bazzaz FA, Coleman J, Morse SR (1990) Growth responses of seven major co-occurring tree species of the northeastern United States to elevated CO_2. *Canadian Journal of Forest Research*, 20, 1479–1484.

Beaulieu J, Perron M, Bousquet J (2004) Multivariate patterns of adaptive genetic variation and seed source transfer in *Picea mariana*. *Canadian Journal of Forest Research*, 34, 531–545.

Bell FW, Ter-Mikaelian MT, Wagner RG (2000) Relative competitiveness of nine early-successional boreal forest species associated with planted jack pine and black spruce seedlings. *Canadian Journal of Forest Research*, 30, 790–800.

Benito Garzón M, Alía R, Robson TM, Zavala MA (2011) Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*, 20, 766–778.

Bigras FJ, Bertrand A (2006) Responses of *Picea mariana* to elevated CO_2 concentration during growth, cold hardening and dehardening: phenology, cold tolerance, photosynthesis and growth. *Tree Physiology*, 26, 875–888.

Bigras FJ, Gonzalez A, Aoust ALD, Hebert C (1996) Frost hardiness, bud phenology and growth of containerized *Picea mariana* seedlings grown at three nitrogen levels and three temperature regimes. *New Forests*, 12, 243–259.

Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, 20, 1–28.

Camarero JJ, Gazol A, Galván JD, Sangüesa-Barreda G, Gutiérrez E (2015) Disparate effects of global-change drivers on mountain conifer forests: warming-induced growth enhancement in young trees vs . CO_2 fertilization in old trees from wet sites. *Global Change Biology*, 21, 738–749.

Canadian Centre for Climate Modelling and Analysis, Canadian Global Circulation Model 3 – www. http://climate-modelling.canada.ca

Chung H, Muraoka H, Nakamura M, Han S, Muller O, Son Y (2013) Experimental warming studies on tree species and forest ecosystems: a literature review. *Journal of Plant Research*, 126, 447–60.

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, 13, 77–81.

van den Driessche R (1991) Effects of nutrients on stock performance in the forest. In: *Mineral nutrition of conifer seedlings* (ed van den Driessche R), pp. 229–260. CRC Press, Boca Raton, Florida.

Green DS (2005) Adaptive strategies in seedlings of three co-occurring, ecologically distinct northern coniferous tree species across an elevational gradient. *Canadian Journal of Forest Research*, 35, 910–917.

Hartmann DL, Klein Tank AMG, Rusticucci M, Alexander LV, Brönnimann S, Charabi Y, Dentener FJ, Dlugokencky EJ, Easterling DR, Kaplan A, Soden BJ, Thorne PW, Wild M, Zhai PM (2013) Observations: Atmosphere and Surface. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Johnsen KH, Seiler JR (1996) Growth, shoot phenology and physiology of diverse seed sources of black spruce: I. Seedling responses to varied atmospheric CO_2 concentrations and photoperiods. *Tree Physiology*, 16, 367–373.

Johnsen KH, Seiler JR, Major JE (1996) Growth, shoot phenology and physiology of diverse seed sources of black spruce: II. 23-year-old field trees. *Tree Physiology*, 16, 375–380.

Jump AS, Peñuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, 8, 1010–1020.

Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature*, 382, 146–149.

Khalil MAK (1984) All-range black spruce provenance study in Newfoundland: performance and genotypic stability of provenances. *Silvae Genetica*, 33, 63–71.

Lamhamedi M, Bernier P (1994) Ecophysiology and field performance of black spruce (*Picea mariana*): a review. *Annals of Forest Science*, 51, 529–551.

Mcleod TK (2001) *The ecology of* Picea glauca *(Moench) Voss at its range limits in northwest Canada*. University of British Columbia, 198 pp.

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Aha R, Alm-Kübler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl Å, Defila C, Donnelly A, Filella Y, Jatczak K, Måge F, Mestre A, Nordli Ø, Peñuelas J, Pirinen P, Remišová V, Scheifinger H, Striz M, Susnik A, Van Vliet AJH, Wielgolaski F-E, Zach S, Zust A (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12, 1969–1976.

Morgenstern EK, Mullin TJ (1990) Growth and survival of black spruce in the range-wide provenance study. *Canadian Journal of Forest Research*, 20, 130–143.

Morison JIL, Gifford RM (1984) Ethylene contamination of CO_2 cylinders: effects on plant growth in CO2 enrichment studies. *Plant Physiology*, 75, 275–277.

Murray MB, Smith RI, Leith ID, Fowler D, Lee HSJ, Friend AD, Jarvis PG (1994) Effects of elevated CO_2, nutrition and climatic warming on bud phenology in Sitka Spruce (*Picea sitchensis*) and their impact on the risk of frost damage. *Tree Physiology*, 14, 691–706.

Oleksyn J, Modrzynski J, Tjoelker MG, Z.ytkowiak R, Reich PB, Karolewski P (1998) Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Functional Ecology*, 12, 573–590.

Park YS, Fowler DP (1988) Geographic variation of black spruce tested in the Maritimes. *Canadian Journal of Forest Research*, 18, 106–114.

Parker WH, Niejenhuis AV, Charrette P (1994) Adaptive variation in *Picea mariana* from northwestern Ontario determined by short-term common environment tests. *Canadian Journal of Forest Research*, 24, 1653–1661.

Pierret A, Gonkhamdee S, Jourdan C, Maeght JL (2013) IJ_Rhizo: An open-source software to measure scanned images of root samples. *Plant and Soil*, 373, 531–539.

Reich PB (2014) The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102, 275–301.

Salifu KF, Timmer VR (2003) Optimizing nitrogen loading of *Picea mariana* seedlings during nursery culture. *Canadian Journal of Forest Research*, 33, 1287–1294.

Savolainen O, Bokma F, García-Gil R, Komulainen P, Repo T (2004) Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of *Pinus sylvestris* to climatic changes. *Forest Ecology and Management*, 197, 79–89.

Sigurdsson BD (2001) Elevated [CO_2] and nutrient status modified leaf phenology and growth rhythm of young *Populus trichocarpa* trees in a 3-year field study. *Trees - Structure and Function*, 15, 403–413.

Sultan SE (1995) Phenotypic plasticity and plant adaptation. *Acta Botanica Neerlandica*, 44, 363–383.

Sultan SE (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, 5, 537–542.

Tjoelker MG, Oleksyn J, Reich PB (1998) Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. *Tree Physiology*, 18, 715–726.

Vitasse Y, Hoch G, Randin CF, Lenz A, Kollas C, Scheepens JF, Körner C (2013) Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia*, 171, 663–678.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature*, 416, 389–395.

Way DA, Sage RF (2008) Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.]. *Global Change Biology*, 14, 624–636.

Way DA, Ladeau SL, McCarthy HR, Clark JS, Oren R, Finzi AC, Jackson RB (2010) Greater seed production in elevated CO_2 is not accompanied by reduced seed quality in *Pinus taeda* L. *Global Change Biology*, 16, 1046–1056.

4.8. Tables

Table 4.1. ANOVA table for the generalized linear mixed effects model of black spruce seedling height from three populations (Prince Albert SK, Fort McMurray AB, and Inuvik NT) over the course of the experiment. Individual nested in block was included as a random effect. Denominator degrees of freedom calculated using a Satterthwaite approximation.

	Sum of squares	**Mean squares**	**Numerator DF**	**Denominator DF**	**F-value**	**p-value**
Population	4.097	2.049	2	38.330	23.230	<0.0001
CO_2	0.051	0.051	1	37.560	0.577	n.s.
Time	79.513	9.939	8	328.720	112.713	<0.0001
Population*CO_2	0.031	0.016	2	38.740	0.176	n.s.
Population*Time	9.996	0.625	16	328.740	7.085	<0.0001
CO_2*Time	1.551	0.194	8	328.720	2.198	0.027
Population*CO_2*Time	1.564	0.0977	16	328.730	1.108	n.s.

