

TREE RING RESPONSES TO CLIMATE: DROUGHT STRESS SIGNALS DECREASED
RESILIENCE OF NORTHERN BOREAL FORESTS

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By

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ABSTRACT

Unprecedented rates of climate change have increased forest stress and mortality worldwide. Previous research in the boreal forest has largely documented negative growth responses to climate in forest species and habitats characteristic of drier conditions, emphasizing the sensitivity of drier or warmer landscape positions to climate warming. Tree growth responses to recent climate warming may signal changes in the susceptibility of forest communities to compositional change and consequently impact a wide range of ecosystem processes and services. In this study, I explored relationships between climate and radial growth of black spruce, a dominant tree species typical of cool and moist habitats in the boreal forests of North America. I assessed how growth-climate responses varied with stand characteristics and landscape position across four different regions in Alaska and Yukon Territory and found widespread negative correlations between growth and temperature. Decreased tree growth in association with increasing temperatures is generally accepted as a signal of temperature induced drought stress. However, variations in tree growth alone do not reveal the physiological mechanisms behind recent changes in tree growth. Thus, I used stable carbon isotopes to test if the changes in growth were due to physiological drought stress. My results highlight the prominence of drought stress in the boreal forest, even for trees located in cool and moist landscape positions. As mature trees might be able to survive in stressful environmental conditions that do not permit successful post-fire recruitment and survival of seedling, drought stress could affect the resilience of the boreal forest ecosystem to disturbance from fire. I assessed drought stress in pre-fire trees and used post-fire forest compositional changes as a proxy for ecosystem resilience. My results suggest that forest stands with the lowest resilience to disturbance are those that experienced the compounding effects of climate induced drought stress and high fire severity. These sites were generally located at warmer and drier landscape positions, suggesting they are less resilient to disturbance than sites in cool and moist locations. I conclude that as temperatures continue to warm, the loss of boreal forest resilience to disturbance from fire will vary in association with environmental heterogeneity across the landscape.

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CHAPTER 1: INTRODUCTION

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Climate change is affecting the structure and function of forests around the world. Changes to forests such as reduced biomass or altered community structure may compromise the capacity of forest ecosystems to recover from disturbance (Lenton *et al.*, 2008) and possibly push forest ecosystems into alternate states of vegetation cover (IPCC, 2013, Reyer *et al.*, 2015). Resilience theory is a useful framework from which to study the impacts of climate change on forested ecosystems. This theory suggests that forest ecosystems reach a critical threshold response to changing climate and will subsequently shift towards a new regime (Scheffer & Carpenter, 2003). We therefore define resilience as the ability of an ecosystem to absorb the disturbance, re-organize, and maintain structural and functional integrity (Scheffer *et al.*, 2009). When the ecosystem's resilience is exceeded, it will transform to a new state that has different properties, functions, and feedbacks, and from which the probability of return to the previous state is low (Folke, 2006). Environmental stresses can act to decrease ecosystem resilience and in the face of perturbation cause abrupt ecosystem change and shifts to new states (fig 1.1). Forecasting these changes in ecological communities is a major challenge in ecology (Peterson *et al.*, 2003). Moreover, studying ecosystem resilience and the possible factors indicative of decreased resilience will enhance our ability to predict changes in ecological communities in response to rapid climate change and novel environmental conditions.

The boreal forest is an ideal ecosystem to study changing resilience to disturbance. It has undergone significant warming in recent decades, is frequently disturbed by large fires, and recent studies indicate variation in the resilience of this ecosystem to disturbance, resulting in changes in species composition following fire. Boreal forests in northwestern North America have warmed at nearly twice the rate of the global average during the 20th century (ACIA, 2005, IPCC, 2013). In interior Alaska the mean annual air temperature has increased by 1.38°C over the last 50 years (Shulski & Wendler, 2006), whereas precipitation has only increased by 7mm (Hinzman *et al.*, 2005). The slight increases in precipitation in conjunction with large increases in temperature results in higher evapotranspiration rates. This causes reductions in available moisture through changing the precipitation-potential evapotranspiration ratio, resulting in drier growing conditions. Warmer and drier summers in interior Alaska will directly and indirectly effect boreal forest growth, disturbance regimes, and successional trajectories (Haufler, 2010).

In response to the increase in summer temperatures during the last half of the 20th century, recent research in Alaska and northwestern Canada has shown that the growth of coniferous trees has decreased (eg. Barber *et al.*, 2000, Pisaric *et al.*, 2007, Wilmking *et al.*, 2005). The negative correlations between growth and temperature have been attributed to temperature induced moisture stress, summer temperatures surpassing physiological thresholds, increased winter precipitation, decreased amounts of solar radiation due to increased cloudiness, and rapid changes in climate (D'Arrigo *et al.*, 2008 and references within). However, temperature induced moisture stress or drought stress is the most widely accepted explanation for the decrease in conifer tree growth as summer temperatures increase (Barber *et al.*, 2000, Lloyd & Bunn, 2007).

Although vegetation change will likely occur in direct response to climate change, specifically due to drought stress, the most dramatic shifts in vegetation are likely to come from changes in climate altering the patterns of fire disturbance (Allen & Breshears, 1998, Jentsch *et al.*, 2007). Fire is the primary large-scale disturbance agent in the boreal forest of Alaska and northwestern Canada. The fire regime includes attributes of fire such as size, frequency, seasonality, and severity (Weber & Flannigan, 1997). These attributes are strongly linked to weather, and as such, changes in climate will strongly affect the fire regime. In fact, boreal forest fire regimes have already changed in response to warming and drying climatic conditions and continued increases in fire frequency, extent, severity, and fire season length are expected (Balshi *et al.*, 2009, Flannigan *et al.*, 2005, Kasischke & Turetsky, 2006, Stocks *et al.*, 2000).

Changes to the fire regime will strongly influence the successional trajectory of boreal forests (Johnstone *et al.*, 2010a). For example, a shortened fire return interval can result in stands burning when they have not yet reached reproductive maturity and as such are unable to regenerate at densities sufficient to replace pre-fire vegetation (Brown & Johnstone, 2012, Johnstone & Chapin, 2006b). Fire severity and the consumption of surface organic layers is probably one of the most important factors of the fire regime in terms of succession. Severe fires, that decrease the depth of organic matter, will alter the seedbed quality and strongly influence pattern of regeneration (Johnstone & Chapin, 2006a). For example, Johnstone *et al.* (2010a) examined how environmental conditions, fire severity, and stand structure affected successional trajectories in interior Alaska. They found that black spruce stand self-replacement was most

likely to occur at moist sites that burned at low severities, whereas deciduous trees dominated post-fire when the sites were severely burned.

The post-fire successional trajectory is also dependent on pre-fire species composition and their ability to regenerate and establish post-fire. Black spruce, the dominant tree species in the northern boreal forest and the focal species of my thesis, is adapted to the fire-prone boreal forest through the development of large seeds stored in aerial seedbanks. Black spruce is able to produce viable seed at approximately 25 years of age and by 50-100 years of age consistently produces adequate seed for post-fire self-replacement (Viglas *et al.*, 2013). Black spruce has adapted to fire through the production of semi-serotinous cones, meaning the seeds are kept inside the cones with a resinous seal until extreme heat melts the resin and allows large quantities of seeds to disperse (Zasada *et al.*, 1992). The development of aerial seedbanks, resulting from this serotiny (Lamont, 1991), and the production large seeds with adequate carbohydrates enable black spruce to establish following fire, despite the thick, nutrient poor organic layer on which they are commonly located (Viereck *et al.*, 1983). Trembling aspen and paper birch, the dominant deciduous species in northern boreal forests, have light seeds allowing long distance dispersal. The small seeds have fewer reserves, relative to spruce seeds, and therefore cannot support fast rates of seedling root growth, resulting in a poor ability to establish on thick organic layers (Greene *et al.*, 2007, Johnstone & Chapin, 2006a). Therefore they are predominant in areas with a thin organic soil layer (Viereck *et al.*, 1983). Despite their ability for long distance seed dispersal, post-fire establishment of aspen and birch usually occurs asexually as fire promotes root suckering (Lavertu *et al.*, 1993, Rinne *et al.*, 1987). Thus, even low densities of aspen or birch present in the pre-fire stand can result in high densities of young aspen and birch establishing post-fire through suckering (Lavertu *et al.*, 1993). The rates of seedling establishment vary with substrate and the organic layer thickness is particularly important in determining post-fire species establishment and survival. In general, conifer species are likely to persist on sites with a thick organic layer and deciduous species on sites with a shallow organic layer.

A switch from black spruce dominated landscape to more deciduous species is representative of an alternate successional trajectory. Historically, the boreal forest has undergone abrupt changes in species composition following climate change and disturbance. For example, warm periods which increased fire frequencies resulted in more deciduous cover and

cooler periods which experienced fewer fires were dominated by spruce (Kelly *et al.*, 2013). However, we are now reaching a point where climate and the associated effects of climate on the fire regime are beyond the historical range of variability (Kelly *et al.*, 2013). As such black spruce ecosystems may undergo alternate successional trajectories. Successional processes within black spruce boreal forests have historically been observed as a simple cycle of stand self-replacement, with forests burning and recovering to pre-fire vegetation composition at approximately 100 year intervals (Van Cleve & Viereck, 1981). The boreal forest of interior Alaska has maintained this cycle of stand self-replacement for the past 6000 years, indicating that it has been a resilient ecosystem (Chapin *et al.*, 2010, Kelly *et al.*, 2013). However, an altered fire regime acting on an ecosystem undergoing environmental stress, may result in decreased resilience and cause abrupt ecosystem change (fig 1.1). The impacts of climate change on conifer tree growth and productivity could be indicative of the resilience of the boreal forest ecosystem (Johnstone *et al.*, 2010b). Specifically, current regeneration conditions likely differ from those experienced when the previous stand established and mature trees might be able to survive in stressful environmental conditions that do not permit successful post-fire recruitment and survival (Bouchon & Arseneault, 2004). Thus with disturbance from fire, forest stands may be less likely to recover to pre-fire stand densities, resulting in alternate successional trajectories (Johnstone *et al.*, 2010b). As environmental stresses can decrease ecosystem resilience and in the face of disturbance cause changes in stability domains (fig 1.1), we expect that the greatest loss of ecosystem resilience should occur where species are found at their physiological tolerance limits. As such the climate-induced drought response of boreal forest tree growth has the potential to predict landscape variations in resilience.

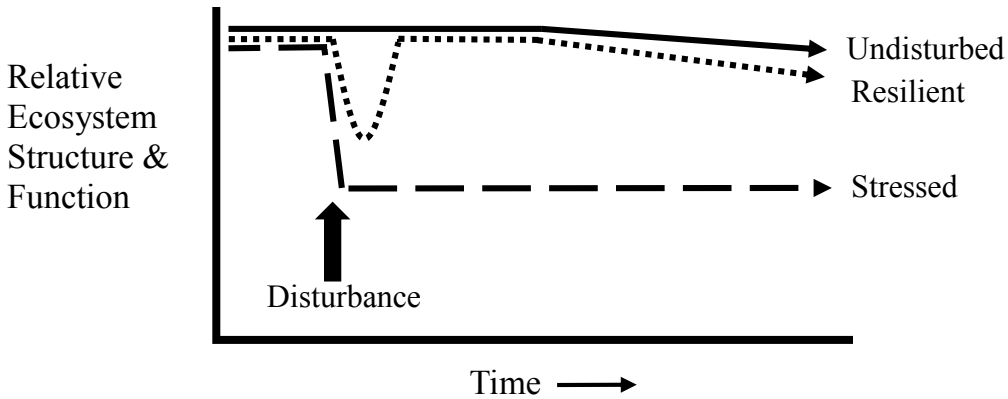


Figure 1.1 Conceptual diagram to depict temporal changes in ecosystem structure and function in association with disturbance and predisposing environmental stress. An undisturbed ecosystem (solid line) may experience gradual changes in relative ecosystem structure and function (i.e. species composition) over time. A resilient ecosystem (dotted line) may temporarily change to a new configuration in response to disturbance, but will soon return to the previous configuration and may then gradually change in the absence of disturbance. An ecosystem experiencing predisposing stress (dashed line) may rapidly change to a new ecosystem state with different structure and function in response to disturbance.

1.2 Tree-Ring Analyses

In response to climate change, forested ecosystems worldwide have experienced drought induced mortality (Allen *et al.*, 2010) and the occurrence of drought stressed trees is becoming significantly more common throughout the boreal forest (Lloyd & Bunn, 2007). Forest drought stress has been identified by satellite based studies (Beck *et al.*, 2011, Verbyla, 2011), long term research plots (Ma *et al.*, 2012), and tree ring analyses (Barber *et al.*, 2000, Lloyd & Bunn, 2007). As the processes involved in tree ring formation integrate the previous and current seasons climatic conditions (Fritts, 1976), the study of the relationship between annual tree rings and climate, known as dendroclimatology, is useful for identifying climatic impacts on forested ecosystems (Fritts, 1976). Understanding the direct and indirect effects of climate on the processing governing tree growth is central for successful dendroclimatic analyses.

Of the climatic factors directly effecting tree growth, temperature is one of the most limiting, through its control on respiration and assimilation processes (Fritts, 1976). The effects of temperature on radial growth are most often associated with growth initiation, as cold weather at the beginning of the season can delay cambial activity resulting in a narrow ring (Fritts, 1976). Once growth has started other factors usually become more limiting, but any period of extremely cool weather, especially at high elevations or latitudes, can limit growth (Fritts, 1976). However, increases in temperature that lead to soil drying through heightened evaporative demands can also negatively impact tree growth. This type of temperature induced moisture stress or drought stress results in decreased conifer tree growth as summer temperatures warm (Barber *et al.*, 2000, Lloyd & Bunn, 2007). Drought stress can be defined as the absence of precipitation for a period of time long enough to result in a shortage of water and injury to the plant (Kramer & Boyer, 1995, Trenberth *et al.*, 2007). Water is essential for plant health and survival. It supplies electrons for photosynthesis, transports mineral and nutrients from the soil to enable plant growth, provides mechanical stability to leaves, prevents overheating, and is the basis of the cytoplasm (Hartmann, 2011). During drought events, soil water conductance is lower than the rate of water uptake by the plant, creating a negative pressure within the xylem (Tyree & Zimmerman, 2002). Once this pressure reaches a threshold, embolisms within the vascular cells occur and the water column ruptures, leading to a partial loss of xylem conductance (Tyree & Zimmerman, 2002). When the drought persists for an extended period of time a total loss of

conductance can occur, causing reduced photosynthetic rates and significant reductions in annual tree ring width (Flexas *et al.*, 2006, Vaganov *et al.*, 2006)

A combination of temperature and precipitation changes throughout the growing season largely determines the overall size and internal structure of the annual ring formed in that particular year (Vaganov *et al.*, 2006). In temperate and boreal forests, low precipitation is generally associated with high temperatures, which enhances water loss and leads to the formation of a narrow annual ring (Fritts, 1976). Not only does the combination of low precipitation and high temperatures in the current season produce a narrow ring but the combination of these environmental variables in the growing seasons prior to ring formation can also lead to a narrow ring (Fritts, 1976). Water stress caused by high temperatures in the years prior to ring formation often result in fewer and smaller leaves, buds, and roots, thus reducing photosynthetic and absorptive tissues on the tree and the storage of carbohydrates (Fritts, 1976). The lack of photosynthetic and absorptive tissue due to past climatic conditions, can limit the radial growth when climatic conditions in the year of ring formation are actually favourable for growth (Fritts, 1976).

Soil temperature, moisture, and content of mineral elements can also significantly influence tree growth (Vaganov *et al.*, 2006). Soil warming and the mobility of moisture within the soil depends on the soil structure; sandy soils will heat faster and to a greater depth and have more available moisture than heavy clay (Lal & Shukla, 2004). Colder soils restrict water uptake and can therefore inhibit growth through limiting hydration (Fritts, 1976). Water movement also brings mineral nutrients to the growth tissues, thus soil moisture content and the ability of the tree to access the water restricts growth through limiting mineral nutrients (Luxmoore, 1991). Trees growing in nutrient and water rich conditions tend to have an increased sensitivity to climatic parameters as they can rapidly adjust to climate variability, whereas trees growing on sites poor in nutrients and water have low amounts of reserves, inhibiting rapid adjustments to annual variations in climate (Leonelli *et al.*, 2008).

Tree growth can also vary relative to aspect, elevation, and latitude. In the northern hemisphere, trees located on south-facing slopes receive more solar energy than those located on northern slopes, resulting in variations of radial growth between individuals otherwise influenced by the same climate (Vaganov *et al.*, 2006). However, the main variations in growth related to aspect, elevation, and latitude are due to differences in growth initiation dates associated with

temperature or photoperiod (Vaganov *et al.*, 2006). Soils on north facing slopes can remain frozen and snow covered for long periods of time, causing a delay in the initiation of growth (Fritts, 1976). Thus, trees located on north slopes, at high elevations, and/or at high latitudes will begin growing later in the season than trees on south facing slopes, lower elevations, and/or lower latitudes (Vaganov *et al.*, 2006). Additionally, at high elevations and northern latitudes soils are often underlain by discontinuous or continuous permafrost. The presence of permafrost and its proximity to soil surface effects drainage and moisture availability and can subsequently influence tree growth (Vaganov *et al.*, 2006).

As tree growth is strongly influenced by climate, dendroclimatological analyses are a valuable method for understanding the impacts of environmental change on forested ecosystems. However, factors associated with topography and soils can significantly impact growth-climate responses resulting in tree ring sensitivity to climate being heterogeneous across the landscape. In order to accurately assess the impacts of environmental change on boreal forest tree growth it is therefore necessary to include the heterogeneity associated with the non-climatic processes governing tree growth.

1.3 Research Objectives and Dissertation Structure

This thesis is organized into three manuscript-styled chapters (Chapters 2-4). Each chapter has been or will be published in peer-reviewed journals and the complete citation and recognition of the copyright holder can be found at the beginning of each chapter. The key research objectives and novel aspects associated with each of the manuscript-styled chapters are as follows.

In Chapter 2 I assess the effects of environmental gradients on the sensitivity of black spruce tree growth to climate throughout the northwestern boreal forest. Although black spruce is a dominant species in the northwestern boreal forest, its response to recent climate warming is poorly documented. I used a novel approach to assess which environmental parameters influenced growth, including regional scale variations in climate, landscape scale variations associated with topographic gradients, and stand scale variations such as tree density and size. I analyzed growth-climate responses of individual trees within sites and use both multivariate statistics and traditional dendroclimatology methods to determine how responses varied between landscape positions and regions. As black spruce grows in a range of edaphic conditions, I

hypothesized that changing constraints on resource availability from temperature- to moisture-limitation across environmental gradients would correspond to changes in the growth-climate responses.

In Chapter 3 I examine patterns of black spruce growth and carbon isotopic composition in tree rings in response to climate warming and drying in the boreal forest of interior Alaska. This chapter builds on the findings of Chapter 2, in which I interpreted decreased tree growth in association with warm spring and summer temperatures as a signal of temperature induced drought stress. In Chapter 3, I provide a secondary line of evidence for physiological drought stress through examining the stable carbon isotope composition of tree rings. I accounted for potential effects of microclimate and moisture availability by sampling on northern and southern aspects at three nested scales: landscape, toposequence, and a subsample of trees within the toposequence. I hypothesized that if the negative correlations between ring-width and warm temperatures is driven by temperature-induced drought stress then the carbon isotope composition of tree rings would indicate physiological drought stress.

In Chapter 4 I examine landscape variations in forest resilience to disturbance in northern black spruce forests of interior Alaska. In this chapter, I use the growth-climate responses of pre-fire trees (identified in Chapter 2 and 3), as an indication of the direct climate effects on potential recruitment following fire. I assessed post-fire regeneration and used the change in pre-fire to post-fire stand composition as a proxy for ecosystem resilience, with sites experiencing the largest change in composition indicative of decreased resilience and an altered successional trajectory. I tested the influence of environmental heterogeneity, fire characteristics, and predisposing climatic stress on the loss of resilience to disturbance and vulnerability of forests to state changes at the landscape scale. I hypothesized that sites experiencing drought stress in combination with severe fires would be most vulnerable to a loss of resilience to disturbance and that this vulnerability would not be uniform across the landscape.

In the final Chapter of this thesis (Chapter 5) I review the main conclusions from each chapter and highlight the significance of this research. I conclude by making suggestions for future research.

1.4 References

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CHAPTER 2: WIDESPREAD NEGATIVE CORRELATIONS BETWEEN BLACK SPRUCE
GROWTH AND TEMPERATURE ACROSS TOPOGRAPHIC MOISTURE GRADIENTS IN
THE BOREAL FOREST

This chapter has been modified from:

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**: 064016.

2.1 Introduction

Global temperature has increased over the past 100 years at an unprecedented rate (IPCC, 2013). This warming has not been uniform. Northern high latitude ecosystems, where the boreal forest resides, have warmed at nearly twice the rate of the global average, particularly during the last 30 years (ACIA, 2005, IPCC, 2013). This warming is estimated to have had substantial impacts on boreal forest productivity and tree growth (Beck *et al.*, 2011, Lloyd & Bunn, 2007). As radial growth is strongly linked to climate, the study of annual tree rings is useful for understanding historical tree growth responses to climate (Fritts, 1976). Changes in tree growth may signal changes in the susceptibility of forest communities to compositional change and consequently impact ecosystem processes and services (Allen *et al.*, 2010, Soja *et al.*, 2007). Thus, examining past responses of tree growth to climate variability enhances our capacity to predict future changes in boreal forest vegetation as climate continues to change.

Declining tree productivity has been detected in observational studies throughout the boreal forest of interior Alaska (Beck *et al.*, 2011) and Canada (Ma *et al.*, 2012), and in satellite-based studies across larger regions (Beck & Goetz, 2011, Lloyd *et al.*, 2011, Verbyla, 2011). However, signals of declining tree productivity are less frequent in the northern, colder portions of latitudinal climate gradients (Lloyd & Bunn, 2007, Lloyd *et al.*, 2011), or in more humid, maritime climate zones (Juday & Alix, 2012, Wilmking & Juday, 2005). These patterns are consistent with the hypothesis that negative responses of tree growth to warming is caused by temperature induced moisture stress, or drought stress (Barber *et al.*, 2000, D'Arrigo *et al.*, 2008). For example, mean annual air temperatures in interior Alaska have increased by 1.9°C over the past 50 years (Karl *et al.*, 2009), while annual precipitation has remained relatively constant (Hinzman *et al.*, 2005). Negative impacts of this warming on boreal tree growth have been associated with species occupying warmer and drier habitat conditions (e.g. Barber *et al.*, 2000, Juday & Alix, 2012, Wilmking & Juday, 2005) and are less frequent among trees growing in moister landscape positions (Johnstone *et al.*, 2010, Wilmking & Myers-Smith, 2008). This suggests that forest sensitivity to climate warming may depend on local moisture availability (Lloyd & Bunn, 2007). Understanding the importance of local context in driving patterns of climate sensitivity is essential for developing an integrated landscape perspective of ecosystem resilience to climate change.