4.9. Figures

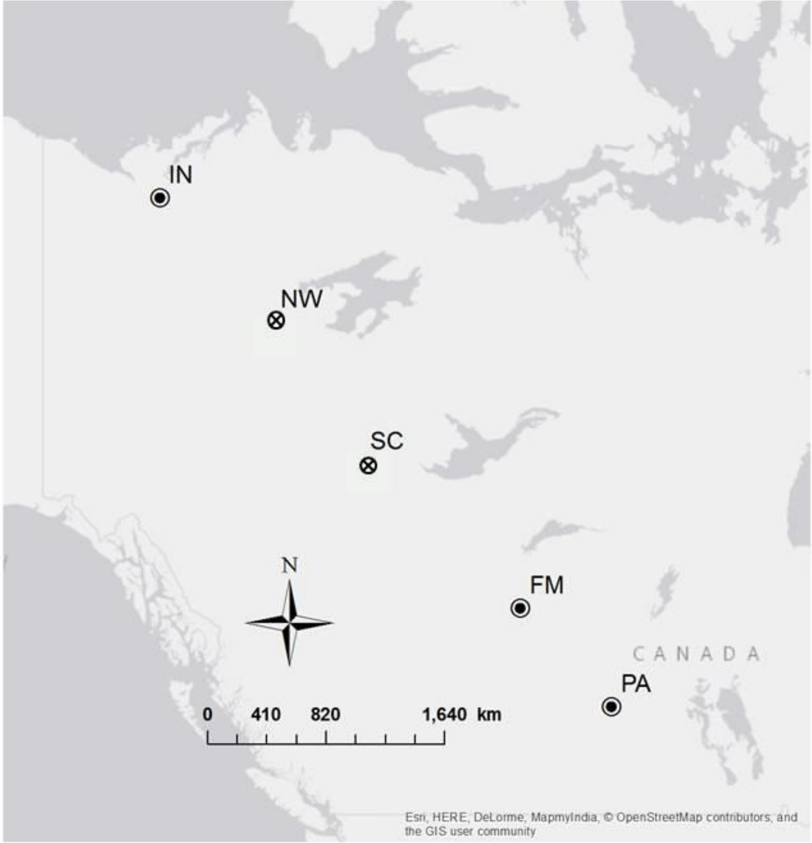

Fig. 4.1. Seed sources for the experiment. IN – Inuvik, NW – Norman Wells, SC – Scotty Creek, FM – Fort McMurray, PA – Prince Albert. Sites marked over with a × indicate populations that suffered extensive mortality before the end of the experiment and could not be included in the analyses. Map inset acquired on ArcMap 10.3, ESRI, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors and the GIS user community.

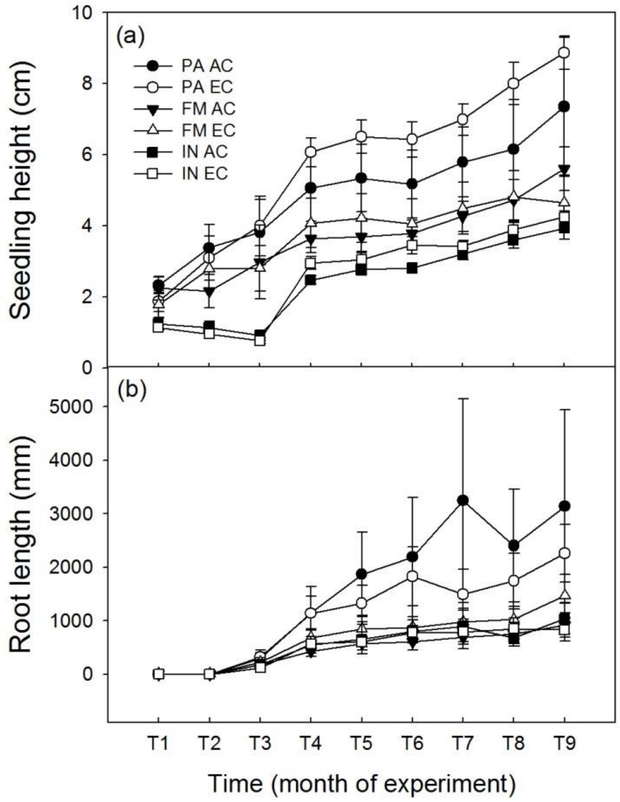

Fig. 4.2. Mean seedling height (a) and root length (b) over the course of the experiment. Each time point corresponds to our monthly measurements throughout three three-month growing seasons (season 1: T1 – T3, season 2: T4 – T6, season 3: T7 – T9). Populations shown are Prince Albert SK (PA), Fort McMurray AB (FM), and Inuvik NT (IN). Ambient CO_2 treatment is represented by filled symbols (AC), while elevated CO_2 is shown as unfilled symbols (EC). Error bars represent standard error. There were significant differences between the height of the three populations throughout the experiment, and how population heights change over time (GLMM results shown in Table 1), while CO_2 treatment did not significantly affect height growth. Neither population nor treatment was a significant term in the GLMM model for root length throughout the experiment.

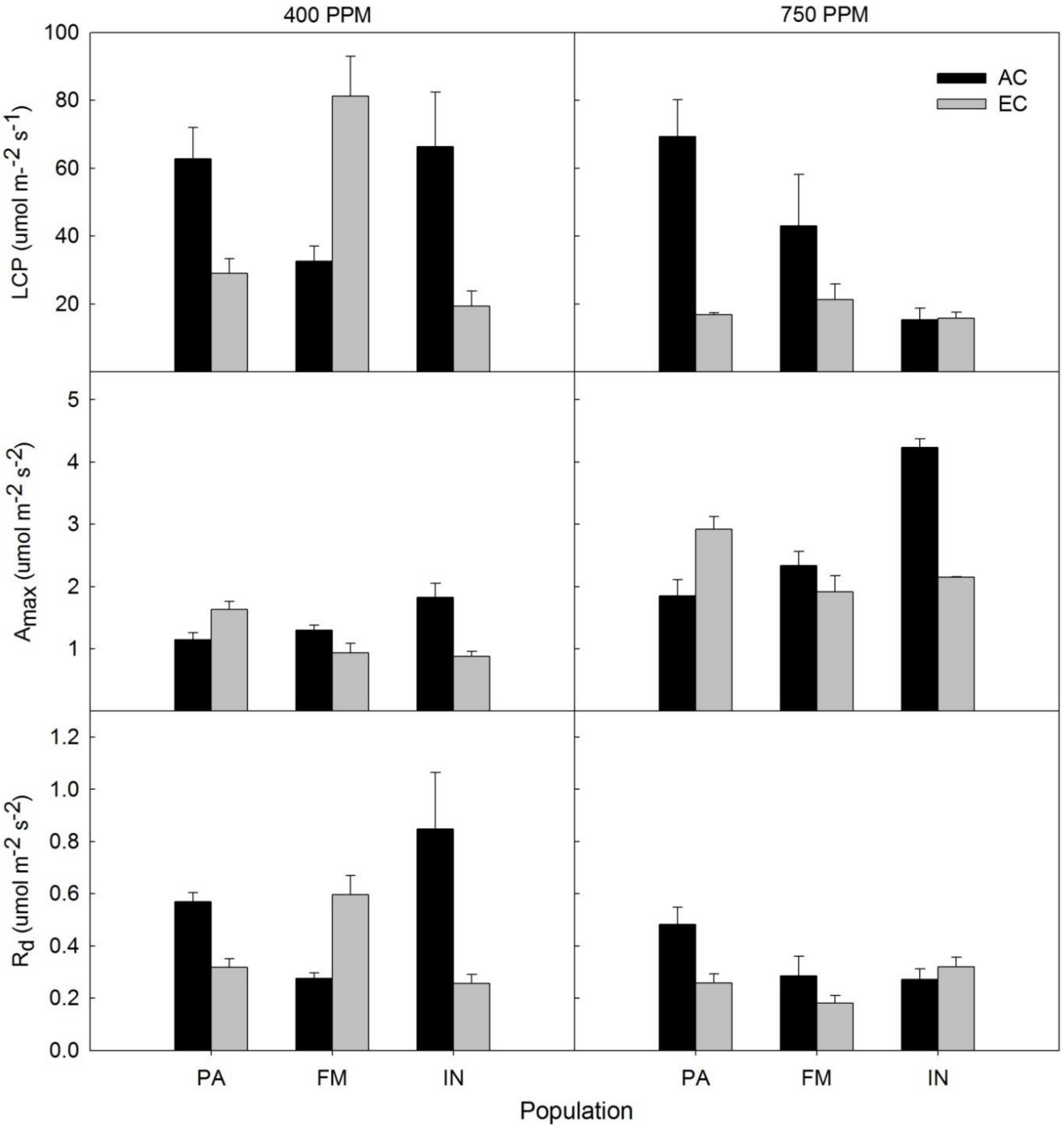

Fig. 4.3. Light compensation point (LCP), maximum photosynthetic rate (A_{max}), and dark respiration (R_d) for each of the populations (IN – Inuvik NT; FM – Fort McMurray AB; PA – Prince Albert SK) and CO_2 treatments (AC – ambient CO_2; EC – elevated CO_2). The CO_2 concentrations under which the gas exchange measurements were made are indicated by the titles above each panel column (400 or 750 ppm). Error bars indicate standard error around the means. There were no significant differences among any of these treatments.

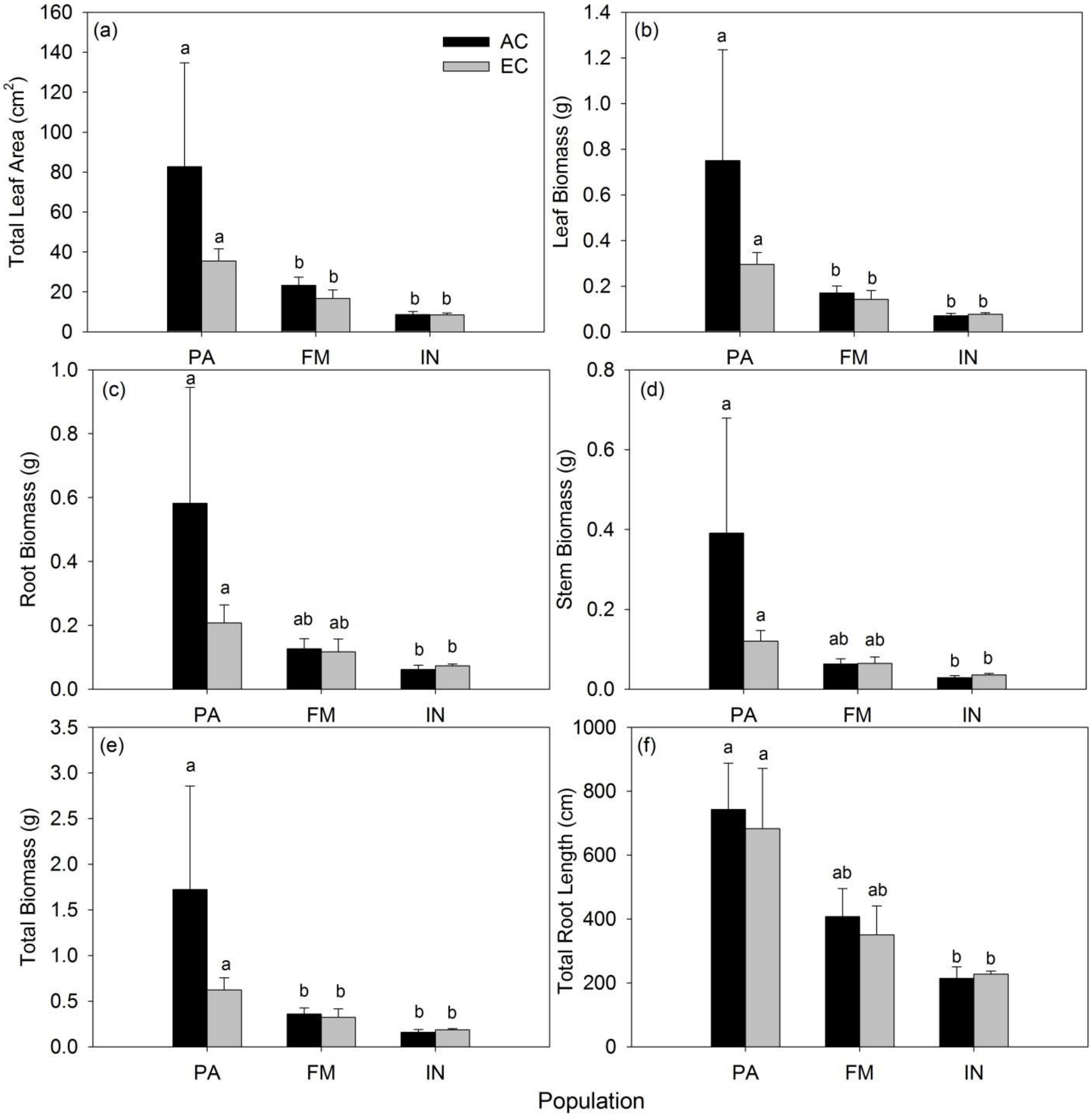

Fig. 4.4. Post-harvest morphological trait measurements that exhibit significant differences. Populations shown are Prince Albert SK (PA), Fort McMurray AB (FM), and Inuvik NT (IN) and CO_2 treatments are Ambient CO_2 (AC) and elevated CO_2 (EC). Error bars indicate standard error around the means. Treatments showing significant differences (ANOVA, Tukey HSD, $p<0.05$) are indicated by different letter codes.