Picea mariana (Mill.) B.S.P. (black spruce) is a dominant tree species in the boreal forests of North America, yet its radial growth response to recent climate change is poorly documented, particularly in rapidly warming regions of western Canada and Alaska (Hinzman *et al.*, 2005). Black spruce grows in a range of edaphic conditions, but is typically found on cold, wet, and nutrient poor soils associated with north-facing slopes and lowlands underlain with permafrost (Viereck *et al.*, 1983). As low soil temperatures restrict nutrient availability and tree growth (Viereck *et al.*, 1983), black spruce forests might respond favourably to recent climate warming. In contrast, if moisture is limiting at drier and warmer sites, then growth at these sites should respond negatively to warming due to temperature induced moisture stress. For example, black spruce in the Tanana flats of interior Alaska showed low sensitivity of radial growth to climate at peatland sites, while trees in higher ground exhibited signals of drought stress (Wilmking & Myers-Smith, 2008). As the distribution of black spruce includes some of the coolest and wettest conditions in the boreal forest, this species provides an excellent system to test the hypothesis that changing constraints on resource availability from temperature- to moisture-limitation across environmental gradients will lead to corresponding changes in the sensitivity of tree growth to climate (Lloyd & Bunn, 2007).

We tested the effect of environmental gradients on the sensitivity of tree growth to climate by examining growth-climate relationships of black spruce trees throughout the northwestern boreal forest. Our approach explicitly incorporated different scales at which environmental parameters may control growth responses, including regional scale variation in climate conditions such as temperature and precipitation; landscape scale variation caused by topographic gradients in elevation, aspect, and slope; and stand scale factors such as tree density and size that influence the local tree environment (Wilmking & Juday, 2005). Traditional dendroclimatology methods consist of building a site chronology by averaging annual ring width measurements of numerous trees within a site and evaluating the chronology's response to climate parameters (Cook & Kairiukstis, 1990). However, opposing tree growth responses (increasing or decreasing) to temperature can occur within a given sample site (Wilmking & Juday, 2005, Wilmking *et al.*, 2004). Here, we analyzed growth-climate responses of individual trees within a site and use both multivariate statistics and traditional dendroclimatology methods to determine how responses varied between landscape positions and regions. Changes in tree growth in response to climate warming may be a key indicator of future alterations in ecosystem

processes and services across heterogeneous forest landscapes (Allen *et al.*, 2010, Soja *et al.*, 2007).

2.2 Methods

2.2.1 Field and Laboratory Methods

In the summer of 2012, we established 36 sites in Alaska, USA and 12 sites in Yukon Territory, Canada in areas with abundant black spruce forest. Sites were located in four regions along the 1) Steese, 2) Dalton, and 3) Taylor Highways in interior Alaska and 4) along the Dempster Highway in northern Yukon Territory (fig 2.1). The four study regions differ in terms of annual and monthly climate conditions (fig 2.2); the Dalton region is relatively cool and dry, the Dempster region cool and moist, the Steese region warm and moist, and the Taylor region warm and dry. Sites were established in pure black spruce stands located within large, recent fire scars dating from 2004 or 2005, to enable planned comparisons between pre-fire tree growth and post-fire regeneration. Site selection was stratified based on broad scale topographic positions affecting drainage (moisture) and incident solar radiation (temperature) (Viereck *et al.*, 1983). Within each region, three sites were selected to represent each category of 1) wet and flat, 2) north-facing midslope (cool), 3) south-facing midslope (warm), and 4) dry and flat positions. Sites in the Steese and Taylor regions have coarse soils and are relatively well drained, whereas a thick cap of fine-grained loess characterizes soils in the Dalton and Dempster regions. The majority (75-80%) of the boreal forest throughout these regions is underlain by permafrost (Osterkamp & Romanovsky, 1999), with the exception of south-facing slopes and floodplains near major rivers (Viereck *et al.*, 1983).

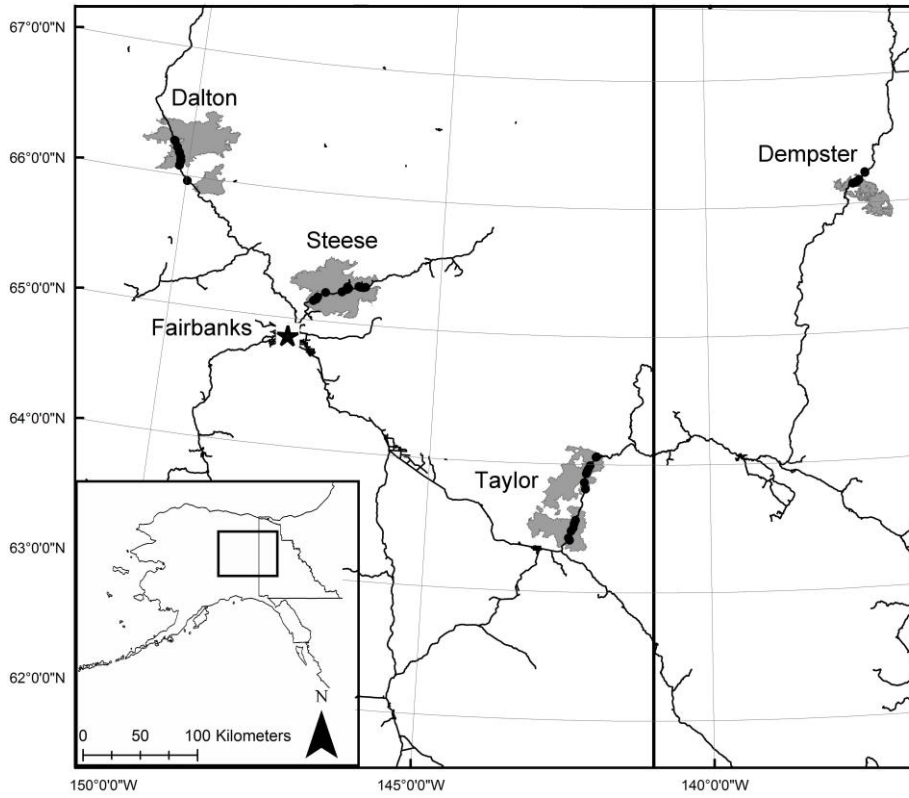


Figure 2.1 Location of forty-eight study sites (black dots) within four regions of recently burned forest (grey), along the Dalton, Steese, and Taylor Highways in interior Alaska and the Dempster Highway in Yukon Territory.

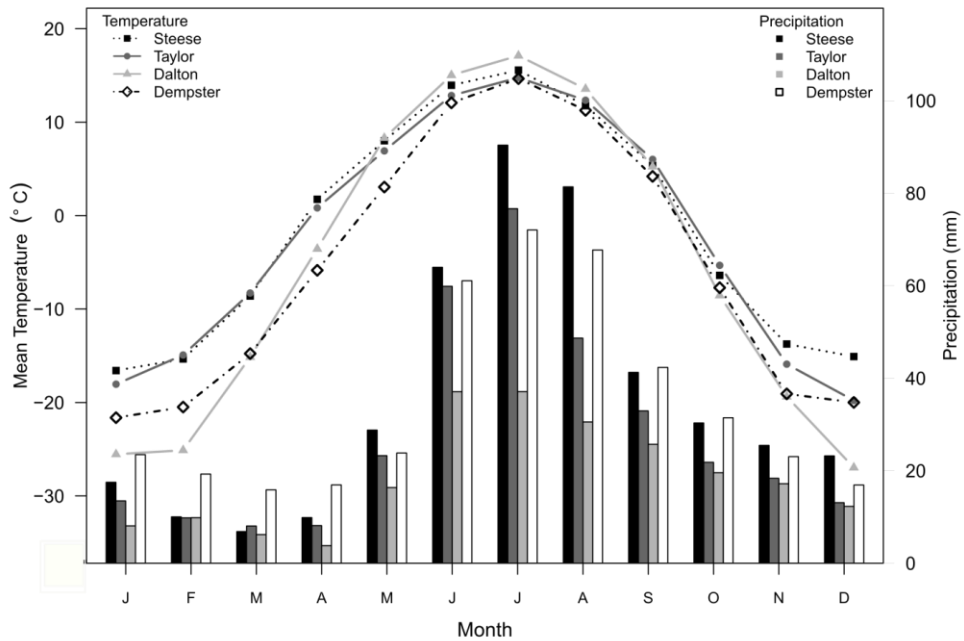


Figure 2.2 Mean monthly temperature (points) and total monthly precipitation (bars; averaged over the period 1974-2003) for each of the four regions examined in this study. Climate data were obtained from the Scenarios Network for Alaska and Arctic Planning (2013).

At each site, we characterized topographic and soil characteristics, and measured the structure and composition of the pre-fire stand (table A2.1). We recorded latitude, longitude, elevation, slope, and aspect, and used these variables for subsequent calculation of insolation, an index of solar radiation received at a site on the summer solstice (as per Bennie *et al.*, 2006). Soil pH was measured in the field for three random samples of near surface mineral soil (A horizon), using an electronic pH meter (Hanna Instruments) and 1:1 dilution with de-ionized water. Moisture classes, based on topography-controlled drainage and adjusted for soil texture, were assigned to each site on a six-point scale, ranging from xeric to subhygric (Johnstone *et al.*, 2008). Within each site, we measured the diameter at breast height (DBH) of all the pre-fire trees (> 1.4 m in height) originally rooted within two parallel 2 m X 30 m belt transects to calculate stand basal area (m²/ha of trees >1.4 m in height). At each site, we collected a total of 10 stem disks at the standard height of 1.4 m from randomly selected pre-fire black spruce trees along two belt transects. In the laboratory, the disks were sanded with increasingly fine sandpaper (up to 400 grit) to produce visible rings. Annual rings widths were measured (resolution 0.001 mm) on two radii per stem disk using WinDENDRO software version 2012c (Regent Instruments, 2011).

2.2.2 Statistical analysis

To prepare the ring width measurements for growth-climate analyses, we visually cross-dated each tree-ring series against master chronologies developed for each site and region. We quality-checked our crossdating using COFECHA version 6.06 (Grissino-Mayer, 2001). Successfully dated ring-width series were analyzed in R version 3.0.2 (R Development Core Team, 2011). Non-climatic trends in ring growth were removed by detrending raw ring widths with a smoothing spline, with a frequency response of 0.5 at a wavelength of $0.67 * n$ years (Zang, 2010) in the package ‘dplR, version 1.5.7’ (Bunn, 2010). This detrending option is known to remove variances of low frequencies (i.e. longer wavelengths) with little or no removal of variance of high frequencies (i.e. shorter wavelengths) (Cook & Holmes, 1996). Dividing actual ring-widths by the curve-fitted value in each year produced a dimensionless width index for each series (Bunn, 2010, Cook & Briffa, 1990). Individual tree chronologies were constructed by averaging the two detrended ring-width series for each tree.

We determined the growth-climate response of individual trees by calculating bootstrapped correlations between ring widths and mean monthly temperatures and total monthly

precipitation for 1975 to 2003 using the package ‘bootRes, version 1.2.3’ (Zang, 2010). We chose to analyze growth-climate responses over this thirty-year period to maximize the number of trees to include in the analysis and to circumvent the divergence problem (D'Arrigo *et al.*, 2008). We used downscaled climate data from SNAP (Scenarios Network for Alaska and Arctic Planning 2013) to provide climate records for each of the four regions examined in this study (see Appendix 1). We calculated growth-climate correlations using a 17-month climate window, extending from April of the year preceding growth to August of the current year of growth (Fritts, 1976). The significance of each of the 34 climate correlations was determined from 95% confidence intervals (Zang, 2010).

We grouped trees within each region according to their dendroclimatic responses through a hierarchical agglomerative cluster analysis (HCA) using Euclidean distances and Ward's linkage method in the package ‘vegan, version 2.0-10’ (Oksanen *et al.*, 2013). HCA begins with each object (individual trees in this case) in a separate cluster and then joins objects into groups based on their similarity (growth-climate correlations in this case) (Legendre & Legendre, 2012). The outcome is a grouping in which trees that are in the same cluster resemble each other in terms of their dendroclimatic responses. Long stems indicate natural groups in the dendrogram; consequently, we examined branch length to identify the optimal number of clusters (Legendre & Legendre, 2012). We characterized the growth-climate responses of each HCA groups by calculating the average correlation between individual chronologies in a group and the climate variables representing mean monthly temperature and total precipitation over 17 months. Significance of average correlations was based on 95% confidence intervals.

We completed a simple redundancy analysis (RDA) (Legendre & Legendre, 2012) in ‘vegan’ to determine whether environmental and stand variables collected at each site (table A2.1) could explain the observed variability in dendroclimatic responses. We included geographic coordinates in the explanatory matrix to account for spatial non-independence, and tree DBH to capture any size-related effects. RDA is an ordination technique based on a multiple linear regression model, which relates the variability in multivariate responses to a set of explanatory variables (Legendre & Legendre, 2012). To identify the individual variables within the explanatory dataset that were significantly associated with variation in dendroclimatic responses, we ran a stepwise forward selection, using model adjusted R^2 and variable retention at

a permutation value of 0.05 (Blanchet *et al.*, 2008). The significant variables from this selection process were retained for the RDA.

To visualize multivariate differences in dendroclimatic responses among the groups obtained from the HCA, we performed a principle component analysis (PCA) using the package ‘labdsv, version 1.6-1’ (Roberts, 2013). We explored which environmental and stand variables were associated with the variance in dendroclimatic responses by calculating vectors overlays of explanatory variables in ‘vegan’. The significance of the fitted vectors was determined using 999 permutations of the explanatory variables and tested using the 95 percentile range. We then plotted the significant vectors ($p < 0.05$) as radiating lines from the centroid of PCA ordination scores, where the angle and length of the vectors indicate the direction and strength of the relationship (McCune & Grace, 2002). Additionally, we plotted the proportion of individuals for each site type belonging to each climate response group defined by the HCA.

To assess how site types varied in their growth responses to climate, we took a more traditional dendrochronology approach and created mean chronologies based on topographic classes (dry flat, wet flat, north facing slope, and south facing slope) in the package ‘dplR, version 1.5.7’ (Bunn, 2010). General chronology statistics of mean correlation between trees (R), mean sensitivity (MS), signal to noise ratio (SNR), autocorrelation (AR), and expressed population signal (EPS) for each of the standard chronologies developed per site type and region were calculated to ensure that all the chronologies were suitable for growth-climate analyses (Speer, 2010). We then determined the growth-climate responses of each site type using the same methods as for individual chronologies (see above).

2.3 Results

Two distinct groups of growth-climate responses were identified by the HCA in each region (fig 2.3(a,b,c,d)). Slightly more than half of the trees were classified as ‘Group 1’ in the Taylor, Dalton, and Dempster regions (53.9, 53.2, and 57.3 % respectively). In contrast, more trees (58.9 %) were classified as ‘Group 2’ in the Steese region. Correlations between temperature variables and ‘Group 1’ trees were not consistent between the four regions. This group showed positive responses to current summer temperatures in the Steese (fig 2.3(e)) and Dalton (fig 2.3(g)) regions, and negative responses to winter temperatures in the Steese (fig 2.3(e)), Dalton (fig 2.3(g)), and Dempster (fig 2.3(h)) regions. Further, positive correlations

between ‘Group 1’ trees and previous growing season temperatures were found for trees in the Dempster region (fig 2.3(h)). As ‘Group 1’ trees did not consistently respond to temperature among the different regions, we refer to them as ‘mixed responders’. This naming reflects the lack of consistent, significant correlations detected between growth of ‘Group 1’ trees and spring and summer temperatures. ‘Group 2’ trees from all four regions had ring-width chronologies that were consistently and negatively associated with temperature variables (fig 2.3 (e,f,g,h)), thus we refer to these trees as ‘negative responders’. Negative responders across all regions showed consistent negative correlations between growth and temperature in current April, current May, and previous July.

Correlations with precipitation were more variable and not consistent among regions or groups. In the Steese (fig 2.3(i)) and Dalton (fig 2.3(k)) regions, ‘Group 1’ mixed responders were positively correlated to precipitation, whereas in the Taylor (fig 2.3(j)) and Dalton (fig 2.3(l)) regions, mixed responders were predominantly negatively correlated with precipitation throughout the year. Correlations with precipitation and ‘Group 2’ negative responders were highly variable: few correlations were observed in the Steese (fig 2.3(i)) and Dalton (fig 2.3(k)) regions, positive correlations with previous growing season and winter precipitation were observed in the Taylor region (fig 2.3(j)), and negative correlations with winter precipitation were observed in the Dempster region (fig 2.3(k)).

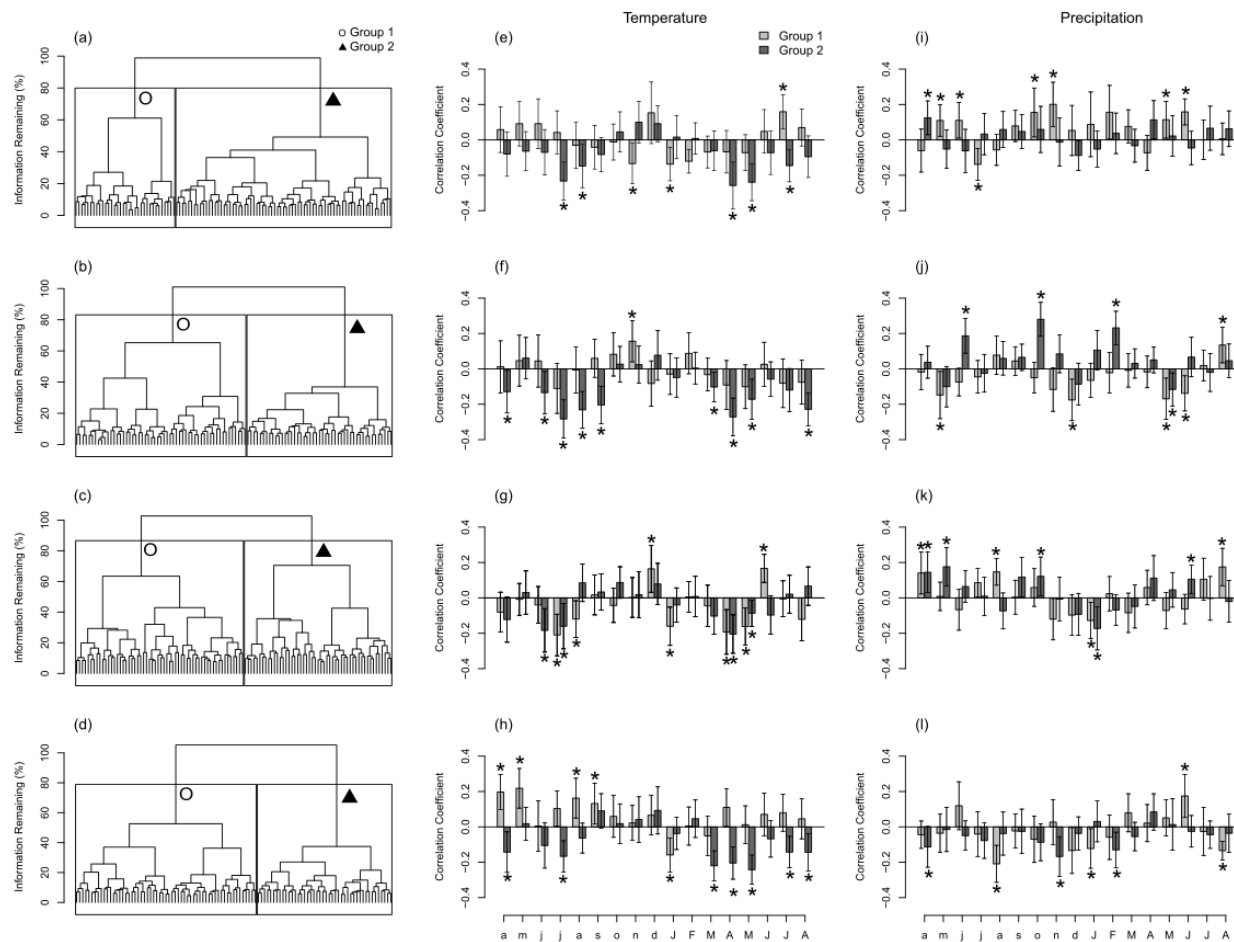


Figure 2.3 Hierarchical agglomerative clustering analysis (HCA) dendrograms and average correlations between mean monthly temperature and precipitation for trees in the Steese (a,e,i), Taylor (b, f, j), Dalton (c,g,k), and Dempster (d,h,l) regions. Dendrograms separate (a) 107 trees, (b) 102 trees, (c) 109 trees, and (d) 103 trees into two distinct groups based on dendroclimatic correlation coefficients. Length of nodes represents distinctness of groups. Individual tree ring width series from group 1 (light grey) and group 2 (dark grey), defined by the HCA, were used to calculate average correlations between mean monthly temperature and precipitation over a 17 month climatic window. Y-axes in e-l represent correlation coefficients with 95% confidence intervals (* =significant) and X-axes represent months of year (lower case= year prior to ring formation, uppcase=year of ring formation).

Negative and mixed responders were located in all of the topographic classes we sampled across all four regions, and were not strongly associated with the environmental and stand covariates that we measured. Stepwise selection of covariates chose two to four significant variables for each region (table 1). RDA ordination of dendroclimatic responses constrained by these covariates indicated that the measured environmental variables explained a small portion of the variation in dendroclimatic responses, e.g. between 6.1 and 12.1% of the variation in growth-climate responses within each region (table 1 and table A2.2). The PCA correlation biplot of dendroclimatic responses overlaid with vectors of significant covariates suggests that there were some associations between environmental variables and groups defined by the HCA, but these associations were not consistent among regions (fig 4). The proportion of individuals in each of the HCA response groups did not consistently vary across topographic classes (fig 4). However, there was some indication that negatively responding trees dominated south facing slopes in interior Alaska, particularly in the Steese region. In contrast, in the Dempster region, we observed a slight tendency for negatively responding trees to be found on north facing slopes or wet lowlands (fig 4).

Table 2.1 Environmental and stand covariates selected by forward stepwise selection for redundancy analysis. The order of variable selection is shown. Individual R^2 of each individual variable is based on RDA analyses with only the single covariate included. The total variation is for the full RDA model with all selected covariates included.