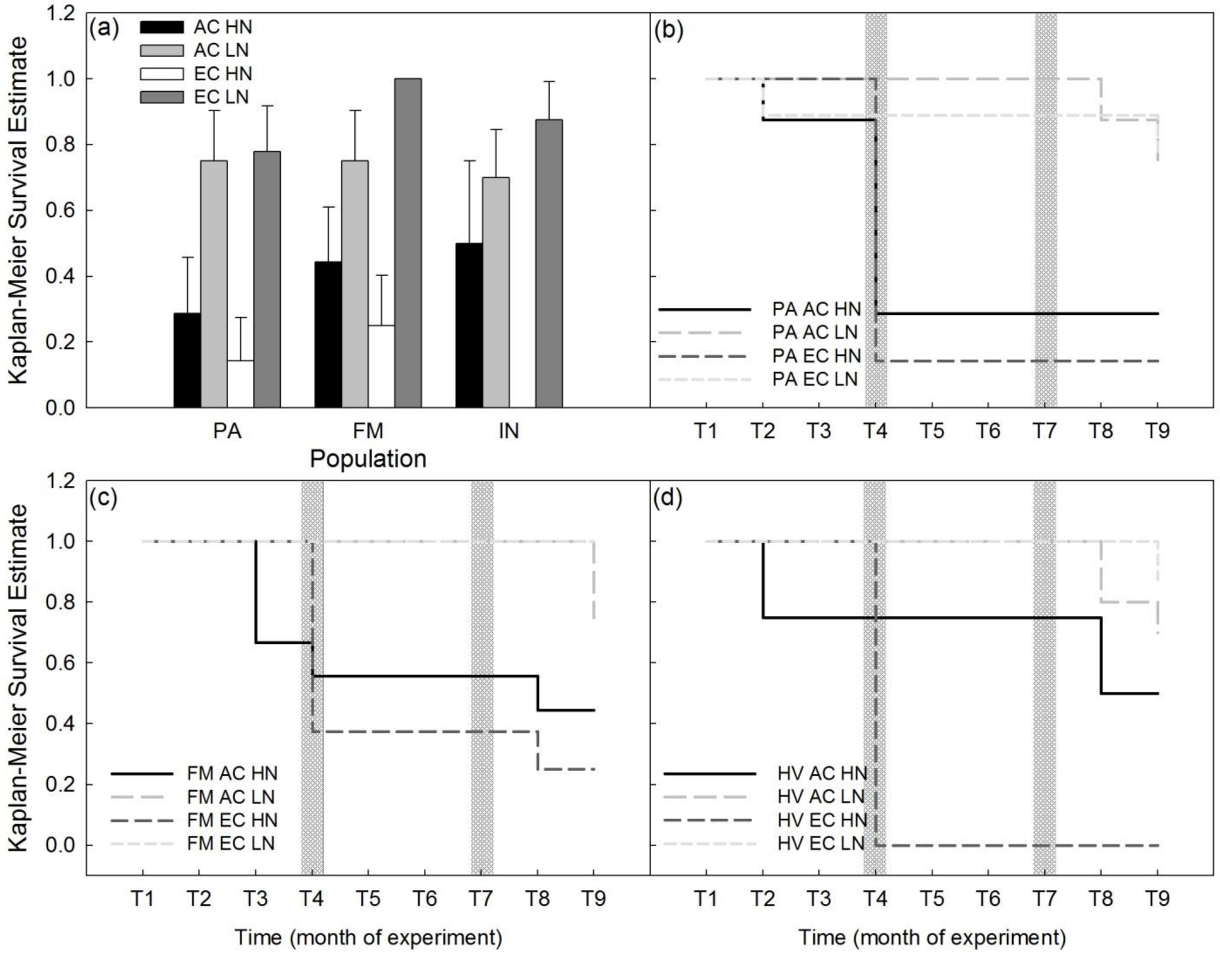

Fig. 4.5. (a) Mean cumulative Kaplan-Meier survival estimate of seedlings under each treatment in the experiment. (b-d) Survival curves showing Kaplan-Meier survival estimates throughout the experiment for each population. Populations shown are Prince Albert SK (PA), Fort McMurray AB (FM), and Inuvik NT (IN), CO_2 treatments are Ambient CO_2 (AC) and elevated CO_2 (EC), and nutrient treatments are low nutrient (LN) and high nutrient (HN). Error bars indicate standard error around the means. Grey vertical bars on panels b-d indicate the first month of measurements post-winter. Each time point corresponds to our monthly measurements throughout three three-month growing seasons (season 1: T1 – T3, season 2: T4 – T6, season 3: T7 – T9).

4.10. Supplementary Information

The supporting information provided includes definitions of acronyms, tables and figures from non-significant test results, additional methodological details, and additional non-essential figures that present information supporting hypotheses brought up in our discussion.

Table S4.1. List of acronyms and their definitions.

A_{max}	Maximum photosynthetic rate
LCP	Light compensation point
LMR	Leaf mass ratio
R_d	Dark respiration rate
R:S	Root to shoot ratio
RMR	Root mass ratio
SLA	Specific leaf area
SMR	Shoot mass ratio
SRL	Specific root length
TLA	Total leaf area
TRL	Total root length

Table S4.2. F tables from non-significant analysis of variance performed on physiological traits.

Trait		**DF**	**SS**	**Mean Sq**	**F-value**	**p-value**
LCP – 400	Population	2	1.293	0.6467	0.598	0.566
	CO_2	1	0.976	0.9755	0.902	0.361
	Block	8	4.388	0.5485	0.507	0.829
	Residuals	12	12.980	1.0817		
LCP – 750	Population	2	3.241	1.6203	1.650	0.236
	CO_2	1	1.755	1.7552	1.787	0.208
	Block	8	10.179	1.2724	1.295	0.337
	Residuals	11	10.804	0.9822		
Amax – 400	Population	2	0.349	0.1747	0.380	0.692
	CO_2	1	0.444	0.4437	0.965	0.345
	Block	8	2.134	0.2668	0.580	0.776
	Residuals	12	5.518	0.4598		
Amax – 750	Population	2	4.935	2.468	3.174	0.0856
	CO_2	1	1.376	1.376	1.770	0.2129
	Block	8	7.277	0.910	1.170	0.4000
	Popn:CO_2	2	6.835	3.418	4.396	0.0427
	Residuals	10	7.774	0.777		
Rd – 400	Population	2	0.0665	0.03323	0.147	0.865
	CO_2	1	0.1834	0.18338	0.812	0.385
	Block	8	0.8392	0.10490	0.465	0.859
	Residuals	12	2.7089	0.22574		
Rd – 750	Population	2	0.0751	0.03757	1.136	0.353
	CO_2	1	0.0524	0.05244	1.585	0.232
	Block	8	0.3960	0.04950	1.496	0.255
	Residuals	12	0.3970	0.03308		

Table S4.3. F tables from non-significant analysis of variance performed on allocation traits.

Trait		**DF**	**SS**	**Mean Sq**	**F-value**	**p-value**
LCP – 400	Population	2	1.293	0.6467	0.598	0.566
	CO_2	1	0.976	0.9755	0.902	0.361
	Block	8	4.388	0.5485	0.507	0.829
	Residuals	12	12.980	1.0817		
LCP – 750	Population	2	3.241	1.6203	1.650	0.236
	CO_2	1	1.755	1.7552	1.787	0.208
	Block	8	10.179	1.2724	1.295	0.337
	Residuals	11	10.804	0.9822		
Amax – 400	Population	2	0.349	0.1747	0.380	0.692
	CO_2	1	0.444	0.4437	0.965	0.345
	Block	8	2.134	0.2668	0.580	0.776
	Residuals	12	5.518	0.4598		
Amax – 750	Population	2	4.935	2.468	3.174	0.0856
	CO_2	1	1.376	1.376	1.770	0.2129
	Block	8	7.277	0.910	1.170	0.4000
	Popn:CO_2	2	6.835	3.418	4.396	0.0427
	Residuals	10	7.774	0.777		
Rd – 400	Population	2	0.0665	0.03323	0.147	0.865
	CO_2	1	0.1834	0.18338	0.812	0.385
	Block	8	0.8392	0.10490	0.465	0.859
	Residuals	12	2.7089	0.22574		
Rd – 750	Population	2	0.0751	0.03757	1.136	0.353
	CO_2	1	0.0524	0.05244	1.585	0.232
	Block	8	0.3960	0.04950	1.496	0.255
	Residuals	12	0.3970	0.03308		

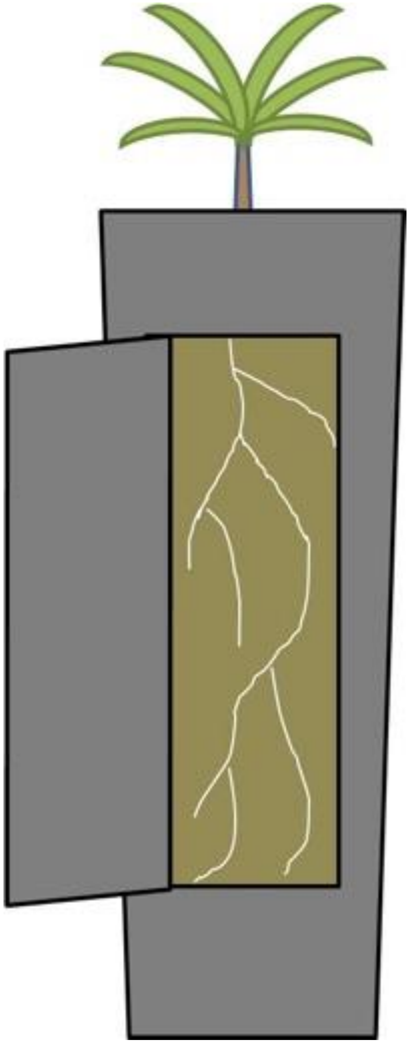

Fig. S4.1. Schematic of the “windows” created in seedling pots to monitor root growth measurement throughout the experiment. The window was created by inserting a transparency sheet into the pot.