Highway	Variable	R²	Order selection
Steese	Insolation	0.062	1
	Longitude	0.053	2
	Total Variation	0.087	
Taylor	Black Spruce Density	0.042	1
	Moisture Class	0.034	2
	Total Variation	0.061	
Dalton	Latitude	0.032	1
	Slope	0.025	2
	Aspect	0.022	4
	Black Spruce density	0.026	5
	Total Variation	0.121	
Dempster	DBH	0.041	1
	Soil pH	0.031	2
	Elevation	0.013	3
	Total Variation	0.089	

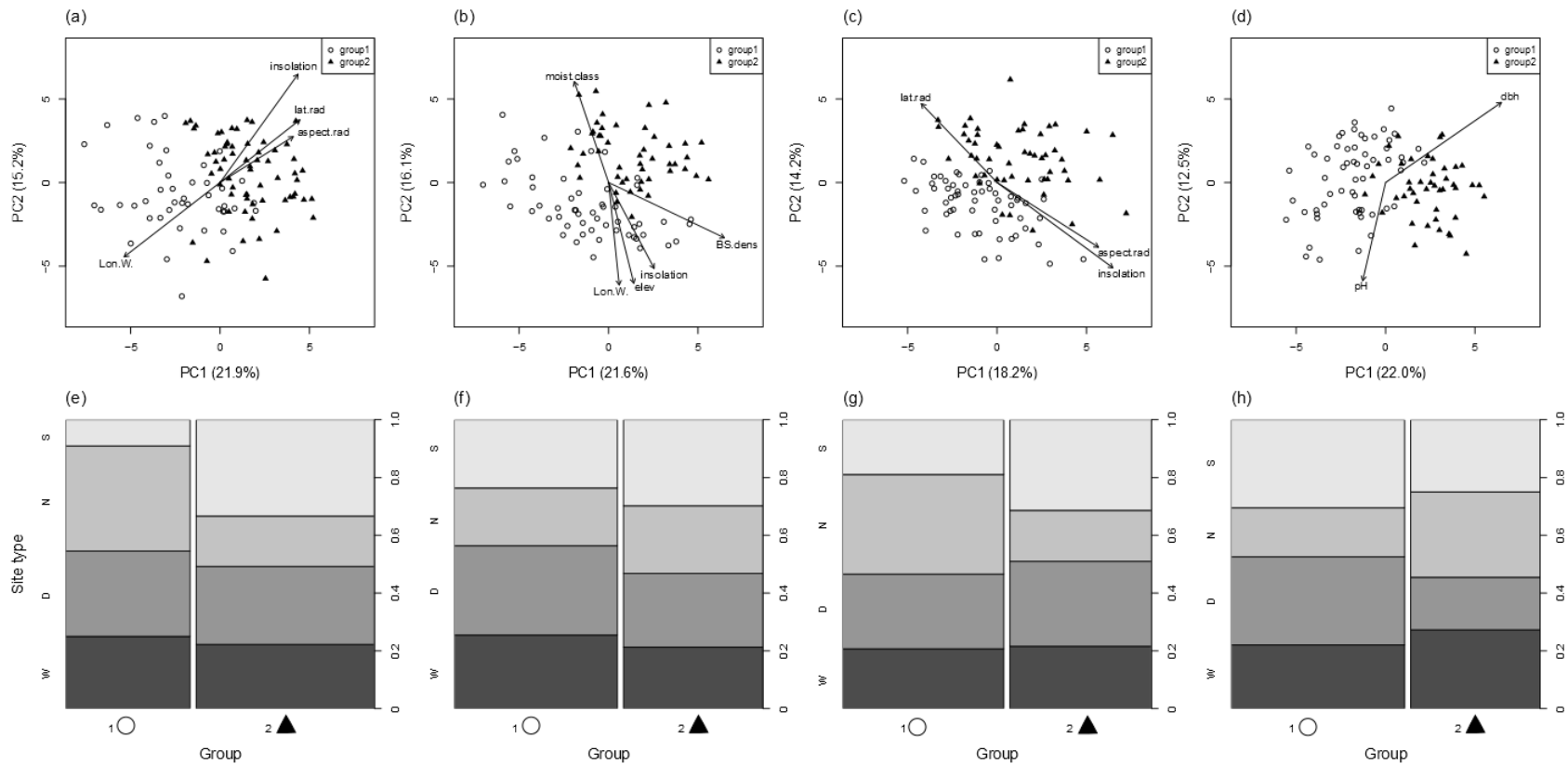


Figure 2.4 Principal component analysis (PCA) correlation biplot of dendroclimatic responses overlaid by the significant vectors of environmental covariates. Separate panels show trees sampled in the (a) Steese, (b) Taylor, (c) Dalton, (d) and Dempster regions. Points represent individual trees belonging to each group (Group 1 = mixed responders (O), Group 2 = negative responders (▲)). The lower panels show the proportion of individual trees associated with each topographic class (S=south, N=north, D=dry, W=wet) belonging to each group, in the (e) Steese, (f) Taylor, (g) Dalton, and (h) Dempster regions.

Standard, averaged chronologies based on site types within regions produced chronology statistics indicating they were suitable for climate analysis (table 2). Within the interior Alaska regions, these chronologies demonstrated a negative growth response to previous growing season temperature (July) and current spring temperatures (April and May) at most site types (fig A2.1). Radial growth responses of trees to temperature in the Dempster region did not follow a similar pattern to trees in interior Alaska; they responded negatively to previous August and December precipitation and did not show consistent temperature responses across site types (fig A2.2).

Table 2.2 Statistics of mean correlation between trees (R), mean sensitivity (MS), signal to noise ratio (SNR), autocorrelation (AR), and expressed population signal (EPS) for each of the standard chronologies developed per topographic site class and region.

Region	Site class	# Trees	R	MS	SNR	AR	EPS
Steese	South facing slope	25	0.576	0.194	33.962	0.223	0.917
	North facing slope	27	0.331	0.186	13.359	0.311	0.713
	Dry - flat	29	0.330	0.173	14.284	0.251	0.707
	Wet - flat	25	0.460	0.214	21.296	0.176	0.848
Taylor	South facing slope	27	0.423	0.191	19.794	0.319	0.836
	North facing slope	22	0.367	0.179	12.755	0.316	0.706
	Dry - flat	29	0.375	0.205	17.400	0.380	0.869
	Wet - flat	24	0.316	0.202	11.088	0.382	0.628
Dalton	South facing slope	27	0.465	0.214	23.467	0.242	0.863
	North facing slope	29	0.595	0.204	42.605	0.181	0.936
	Dry - flat	30	0.397	0.217	19.751	0.297	0.823
	Wet - flat	23	0.435	0.211	17.707	0.139	0.813
Dempster	South facing slope	29	0.488	0.241	27.641	0.280	0.877
	North facing slope	25	0.448	0.231	20.290	0.300	0.797
	Dry - flat	27	0.540	0.243	31.696	0.157	0.902
	Wet - flat	26	0.426	0.224	19.296	0.301	0.801

2.4 Discussion

The most common and consistent pattern of black spruce growth responses to climate was a negative response to warmer temperatures in the previous growing season and current spring. In contrast to our expectations, landscape position was a poor predictor of the variation in growth responses to climate in any of our studied regions. Previous studies have found that climate responses of boreal conifers varied within sites and the proportion of trees with negative responses to summer temperatures changed across longitudinal or latitudinal gradients of precipitation and temperature (Juday & Alix, 2012, Lloyd *et al.*, 2011, Wilmking & Juday, 2005), or across local moisture gradients (Johnstone *et al.*, 2010, Wilmking & Myers-Smith, 2008). Thus, we expected that signals of temperature-induced drought stress in tree growth responses would vary among regions and topographic classes based on relative moisture availability. However, in interior Alaska, we found only weak evidence for our hypothesized association between negative temperature responses and warmer, drier landscape positions, and in the Yukon, negative responders showed a tendency to be associated with cooler and wetter landscape positions. Irrespective of topography, radial growth was typically negatively correlated with temperature variables and showed inconsistent responses to precipitation, except in the cool and moist Dempster region, where tree growth showed consistent negative associations with precipitation. Our results indicate that future warming, particularly in spring (April and May), may negatively influence the radial growth of black spruce trees across a broad region, and that this response is not ameliorated by local gradients in moisture availability. We discuss our results in terms of the heterogeneity in black spruce growth-climate responses we observed between regions, among landscape positions, and within sites.

The most widely accepted explanation for negative growth responses to warm spring and summer conditions is temperature-induced moisture stress (Barber *et al.*, 2000, Lloyd & Bunn, 2007). Warmer temperatures during the previous growing season can result in a reduction of photosynthetic tissue, which limits radial growth the following year (Fritts, 1976). Increased spring (April and May) temperatures may also induce drought stress through stimulation of photosynthesis and transpiration of evergreen foliage prior to soil thaw, when there is insufficient water transport from roots to support evaporative demands (Berg & Chapin, 1994). Because moisture limitation is more likely in warmer and drier landscape positions (e.g. Lloyd & Bunn, 2007), we expected to see negative temperature responses in upland and south-facing slopes, but

were surprised to find these equally prevalent in cooler and wetter landscape positions. Studies of white spruce in Alaska have documented similar patterns of reduced tree growth in response to warm spring temperatures at cool and moist sites near treeline (Ohse *et al.*, 2012, Wilmking & Juday, 2005). We hypothesize that negative temperature responses in cool and wet locations are associated with vertical patterns in the distribution of roots. Trees in cool and wet locations often have roots that are confined to shallow surface layers to avoid anaerobic and cold soil conditions in deeper soil layers (Islam & Macdonald, 2004, LeBarron, 1945). This rooting structure may render black spruce trees ineffective at water and nutrient uptake during periods when the active layer depth increases and the water table lowers (Dang & Lieffers, 1989), particularly on north facing slopes where moisture may drain downslope as the active layer thaws (Jorgenson & Osterkamp, 2005). Likewise, cooler landscape positions may experience delays in the timing of spring thaw, thus extending the risk of early season moisture deficits when roots are frozen (Berg & Chapin, 1994).

Although there were widespread similarities in the pattern of black spruce radial growth responses to previous growing season and current spring temperatures, we did detect some regional differences in dendroclimatic responses. Specifically, radial growth in the Dempster region exhibited a consistent and negative response to fall and winter precipitation, whereas radial growth in interior Alaska was more strongly correlated with spring and summer temperature variables. These regional differences in dendroclimatic responses likely reflect different climatic constraints on tree growth among study regions. Specifically, the Dempster region was relatively cooler and wetter in winter over the study period than the interior Alaska regions, and thus Dempster trees were more likely to experience conditions of adequate moisture during summer. Negative responses of Dempster trees to autumn and winter precipitation may reflect indirect effects on growth caused by mechanical damage from a heavy snow load. Additionally, precipitation that falls as snow has been linked to a delay in the start of the growing season and reduced radial growth (Vaganov *et al.*, 1999).

In this study, we used both multivariate statistics and traditional methods of tree ring analysis to explore black spruce growth-climate responses. The multivariate analysis indicated common patterns of negative growth responses to previous growing season and current spring temperatures, and highlighted the heterogeneity in growth-climate responses among individual trees within sites. This within site variability is often missed in standard dendrochronology

studies, where individual tree chronologies are averaged together. Previous research examining individual tree growth of white spruce near treeline in Alaska found that growth responses to warming were positive, negative, or neutral and could not be predicted by landscape position or site type (Wilmking & Juday, 2005). Our study expands upon this research to document variations in black spruce responses that were largely unrelated to topographic gradients in moisture availability for a species that dominates cool and moist environments within the contiguous boreal forest (Viereck *et al.*, 1983). Individual tree characteristics and their ability to compete for resources may explain some of the within site variability we detected. However, we found no relationship between growth-climate responses and factors likely to be associated with competition, such as stand density, tree age, and tree DBH. Within site variation in dendroclimatic responses could also be due to genetic variation between individuals (Wilmking & Juday, 2005) or small-scale variability in soil conditions and nutrient availability (Pastor *et al.*, 1999). We did not address these possibilities but believe they warrant further investigation.

2.5 Conclusion

Our assessment of dendroclimatic responses within interior Alaska and northern Yukon suggests that the effects of continued warming on black spruce tree growth will largely be negative. Negative responses to spring and summer temperature were widespread, occurring at all landscape positions and in all regions. As black spruce is a dominant tree species in the boreal forest, its response to continued warming will play a key role in driving forest responses to climate change. Our results suggest that black spruce productivity is likely to decline across broad areas of boreal forest with continued warming. This response is apparent even in cool and moist environments that are expected to be resistant to temperature-induced drought stress (e.g. Lloyd & Bunn, 2007), and where black spruce has dominated for millennia (Hu *et al.*, 1993). The widespread pattern of negative growth responses of black spruce to temperatures that we observed across topographic moisture gradients may be an important warning signal of broad-scale vulnerability of boreal forests to ongoing climate change.

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CHAPTER 3: STABLE CARBON ISOTOPE ANALYSIS REVEALS WIDESPREAD
DROUGHT STRESS IN BOREAL BLACK SPRUCE FORESTS

This chapter has been modified from:

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

Unprecedented rates of climate change over the past century have impacted forested ecosystems worldwide (IPCC, 2013). Specifically, the combination of altered disturbance regimes and climate warming has increased forest stress and mortality over the past decade (Allen *et al.*, 2010, Carnicer *et al.*, 2011). As models project continued climate change and widespread increases in aridity, drought stress and associated forest dieback is a global concern (IPCC, 2013, Seager *et al.*, 2007). Increases in drought stress could alter the composition, structure, and biogeography of forests, fundamentally changing a wide range of ecosystem processes and services (Allen *et al.*, 2010, Soja *et al.*, 2007). Although much research has focused on drought in semi-arid forested regions, drought is also of serious concern for continental regions of boreal Alaska, Canada, and Eurasia (Soja *et al.*, 2007). As boreal forests contain approximately 30% of global terrestrial carbon (McGuire *et al.*, 2009), changes in boreal forest productivity, structure, and/or composition could alter the global carbon balance and have significant implications for the global climate system (Ma *et al.*, 2012, Piao *et al.*, 2008). Thus, understanding how warming has affected boreal forests is imperative for predicting future climate change through vegetation/climate feedbacks of carbon cycling and other ecosystem processes (Euskirchen *et al.*, 2010, Tarnocai *et al.*, 2009).

Tree rings have long been used as a proxy for past climatic conditions and environmental changes (Fritts, 1976), however there is still uncertainty regarding the specific mechanisms by which climate conditions, particularly drought, affect tree ring width (Vaganov *et al.*, 2006). Tree growth occurs when carbon dioxide is captured from the atmosphere and fixed into carbohydrates via photosynthesis. The physical processes and chemical reactions that take place during photosynthesis determine the carbon isotopic composition of the plant material. Specifically, environmental conditions that control the rate of stomatal conductance and photosynthesis influence the stable carbon isotope ratios in tree rings (McCarroll & Loader, 2004). For example, when a tree is moisture stressed, stomatal closure reduces the uptake of CO₂ and reduces discrimination against ¹³CO₂ during photosynthesis, resulting in a higher ratio of ¹³C to ¹²C in tissue produced. Taking into account the isotopic composition of atmospheric CO₂, these ratios are expressed as the carbon isotope discrimination ($\Delta^{13}\text{C}$), which represents discrimination against ¹³CO₂, thus lower $\Delta^{13}\text{C}$ values indicate increased stomatal regulation and physiological moisture stress (McCarroll & Loader, 2004).

In the North American boreal forest, decreased tree growth in response to increasing summer temperatures is generally accepted as a signal of temperature induced moisture stress or drought stress (Barber *et al.*, 2000, Lloyd & Bunn, 2007). As tree ring stable carbon isotopes are controlled by photosynthetic rate and stomatal conductance in response to environmental conditions (McCarroll & Loader, 2004), they can provide evidence of physiological moisture stress in response to climatic variations (e.g. Barber *et al.*, 2000). However, growth and $\Delta^{13}\text{C}$ responses to regional climate may be affected by site-specific topographic factors, as differences in solar insolation associated with slope and aspect, as well as drainage class, results in microclimate variability (Daly *et al.*, 2002). A key component of forest microclimate is soil moisture availability, which is driven by variations in soil and air temperature, evaporation and transpiration rates, solar radiation, and edaphic conditions, and often varies along topographic gradients (Chen *et al.*, 2007, Devito *et al.*, 2005). It has long been recognized that such gradients in soil moisture availability can influence forest ecosystem structure and function (Whittaker, 1956), and affect tree photosynthetic capacity, growth, and physiological stress responses (Chen *et al.*, 2007). For example, when water availability is limiting, higher solar radiation and evaporation rates associated with southern aspects may enhance the physiological impacts of soil dryness (Devito *et al.*, 2005).

In this study, we investigated the variation of black spruce radial growth and carbon isotope discrimination in tree rings in relation to climate in interior Alaska. Interior Alaska has experienced a mean annual air temperature increase of 1.9°C over the past 50 years (Karl *et al.*, 2009), and widespread declines in the productivity of boreal tree species over this period have been interpreted as a sign of drought stress (Beck *et al.*, 2011). Negative associations between radial growth and temperature, initially identified in upland white spruce (Barber *et al.*, 2000), have now been found to be widespread in black spruce, even within the cooler and moister parts of its distribution in Alaska and NW Canada (Walker & Johnstone, 2014, Wilmking & Myers-Smith, 2008). However, it remains unclear if these growth-climate associations in cool and moist microclimates arise from the same processes that have been detected from sites where warm, well-drained soils make drought stress a highly plausible mechanism. Our first objective was to assess if black spruce radial growth varied between stands on southern versus northern aspects. Secondly, we identified the climatic factors influencing radial growth in order to confirm the expected signals of moisture stress observed in broad scale studies of ring-width chronologies of

black spruce across interior Alaska and Yukon (Beck *et al.*, 2011, Walker & Johnstone, 2014). Our third objective was to assess if tree-ring $\Delta^{13}\text{C}$ responses supported the interpretation of drought stress as the proximal driver of radial growth responses to climate. Specifically, we hypothesized that if temperature-induced drought stress is driving the widespread patterns of negative ring-width correlations with temperature then the C isotope composition of tree rings should be consistent with the isotopic signature of physiological drought stress, specifically the $\Delta^{13}\text{C}$ time series should be negatively correlated with temperature. Our expectation was that trees on a southern aspect would be more vulnerable to temperature induced moisture stress, and would therefore have lower $\Delta^{13}\text{C}$, compared to trees on a northern aspect. Our results provide an alternate line of evidence to investigate whether increases in drought stress associated with warmer temperatures are sufficient to explain the widespread negative correlations between tree growth and temperature across topographic gradients in microclimate in the northern boreal forest.

3.2 Material and Methods

3.2.1 Field and Laboratory Methods

In the summer of 2012, we established 18 sites in three regions of interior Alaska (fig 1). Within each region, we sampled six sites, three on north facing and three on south facing slopes, in order to capture microclimate variability associated with topographic gradients. Additionally, we sampled six sites on a toposequence within the Poker Flats Research Range (PFRR), in the Steese Highway sample region, where there was a site on the upper ridge, midslope, and toeslope portions of a north facing and a south facing slope, respectively. At each site, based on topography, soil texture, and drainage conditions, we classified site moisture on a six-point scale, ranging from xeric to subygric (Johnstone *et al.*, 2008) and measured the structure and composition of the pre-fire stand (table 3.1). All sites were established in pure black spruce stands located within large, recent fire scars dating from 2004, which allowed us to collect complete stem disks without concerns for causing tree mortality. The 2004 fires had killed close to 100% of the trees at all sampled sites, but rarely consumed more than the needles and fine twigs on the trees (Boby *et al.*, 2010), and stem sections were complete and undamaged at the time of sampling. At each site, we collected 10 stem disks at the standard height of 1.4 m from randomly selected pre-fire black spruce trees along two belt transects. Stem disks were sanded

with increasingly finer sandpaper, up to 400 grit, to produce clearly visible rings. There were no signs of decomposition in the sampled disks, and stem wood is typically well-preserved for decades in these northern post-fire stands (Boulanger & Sirois, 2006). Total annual ring widths were measured (resolution 0.001 mm) on two radii per stem disk using WinDENDRO software version 2012c (Regent Instruments, 2012). For the subsampled trees on the toposequence, we also measured and recorded earlywood width. The placement of the earlywood to latewood boundary was identified by setting the definition parameter in WinDENDRO to 25% of the difference between maximum and minimum light intensity. We visually cross-dated each tree-ring series against master chronologies developed for each site and region. We quality-checked our crossdating using COFECHA version 6.06 (Grissino-Mayer, 2001). Successfully dated ring-width series were analyzed in R version 3.0.2 (R Development Core Team, 2012).

Table 3.1 Site ID, location, environmental variables, and stand characteristics of the 24 sample sites.

	Site Type ^a and ID	Latitude (N)	Longitude (W)	Elevation (m.a.s.l)	Slope	Aspect	Insolation ^b	Moisture Class ^c	Black Spruce basal area (m ² /ha)	Black Spruce Density (stems/m ²)	Age (# rings)	Diameter Breast Height (cm)
Steese Region	N1	65.15128	147.3421	271	20.5	330	0.488	3	2.5	0.208	59	5.9
	N2	65.16572	147.29	252	27	320	0.42	3	0.02	0.002	104	5.7
	N3	65.28393	146.7349	507	16	330	0.549	3	4.97	0.283	47	6.0
	S1	65.26212	146.7543	387	0	170	0.74	2	11.06	0.442	64	6.1
	S2	65.29468	146.5243	468	12.75	170	0.868	2	10.14	0.242	63	8.5
	S3	65.29327	146.3917	485	14	219	0.845	2	4.3	0.167	63	6.6
Dalton Region	N1	66.26032	150.3361	523	6.5	330	0.656	2	8.13	0.117	57	10.1
	N2	66.21182	150.2578	464	11.5	20	0.585	3	6.79	0.550	59	5.5
	N3	66.11195	150.1569	464	8.5	342	0.626	2	6.9	0.167	53	9.1
	S1	66.2556	150.321	518	4.25	150	0.77	2	10.91	0.158	56	12.4
	S2	66.073	150.1684	218	15	168	0.88	1	12.48	1.075	56	5.4
	S3	66.07135	150.1691	194	8.5	160	0.818	2	11.98	0.558	55	6.0
Taylor Region	N1	66.9617	142.163	665	5.5	31	0.659	5	4.83	0.708	65	4.7
	N2	63.56224	142.3734	857	8.5	12	0.657	3	14.12	0.267	93	7.2
	N3	63.42263	142.4914	840	21.75	33	0.502	2	10.99	0.208	122	7.4
	S1	63.94592	142.1853	611	10	220	0.831	3	23.72	0.550	128	9.0
	S2	63.53502	142.3952	870	6.25	195	0.824	2	29.34	0.708	72	6.1
	S3	63.47665	142.4491	825	5	210	0.807	2	11.34	0.708	68	6.2
Rocket Range Toposequence	N1	65.12058	147.4474	374	16.5	10	0.522	5	3.11	0.258	101	5.3
	N4	65.11866	147.4455	442	12.75	10	0.577	3	4.16	0.467	62	5.8
	N5	65.11803	147.4448	457	8.5	10	0.636	3	9.22	0.633	51	4.6
	S1	65.11415	147.4317	470	11.5	190	0.859	2	10.29	0.208	55	10.1
	S4	65.11598	147.4317	496	3.5	190	0.781	2	12.52	0.242	50	9.8
	S5	65.11656	147.4314	498	2.5	190	0.77	1	10.95	0.300	59	8.5

^a Site Type N=north facing, S=south facing

^b A calculated index of the amount of solar radiation received at a site on the summer solstice.

^c Ranking of site moisture: 1=xeric, 2=subxeric, 3=subxeric to mesic, 4=mesic, 5=submesic

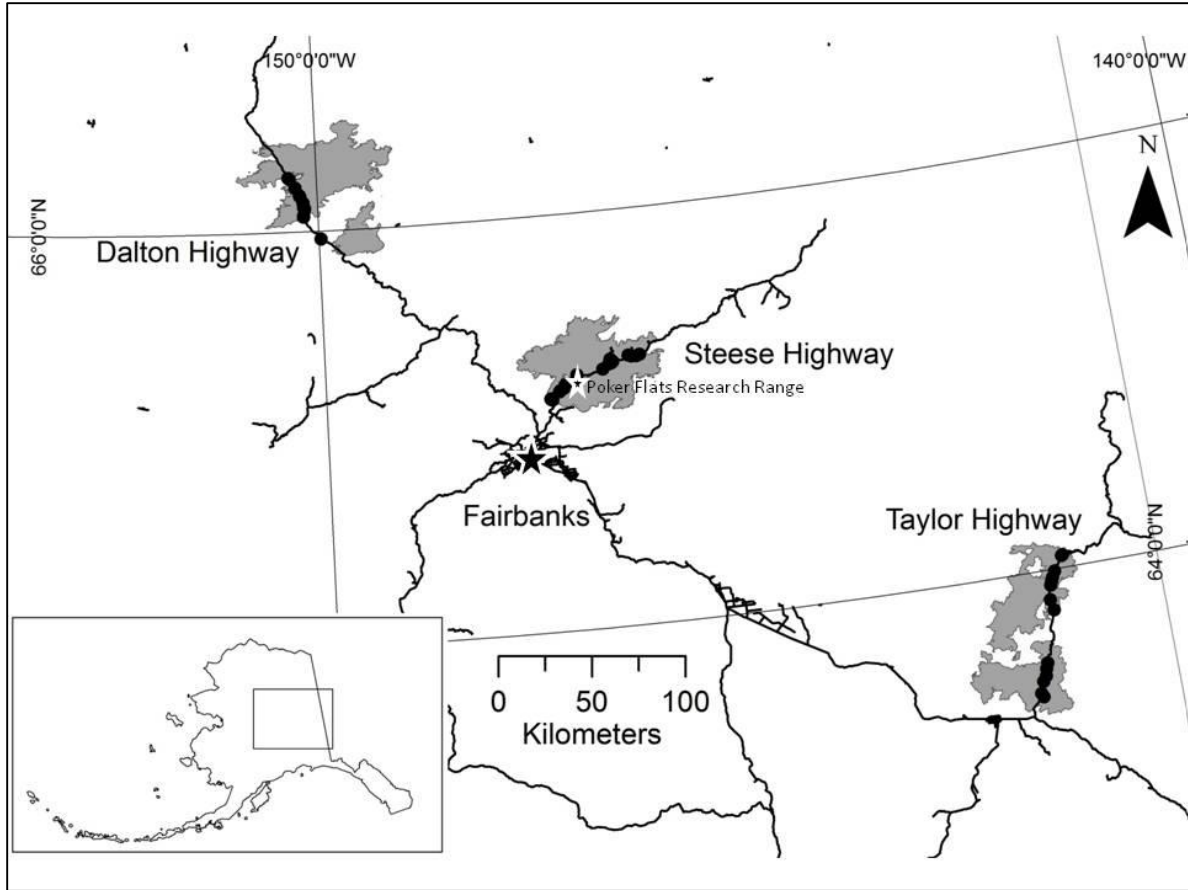
1 3.2.2 *Ring Width Index*

2 To maximize the common climatic signal between trees and determine how monthly
3 climate parameters might influence growth (Cook & Kairiukstis, 1990), we detrended raw ring
4 widths with a smoothing spline, with a frequency response of 0.5 at a wavelength of $0.67 \cdot n$
5 years (Zang, 2010) in the package ‘dplR’ (Bunn, 2010). This detrending option is known to
6 remove variances of low frequencies (i.e. long-term growth rates) with little or no removal of
7 variance of high frequencies (i.e. year to year variation in growth). Dividing actual ring-widths
8 by the curve-fitted value in each year produced a dimensionless width index for each series
9 (Bunn, 2010). Individual tree chronologies were constructed by averaging the two detrended
10 ring-width series for each tree. We built detrended annual ring width chronologies for trees at
11 each of three nested scales: 1) within the three regions of interior Alaska (n=180 trees), 2) within
12 the complete toposequence (n=60), and 3) subsampled trees within the toposequence (n=18).

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17 Figure 3.1 Location of 18 study sites (black dots), located in three separate 2004 burn complexes
 18 (grey), along the Dalton, Steese, and Taylor Highways in interior Alaska. Note: an additional six
 19 sites were sampled on a toposequence within the Poker Flats Research Range (PFRR) along the
 20 Steese Highway.

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3.2.3 Carbon Isotope Composition

To determine the extent of annual variation in carbon isotope composition, we randomly selected three trees per site within the PFRR toposequence. This resulted in 18 trees sampled, evenly distributed between the south and north aspect. We manually separated annual rings from the outer twenty-five years (1979-2003) on two perpendicular radii (2.5 x 2.5 cm) per tree using a dissecting scope, razor, and chisel. Wood from the two radii were homogenized into one sample and cut into fine particles using scissors to minimize sample loss. The samples (n=450) were then oven-dried at 60°C for 48 hrs. We encased approximately 2.5 mg of each sample in a tin cup for isotopic analysis. There is considerable debate regarding which wood component to isolate for carbon isotope composition (McCarroll & Loader, 2004) and alpha-cellulose is widely accepted as the standard in dendroisotopic analysis (Harlow *et al.*, 2006, Leavitt & Danzer, 1993). However, numerous studies have shown significant similarity in carbon isotopes of cellulose and wholewood, supporting the use of whole wood for dendroisotopic analysis (e.g Au & Tardif, 2009, Borella *et al.*, 1998, Loader *et al.*, 2003). We chose to use whole wood for this analysis based on the results obtained from analyzing carbon isotopes of a subsample of whole wood, extractive-free wood, holocellulose and alpha-cellulose, which showed no difference in isotopic signatures between whole wood and wood sub-components (Appendix 3).

The carbon isotope composition of tree rings is determined by the isotopic composition of CO₂ in the atmosphere and two main fractionation processes. The first fractionation occurs during diffusion of CO₂ through stomata into the leaf, where ¹³CO₂ diffuses slower than ¹²CO₂ (Farquhar *et al.*, 1989). The second occurs during carboxylation, where the enzyme ribulose-1,5-biphosphate carboxylase (RuBisCo) reacts with ¹²CO₂ molecules faster than with ¹³CO₂ molecules (Farquhar *et al.*, 1989). These fractionation processes result in the tree ring being more depleted in ¹³C than atmospheric CO₂. Carbon isotopic composition was measured using a continuous flow, stable-isotope mass spectrometer at the Light Stable Isotope Mass Spec Lab, Department of Geological Science, University of Florida. The C¹³ abundance relative to C¹² is expressed as δ¹³C:

$$\delta^{13}\text{C}(\text{‰}) = [(R_{\text{sample}}/R_{\text{VPDB}})-1] \times 1000 \quad (\text{Eq. 3.1})$$

where R_{sample} and R_{VPDB} represent the ¹³C/¹²C ratios of the sample and the Vienna PeeDee belemnite (VPDB) standard, respectively (Coplen 1995).

As the combustion of isotopically light fossil fuels has led to a decrease in the $\delta^{13}\text{C}$ of atmospheric CO_2 over the last two centuries, it is necessary to eliminate the effects of this change on tree ring $\delta^{13}\text{C}$. Thus, we calculated the carbon isotope discrimination (Δ) for each sample:

$$\Delta = (\delta^{13}\text{C}_{\text{atmo}} - \delta^{13}\text{C}_{\text{tree}}) / (1 + \delta^{13}\text{C}_{\text{tree}}/1000) \quad (\text{Eq. 3.2})$$

where $\delta^{13}\text{C}_{\text{atmo}}$ and $\delta^{13}\text{C}_{\text{tree}}$ are the isotopic values of the atmosphere and tree CO_2 , respectively.

The $\delta^{13}\text{C}_{\text{atmo}}$ values were obtained from Antarctic ice core data and direct measurements, summarized by McCarroll and Loader (2004). $\Delta^{13}\text{C}$ is related to the intercellular CO_2 concentration (C_i) and the ambient CO_2 concentration (C_a) by the following (Farquhar et al. 1989):

$$\Delta^{13}\text{C}\text{‰} = a + (b-a) (C_i/C_a) \quad (\text{Eq. 3.3})$$

where a ($=4.4\text{‰}$) is the fractionation between $^{13}\text{CO}_2$ and $^{12}\text{CO}_2$ during diffusion of CO_2 through the stomata, and b ($=27\text{‰}$) is the RuBisCo enzymatic biologic fractionation (Farquhar *et al.*, 1989). $\Delta^{13}\text{C}\text{‰}$ represents discrimination against the heavier CO_2 molecule ($^{13}\text{CO}_2$), thus lower values indicate a higher ratio of ^{13}C to ^{12}C due to increased stomatal regulation associated with physiological moisture stress (McCarroll & Loader, 2004).

3.2.4 Climate data

We used climate data of mean monthly temperature and total monthly precipitation from SNAP (Scenarios Network for Alaska and Arctic Planning 2013) corresponding to our study regions. SNAP data uses the outputs from the five best performing Global Climate Models (GCMs) for Alaska (Walsh *et al.*, 2008) and downscales data using a Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly *et al.*, 2002). This downscaling procedure accounts for slope, elevation, and proximity to coastlines, and is the same approach used in UK Climate Research Unit (CRU - www.cru.uea.ac.uk/) data (www.snap.uaf.edu). As weather observation stations throughout interior Alaska are sparse, the downscaled climate data accounts for differences corresponding our three study regions. In addition to the temperature and precipitation data, a monthly climatic moisture index (CMI), which represents total monthly precipitation minus monthly potential evapotranspiration (PET), which is a function of temperature, was calculated using the simplified Penman–Montieth method of Hogg (1997). Annual CMI was calculated by taking the sum of the monthly moisture indices. Low CMI values represent moisture limitation, whereas higher values suggest surplus moisture. To interpret annual changes in the climate data, we calculated deviations from the historical mean (1950-

2003) for each of temperature, precipitation, and CMI over the period 1979-2003 (fig. 3.2 and fig. A4.1).

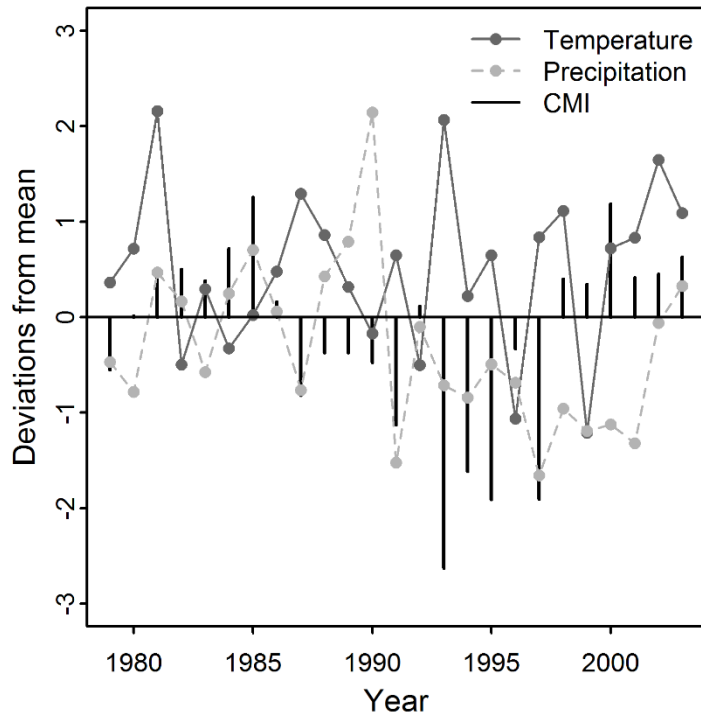


Figure 3.2 Temperature, Precipitation and Climate Moisture Index (CMI), deviations (1979-2003) from the historical mean (1950-2003) for the Steese region. Temperature and Precipitation data was obtained from Scenarios Network for Alaska and Arctic Planning, and the CMI was calculated using the simplified Penman–Montieth method of Hogg (1997). Climate deviations for the Taylor and Dalton are similar and are available in supplementary material (fig A4.1).

3.2.5 Data analysis

To assess differences in radial growth and isotope composition, we recorded annual ring width and $\Delta^{13}\text{C}$ over the period 1979-2003. For all trees within the three regions of interior Alaska (n=180 trees), trees within the PFRR toposequence (n=60), and the subsampled trees within the toposequence (n=18) we determined if mean ring width differed between trees on the northern versus southern aspects using a student's t-test. For the subsampled toposequence (n=18), we used the same approach to test if the ratio of earlywood to total annual ring width differed between trees on the north versus south aspect. Additionally, differences in mean $\Delta^{13}\text{C}$ were tested between subsampled trees on the northern versus southern aspects. T-test results were similar to those obtained using mixed-models with site type (north vs. south aspect) as a fixed effect and tree and year as random effects, and are presented here for simplicity. We chose to test differences based on aspect (north vs. south) rather than individual sites, as microclimate, based on incident solar radiation, is different between aspects. Additionally, initial data analysis showed larger differences in ring width between trees located on the two aspects, than between individual sites. We calculated Pearson's correlation coefficients between mean ring widths on the southern and northern aspects at each of the examined scales and for percent earlywood and $\Delta^{13}\text{C}$ on the subsampled trees.

To determine the extent to which radial growth is influenced by climate we used detrended ring-width chronologies and calculated Pearson's correlation coefficients with annual deviations from the historical means (1950-2003) of temperature, precipitation, and climate moisture index (Hogg, 1997). This was completed over the period 1979-2003 at each of the examined scales. We used the same method to assess correlations between $\Delta^{13}\text{C}$ of the subsampled trees and climate parameters. Additionally, the relationship between radial growth and $\Delta^{13}\text{C}$ on both aspects was assessed with Pearson's correlation coefficients.

We calculated bootstrapped correlations of mean monthly temperatures, total monthly precipitation, and mean monthly CMI with detrended ring-width chronologies over the period 1979 to 2003 using the package 'bootRes, version 1.2.3' (Zang, 2010). We calculated correlations using a 17-month climate window, extending from April of the year preceding growth to August of the current year of growth (Fritts, 1976). The significance of each of the 51 climate correlations was determined from 95% confidence intervals (Zang, 2010). As individual tree responses to climate may vary within sites (Walker & Johnstone, 2014), we did not base our

analysis on average indices of all individual trees at a site, as is typical in dendroclimatology (Cook & Kairiukstis, 1990). Instead, we maintained the variability associated with each tree and categorized the growth response of each individual tree to temperature into one of four types (as per Lloyd *et al.*, 2011): positive (>67% of significant correlations were positive), negative (>67% of significant correlations were negative), mixed (between 33 and 67 % of significant correlations were negative) or none (no significant correlations). The growth response of each tree to precipitation and CMI was categorized in the same manner. We then calculated the proportion of trees in each temperature, precipitation, and CMI response category on north and south aspects. This was completed for trees within the three regions of interior Alaska (n=180 trees), trees within the PFRR toposequence (n=60), and the subsampled trees within the toposequence (n=18). We used a X^2 test in the package ‘gmodels’ (Warnes, 2009) to assess if the proportion of individuals within each of the four response categories differed between northern and southern aspects.

To examine both the radial growth and $\Delta^{13}\text{C}$ responses of the subsampled trees at the site-type level, we created mean chronologies for the tree ring parameters of ring width and $\Delta^{13}\text{C}$ for each aspect (north and south) in the package ‘dplR, version 1.5.7’ (Bunn, 2010). General chronology statistics of mean correlation between trees (R), mean sensitivity (MS), autocorrelation (AR), and expressed population signal (EPS) for each of the standard chronologies developed per site type and region were calculated to ensure that all the chronologies were suitable for growth-climate analyses (table 3.2) (Speer, 2010). We then determined the climate responses of each chronology by calculating bootstrapped correlations in the same manner as for individual trees (see above).

Table 3.2 Statistics of mean correlation between trees (R), mean sensitivity (MS), autocorrelation (AR), and expressed population signal (EPS) for ring width and $\Delta^{13}\text{C}$ chronologies (n=9 trees/chronology).

Chronology	Aspect	R	MS	AR	EPS
Ring Width	North	0.842	0.175	0.581	0.951
	South	0.834	0.200	0.520	0.946
$\Delta^{13}\text{C}$	North	0.703	-0.010	0.456	0.876
	South	0.633	-0.013	0.488	0.819

3.3 Results

3.3.1 Stand structure and radial growth

The 18 sites we sampled on north and south aspects throughout interior Alaska captured a large gradient in black spruce stand structure (table 3.1). Stand basal area spanned three orders of magnitude, from a minimum of 0.02 m²/ha on a north aspect, to a maximum of 29.34 m²/ha on a south aspect. On average, sites on southern aspects had a significantly greater basal area (13.64 vs. 6.46 m²/ha; $t=-3.11$; $p<0.01$) and stand density (0.52 vs. 0.28 stems/m²; $t=-5.89$; $p<0.01$) than northern aspects. These differences did not correspond to any differences in average dbh (7.25 vs. 6.88 cm; $t=-0.73$, $p=0.47$) or average stand age (68.36 vs. 69.89 years; $t=0.35$, $p=0.72$) between southern and northern aspects. Stands also encompassed a range of moisture classes, ranging from submesic on northern aspects to xeric on southern aspects. Similarly, southern aspects received a higher relative amount of incident solar radiation on the summer solstice (solar insolation index) on average than northern aspects (0.82 vs. 0.57; $t=-9.40$; $p<0.01$).

The six sites we sampled along the toposequence are representative, in terms of stand basal area, density, age, moisture, and insolation, of the wider range of stand structures throughout interior Alaska (table 3.1). However, differences in ring widths between aspects in the Steese toposequence were larger than mean differences between aspects in the regional sample (fig. 3.3 and table 3.3), indicating that the toposequence population represents relatively extreme differences between topographic units.

Within the toposequence, we also assessed the proportion of earlywood to total annual ring width and found that tree rings on the south aspect were composed of a larger proportion of earlywood than trees on the north aspect (70 vs. 61%; $t=8.29$, $p<0.001$). Despite the difference in mean ring widths between aspects, interannual variations in radial growth, earlywood, and $\Delta^{13}\text{C}$ were highly correlated between aspects (fig. 3.3 and table 3.3).

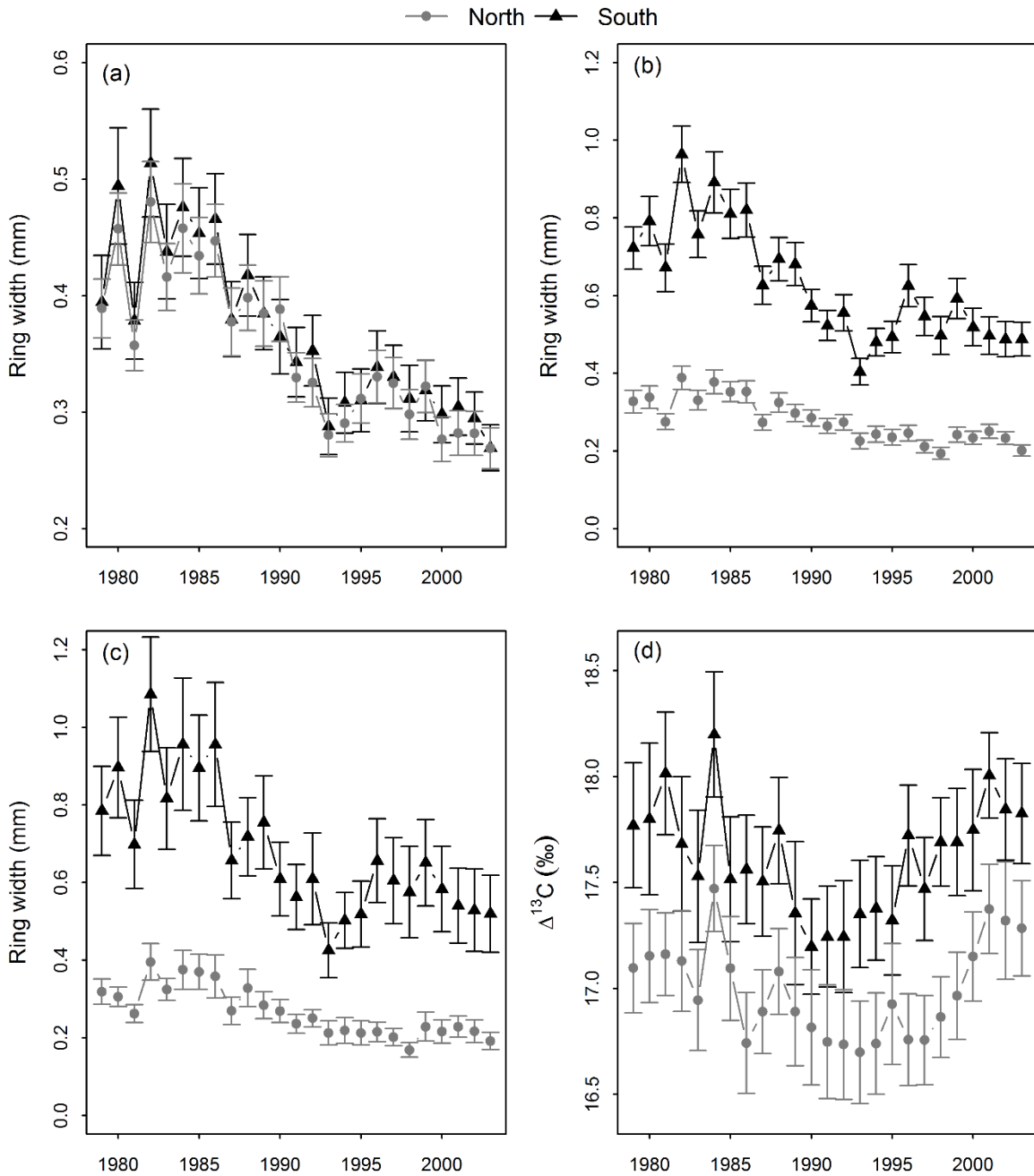


Figure 3.3 Mean black spruce ring widths (mm) per year on northern and southern aspects for a) all sampled trees within interior Alaska (n=180), b) within the toposequence (n=60), and c) the subsampled trees within the toposequence (n=18), along with d) mean $\Delta^{13}\text{C}$ per year on the south and north aspect for subsampled trees within the toposequence (n=18). Error bars represent standard error of the mean.