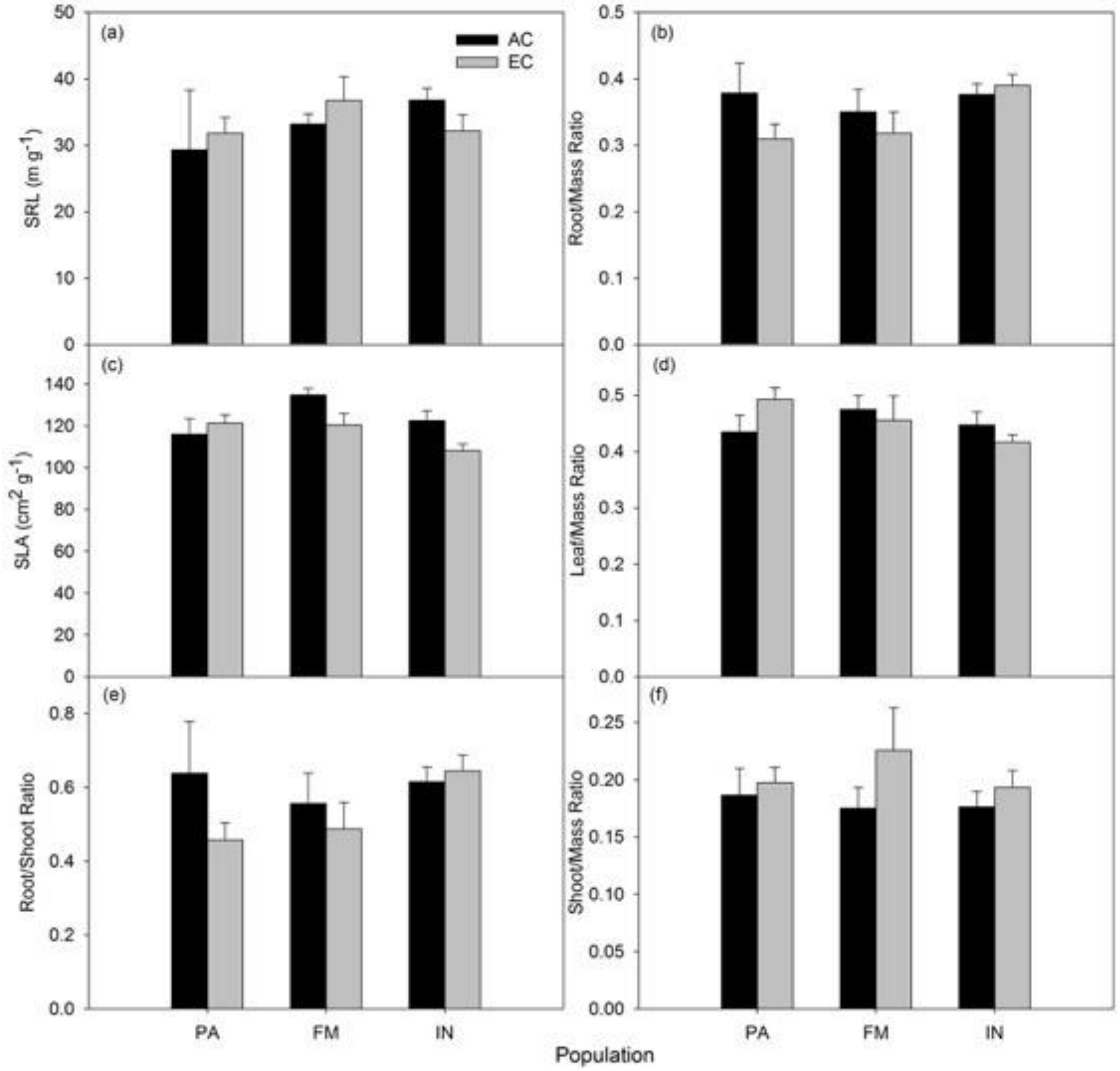

Fig. S4.2. Post-harvest allocation trait measurements. Populations shown are Prince Albert SK (PA), Fort McMurray AB (FM), and Inuvik NT (IN) and CO_2 treatments are ambient CO_2 (AC) and elevated CO_2 (EC). Error bars indicate standard error around the means. There were no significant differences among any of these treatments.

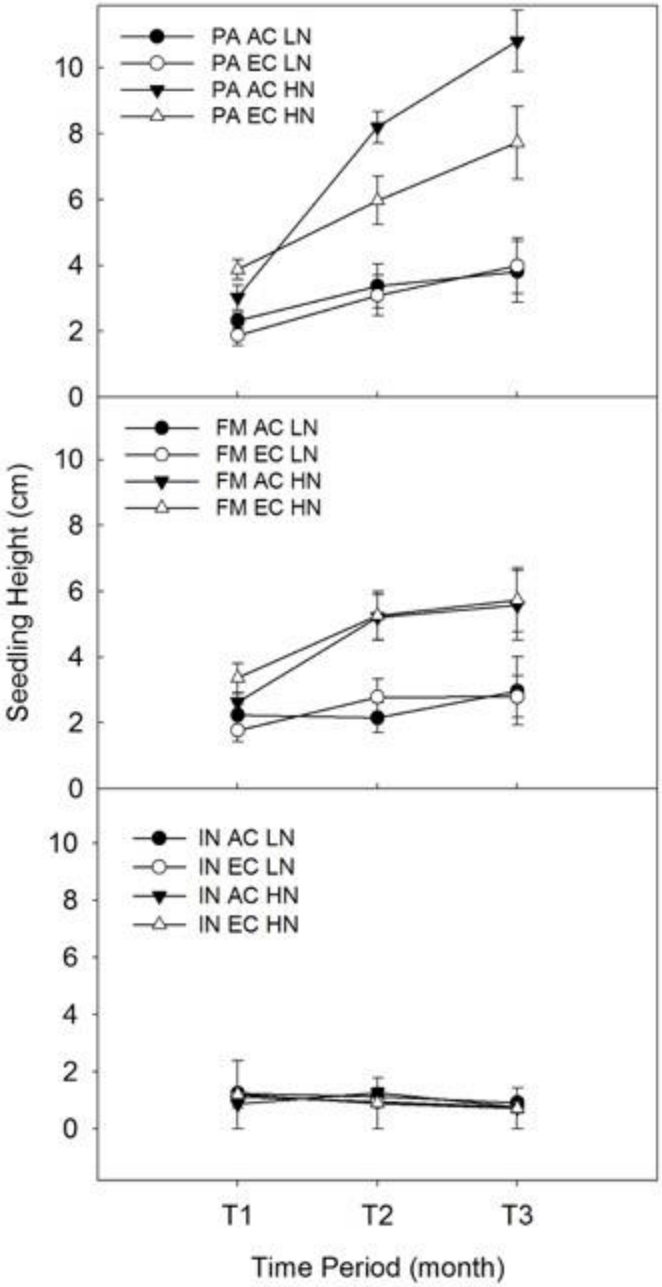

Fig. S4.3. Mean seedling height over the first three-month-long growing season. Populations shown are Prince Albert SK (PA), Fort McMurray AB (FM), and Inuvik NT (IN). Ambient CO_2 treatment is represented by filled symbols (AC), while elevated CO_2 is shown as unfilled symbols (EC). Error bars represent standard error.

Chapter 5: Conclusions

5.1. Introduction

The boreal forest is experiencing dramatic changes in climate, particularly across northwestern North America. Through my doctoral research, I have captured the changes in growth patterns of black spruce (*Picea mariana*) in the northwestern boreal forest over a time period which encompasses the most rapid rate of warming that these contemporary forests have faced (Hartmann *et al.*, 2013). I have investigated the influence of climate change on growth patterns across the range of the species, and investigated in a more detailed fashion the effects of permafrost degradation on growth at a rapidly thawing peatland site. To try to address mechanisms of differential growth-climate responses, I investigated the trait plasticity of seedlings grown from sites across the latitudinal extent of black spruce in northwestern Canada. The results of these components of my doctoral research serve to (1) provide an important history of the major influences on productivity from wide-ranging black spruce forests, which can be used to predict the fate of this species under future climate forecasts, and (2) quantify the plasticity of key black spruce seedling traits in order to anticipate the ability of young populations to adapt to changing conditions.

5.2. Summary of Research

In Chapter 2, I observed a steady decline in the average annual growth of black spruce since the mid-1900s at Scotty Creek, a discontinuous permafrost peatland site that has experienced extensive permafrost degradation over recent decades. Despite the obvious effects of permafrost thaw on forests within this landscape, wherein “drunken trees” topple as the permafrost plateaus on which they are established thaw to become wetland features (Quinton *et al.*, 2011), I did not find that the magnitude of growth of trees was influenced by being within a

10 m “edge zone” of a wetland or on permafrost plateaus with high rates of lateral permafrost degradation. However, the results of this chapter indicate that declining growth at this site may instead be driven by vertical permafrost thaw (a deepening active layer), which impacts a higher proportion of the stems at the site. A deepening active layer as a result of sustained warming over recent decades is likely lowering the water table and driving drought stress in these shallow-rooted black spruce forests.