Table 3.3 Results of t-test to assess the difference in average ring width (RW - mm), % earlywood, and $\Delta^{13}\text{C}$ ‰ between northern and southern aspects and correlation coefficients between the mean ring width, % earlywood, and $\Delta^{13}\text{C}$ of northern and southern aspects. Values represent mean (\pm standard error) of black spruce ring width (mm) at the three examined scales, on the north and south aspects from 1979-2003, the average percent of earlywood (\pm standard error) and mean $\Delta^{13}\text{C}$ of the subsampled trees.

	North	South	t.value	Corr. coeff
	(mean \pm S.E)	(mean \pm S.E)	(p-value)	(p-value)
RW Landscape (n=180)	0.356 \pm 0.024	0.370 \pm 0.032	0.658 (0.514)	0.984 (<0.001)
RW Toposequence (n=60)	0.279 \pm 0.022	0.628 \pm 0.052	11.125 (<0.001)	0.933 (<0.001)
RW Subsample (n=18)	0.266 \pm 0.032	0.684 \pm 0.112	11.539 (<0.001)	0.914 (<0.001)
% Earlywood Subsample (n=18)	61.4 \pm 3.917	69.6 \pm 2.329	7.556 (<0.001)	0.415 (<0.05)
$\Delta^{13}\text{C}$ ‰ Subsample (n=18)	16.992 \pm 0.046	17.617 \pm 0.054	9.030 (<0.001)	0.830 (<0.001)

3.3.2 Radial growth – climate responses

Climate parameters of temperature, precipitation, and CMI, were similar between the three examined regions (fig. 3.2). We observed a decreasing trend of CMI over the period of examination (1979-2003), however this was not significant ($p>0.05$). Climate parameters of temperature and precipitation exhibited no significant trends. In general, CMI is negatively related to temperature and positively related to precipitation, however these relationships were not significant over the period of examination ($p>0.05$; fig. 3.2). In response to annual deviations in climate, detrended radial growth of trees on both aspects were significantly negatively correlated to mean annual temperature and positively correlated to annual CMI at each of the examined scales (table 3.4). Positive correlations between radial growth and annual precipitation were detected at the toposequence and subsample scale (table 3.4). Based on growth correlations with monthly climate parameters, trees on northern and southern aspects showed no differences in the proportion of individuals within response categories at any of the examined scales (fig. 3.4 and table A4.1). The most consistent response we observed was a negative radial growth response to temperature and positive to precipitation and CMI. Specifically, radial growth of the 18 subsampled trees was negatively correlated to temperature and positively correlated to CMI in both the previous growing season and current spring (fig. 3.5).

Table 3.4 Pearson's correlation coefficients between black spruce detrended ring width index (RW) and carbon isotope discrimination ($\Delta^{13}\text{C}$), on northern and southern aspects and annual deviations from the historical means (1950-2003) of precipitation, temperature, and climate moisture index (CMI). Bold text indicates significant correlations (p-value <0.05).

	RW (Landscape)		RW (Toposequence)		RW (Subsample)		$\Delta^{13}\text{C}$ (Subsample)	
	North	South	North	South	North	South	North	South
Temperature	-0.182	-0.145	-0.281	-0.404	-0.268	-0.418	0.042	0.039
Precipitation	0.008	0.003	0.223	0.160	0.275	0.129	0.049	-0.019
CMI	0.152	0.163	0.322	0.438	0.375	0.474	0.200	0.184

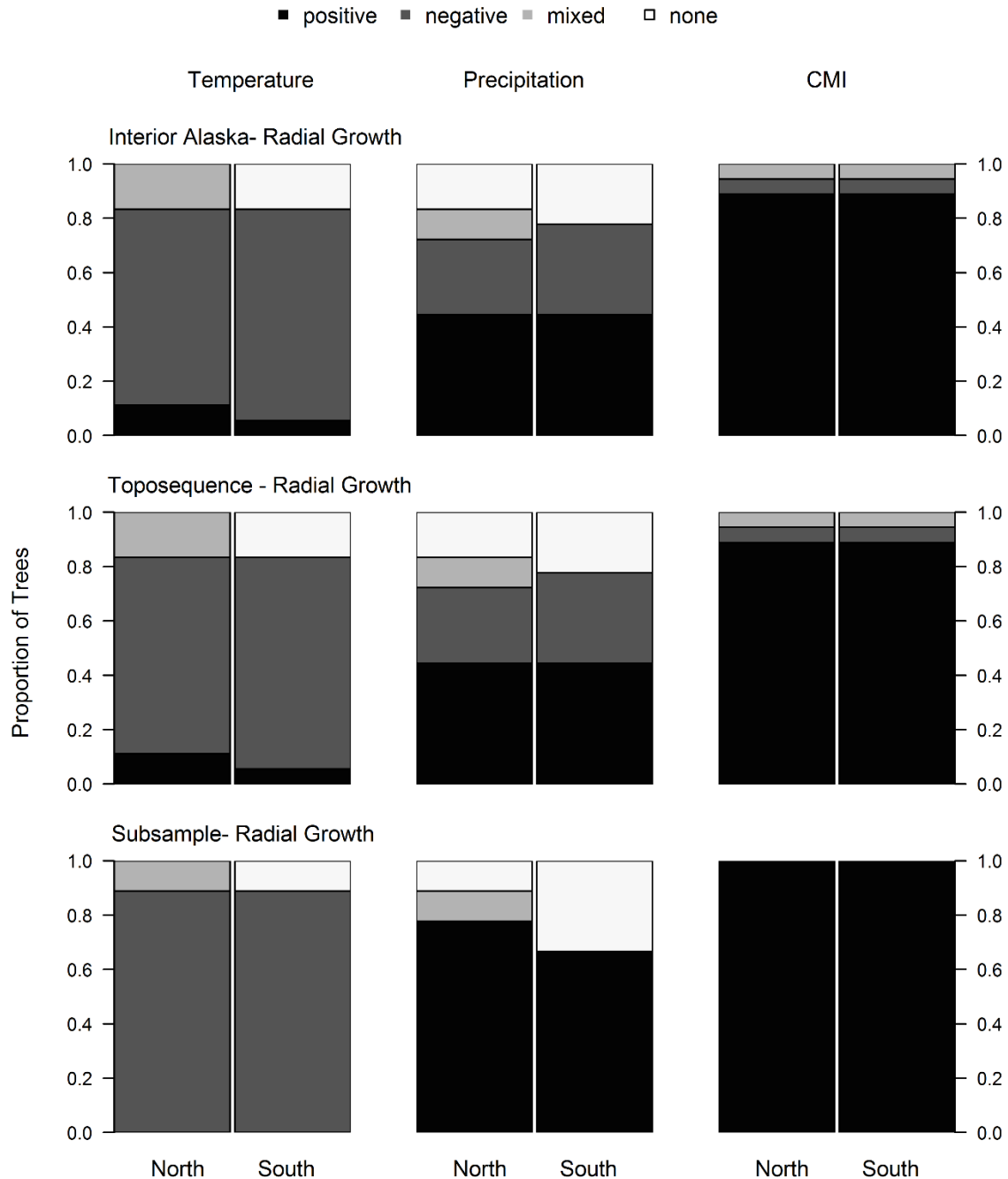


Figure 3.4 The proportion of trees on northern and southern aspects within interior Alaska (n=180 – top row), within the toposequence (n=60 – middle row), and among subsampled trees within the toposequence (n=18 – bottom row) whose variability in ring width responded positively, negatively, mixed, or exhibited no response. Columns represent responses to temperature (left column), precipitation (middle column), or climate moisture index CMI (right column). Response categories are defined in the methods. There were no significant differences in the proportions of trees in response categories between the northern and southern aspects (see Table A4.1 for statistical results).

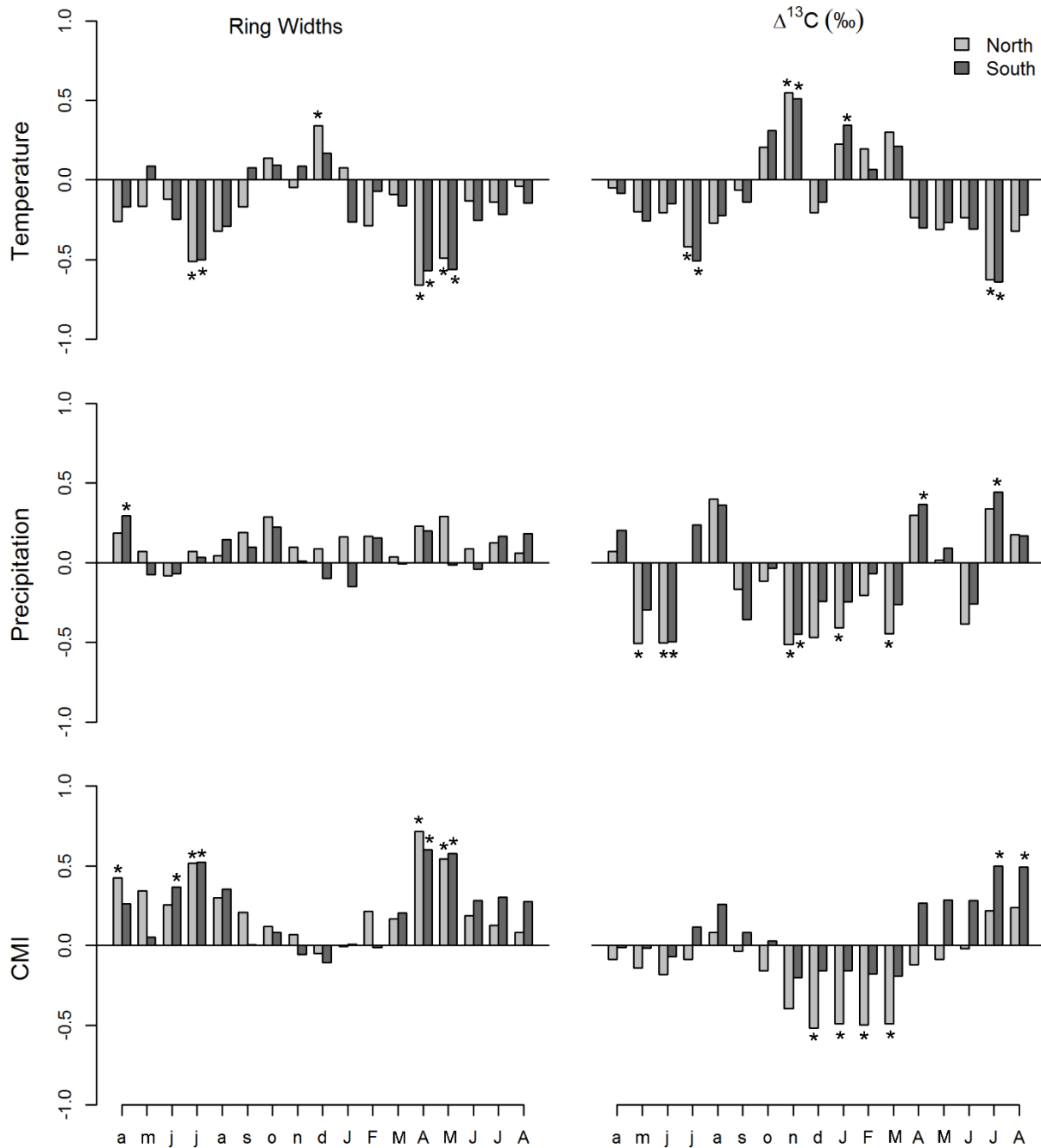


Figure 3.5 Averaged chronologies of ring widths and $\Delta^{13}\text{C}$ correlated with 17-month climatic window of temperature, precipitation, and climate moisture index (CMI) from 1979-2003. Each of the North and South facing chronologies are composed of 9 trees each. Y-axes represent correlation coefficients (* =significant) and X-axes represent months of year (lower case= year prior to ring formation, uppercase=year of ring formation).

3.3.3 Stable Carbon Isotope Analysis

$\Delta^{13}\text{C}$ of subsampled black spruce trees significantly differed between aspects; ranging from 16.1‰ for a tree on the northern aspect to 18.9‰ for a tree on the southern aspect (table 3.3). On the northern aspect, $\Delta^{13}\text{C}$ was positively correlated to radial growth ($cor = 0.164$, $p < 0.05$) but not on the southern aspect ($cor = -0.009$, $p = 0.887$). However, interannual variations in $\Delta^{13}\text{C}$ were highly correlated between trees on both aspects (fig. 3.3 and table 3.3). The period of lowest $\Delta^{13}\text{C}$ occurred in the early 1990s (fig. 3.3), which corresponds to a period of low CMI (fig. 3.2); $\Delta^{13}\text{C}$ was positively correlated to CMI on both the north and south aspect (table 3.3). Radial growth responses to temperature were similar on both aspects; negatively correlated to previous and current July and positively correlated to November (fig 3.5). $\Delta^{13}\text{C}$ was more strongly negatively correlated with precipitation and CMI on the north compared to the south aspect, specifically throughout the winter months (fig 3.5). Additionally, $\Delta^{13}\text{C}$ on the south aspect was positively correlated to CMI in the current growing season (fig. 3.5).

3.4 Discussion

Black spruce trees are sensitive to moisture limitation on both northern and southern aspects, suggesting that few habitats are likely to be resistant to drought-induced growth declines in the northern boreal forest. We observed a consistent negative radial growth response to temperature and a positive response to precipitation and CMI, regardless of scale or aspect. Sensitivity of tree ring widths to warm temperatures has been observed in numerous studies throughout the boreal forest and have been attributed to changes in seasonality, decreased amounts of solar radiation due to increased cloudiness, and drought stress (D'Arrigo *et al.*, 2008). When a tree is drought stressed the rate of stomatal conductance to photosynthesis is low, which reduces the flow and internal concentration of CO₂ and augments the utilization of ¹³C (McCarroll & Loader, 2004). Lower $\Delta^{13}\text{C}$ is therefore expected in tree-rings formed during dry years or in trees growing on particularly dry sites. In support of the drought stress hypothesis, we found that both north and south facing populations had lower $\Delta^{13}\text{C}$ and smaller ring widths during years of low moisture conditions. However, climatic parameters influencing boreal forest trees are often different for ring width and carbon isotopic composition (Au & Tardif, 2009, Brooks *et al.*, 1998). We found that tree growth was limited by climate parameters in the previous growing season and current spring, whereas $\Delta^{13}\text{C}$ was more sensitive to snow accumulation and current growing season moisture availability. Furthermore, trees on the north aspect had consistently lower $\Delta^{13}\text{C}$, contrary to our expectation that trees in colder and wetter landscape positions would be less moisture limited.

Radial growth responses to climate were similar regardless of the scale or the aspect. Warm spring temperatures and associated low CMI resulted in reduced radial growth, which can be explained by spring desiccation, where trees begin transpiring prior to soil thaw (Berg & Chapin, 1994). Lower CMI and warmer temperatures in the previous growing season also influenced radial growth. Climate conditions which limit the production of photosynthetic and absorptive tissue can lead to reduced radial growth in subsequent years (Fritts, 1976). Similar responses have been observed in black spruce trees across topographic moisture gradients in the northern boreal forest of Alaska and Yukon (Walker & Johnstone, 2014) and white spruce at cool and moist sites near treeline in Alaska (Ohse *et al.*, 2012, Wilmking & Juday, 2005). As growth-climate responses were similar at all examined scales, we believe that the $\Delta^{13}\text{C}$ responses examined on subsampled trees are representative of the wider region.

Contrary to our expectation that trees at the cooler and wetter part of the distribution would be more drought resistant, trees on the north aspect had consistently lower $\Delta^{13}\text{C}$, indicating they are more moisture limited than trees on the south aspect. In agreement, only trees on the north aspect exhibited a positive association between radial growth and $\Delta^{13}\text{C}$, and a positive radial growth response to annual precipitation. These positive associations confirm growth is primarily limited by moisture availability (McCarroll & Loader, 2004). However, $\Delta^{13}\text{C}$ signatures reveal that in years of high winter precipitation trees are more moisture stressed, particularly on the north aspect. This is likely due to high snow loads delaying the start of the growing season and impeding photosynthesis through low soil temperatures in the spring (Vaganov *et al.* 1999). Specifically, high snow loads can extend the period where roots are frozen in the spring. During this time, warm air temperatures increase the evaporative demand of leaves but low soil temperatures reduce plant hydraulic conductance and constrain water uptake (Kramer & Boyer 1995). This limits stomatal conductance and leads to enriched ^{13}C fixed during that time.

Similar responses to winter precipitation have been observed for *Pinus banksiana* in northern Manitoba (Brooks *et al.*, 1998). The lower $\Delta^{13}\text{C}$ and higher sensitivity to winter precipitation of trees on the north aspect could be due to their shallow rooting structure (Islam & Macdonald, 2004, LeBarron, 1945), which may render them ineffective at water uptake during the seasonal thaw when water table is lower (Dang & Lieffers, 1989). Indeed, increased organic layer thickness and higher water tables associated with northern aspects results in black spruce producing adventitious roots (Lieffers & Rothwell, 1987), and effectively restricts the rooting zone to soil organic matter instead of mineral soil (Ruess *et al.*, 2003).

The consistently higher $\Delta^{13}\text{C}$ of trees on the south aspect compared to the north could be attributed to a larger proportion of earlywood, as tree rings on the south aspect had a greater percentage of earlywood than those on the north aspect. Earlywood is often partially composed of stored carbohydrates from the previous growing season and has been shown to be isotopically lighter (ie. higher $\Delta^{13}\text{C}$) than latewood (Jäggi *et al.*, 2002). Despite trees on the south aspect being isotopically lighter than those on the north, they still experienced moisture stress. However, their sensitivity was linked to summer conditions, as has previously been identified for *Picea glauca*, a species characteristic of warm and dry uplands (Barber *et al.* 2000), and for black spruce at one site (Beck *et al.* 2011). Specifically, $\Delta^{13}\text{C}$ was positively associated with

CMI in July and August, confirming that trees on the south aspect are sensitive to moisture availability during the growing season.

Through combining growth-climate and carbon isotopic analyses, we were able to identify that black spruce forests have experienced moisture stress in interior Alaska. This signal of reduced discrimination against ^{13}C in response to decreased moisture availability was present in the majority of trees, regardless of topographic location and associated gradients in potential evapotranspiration and heatload. However, and contrary to our expectations, we found that north facing populations had consistently lower discrimination against ^{13}C . We hypothesize that the lower $\Delta^{13}\text{C}$ for trees on the north aspect is partly due their shallow rooting structure, making them less effective at water uptake than trees on southern aspects. Our results indicate that low productivity forests in cool microsites are not buffered from climate change effects through increased moisture availability, but instead may be even more vulnerable to drought stress with climate change than forests in warmer microsites. We conclude that if temperatures continue to warm, we can expect widespread drought stress and associated declines in productivity throughout the boreal forest of interior Alaska. The moisture stress signals we observed may be an important warning signal of broad-scale vulnerability of boreal forests to ongoing climate change (Allen *et al.*, 2010, Soja *et al.*, 2007). Such compositional change would subsequently compromise ecosystem processes and services, including feedbacks to future climate warming through altering the global carbon balance.

3.5 References

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CHAPTER 4: PREDICTING ECOSYSTEM RESILIENCE TO FIRE FROM TREE RING
ANALYSIS IN BLACK SPRUCE FORESTS

This chapter is in preparation for:

Walker XJ, Johnstone JF. Predicting ecosystem resilience to fire from tree ring analysis in black spruce forests. *In preparation*. *Ecography*.

4.1 Introduction

Forest ecosystem types and species distributions are fundamentally linked to climate and as such are expected to alter in response to climate change (Soja *et al.*, 2007). Unprecedented rates of climate warming over the past decade have increased forest drought stress and mortality worldwide (Allen *et al.*, 2010). However, the most dramatic shifts in forested ecosystems are not expected to be in direct response to climate change, but are more likely to stem from climate altering disturbance dynamics (Jentsch *et al.*, 2007). Changes to a disturbance regime can significantly alter forest ecosystem structure, growth, and post-disturbance succession (McCullough *et al.*, 1998). As environmental conditions continue to change, the occurrence, severity, and impact of disturbances on forested ecosystems are increasing across the globe (Flannigan *et al.*, 2009, Seidl *et al.*, 2014, Turner, 2010). As such there is a need to identify factors that may signal changes in the vulnerability of forested ecosystems to disturbance.

The theory of ecological stability is a useful framework from which to study the vulnerability of ecosystems to disturbance. Ecosystem stability is the ability of an ecosystem to defy change in the face of disturbance and has two main components: resistance and resilience (Pimm, 1984). Ecosystem resistance refers to the ability to withstand disturbance and ecosystem resilience is the ability to recover from disturbance (Pimm, 1984). When the ecosystem's resilience is exceeded, it will transform to a new state that has different properties, functions, and feedbacks, and from which the probability of return to the previous state is low (Folke, 2006). Depending on the ecosystem and the factors influencing resilience, shifts to new states can be gradual or abrupt. Environmental stresses can act to decrease ecosystem resilience and in the face of disturbance cause abrupt changes in stability domains (Rapport & Whitford, 1999). Thus the ability to detect changes in ecological resilience prior to disturbance is central for predicting changes in stability domains and shifts in ecological communities under rapid climate change and novel environmental conditions.

The boreal forest is an ideal ecosystem to study changes in resilience to disturbance and factors indicative of these changes. Boreal forests have warmed at nearly twice the rate of the global average during the last 30 years (IPCC, 2013), are frequently disturbed by large fires (Johnson, 1992), and are considered one of the most vulnerable ecosystems to shifts in vegetation communities as climate continues to change (Gonzalez *et al.*, 2010). However, ecological resilience, post-disturbance successional trajectories, and subsequent forest

composition are influenced by numerous factors including pre-disturbance species composition, type and magnitude of disturbance, landscape heterogeneity in environmental conditions, and climate change (Thompson *et al.*, 2009). Therefore, changes in resilience are unlikely to be homogenous across the landscape and there is substantial uncertainty regarding the factors contributing to possible threshold changes in boreal forest stability.

Decreased ecosystem resilience to disturbance and subsequent changes in boreal forest states are most likely to arise from the compounding effects of changing disturbance characteristics and changes in climate that affect regeneration conditions. Since the arrival of black spruce (*Picea mariana*) in the northwestern North America boreal forest approximately 6000 years ago, there have been periods of vegetation change promoted by feedbacks between climate change, disturbance, and species composition (Kelly *et al.*, 2013). However, the fire regime of recent decades has become more severe and frequent, causing a change in the relatively stable cycle of black spruce burning and recovering to pre-fire vegetation (Chapin *et al.*, 2010, Kelly *et al.*, 2013). Specifically, alternate successional trajectories, shifting from pre-fire black spruce forests to more mixed-deciduous communities post-fire have been observed when forests experienced fires of high severity or increased frequency (Johnstone & Chapin, 2006b, Johnstone *et al.*, 2010a). Post-fire regeneration is also affected by environmental conditions corresponding with topographic position (Dodson & Root, 2013, Johnstone *et al.*, 2010b) and directly influenced by temperature and precipitation regimes (Hogg & Wein, 2005). Specifically, warm and dry conditions can impede conifer regeneration and promote deciduous dominance post-fire (Johnstone *et al.*, 2010b). As mature trees might be able to survive in stressful environmental conditions that do not permit successful post-fire recruitment and survival (Bouchon & Arseneault, 2004), the impacts of climate on conifer tree growth could be indicative of the resilience of the boreal forest ecosystem to disturbance.

In this study we examine landscape variations in forest resilience to disturbance throughout interior Alaska, an area which has undergone significant warming in the last three decades (ACIA, 2005, IPCC, 2013). Warmer and drier growing conditions have resulted in drought stress across regional and topographic moisture gradients in these black spruce forests (Walker & Johnstone, 2014, Walker *et al.*, 2015). Thus, we examined the growth-climate responses of pre-fire trees as an indication of the direct climate effects on potential recruitment. Studies in the boreal forest have found that the initial 3-7 year period of post-disturbance

regeneration is representative of future forest canopy composition (Gutsell & Johnson, 2002, Johnstone *et al.*, 2004, Shenoy *et al.*, 2011). Therefore, we assessed the change in pre-fire to post-fire stand composition and used this as a proxy for ecosystem resilience, with sites experiencing the largest change in composition indicative of decreased resilience and an altered successional trajectory. We test the relative influence of environmental heterogeneity, fire characteristics, and pre-disposing climatic stress on the loss of resilience to disturbance and vulnerability of forests to state changes. We hypothesize that growth-climate responses might be a useful indicator of stand vulnerability to continued climate change, with stands experiencing the largest post-fire compositional change showing the greatest degree of pre-fire drought stress. As changes in ecological resilience are unlikely to be homogenous across the landscape, our analysis provides insight regarding how ecological resilience, post-disturbance successional trajectories, and future forest composition may vary at the landscape scale.

4.2 Methods

4.2.1 Study Area

This study took place in interior Alaska, an area bounded by the Brooks Range to the north and the Alaskan Range to the south (Viereck *et al.*, 1983). The average annual temperature is -2.5°C , mean monthly temperatures range from -23.1°C in January to $+22.8^{\circ}\text{C}$ in July, and there is a relatively short growing season of 135 days or less (Hinzman *et al.*, 2005). Annual precipitation is low and decreases from west to east, averaging 286 mm/year, 35% of which falls as snow (Hinzman *et al.*, 2005). The majority (75-80%) of the Alaskan boreal forest is underlain by permafrost (Osterkamp & Romanovsky, 1999), with the exception of south-facing slopes and floodplains near major rivers (Van Cleve *et al.*, 1983).

4.2.2 Field and Laboratory Methods

In the summers of 2012 and 2013 we established 72 sites within three separate 2004 burn complexes; the Boundary Fire, Dalton Complex, and Taylor Complex (fig 2.1). Within each burn complex, we established 24 sites based on the pre-fire stand composition; 12 in pure black spruce stands, and 12 in mixed black spruce/deciduous stands. Black spruce dominated the pre-fire stands at all the examined sites. Although tree mortality from the fires was close to 100%, fires rarely consume more than fine twigs on trees in mature stands (Boby *et al.*, 2010), so pre-fire tree species were easily identifiable and stem sections were well preserved at the time of

sampling. The selection of black spruce sites was based on broad scale landscape positions, with three sites each of 1) moist lowland (M), 2) north facing midslope (N), 3) south facing midslope (S), and 4) dry upland (D) within each burn complex. Within each burn complex we also established six sites each in mixed trembling aspen/black spruce stands (TA) and mixed paper birch/black spruce stands (PB), which were generally located in drier and warmer landscape positions.

Each site consisted of two parallel 30 m transects separated by 20 m. At each site, we recorded latitude, longitude, and elevation via a handheld GPS, and the slope and aspect with a clinometer and compass. Using these measurements, we calculated a unitless index of the relative solar insolation received at each site on the summer solstice (Bennie *et al.*, 2006) and a unitless index of heatload (McCune & Keon, 2002). Soil texture class was assessed in the field by hand texturing the uppermost mineral horizon, following the Canadian System of Soil Classification (Branch *et al.*, 1987). Understory composition was noted, in particular the presence of indicator species outlined by Hollingsworth *et al.* (2006). Based on understory composition, topography, and drainage conditions adjusted for soil texture, site moisture classes were estimated on a six-point scale, ranging from xeric to subhygric (Johnstone *et al.*, 2008).

We evaluated pre-fire and post-fire stem density and forest composition by measuring dead trees and new seedlings 8-9 years post-fire, when we expected that the seedlings that comprise the future canopy would have established (Gutsell & Johnson, 2002, Johnstone *et al.*, 2004, Shenoy *et al.*, 2011). Decomposition in these northern forest stands is relatively slow and trees killed in the fire typically remain well-preserved for decades (Boulanger & Sirois, 2006), enabling us to identify and measure the structure and composition of the pre-fire stand. As fires typically occur at a frequency of 50-200 years, the pre-fire stand we examined likely originated from fire. To determine the density of each species in the pre-fire stand, all standing dead or fallen deadwood that were originally rooted in two perpendicular 2m x 30m belt-transects were identified to species and the diameter at breast height (dbh) was measured on all individuals with stems >1.4 m in height. The total density (stems ha⁻¹) of each tree species in the pre-fire stand was then calculated. As initial post-disturbance regeneration is representative of future forest composition (Gutsell & Johnson, 2002, Johnstone *et al.*, 2004, Shenoy *et al.*, 2011), we measured post-fire seedlings along the same two transects used for pre-fire stand measurement. Thus, we measured post-fire seedlings along the same two transects used for pre-fire stand

measurement. Ten 1 m X 1 m quadrats were randomly selected and a careful search for all tree seedlings was completed. We identified each seedling to species and calculated the proportion of spruce stems relative to total stems in both the pre-fire and post-fire stand for each site.

At each site, we collected 10 stem disks at the standard height of 1.4 m from randomly selected pre-fire black spruce trees along two belt transects. For each tree, the diameter at breast height (dbh) and distance to the closest three surrounding trees was recorded. Stem disks were sanded with increasingly finer sandpaper, up to 400 grit, in order to produce visible rings. (Cook & Kairiukstis, 1990). Annual rings widths were measured on two radii per stem disk (WINDENDRO, resolution 0.001 mm). We visually cross-dated each tree-ring series against master chronologies developed for each site and region. We quality-checked our cross-dating using COFECHA version 6.06 (Grissino-Mayer, 2001).

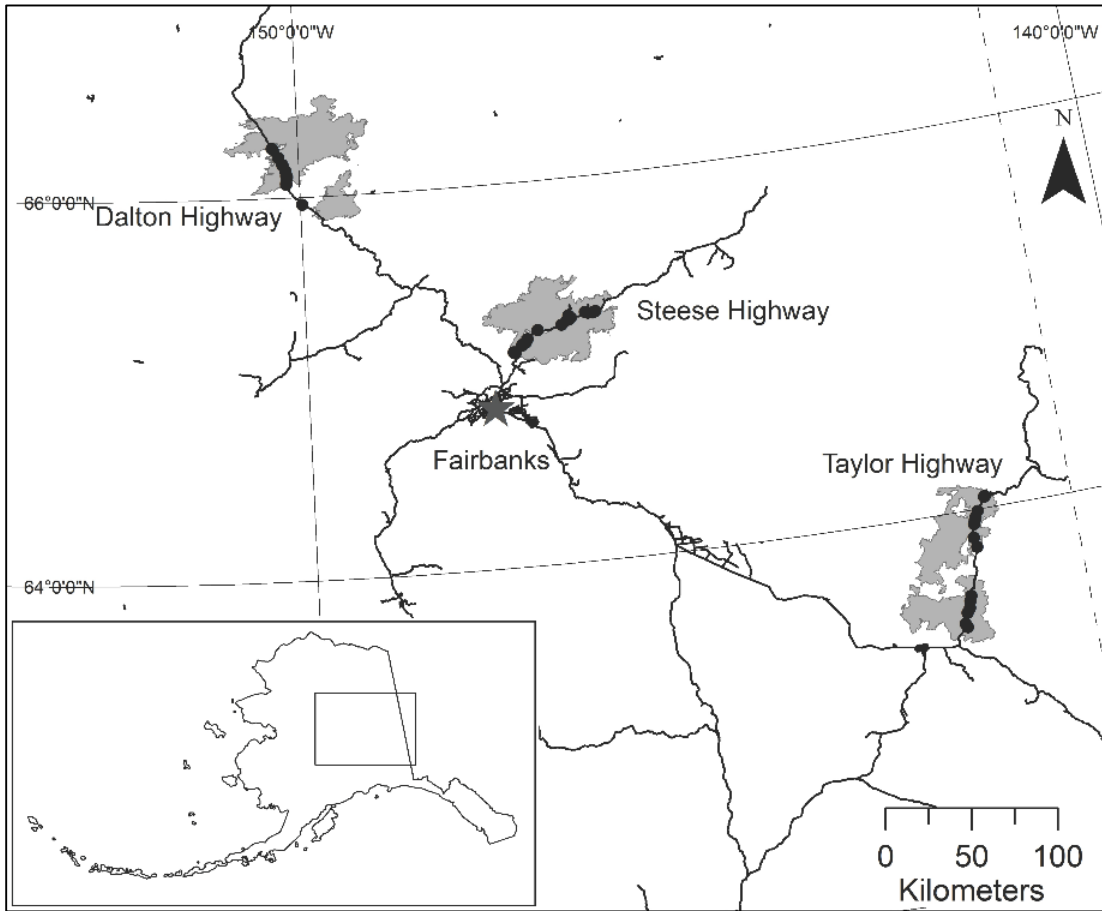


Figure 4.1 Location of 72 study sites (black dots), located in three separate 2004 burn complexes (grey), along the Dalton, Steese, and Taylor Highways in interior Alaska.

4.2.3 Growth-Climate Responses

Climate data of mean monthly temperature and total monthly precipitation corresponding to each of our study regions was obtained from SNAP (Scenarios Network for Alaska and Arctic Planning 2013) (as per Walker & Johnstone 2014). We also calculated a monthly climatic moisture index (CMI), which represents total monthly precipitation minus monthly potential evapotranspiration (PET), a function of temperature as per Hogg (1997). Thus, higher CMI values signify greater moisture availability. Detrending of ring-width chronologies and growth-climate analyses were completed using the R statistical package (R Development Core Team, 2012) and followed the methods outlined in Walker & Johnstone (2014) and Walker et al. (2015). We calculated bootstrapped correlations of mean monthly temperatures and total monthly precipitation with detrended ring-width chronologies over a 17 month climatic window, extending from April of the year preceding growth to August of the current year of growth for the period 1975 to 2003. We categorized the growth response of each individual tree to temperature and precipitation as positive, negative, mixed, or no response and calculated the proportion of trees in each temperature and precipitation category for each site (see details in Walker et al. 2015). Based on *a priori* hypothesis and previous analysis indicating a temperature induced moisture stress in these forest stands (Walker & Johnstone, 2014) we used the proportion of trees responding negatively to temperature and positively to precipitation for subsequent analyses. We also created mean site ring-width chronologies and determined the climate responses by calculating bootstrapped correlations between site chronologies and mean monthly temperatures, total monthly precipitation, and monthly CMI. This resulted in 51 radial growth correlations to monthly climate parameters at each site. For subsequent analyses we used only those growth-climate responses that elicited a significant response in at least 20% of the sites and that were not highly collinear, resulting in five variables associated with CMI.

4.2.4 Data Analysis

As a proxy for ecosystem resilience we determined if there was a change in species composition after fire by calculating the proportional change in black spruce from the pre-fire to the post-fire stand. This was done by subtracting the proportion of spruce trees to total trees in the post-fire stand by this proportion in the pre-fire stand. Thus, negative values represent a decrease in the proportion of black spruce trees in the post-fire stand. All following data analyses were performed using the R statistical package (R Development Core Team, 2012). To

assess if we could predict the proportional change in black spruce density from the pre-fire to the post-fire stand we used three sets of explanatory variables; those associated with pre-fire stand composition (*pre-fire*; 7 variables), variables associated with site environmental conditions (*site*; 10 variables), and dendroclimatic variables (*dendro*; 8 variables) (table 4.1). In addition to the two climate-growth responder categories and the five climate-growth responses associated with CMI (see above) we included average radial growth from 1975-2003 for each of the site chronologies in the *dendro* explanatory matrix (table 4.1).

To determine if variables associated with pre-fire stand composition, site environmental conditions, and dendroclimatic responses (table 4.1) could explain the proportional change in black spruce, we completed variation partitioning with partial regression using the package ‘vegan’ (Oksanen *et al.*, 2013). To identify the individual variables within each of three explanatory datasets that were significantly associated with the variation in proportional change of black spruce, we ran a stepwise selection process, using model adjusted R^2 and variable retention at a permutation value of 0.05 (Blanchet *et al.*, 2008). The significant variables from this selection process were retained for the variation partitioning analysis. By calculating the shared and unique variation explained by the significant variables in each of the explanatory matrices we were able to determine the relative influence of each set of explanatory variables on post-fire tree composition. The unique variation is the portion of variation a set of variables accounts for after controlling for all other measured variables. The shared variation is the explained variation that is common to more than one set of explanatory datasets (Legendre & Legendre, 2012).

To further explore which variables in the explanatory datasets (table 4.1) could predict the change in proportion of black spruce from pre-fire to post-fire stands, we completed boosted regression tree analysis (BRT) in the packages ‘gbm’ (Ridgeway *et al.*, 2013) and ‘dismo’ (Hijmans *et al.*, 2013). This is a machine learning approach based on regression and classification trees that incorporates different data types, is non-parametric, and provides a relatively easy interpretation of the relationships between response and explanatory variables (Elith *et al.*, 2008). As BRT are vulnerable to over-fitting when input variables are highly correlated, we only included the explanatory variables that were significant based on partial stepwise linear regression as used in the variable partitioning analysis (see above). Additionally, we removed any variables that were strongly correlated to other explanatory variables ($\rho > 0.4$),

based on the nonparametric Spearman's rank correlation coefficient. We fitted BRT models using five-fold cross-validation to identify the optimum number of trees (as per Elith *et al.*, 2008) and the following parameters: Gaussian error distribution, a learning rate of 0.001, a bag fraction of 0.5, and tree complexity of three. Next, we used a stepwise selection process that began with all predictor variables (table 4.1) and tested if the model could be simplified based on changes in the cross validation (cv) deviance (Elith *et al.*, 2008). The lowest cv deviance was obtained by dropping five of the nine predictor variables. We then ran the model with reduced interactions (two way or only the main effects) and found no substantial increase in cv deviance, so opted to model the main effects. Finally, we monotonically constrained the partial dependencies of the response variable to the predictive variables and as these constraints did not increase cv deviance we used them in the final model (Elith *et al.*, 2008). We examined the relative influence of the predictor variables by creating partial dependency plots, which represent the effects of each variable on the change in proportion of black spruce after accounting for the average effects of the other variables included in the BRT model (Elith *et al.*, 2008).

To determine how ecosystem resilience may vary across the landscape, we assessed how our site type categories related to the proportional change in black spruce and the most important variables explaining this proportional change (identified with the BRT model). We tested the statistical significance of differences between means using a mixed model approach in the 'lme4' package (Bates *et al.*, 2009). The response variables tested were the top three most important variables (table 4.1) identified in the BRT analysis and the change in black spruce proportions. Variability due to individual sites were set as random effects. To visualize the differences between sites we created boxplots of each of the variables stratified by site type.

Table 4.1 Variables included in each explanatory matrix

Matrix	Variable
Pre-fire composition	Black Spruce Density
	Black Spruce Basal Area * + #
	Trembling Aspen Density *
	Trembling Aspen Basal Area
	Paper Birch Density
	Paper Birch Basal Area *
	Total Deciduous Density
Site variables	Latitude (radians) * +
	Moisture Class (1-6)
	Elevation (m.a.s.l) * +
	Slope (radians) *
	Aspect (radians) *
	Heatload * +
	Insolation
	pH * +
	Organic Layer Depth (cm) * + #
	Mean Stand Age (Based on ring count at DBH)
Dendroclimatic variables	CMI Previous July
	CMI Previous August
	CMI Current April
	CMI Current May *+ #
	CMI Current August * +
	Proportion of Trees responding negatively to temperature (Prop Temp Neg) * +
	Proportion of Trees responding positively to precipitation (Prop Precip Pos)
Average Radial Growth (1970-2003)	

*Variables included in the variance partitioning analysis

+Variables included in the boosted regression tree analysis.

Variables tested in the mixed effect models.

4.3 Results

4.3.1 Site measurements and pre-fire stand composition

The 72 sites we sampled in three 2004 Alaskan burn complexes (fig 4.1) captured a large gradient in environmental conditions in which black spruce is found in the interior Alaskan boreal forest. Black spruce dominated the pre-fire stands at all the examined sites. Stands encompassed a range of moisture classes, from mesic in lowland sites to xeric on south facing slopes. Similarly, depths of the residual, post-fire organic layer varied from ~1cm in a mixed stand to >40 cm on a north facing slope. By sampling on both north and south facing slopes, we also captured a gradient in slope, aspect, and incident solar radiation on the summer solstice (solar insolation index) that ranged from 0.42 on a north slope to 0.90 on a south slope. Pre-fire stand mean (n=10) ring counts at 1.4 m height ranged from 35 to 130, with an average count of 60 years. Black spruce stems comprised on average 98% of stems in sampled black spruce stands and 65% of stems in mixed stands pre-fire. Black spruce basal area ranged across three orders of magnitude from a minimum of 0.02 m² ha⁻¹ on a north facing slope, to a maximum of 34.54 m² ha⁻¹ on a dry upland site. The density of black spruce stems in pre-fire stands ranged from near zero, on a sparsely treed north facing slope, to 1.7 stems m⁻² in a mixed stand (fig. 4.2). The density of deciduous trees in pre-fire stands was near zero in all the black spruce sites and reached a maximum of 0.28 stems m⁻² in the mixed stands.

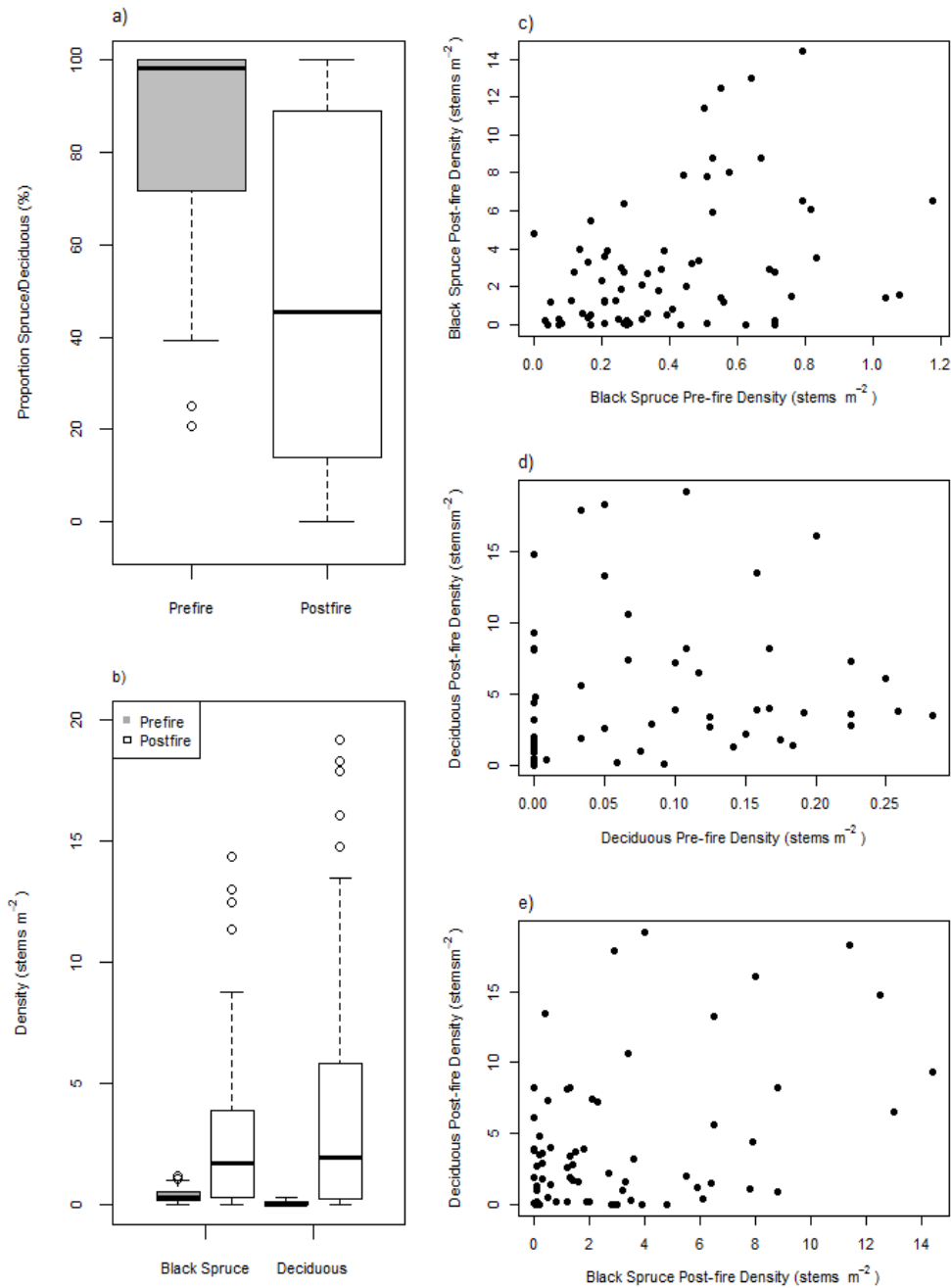


Figure 4.2 Plots showing: a) the distribution of the proportion of black spruce trees (%) in the pre-fire and post-fire stands, b) the distribution of pre-fire (grey boxes) and post-fire (white boxes) stem densities of black spruce and deciduous trees, c) the relationship between pre-fire and post-fire black spruce density ($\rho=0.357$, $p<0.05$), d) the relationship between pre-fire and post-fire deciduous density ($\rho=0.536$, $p<0.05$), and e) the relationship between post-fire seedling densities of black spruce and deciduous trees (not significant, $p\text{-value}>0.05$).