Across the latitudinal extent of black spruce forests studied in Chapter 3, Scotty Creek is the only site which is currently experiencing this effect of permafrost thaw. In fact, of the four sites that were sampled across 15° of latitude, Scotty Creek (the representative mid-latitude site) is the only site showing growth decline over time in site chronology. The timberline and treeline sites (Inuvik and Trail Valley Creek, respectively) are both exhibiting positive growth trends which seem to be driven by warmer, longer growing seasons in recent decades. At the southern limit of black spruce (Southern Old Black Spruce - SOBS), there were no significant temperature or precipitation drivers of recent growth patterns. Although temperature at this site has increased over time, precipitation has also increased and I found that the Climate-Moisture Index (CMI) trends indicate reduced drought stress conditions which has likely contributed to the increase in growth over recent decades. I also found that carbon isotope compositions at SOBS and Scotty Creek showed a decrease in discrimination against ^{13}C. At Scotty Creek, the combination of decreased growth and decreased discrimination against ^{13}C indicates drought stress signals within the trees. On the other hand, SOBS maintains an increase in growth while discrimination against ^{13}C decreases, which implies that carbon fertilization may be occurring at this site (Silva & Anand, 2013).

In Chapter 4, I investigated traits in seedlings that would influence the ability of black spruce to withstand climate change. By using a common garden to grow black spruce seedlings from seed collected from across the latitudinal extent of black spruce in northwestern Canada, I was able to determine that there is evidence for local adaptation in growth and biomass traits; I found that seedlings from the south had greater height, leaf area and leaf biomass, root length and root biomass, stem biomass, and total biomass than the northern seedlings. Conversely, I found that physiological and allocational traits did not differ among populations. Although I applied two treatments in a fully factorial design (high/low nutrient and ambient/elevated CO_2), there were no significant differences between treatments in any of the traits measured. However, I did find that the survival of seedlings with the high nutrient treatment was much lower than in the low nutrient treatment. The concentration of nutrients added to this treatment was well below toxic levels for black spruce (Salifu & Timmer, 2003) indicating that this is not likely a case of nutrient toxicity, however I did find that die-off coincided with the winter cycles. Based on observations of growth patterns of the high nutrient treatment seedlings leading up to their "winter" mortality, I speculate that the increase in available resources triggered riskier growth strategies, leaving these seedlings with unhardened needles going into the winter cycle and ultimately resulting in mortality.

5.3. Implications of Climate Warming in Northwestern Boreal Forests

The results of my research have provided valuable insight into the responses of black spruce to recent climate change, as well as identifying locally adaptive seedling traits that will contribute to the species' ability to tolerate future changes. By integrating the results of the three chapters of my research – Ch. 2 and 3 which address historical changes in black spruce growth patterns, and Ch. 4 which has implications on how seedlings respond under changing conditions

– I have data that can provide the basis for predictions about the fate of the boreal forest in northwestern Canada.

5.3.1. Effects of climate change in recent decades

It is apparent from my research that for southern and mid-latitude populations of black spruce in western Canada, moisture limitation is a key constraint on growth of mature trees. At the site at the southernmost extent of black spruce forests (SOBS), neither temperature nor precipitation were identified as significant drivers of growth. However, Climate-Moisture Index (CMI – a measure of drought stress in a system) trends match the increasing in growth of trees at SOBS, which suggests the importance of water balance (the difference between precipitation and potential evapotranspiration) of the system in influencing the productivity of black spruce.

While water balance also plays an important role in black spruce growth in mid-latitude discontinuous permafrost peatlands in the boreal forest, the effect of warming on permafrost conditions complicates water access. Even when precipitation meets the evapotranspirative demands of a system, productivity of black spruce can be hampered due to vertical permafrost thaw. In these discontinuous permafrost peatland ecosystems, forests establish only on the raised permafrost plateaus. In my research of growth dynamics of black spruce at Scotty Creek (Chapter 2) in conjunction with work by Patankar *et al.* (2015) and Warren (2015), it is apparent that the shallow root systems of mature black spruce on the permafrost plateaus cannot access the water table as the active layer (seasonally thawed soil atop the permafrost) becomes increasingly deeper. This is supported by the increase in negative responses of growth to warming in recent decades; as temperature has steadily increased over time, it indirectly results in drought stressed conditions for black spruce by promoting thawing of the active layer.

At the northernmost extent of black spruce in western Canada, growth is primarily driven by constraints on the short, cool growing season rather than water balance. Although precipitation does play a role in influencing annual growth, it is winter precipitation (snow) which serves as an important climatic driver of productivity. Contrary to the positive association between precipitation and productivity in the southern regions of the boreal forest, this relationship with winter precipitation is negative; rather than winter precipitation providing necessary moisture to the system, years of high snow accumulation constrain the length of the growing season because it takes longer for this large amount of snow to melt, and delays growth initiation. Likewise, warmer spring temperatures and summer temperatures both positively influence productivity at timberline and treeline systems in the western boreal forest, which both contribute to increased growing degree days.

5.3.2. Projections for black spruce productivity under future climate scenarios

Given the known responses of black spruce to climate conditions described in the previous section, predictions can be made about the future of black spruce productivity across the latitudinal extent of this study through evaluating the potential responses of the species to future climate scenarios. For the purposes of making these predictions, I have investigated Environment Canada's projected change in mean surface temperature and precipitation in North America for the year 2090, relative to 1990 for two IPCC climate model scenarios (B1 – a conservative projection for carbon emissions, and A1B – a moderate range projection for carbon emissions). These temperature and precipitation predictions for the weather stations associated with each of the three main study sites (SOBS, Scotty Creek, and Inuvik) are shown in Table 5.1.

At all sites, both temperature and precipitation are expected to increase (Table 5.1). Both climate models predict that Inuvik is going to experience some of the most extreme warming (over 4°C) by the late 21st century. Given the results of my investigation of black spruce growth dynamics at this timberline site in Chapter 3, this increase in temperatures is likely to continue to promote growth of this species at its northern margin. However, an important consideration of this growth projection is the influence of warming on the integrity of the permafrost at the northern extent of black spruce forests in western Canada.

As described in Chapter 2, discontinuous permafrost can influence tree growth in many ways, such as mechanical damage and loss of ground stability as permafrost degrades, or by impeding access to the water table as the active layer deepens. Discontinuous permafrost can occur in areas where mean annual air temperature is above -5°C (Brown, 1969). Although this is near the mean annual temperature expected for the Inuvik region by the end of the 21st century under scenario A1B (Table 5.1), the effects of warming on permafrost can be buffered by the ecosystem (Shur & Jorgenson, 2007; Jorgenson *et al.*, 2010) and discontinuous permafrost will not form immediately upon reaching these temperatures. During the next century, active layer thickening will be the greatest permafrost-driven influence on tree growth in the Inuvik area. The soil foundation will likely be more stable in comparison to Scotty Creek, as a result of the shallower organic layer. There is the potential that this thickening active layer may result in drought stress of trees through the same mechanism as forests are currently experiencing at Scotty Creek (e.g., Chapter 2; Warren, 2015), however this will depend on the local soil conditions. The capacity of mineral soil to retain water is higher than the thick organic layer that typifies Scotty Creek (Boelter, 1968), so this is likely to contribute to maintaining high productivity at this northern forest margin.