4.3.2 Radial growth-climate responses

Average radial growth of black spruce from 1975-2003 ranged from $<1.5 \text{ mm year}^{-1}$ in stands on north facing slopes and moist lowlands to $>9 \text{ mm year}^{-1}$ on south facing slopes and mixed black spruce deciduous stands. Of all the growth-climate responses examined, correlations with CMI in the previous and current growing season were the strongest, eliciting significant responses in over 40% of the stands (table A5.1). Specifically, correlations with CMI in May of the current growing season were significant in over 50% of stands and on average, radial growth positively correlated ($corr = 0.32$) to this climate parameter. A positive response to CMI in May signifies that radial tree growth is greater when more moisture is available in the spring. However, we did observe a range in growth responses to CMI in current May, with some moist lowland stands negatively responding. The strongest positive responses were in dry upland sites and mixed black spruce deciduous stands. In accounting for the individual variability in growth-climate responses within a stand, we found that the majority of trees responded negatively to temperature and positively to precipitation within each stand.

4.3.3 Predicting post-fire composition

Although few mature deciduous trees were encountered in the pre-fire pure black spruce stands, we observed many post-fire deciduous seedlings. The relative proportion of black spruce trees to total trees decreased from pre-fire to post-fire in over 85% of sites (fig 4.2(a)). Post-fire stem densities of both black spruce and deciduous trees (trembling aspen and paper birch combined) were greater than pre-fire stem densities (fig 4.2(b)). As expected, post-fire spruce density was positively correlated with pre-fire spruce density ($\rho=0.357$, $p<0.05$) (fig 4.2(c)). Similarly, post-fire deciduous density was positively correlated with pre-fire deciduous density ($\rho=0.536$, $p<0.05$) (fig 2d). However, we did not observe any relationship between post-fire spruce and deciduous seedling densities ($p\text{-value}>0.05$) (fig 4.2(e)).

In modelling the change in proportion of spruce stems to total stems from the pre-fire to post-fire stands, initial stepwise selection chose three of seven pre-fire stand composition variables, three of nine dendroclimatic response variables, and seven of nine site environmental variables (table 4.2). The overall variance partitioning model including all explanatory data sets explained approximately 32% of the variation in the response variable (fig 4.3(a)). Only the explanatory datasets of site and dendroclimatic variables had significant total and unique

explanatory contributions; the pre-fire stand composition explained approximately 8 % of the variation, but had no unique explanatory contributions (fig 4.3(b, c, d)).

The final model of the BRT analysis explained approximately 25% of the variation in the change in the proportion of black spruce following fire. This model consisted of four of the possible nine predictor variables, modelled with only the main effects, and was constrained to monotonicity. Of the four explanatory variables included in the final BRT model, organic layer depth had the strongest relative influence (~40%) (fig 4.4). Growth response to CMI in May, pre-fire black spruce basal area, and elevation also contributed to explaining the proportional change in black spruce composition (fig 4.4). Partial dependency plots indicate that the greatest change in black spruce occurred at sites with thin post-fire organic layers, a positive response to CMI in May, and a relatively large black spruce basal area (fig 4.4).

In exploring how our predetermined site type classification corresponded to the change in black spruce proportions, we found that the south (S) and mixed (TA and PB) stands experienced the greatest amount of change (table 4.3 and fig 4.5). Organic layer depth varied between site types, with the lowest depth in mixed (TA and PB) stands, and greatest depth in moist (M) stands. Furthermore, we observed differences in black spruce basal area between site types, with the lowest in moist sites (table 4.3 and fig 4.5). We did not detect any significant differences between site types in stand level responses to May CMI (table 4.3 and fig 4.5).

Table 4.2 Explanatory variables selected by stepwise selection for variation partitioning modelling the change in proportion of black spruce from pre-fire to post-fire. Variables are listed in order of importance, based on p-values, in the full model. The adjusted R^2 are for the univariate relationships with bolded values indicating significance (p-value<0.05). R^2 for the model with all selected variables is also included.

Explanatory Set	Variable	R^2
Pre-fire	Trembling Aspen Density	0.029
	Black Spruce Basal Area	0.015
	Paper Birch Basal Area	0.005
	R^2 Full Model	0.078
Site	Organic Layer Depth	0.179
	Aspect	0.103
	pH	0.001
	Heatload	-0.003
	Slope	-0.002
	Elevation	0.008
	Latitude	-0.013
R^2 Full Model	0.308	
Dendro	CMI Current May	0.100
	CMI Current Aug	0.032
	Prop Temp Neg	-0.007
	R^2 Full Model	0.153

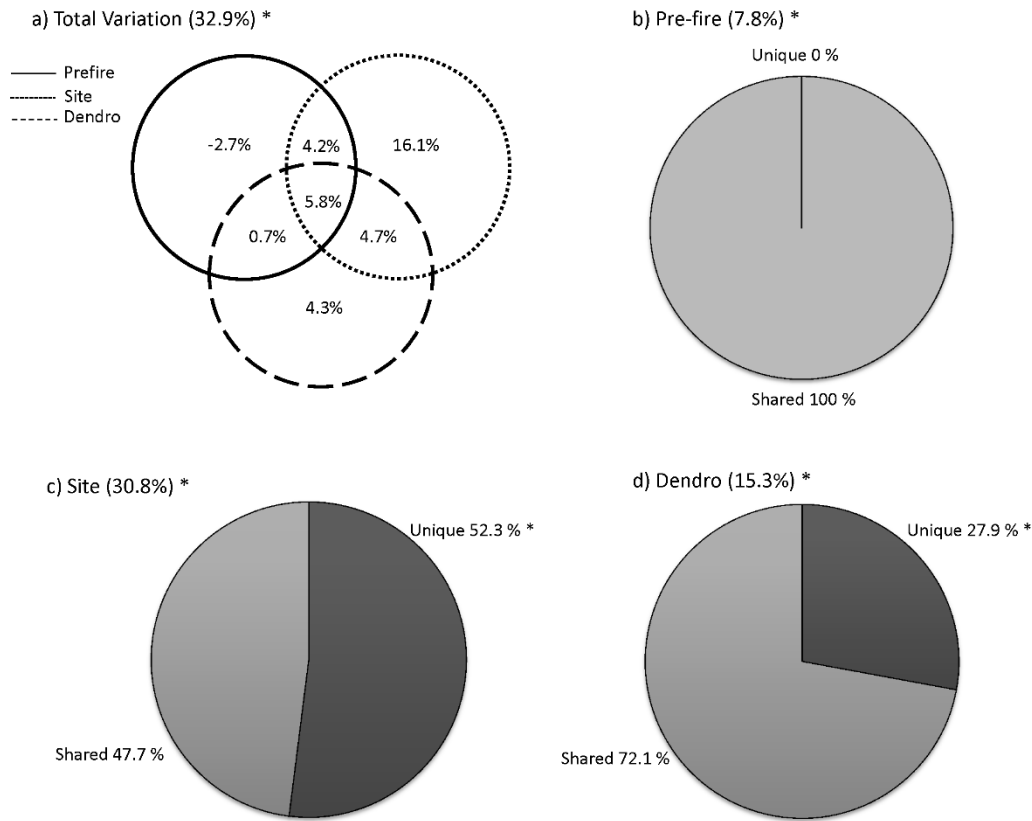
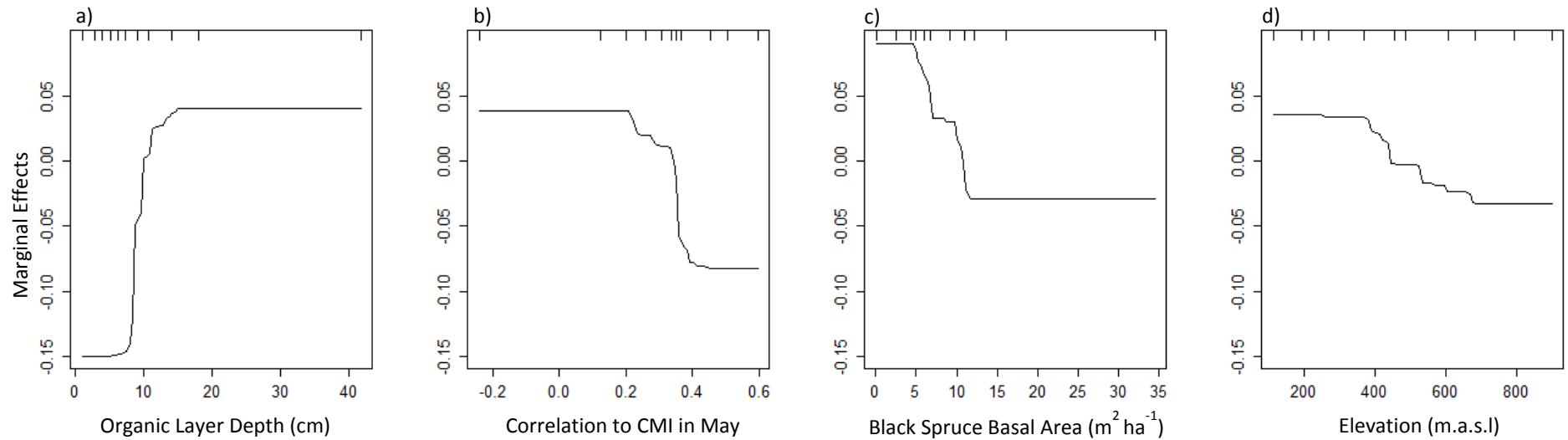


Figure 4.3 Variance partitioning results: a) Venn diagram of variation partitioning of the change in proportion of black spruce from pre-fire to post-fire among the three explanatory datasets. The non-overlapping sections represent the proportion of unique explained variation and the overlapping sections represent the shared portion of explained variation by each explanatory dataset. Total, unique, and shared, variation (%) of post-fire tree regeneration explained by: a) pre-fire stand composition, b) site characteristics, and c) dendroclimatic responses of the pre-fire stand. See table 4.1 for specific variables within each explanatory variable set. The significance (*) is based on adjusted R^2 values with $p < 0.05$. Note: the significance of the shared variation of each explanatory dataset cannot be tested.



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Figure 4.4 Partial dependency plots from the boosted regression tree (BRT) explaining approximately 25% of the variation in the change in proportion of black spruce from the pre-fire to post-fire stand. Plots represent the marginal effects for each of: a) organic layer depth (cm) (relative influence: 42.3%), b) radial growth correlation to climate moisture index in May of the current growing season (relative influence: 22.9%), c) black spruce pre-fire basal area ($\text{m}^2 \text{ha}^{-1}$) (relative influence: 22.5%), and d) elevation (meters above sea level) (relative influence: 12.3%), when all other variables are held constant. The BRT included only the main effects and was constrained to monotonicity. Tick marks at the top of each plot represent the 10% quantiles of the explanatory variable distributions.

Table 4.3 Mixed effect models to test for differences between site types in black spruce proportion change from pre to post-fire, organic layer depth, black spruce pre-fire basal area, and the stand response to CMI in current May.

Model coefficients (Site Types)	Black Spruce Proportion (1 to -1)	Organic Layer Depth (cm)	Black Spruce Basal Area (m ² /ha)	Correlation to CMI current May
Intercept (Dry)	-0.237±0.079	12.290±1.961	12.026±1.969	0.305±0.049
North	-0.042±0.112	3.690±2.772	-5.442±2.783	-0.102±0.069
South	-0.156±0.096	-3.367±2.772	1.893±2.783	0.055±0.069
Moist	0.161±0.096	-5.967±2.772	-9.224±2.783	-0.102±0.069
Trembling Aspen	-0.230 ±0.097	-7.533±2.401	-5.390±2.410	0.065±0.060
Paper Birch	-0.182±0.097	-6.252±2.401	-0.787±2.410	0.035±0.060

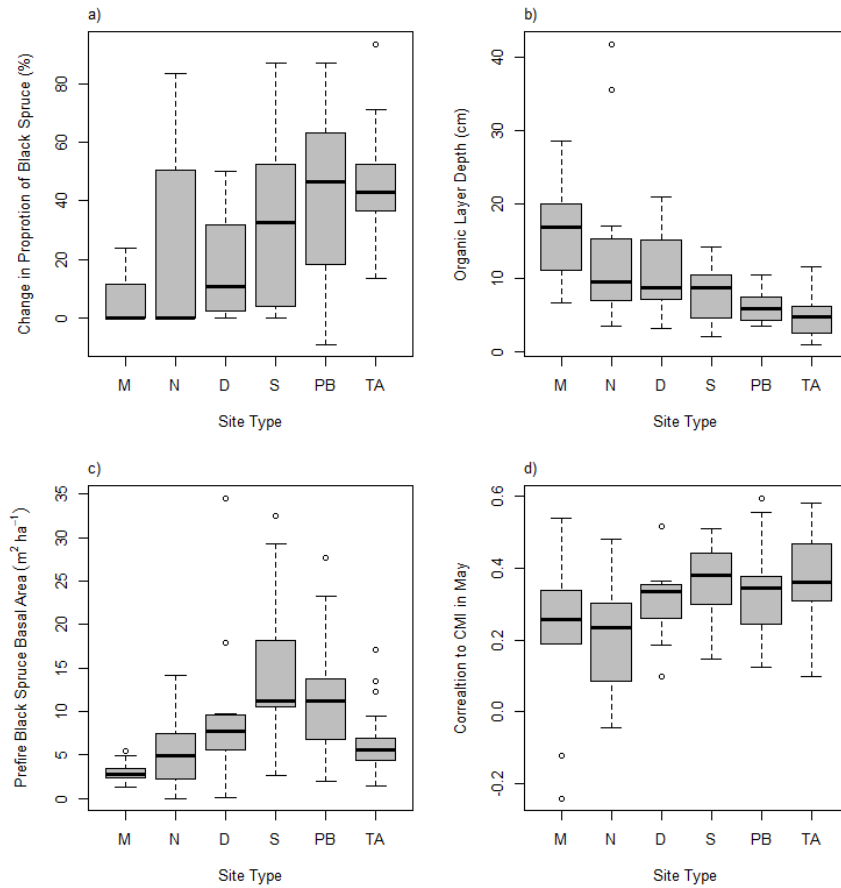


Figure 4.5 Boxplots showing the variability between site types (M=moist, N=north, D=dry, S=south, PB=paper birch, TA= trembling aspen) for each of: a) change in black spruce proportion (%), b) organic layer depth (cm), c) black spruce pre-fire basal area ($m^2 ha^{-1}$), and d) the stand response to CMI in current may (correlation coefficient).

4.4 Discussion

Using the change in proportion of black spruce from the pre-fire to post-fire stand as a proxy for ecosystem resilience, our results suggest substantial landscape variations in black spruce resilience to fire that were related to environmental gradients and tree ring indicators of climatic stress. We observed a decrease in the proportion of spruce relative to total trees from the pre-fire to the post-fire stand in nearly all examined stands, indicating a shift from black spruce dominated stands to mixedwood or deciduous dominated stands. However, our results suggest that this shift or loss of ecosystem resilience is not homogenous across the landscape.

Specifically, forest stands with the lowest resilience to disturbance are those that had relatively thin post-fire organic layer depths and experienced climate induced drought stress indicated by pre-fire growth-climate correlations. These sites were generally located at warmer and drier landscape positions, suggesting they are less resilient to disturbance than sites in cool and moist locations. Our results indicate that ecological resilience and post-disturbance successional trajectories will vary at the landscape scale, and as such we believe they are useful for predicting the future of forested ecosystems under conditions of environment change and novel ecological conditions.

A primary factor underlying resilience of northern boreal black spruce forests through several fire cycles is how fire affects soil organic layer depth. Historically, low severity fires in moist and cool black spruce forests leave a considerable portion of the organic layer intact. In order for successful establishment to occur on the partially combusted surface organic layers, a high seed input, such as that from the aerial seed bank stored in black spruce semi-serotinous cones is needed. Small seeded deciduous species, such as aspen and birch are rarely able to establish on this low quality seedbed (Johnstone & Chapin, 2006a). However, with increasing fire frequency, extent, and severity in response to warmer temperatures and more frequent droughts (Wotton *et al.*, 2010, Xiao & Zhuang, 2007), shifts in boreal vegetation from a spruce- to a broadleaf dominated landscape have occurred (Johnstone *et al.*, 2010a). Specifically, when severe fires consume a large portion of the organic layer, leaving an average of less than 5-10 cm depth, deciduous trees can establish at much higher densities (Johnstone *et al.*, 2010a). We found a similar threshold, where stands with less than ~ 10 cm depth experienced the greatest change in proportion of black spruce. However, post-fire organic layer depth is not only a function of fire consumption but it is also associated with the pre-fire organic layer depth, and thus represents a

combination of fire history and environmental conditions at the site. In terms of the predetermined site types, we found that post-fire organic layer depth was greatest in moist sites. Moist sites with deep organic layers are of poor quality for deciduous establishment and success, suggesting that these areas might be less vulnerable to a change in successional trajectory following disturbance.

Although fire characteristics such as burn severity can decrease ecosystem resilience to disturbance, changes in climate that affect regeneration conditions are also likely important controls on resilience. In this study, we assessed if pre-disturbing climatic stress resulted in a loss of resilience to disturbance and a change in forest successional trajectory. Although seedlings and mature trees are limited by different factors, seedlings are more sensitive to stressful conditions, thus mature trees might be able to persist in environmental conditions that prevent their successful recruitment under the same conditions (Bouchon & Arseneault, 2004). We used tree ring responses to climate as an indication of the climate effects on potential recruitment and found that the radial growth response to CMI in May of the current growing season was the strongest predictor of ecosystem resilience. A strong positive response to CMI in May signifies that low moisture availability in the early growing season results in reduced radial growth. This response can be explained by warm air temperatures in spring increasing the evaporative demand of leaves but low soil temperatures constraining water uptake (Berg & Chapin, 1994). Stands that were strongly and positively correlated to CMI (i.e. drought stressed) experienced the greatest change in stand composition. Although sites at the warmest end of the spectrum were slightly more sensitive to CMI in current May we did not observe any significant differences between the site types. This suggests that mature black spruce trees are able to survive in stressful environmental conditions that are not conducive to post-fire recruitment and survival. Furthermore, these results highlight that growth-climate responses of pre-fire trees are a useful tool for predicting changes in ecological resilience. Our results are similar to a study of white spruce stands in south central Yukon, where the greatest change in pre-fire to post-fire composition coincided with pre-fire trees experiencing a negative response to summer temperatures (Johnstone *et al.*, 2010b). As drought stress is widespread in the boreal forest of interior Alaska, occurring throughout topographic gradients in moisture availability and prominent even in the coolest and wettest microclimates (Walker & Johnstone, 2014), we believe

that the boreal forest might be even more vulnerable to ongoing climate change than previously anticipated.

Despite pre-fire stand composition being an overall poor indication of ecosystem resilience, we did find that stands with relatively higher pre-fire black spruce basal area were most likely to show a loss of resilience and switch to deciduous dominance. Stands with a relatively higher pre-fire black spruce basal area are found in warmer and drier landscape positions and/or in association with deciduous species. The presence of deciduous trees in the pre-fire stand would provide a budbank for asexual regeneration and facilitate rapid post-fire colonization (Chen *et al.*, 2009, Greene & Johnson, 1999). This is in agreement with our observation that sites with even a few deciduous trees present in the pre-fire stand experienced a large decrease in the proportion of black spruce to deciduous following fire. However, as pre-fire stand composition was not a strong predictor of the change in black spruce proportions, it supports our interpretation that fire and environmental conditions, rather than strong legacy effects are more important controls on post-fire regeneration patterns.

A central assumption of our interpretation of forest resilience is based on patterns of early seedling regeneration reflecting future forest stands. Although we expect sites with high seedling densities to undergo self-thinning, the relative abundance of species in the initial 3-7 year period of post-disturbance regeneration is known to be representative of future canopy composition (Gutsell & Johnson, 2002, Johnstone *et al.*, 2004, Shenoy *et al.*, 2011). This short post-fire recruitment window is strongly influenced by the decrease in seedbed quality associated with post-fire recovery and regeneration of understory moss and vegetation, which effectively impairs continuous seedling establishment and results in relatively even aged stands (Johnstone & Chapin, 2006a). Although it is possible for black spruce recruitment to occur several decades after fire, delayed recruitment is hindered by seed availability as semi-serotinous cones require fire to release adequate seed for successful establishment. Thus, delayed recruitment is unlikely to alter the patterns we observed in initial post-fire forest composition. Alternatively, it is possible that the mixed black spruce/deciduous stands could undergo relay succession, during which deciduous trees may initially dominate but their shorter life-spans and shade intolerance would lead to increasing spruce dominance over time. However, ageing of mixed stands in interior Alaska indicate that canopy succession to spruce dominance is rare even after more than 200 years (Kurkowski *et al.*, 2008). This, in combination with the relatively short fire cycle or

boreal forests (<100 years), indicates that the observed pre-fire composition at each site only included trees that had established following the previous fire cycle. Thus the initial patterns of forest composition we observed post-fire are likely to persist for at least the lifespan of the initial cohort and the duration of the fire free interval (Gutsell & Johnson, 2002, Johnstone *et al.*, 2004).

4.5 Conclusion

We detected a change in species composition following fire in the boreal forests of interior Alaska; an area that has been dominated by black spruce for ~6000 years (Kelly *et al.*, 2013). This switch in successional trajectory from the previous fire cycle highlights a loss of ecosystem resilience to disturbance. Areas most vulnerable to a loss of resilience were those that experienced severe fires, indicated by post-fire organic layer thickness, in combination with pre-disturbance drought stress, which we believe is representative of stressful environmental conditions for post-disturbance regeneration. As models project continued climate change and increased fire severity, frequency, and size (de Groot *et al.*, 2013), we can expect a loss of boreal forest ecosystem resilience to disturbance from fire. However, this loss of resilience will likely be confounded by environmental heterogeneity, and we therefore do not expect a uniform loss of resilience across the landscape. Specially, areas most vulnerable to post-disturbance compositional change are those located at warmer and drier landscape positions and sites at the wetter and cooler end of the spectrum may be more resilient to disturbance. The observed switch from conifer dominated to a more deciduous dominated landscape will affect climate-albedo feedbacks, nutrient cycling and plant productivity, future fire regimes, wildlife habitat use, and natural resources for indigenous subsistence activities (Chapin *et al.*, 2010). As climate change continues, increases in aridity, drought stress, and decreasing ecosystem resilience is of serious concern not only for the boreal forest but for forested ecosystems worldwide (IPCC, 2013, Seager *et al.*, 2007). We believe our results are relevant not only for forecasting and managing the effects of a substantially altered boreal landscape, but the methods employed in this study might be useful for predicting vulnerability of other forested ecosystems.