At Scotty Creek, the climate projections suggest continued declines of black spruce in this discontinuous permafrost peatland. With warming expected to bring mean annual air temperatures very near or possibly above 0°C (Table 5.1), permafrost degradation will continue and permafrost may only exist in sporadic patches by 2090. Using observations of permafrost cover at Scotty Creek by Baltzer *et al.* (2014), I was able to predict (with a linear model) that only 23.4% of the landscape will be underlain by permafrost in the year 2090. The loss of permafrost plateaus and transition to wetlands is likely to result in loss of black spruce forest cover and decreased productivity of forests over this time period. Although it is possible that black spruce may survive permafrost degradation in this peatland (e.g., Site C in Fig. S2.8), productivity will likely decrease. Based on work in thawing peatlands in northern Manitoba (Camill, 1999), it is likely that Scotty Creek will experience a transition to more deciduous shrub species that have a greater tolerance and capacity to establish in the expanding wetland features. Alternatively, it is possible that increased runoff likely resulting from greater hydrological connectivity as permafrost thaws may eventually lead to some drying of the system (Connon *et al.*, 2014). If this occurs before complete die-off of existing black spruce forests, there may be more potential for re-establishment in degraded areas that are sufficiently drained.

At SOBS, balance between precipitation and evapotranspirative demands from increasing temperatures is likely to continue to drive productivity of black spruce forests. Although temperature is expected to increase, precipitation is expected to as well. The seasonality of these projected temperature and precipitation increases, not just overall changes, will be important to water balance; although precipitation and temperature may both be showing an overall increase, there could still be seasonal disparities in precipitation and evapotranspiration leading to drought conditions that these projections cannot capture. If the growing season has higher precipitation than evapotranspiration, I expect that productivity of black spruce at its southern extent will continue to increase. If evapotranspirative demands are higher than precipitation over the growing season, black spruce growth and dominance within this part of the boreal forest is likely to decline with the encroachment of the aspen parkland (Hogg & Hurdle, 1995).

5.3.3. Fate of black spruce regeneration in the future of the boreal forest

To this point, only responses of mature black spruce trees to past, present, and future climate change have been discussed. However, an important component of predicting the future of black spruce forests in northwestern Canada is understanding how establishment is affected by changing conditions. From the results of the common garden study in Chapter 4, I can speculate on how juvenile black spruce will respond to the conditions at each site described above.

Although mature trees at the treeline in northwestern Canada were very responsive to warming temperatures and have increased their productivity over recent decades, seedlings from this site demonstrated a very conservative slow-trait strategy, even under the ideal conditions provided in the common garden study. Although under the current conditions at this site, the slow-trait strategy prevents the seedlings from being damaged by early or late season frosts, warming predicted for the Inuvik region (Table 5.1) may drive more competition from faster-growing plants that could hamper seedling establishment and success (Aitken *et al.*, 2008). The lack of trait plasticity in response to resource availability demonstrated in these seedlings is likely limited by the low resource availability conditions at treeline since trait plasticity is very costly to maintain (DeWitt *et al.*, 1998; Alpert & Simms, 2002). If conditions continue to improve resource availability over the long term, seedlings may begin to exhibit a greater degree of plasticity, or over generations they may adapt to the warmer climate that is predicted for this region.

At Scotty Creek, germinant success is likely to limit any re-establishment of black spruce as mature trees die-off due to the effects of permafrost degradation and warming. In permafrost peatlands degrading into wetland features, *Sphagnum* moss growth has been shown to outcompete black spruce seedlings (Camill *et al.*, 2010), restricting regeneration. Additionally, under the current conditions at Scotty Creek, the quality of seed produced by mature black spruce was very poor, with such low germination rates and poor survival of germinants that this population had to be dropped from the experiment in Chapter 4. Because the conditions for black spruce at Scotty Creek are predicted to continue to deteriorate by the late 21st century (see section 5.3.2), reproductive capacity is unlikely to improve given the poor resource availability (Obeso, 2002). Thus, if the persistence of black spruce at this site falls upon its capacity to regenerate, the outlook for black spruce at this site is poor.

At the southernmost provenance in the common garden study (approximately 100 km south of the SOBS study site in Chapter 3), seedlings performed well in the ideal conditions of the growth chamber. Although I was unable to confirm or deny that black spruce from the southern margins of the species' range exhibited plasticity in their traits, seedlings from this provenance demonstrated greater growth than any other site in this study. Observations from throughout the experiment support that this provenance has a fast-trait strategy, a much riskier approach than the northern population. Although risky, this provenance faces some of the least severe conditions and is less likely to face early frosts and snowfall which would cause die-off of unhardened growth. This fast-trait strategy also gives seedlings from this provenance a better chance to compete with other plant species moving northward as climate warms and may aid in the persistence of black spruce under future climates.

In addition to the constraints that reproductive success and plasticity of traits has on regeneration, fire severity and return interval will play an important role in the persistence of black spruce at all sites. Not only does fire promote the semi-serotinous cones of black spruce to open and disperse seed, it can dramatically change the substrate on which the seedling would establish. For example, in severe burns where the organic material has been largely consumed and mineral soil has become exposed, deciduous tree species such as trembling aspen (*Populus tremuloides*) have greater establishment potential than conifers (Johnstone & Kasischke, 2005; Johnstone & Chapin, 2006). Similarly, wind-dispersed species such as trembling aspen have an advantage over conifers such as black spruce when fire return intervals become shorter; short fire return intervals can reduce seed availability because black spruce may not reach reproductive maturity before experiencing another burn (Brown & Johnstone, 2012). Fire activity is expected to continue to increase into the late 20th century as climate warming continues (Soja *et al.*, 2007), thus making it an important factor to consider in predicting the regeneration and persistence of black spruce in the boreal forest. The fast-trait strategy of the southern seedlings will aid in giving black spruce a competitive advantage in recolonization after fire, while the slow-trait strategy of northern black spruce seedlings may result in recolonization of faster-growing species.

5.4. Differences in Responses between Field and Experimental Studies

A puzzling result of the culmination of these three data chapters is the apparent contrast between responsiveness to changing conditions between the field studies and common garden experiment. In chapter 3, mature black spruce from the Inuvik NT area have responded dramatically to the changing climatic conditions – warming has seemed to have improved growing conditions for black spruce in recent decades, and the effect is apparent. On the other hand, in the common garden study, seedlings grown from seed acquired from this same site exhibited no detectable response to either resource condition that was manipulated in the study, nor did they seem to take advantage of the ideal temperature regime provided in the experiment.

There are several possible reasons for the seemingly contrasting results. Firstly, ontogenetic influences may be playing a role in the different levels of responsiveness between the seedlings in the common garden study and the mature trees sampled in the tree-ring studies. There is considerable evidence of trees showing completely contrasting responses to warming and resource availability between ontogenetic stages (Chung *et al.*, 2013; Camarero *et al.*, 2014). Thus, inconsistencies in responses between seedlings in the common garden study and mature trees in the dendrochronology study may be attributed simply to age class of trees.

Alternatively, it is possible that trees grown under artificial conditions may not demonstrate the same responses as trees in a natural environment. Despite technology allowing for impressive control of many conditions in growth chambers such as those used in this common garden experiment, it was not feasible to mimic the numerous variables such as temperature, photoperiod, humidity, and soils that these black spruce would experience in situ. Any number of these variables could be a factor driving differences in the responsiveness of trees between the common garden and dendrochronological studies.

5.5. Future Directions

This research has made great strides in developing a thorough understanding of growth dynamics of black spruce in northwestern Canada, and has provided framework and direction for continued studies. An important approach to predicting resiliency of trees under changing climate is performing a reciprocal transplant experiment (Sultan, 2000); essentially, common gardens are established at the location of each population, giving the ability to make conclusions not just about the plasticity of each population, but whether the traits exhibited by each population confers competitive advantage at that site thereby demonstrating local adaptation. In addition, pairing these common garden studies of seedlings with functional trait measurements of mature black spruce at each site would provide insight into persistence and functionality of existing trees.

Although edaphic conditions were not a focal point of my research, the belowground environment is implied as a key influence on forest productivity throughout both Chapter 2 and 3. In order to directly address the hypotheses proposed about the role of edaphic conditions in growth patterns and as influences on climate-growth relationships, a more detailed examination of belowground conditions should be undertaken. Investigating factors such as soil temperature, plant-available nutrients, soil moisture dynamics, and deploying tools for monitoring root growth dynamics as the active layer deepens would help support the hypotheses that we have proposed about the mechanisms driving forest productivity in the boreal region.

Increasing the spatial resolution of sampling will allow us to better understand the variability in growth dynamics of this species. However, there are considerable logistical and financial constraints on this sort of sampling in the remote areas comprising the range of black spruce. The non-uniformity in growth dynamics of black spruce within this study, and within the literature as a whole poses challenges with generalizing growth patterns across the boreal. Spatial and temporal variability in the climate-growth responses of black spruce as described above in Chapter 3 make these large-scale generalizations ineffective at predicting the function and persistence of this widespread boreal species. As remote sensing technology becomes more efficient and available, remotely-sensed predictions of growth dynamics coupled with details of soil moisture, landscape, and vegetation in conjunction with ground truthing and targeted sampling in areas with potential for high variability will aid in capturing the array of growth dynamics across microsites and large regions.

5.6. Conclusions

Overall, I have successfully met the objectives of this doctoral research. I have identified climatic drivers of black spruce growth over recent history across the species' 15° latitudinal extent in western Canada, as well as investigated effects of permafrost thaw on growth dynamics in a rapidly-thawing discontinuous permafrost peatland site. Stable carbon isotope analysis has provided insight into mechanisms driving growth dynamics at the study sites. The common garden study performed with black spruce seed from across the latitudinal extent of western Canada identified that several key growth traits did not exhibit plasticity when seedlings were grown under ideal conditions, particularly in the northern provenance. Additionally, at the southern provenance, high resource conditions seemed to increase competitive growth strategies, leading to greater mortality in these treatments. Although there is much work that can still be done to quantify the growth dynamics of black spruce, this research has provided a baseline for projections about the persistence of the most widespread and dominant boreal tree species in the face of a changing climate.

5.7. References

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.

Alpert P, Simms EL (2002) The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evolutionary Ecology*, 16, 285–297.

Baltzer JL, Veness T, Chasmer LE, Sniderhan AE, Quinton WL (2014) Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. *Global Change Biology,* 20, 824–834.

Boelter DH (1968) Important physical properties of peat materials. In: *Proceedings of the Third International Peat Congress*, pp. 150–156. Quebec City.

Brown RJE (1969) Factors influencing discontinuous permafrost in Canada. In: *The Periglacial Environment: Past and Present* (ed Péwé TL), pp. 11–53. McGill-Queen's University Press, Montreal.

Brown CD, Johnstone JF (2012) Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management*, 266, 34–41.

Camarero JJ, Gazol A, Galván JD, Sangüesa-Barreda G, Gutiérrez E (2014) Disparate effects of global-change drivers on mountain conifer forests: warming-induced growth enhancement in young trees vs. CO_2 fertilization in old trees from wet sites. *Global Change Biology,* doi: 10.111/gcb.12787.

Camill P (1999) Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany*, 77, 721–733.

Camill P, Chihara L, Adams B, Andreassi C, Barry A, Kalim S, Limmer J, Mandell M, Rafert G (2010) Early life history transitions and recruitment of *Picea mariana* in thawed boreal permafrost peatlands. *Ecology*, 91, 448–59.

Chung H, Muraoka H, Nakamura M, Han S, Muller O, Son Y (2013) Experimental warming studies on tree species and forest ecosystems: a literature review. *Journal of Plant Research*, 126, 447–60.

Connon RF, Quinton WL, Craig JR, Hayashi M (2014) Changing hydrologic connectivity due to permafrost thaw in the lower Liard River valley, NWT, Canada. *Hydrological Processes*, 28, 4163–4178.

DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, 13, 77–81.

Hartmann DL, Klein Tank AMG, Rusticucci M, Alexander LV, Brönnimann S, Charabi Y, Dentener FJ, Dlugokencky EJ, Easterling DR, Kaplan A, Soden BJ, Thorne PW, Wild M, Zhai PM (2013) Observations: Atmosphere and Surface. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Hogg EH, Hurdle PA (1995) The aspen parkland in western Canada: A dry-climate analogue for the future boreal forest? *Water, Air, and Soil Pollution*, 82, 391–400.

Johnstone JF, Chapin FS (2006) Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems*, 9, 14–31.

Johnstone JF, Kasischke ES (2005) Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. *Canadian Journal of Forest Research*, 35, 2151–2163.

Jorgenson MT, Romanovsky V, Harden J, Shur Y, O'Donnell J, Schuur EAG, Kanevskiy M, Marchenko S (2010) Resilience and vulnerability of permafrost to climate change. *Canadian Journal of Forest Research*, 40, 1219–1236.

Mekis É, Vincent LA (2011) An overview of the second generation adjusted daily precipitation dataset for trend analysis in Canada. *Atmosphere-Ocean*, 49, 163–177.

Nakicenovic N, Alcamo J, Davis G, de Vries B, Fenhann J, Gaffin S, Gregory K, Grübler A, Jung TY, Kram T, Lebre La Rovere E, Michaelis L, Mori S, Morita T, Pepper W, Pitcher H, Price L, Riahi K, Roehrl A, Rogner H-H, Sankobski A, Schlesinger M, Shukla P, Smith S, Swart R, van Rooijen S, Victor N, Dadi Z (2000) *Special Report of Emissions Scenarios (SRES), A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom, 595 pp.

Obeso JR (2002) The costs of reproduction in plants. *New Phytologist*, 155, 321–348.

Patankar R, Quinton WL, Hayashi M, Baltzer JL (2015) Sap flow responses to seasonal thaw and permafrost degradation in a subarctic boreal peatland. *Trees - Structure and Function*, 29, 129–142.

Quinton WL, Hayashi M, Chasmer LE (2011) Permafrost-thaw-induced land-cover change in the Canadian subarctic: implications for water resources. *Hydrological Processes*, 25, 152–158.

Salifu KF, Timmer VR (2003) Optimizing nitrogen loading of *Picea mariana* seedlings during nursery culture. *Canadian Journal of Forest Research*, 33, 1287–1294.

Shur Y, Jorgenson MT (2007) Patterns of permafrost formation and degradation in relation to climate and ecosystems. *Permafrost and Periglacial Processes*, 18, 245–258.

Silva LCR, Anand M (2013) Probing for the influence of atmospheric CO_2 and climate change on forest ecosystems across biomes. *Global Ecology and Biogeography*, 22, 83–92.

Soja AJ, Tchebakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Parfenova EI, Chapin FS III, Stackhouse PW Jr. (2007) Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change*, 56, 274–296.

Sultan SE (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, 5, 537–542.

Warren RK (2015) *Examining the spatial distribution of soil moisture and its relationship to vegetation and permafrost dynamics in a subarctic permafrost peatland*. University of Guelph, 53 pp.

5.8. Tables

Table 5.1. Past and predicted 20-year mean annual temperature and total annual precipitation for each of the study sites – Southern Old Black Spruce (SOBS), Scotty Creek (SC), and Inuvik (INVK). 1981-2000 temperature data were acquired online from the Environment Canada Climate Weather Archives (Environment Canada – www.climate.weather.gc.ca) and precipitation data from Environment Canada's Second Generation Adjusted Precipitation Data (Mekis & Vincent, 2011). Predicted climate data is derived from the Third Generation Coupled Global Climate Model produced by the Canadian Centre for Climate Modelling and Analysis. Two scenarios are shown: B1 – a scenario that incorporates the introduction of clean energy and environmental sustainability practices with low population growth; and A1B – a scenario with low population growth but little change toward more environmental sustainability. These scenarios are both described in detail in the IPCC Emissions Scenarios report (Nakicenovic *et al.*, 2000).

	Temperature (°C)			**Precipitation (mm)**		
	1981-2000	**2081-2100**		**1981-2000**	**2081-2100**	
Site		**B1**	**A1B**		**B1**	**A1B**
SOBS	4.51	6.76 ± 0.25	7.76 ± 0.25	502.0	539.7 ± 12.6	577.3 ± 25.1
SC	-2.78	-1.03 ± 0.25	2.03 ± 0.25	466.2	536.1 ± 23.3	536.1± 23.3
INVK	-8.41	-6.16 ± 0.25	-4.66 ± 0.25	318.3	366.0 ± 15.9	397.9 ± 16.0