4.6 References

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CHAPTER 5: CONCLUSIONS

5.1 Summary of Rational and Objectives

Unprecedented rates of climate change over the past century have impacted forested ecosystems worldwide (IPCC, 2013). However, this warming has not been globally uniform and boreal forest ecosystems have warmed at nearly twice the rate of the global average (ACIA, 2005, IPCC, 2013). Warming temperatures will have significant impacts on boreal forest vegetation and associated ecosystem processes and services (Chapin *et al.*, 2010). As the boreal forest covers approximately 17% of terrestrial earth and contains at least 30% of global terrestrial carbon (Kasischke, 2000), changes in boreal forest productivity, structure, and/or composition is of global concern.

In direct response to warming climatic conditions, declining tree productivity has been detected in observational studies throughout the boreal forest of interior Alaska (Beck *et al.*, 2011) and Canada (Ma *et al.*, 2012), and in satellite-based studies across larger regions (Beck & Goetz, 2011, Verbyla, 2011). The negative impacts of warming on boreal tree growth have generally been associated with trees growing in drier and warmer microsites (e.g Barber *et al.*, 2000, Wilmking & Juday, 2005), suggesting that forest sensitivity to climate will depend on local moisture availability (Lloyd & Bunn, 2007). This sensitivity to climate is also likely to impact regeneration, as current conditions likely differ from those experienced when the previous stand established and mature trees might be able to survive in stressful environmental conditions that do not permit successful post-disturbance recruitment and survival (Bouchon & Arseneault, 2004). Thus with disturbance, forest stands may be less likely to recover to pre-fire stand densities, resulting in alternate successional trajectories (Johnstone *et al.*, 2010b).

In this research, I assessed how black spruce (*Picea mariana* (Mill.) BSP) trees responded to climate. Black spruce forests are typically found on cold, wet, and nutrient poor soils underlain with permafrost and thus provided an excellent opportunity to test if temperature and moisture limitation associated with environmental gradients correspond to changes in growth-climate responses. Specifically, I assessed how the growth-climate responses of black spruce varied with stand characteristics and landscape position across four different regions in Alaska and Yukon Territory (Chapter 2) and if tree-ring $\Delta^{13}\text{C}$ responses supported the interpretation of drought stress as the driver of radial growth responses to climate (Chapter 3). I then tested the possible linkages between ecosystem resilience and the growth-climate

relationship of pre-fire trees, specifically drought stress signals, across topographic moisture gradients throughout interior Alaska (Chapter 4).

5.2 Summary of Results

In this study, I found that approximately half of the trees exhibited reduced radial growth in response to warm temperatures in the previous growing season and current spring, which I interpreted as a signal of drought stress (Chapter 2). Although I found variation in the growth responses of individual trees within sites, both landscape position and stand characteristics were weak predictors of this variability, explaining $\leq 12\%$ of the variation in any region. These results indicate that future warming, particularly in spring, is likely to result in drought stress and a reduction of black spruce radial growth independent of region, landscape position, or stand characteristics. These results were unexpected as we hypothesized that trees in cool and moist habitats would be less vulnerable to drought stress. Based on these unexpected results, I examined the stable carbon isotope responses to temperature to determine whether the negative correlations between growth and temperature in cool and moist microsites were arising from the same processes detected in warm and dry sites where drought stress seems highly plausible (Chapter 3). I found that trees showed ^{13}C isotopic signatures consistent with drought stress on both northern and southern aspects (ie. both moist and dry microsites) and contrary to my expectation, trees on the northern aspect showed the strongest drought signal. These results highlight the prominence of drought stress in northern black spruce ecosystems and suggest that if temperatures continue to warm, we can expect drought induced productivity declines across large regions of the boreal forest, even for trees located in cool and moist landscape positions.

However, the largest changes in boreal vegetation will likely not be in direct response to climate warming, but indirectly through alterations in the fire regime, which will subsequently affect boreal forest regeneration and the successional trajectory. In this research, I identified widespread temperature induced drought stress of black spruce trees (Chapter 2 and 3), which signalled changes in the susceptibility of forest communities to compositional change (Chapter 4). Specifically, the climate-growth responses of pre-fire trees were used to assess ecosystem resilience to disturbance as stressful environmental conditions in mature forests might impede successful post-disturbance recruitment and survival (Chapter 4). I found that in the majority of sites the relative proportion of black spruce trees decreased post-fire, ranging from almost no

change to a 90% decrease and I interpreted this as a loss of resilience to disturbance. The largest shifts in post-fire species composition occurred in sites that experienced the compounding effects of climate induced drought stress and high fire severity, indicated by pre-fire growth-climate correlations, and post-fire organic layer thickness, respectively. These sites were generally located at warmer and drier landscape positions, suggesting they are less resilient to disturbance than sites in cool and moist locations. These result indicate that tree growth-climate responses can provide an estimate of stand environmental stress to ongoing climate change and as such are a valuable tool for determining forest ecosystem resilience and forecasting future forest composition.

5.3 Implications of drought stress and changing resilience to disturbance

As black spruce is the most widespread forest type in interior Alaska (Viereck *et al.*, 1983), its productivity and growth responses to recent climate change have the potential to influence the global carbon cycle and future climate change (Angert *et al.*, 2005, Ma *et al.*, 2012, Piao *et al.*, 2008). Specifically, the boreal forest has historically acted as a carbon sink, absorbing more atmospheric carbon dioxide (CO₂) than it releases (Myneni *et al.*, 2001). Areas of the boreal forest where trees are responding negatively to increasing summer temperatures might limit this carbon uptake and begin acting as carbon source, releasing more CO₂ than it absorbs. Results of this research indicate drought induced productivity declines across large regions of the boreal forest (Chapter 2 and 3) and as such could be indicative of boreal black spruce forests switching from acting as a carbon (C) sink to a source. Although drought stress will have direct impacts on boreal vegetation, the greatest impacts on boreal ecosystem processes and services are likely to result from an altered fire regime acting on an ecosystem of decreased resilience. In this research, I found that the largest shifts in post-fire species composition occurred in sites that experienced the compounding effects of climate induced drought stress and high fire severity (Chapter 4). As ongoing climate change is predicted to increase fire severity, extent, and frequency (de Groot *et al.*, 2013), and also negatively affect the growth and productivity of trees (e.g Barber *et al.*, 2000, Beck *et al.*, 2011, Wilmking *et al.*, 2004 and Chapter 2 and 3) throughout the boreal forest, this ecosystem is vulnerable to post-disturbance shifts in vegetation composition. In agreement, a switch from conifer dominated to deciduous dominance post-fire has been observed in association with changes to the fire regime (e.g. Johnstone *et al.*, 2010a)

and pre-fire stand environmental stress inferred from growth-climate responses (Johnstone *et al.*, 2010b and Chapter 4).

The observed switch from conifer dominated to a more deciduous dominated landscape will significantly impact boreal forest ecosystem processes and services due in part to intrinsic differences between deciduous and black spruce stands. Black spruce grow in dense stands with moist understory conditions and are characterized by slow growth, slow rates of decomposition, and low nutrient availability, which promote a thick organic layer, relatively shallow active layer, and permafrost (Viereck *et al.*, 1983). This means that the proportion of C stored in black spruce stands is generally higher in the soil organic layer than in the actual above ground tree biomass. Black spruce stands are also highly flammable due the high resin and low moisture content of their needles, and large amount of ground fuel connected to the canopy through low-lying branches. Moreover, the thick organic layer and understory mosses and lichens characteristic of black spruce stands are highly flammable (Johnson, 1992). In contrast, deciduous stands have high leaf litter input associated with increased rates of decomposition, higher nutrient availability, and low moss growth, which results in a relatively thin organic layer. This means that the majority of C stored in deciduous stands is in the above ground standing biomass (Viereck *et al.*, 1983). In terms of flammability, deciduous stands have less flammable resins, higher moisture content and fewer ground ladder fuels than spruce stands and are therefore less flammable (Cumming, 2001).

Due to the differences between coniferous and deciduous stands, a switch to deciduous dominance on the landscape will have significant impacts on future climate, carbon storage, nutrient cycling, plant productivity, future fire regimes, wildlife habitat and natural resources for human subsistence use (Chapin *et al.*, 2010). Increased deciduous cover could result in atmospheric cooling due to increases in surface albedo and higher evapotranspiration compared to coniferous stands (Randerson *et al.*, 2006). Above ground carbon pools would likely increase (Alexander *et al.*, 2012), but carbon sequestration might be reduced as deciduous forests accumulate less soil organic matter than spruce ecosystems (Mack *et al.*, 2008). Moreover, the reduced moss and organic layers associated with deciduous cover would enhance permafrost degradation and the release of soil carbon to the atmosphere (Schuur *et al.*, 2008). Fire return intervals are also likely to increase due to lower fuel accumulation, slower rates of fire spread, and reduced flammability of deciduous compared to coniferous forests (Cumming, 2001). A shift

to deciduous dominance will also substantially affect wildlife habitat and human subsistence use. Landscape changes in vegetation will strongly influence mammalian communities in terms of both species composition and distributions (Fisher & Wilkinson, 2005). As communities in northern boreal forests depend on more than 50 wildlife species, including large game animals and edible and medicinal plants, changes to boreal forest vegetation will significantly impact human subsistence activities (Nelson *et al.*, 2008).

5.4 Future Research

In this thesis, I addressed how black spruce trees are responding to climate and how black spruce ecosystem resilience to disturbance from fire may be changing. Despite the results presented here, uncertainties still remain regarding the growth-climate responses of black spruce forest ecosystems and their loss of resilience. Building off of the ideas and results presented throughout this thesis, in the section that follows I provide ideas for future research, specific questions to be addressed, and how these ideas will further our fundamental understanding of boreal forest ecosystem change (see Table 5.1 for a summary).

In this study, I examined growth-climate responses over a thirty year period, which enabled me to examine the greatest number of trees within a site, in addition to circumventing the problem of divergence (D'Arrigo *et al.*, 2008). However, it would be beneficial to understand how black spruce trees responded to climate over a longer period of time, particularly if trees responded to climate differently before 1975, when climate was presumably more favorable for black spruce growth (table 5.1 – Objective 1). For example, a recent study addressing the growth-climate responses of black spruce forest stands in interior Alaska, suggests that prior to 1990 black spruce forests were responding negatively to warm summer temperatures (ie. drought stressed), but post 1990 they began to respond favourably to warming (Ueyama *et al.*, 2005). These results are in direct contrast to the results presented in this thesis. Thus, I believe extending the period of study will provide valuable insight into the possibility of changing growth responses over time and perhaps partially account for the contrasting results between my study and that of Ueyama *et al.* (2015). Another possibility for the discrepancies between our results could be of a more methodological nature. Specifically, their climate responses were calculated from one master chronology that was created from numerous sites that spanned a relatively broad spatial scale. In contrast, I used multivariate statistics for analyzing growth-

climate responses, and believe this type of analyses is valuable, as it retains and accounts for individual variation rather than averaging and losing individual variability as is traditionally used in dendro analyses. Specifically, I found individual variability within stands, with some trees responding negatively and others exhibiting no significant responses. The reasons for this variability remains unclear, but could be due to genetic variation (Wilmking & Juday, 2005), variations in soil conditions and/or nutrient and light availability within the stand, and/or differences in belowground productivity (Pastor *et al.*, 1999), all of which I believe warrants further investigation (table 5.1 – Objective 2). Understanding the reasons for individual variability could not only improve methods for future dendroecological studies, but could also enhance our understanding of the observed climate-growth responses and for forecasting future responses to continued climate change.

In Chapters 2 and 3, I hypothesized that the observed drought signal on north facing slopes could be due to the shallow rooting structure of black spruce trees on sites with thick organic layers and near surface permafrost, which would make them ineffective at water and nutrient uptake when the active layer increases and the water table lowers. However, we currently lack a comprehensive understanding of belowground dynamics, particularly fine root production, in the boreal forest ecosystem (Gower *et al.*, 2001). Therefore more information is needed regarding belowground primary productivity and active layer depths, and if and how these are associated with landscape position (table 5.1 – Objective 3). This is an important knowledge gap to fill, not only for explaining differences between microsites or individual trees in terms of their vulnerability to ongoing climate warming, but also in terms of overall forest productivity and carbon accumulation. It is generally assumed that negative radial growth responses to temperature indicate decreased productivity, but trees could be allocating their resources to belowground productivity through increased root growth. As such, better estimates of belowground productivity need to be obtained in order to understand and predict carbon accumulation in association with temperature induced drought stress.

In Chapter 4, I concluded that we can expect increased vulnerability to compositional change at stands experiencing the compounding effects of an altered fire regime acting on an ecosystem of decreased resilience. In this study, I was unable to disentangle the compounding and interacting effects of fire severity, decreased ecosystem resilience, and environmental gradients in moisture, and how they relate to regeneration (table 5.1 – Objective 4). The largest

shifts in post-fire species composition generally occurred in sites located at warmer and drier landscape positions, with a shallow organic layers, and that experienced a positive growth response to spring moisture. However, higher fire severity is likely to occur in warmer and drier landscape positions and stands occupying similar landscape positions might experience different degrees of post-fire compositional change depending on the degree of fire severity. My study could have addressed this better through using more accurate indications of fire severity, such as composite burn index (CBI) or an estimation of pre-fire organic layer depth using adventitious roots (Boby *et al.*, 2010). Furthermore, my results were based on the assumption that pre-disturbance drought stress was representative of environmentally stressful post-disturbance regeneration conditions. This link could still be empirically tested through transplant and seeding experiments at post-fire sites that experienced different levels of fire severity and different level of pre-disturbance environmental stress. I believe quantitative measurements of fire severity and regeneration conditions would provide additional clarification in regards to differentiating the compounding and interacting effects of an altered fire regime acting on an ecosystem of decreased resilience.

Although uncertainties remain regarding the growth-climate responses of black spruce forest ecosystems and their loss of resilience to disturbance, I believe that the methodology and results presented in this thesis are relevant not only for forecasting and managing the effects of a substantially altered boreal landscape, but could also be useful for predicting vulnerability of other forested ecosystems. Furthermore, as climate change increases the occurrence, severity, and impact of disturbances on forested ecosystems worldwide, there is a growing need to identify factors that contribute to an ecosystem's resilience or that signal changes in the vulnerability of forested ecosystems to disturbance. I believe that my findings, which indicate that tree growth-climate responses can be used as an indication of ecosystem resilience to disturbance are a valuable tool for predicting forest ecosystem resilience and forecasting future forest composition.

Table 5.1 Future research objectives, specific questions to be addressed, and the significance of the proposed research

Future Research Objectives	Questions to Address	Significance
1. Assess the climate-growth responses of black spruce over a longer period of time	<p>a. Has the climate-growth responses of black spruce have changed over time?</p> <p>b. Have black spruce always been drought stressed or is this a recent response to warmer temperatures?</p>	Enhanced predictions of the responses of black spruce trees to continued climate change
2. Determine the reasons for individual variability in climate growth responses within stands	<p>a. Is individual variability attributed to difference in soil conditions or nutrient availability?</p> <p>b. Is individual variability related to belowground differences in productivity?</p> <p>c. Are there genetic differences between trees which could account for the individual variability?</p>	<p>Improved methods in dendroecology sampling and analyses</p> <p>Enhanced understanding of observed climate-growth responses</p>
3. Assess belowground production in black spruce stands	<p>a. How are trees allocating resources to belowground primary production?</p> <p>b. Does belowground productivity differ with climate, active layer depth, landscape position, and/or between individual trees?</p>	Predicting total carbon accumulation in black spruce ecosystems as climate continues to change
4. Clarify the compounding effects of fire severity, decreased ecosystem resilience, and environmental gradients in moisture, and how they relate to regeneration	<p>a. Does post-fire compositional change differ between stands occupying similar landscape positions but experiencing different fire severities?</p> <p>b. Do seedling and transplant survival and growth differ with fire severity, landscape position, and pre-disturbance environmental stress?</p>	Increased ability to forecast ecosystem change

5.5 References

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APPENDIX 2: METHODS FOR DOWNSCALED CLIMATE DATA

Our analyses of tree growth responses to climate used customized downscaled climate data for Alaska and western Canada provided by SNAP (Scenarios Network for Alaska and Arctic Planning 2013). The SNAP data uses the outputs from the five best performing Global Climate Models (GCMs) for Alaska (Walsh et al., 2008) and downscales data using a Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al., 2002). This downscaling procedure accounts for slope, elevation, and proximity to coastlines, and is the same approach used in Climate Research Unit (CRU) data. The primary reason for downscaling GCM data is to provide a finer spatial resolution of climate data that is consistent with the influence of topography at high latitudes.

The historical climate data we used is based on CRU TS3.1 data (Harris et al., 2013) and downscaled by the delta method to match the PRISM climatological data of temperature and precipitation from a 2 km spatial resolution covering Alaska and regions of Canada. The baseline climate data used in the downscaling (PRISM and CRU) has been peer reviewed (Daly et al., 2002; Harris et al., 2013). However, SNAP also assesses the validity of their downscaling process by comparing twentieth century GCM data to actual weather station data. For a full report on the downscaling validation, uncertainty, and specific information regarding the methodology please visit www.snap.uaf.edu.

In this study, the downscaled climate data we used corresponds to each of the four study regions examined, none of which are co-located with long-term climate stations and thus require some form of spatial interpolation to estimate historic climate variations. We obtained values of mean precipitation (mm/year) and mean temperature (Celsius) for every month of every year in each of the regions by averaging all the pixels from the SNAP data within each fire scar. The use of averaged data within each region ensures that our climate data best represent robust patterns of regional variation in climate, and avoids spurious problems with our fine-grained sample locations being arbitrarily clustered within coarser-scale spatial climate pixels. Local effects of topography on microclimate were assumed to be consistent within regions and captured by our topographic stratification of sites.

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APPENDIX 3: SUPPORTING INFORMATION FOR CHAPTER 2.

Table A3.1 Site ID, location, environmental variables, and stand characteristics of the 48 sample sites.

	Site Type ^a and ID	Latitude (N)	Longitude (W)	Elevation (m.a.s.l)	Slope	Aspect	Insolation ^b	pH ^c	Moisture Class ^d	Black Spruce basal area (m ² /ha)
Steese Highway	S1	65.26212	146.75432	387	0	90	0.74	6.72	2	11.06
	S2	65.29468	146.52433	468	0	90	0.87	5.25	2	10.14
	S3	65.29327	146.39170	485	0	90	0.85	5.43	2	4.30
	D1	65.18373	147.26666	236	20.5	330	0.74	5.58	2	9.74
	D2	65.27157	146.70763	378	27	320	0.74	6.46	3	9.49
	D3	65.26613	146.72455	357	16	330	0.74	6.11	3	6.93
	N1	65.15128	147.34212	271	9.5	170	0.49	4.93	3	2.50
	N2	65.16572	147.29003	252	12.75	170	0.42	5.20	3	0.02
	N3	65.28393	146.73490	507	14	219	0.55	4.90	3	4.97
	W1	65.22407	147.13072	279	0	90	0.74	5.37	5	2.54
	W2	65.28942	146.48790	424	0	90	0.74	5.01	6	2.61
	W3	65.15607	147.33268	210	0	90	0.74	5.20	5	3.76
Taylor Highway	S1	63.94592	142.18526	611	0	90	0.831	5.71	3	23.72
	S2	63.53502	142.39516	870	0	90	0.824	5.48	2	29.34
	S3	63.47665	142.44905	825	0	90	0.807	5.84	2	11.34
	D1	63.96244	142.16904	659	5.5	31	0.755	6.46	3	17.96
	D2	63.50164	142.4129	796	8.5	12	0.760	6.58	2	8.69
	D3	63.4045	142.47238	802	21.75	33	0.761	5.74	3	34.55
	N1	66.9617	142.16304	665	10	220	0.659	5.95	5	4.83
	N2	63.56224	142.3734	857	6.25	195	0.657	5.15	3	14.12
	N3	63.42263	142.49141	840	5	210	0.502	4.62	2	10.99
	W1	64.06035	142.02039	595	0	90	0.754	6.29	6	1.61
	W2	63.92665	142.19987	596	0	90	0.756	6.25	6	4.89
	W3	63.80704	142.20879	681	0	90	0.757	6.18	6	2.98
Dalton Highway	S1	66.25560	150.32100	518	0	90	0.77	4.94	2	10.91
	S2	66.07300	150.16837	218	0	90	0.88	6.08	1	12.48
	S3	66.07135	150.16913	194	0	90	0.82	7.60	2	11.98
	D1	66.16902	150.20232	319	6.5	330	0.73	6.53	2	5.51
	D2	66.13817	150.16703	248	11.5	20	0.73	6.48	2	6.74
	D3	65.96183	149.97667	159	8.5	342	0.73	6.91	2	8.63
	N1	66.26032	150.33610	523	4.25	150	0.66	4.78	2	8.13
	N2	66.21182	150.25782	464	15	168	0.59	4.94	3	6.79
	N3	66.11195	150.15693	464	8.5	160	0.63	5.56	2	6.90
	W1	66.11525	150.16475	167	0	90	0.73	6.55	6	3.17
	W2	66.17567	150.21050	130	0	90	0.73	5.22	5	2.30
	W3	66.10715	150.15587	215	0	90	0.73	5.52	6	1.36
Dempster Highway	S1	66.15619	137.1515	613	0	90	0.784	5.45	2	32.55
	S2	66.23415	136.9015	778	0	90	0.782	4.74	2	2.68
	S3	66.16673	137.0663	612	0	90	0.852	4.90	2	10.97
	D1	66.16379	137.0895	652	10	60	0.729	4.91	3	5.78
	D2	66.16853	137.0622	620	6	10	0.729	5.07	2	0.13
	D3	66.18126	137.0221	630	5	11	0.729	4.85	1	2.13
	N1	66.16714	137.082	642	5.5	152	0.659	5.19	4	1.71
	N2	66.16925	137.0604	619	5	200	0.655	6.14	4	1.83
	N3	66.24022	136.9041	782	14.5	148	0.667	4.95	3	3.68
	W1	66.15614	137.1449	598	0	90	0.729	5.09	5	5.43
	W2	66.16157	137.1001	655	0	90	0.729	5.93	6	3.09
	W3	66.16792	137.0659	623	0	90	0.729	5.88	6	2.33

^a Site Type D=dry flat, N=north facing midslope, S=south facing midslope, W=wet flat.

^b A calculated index of the amount of solar radiation received at a site on the summer solstice.

^c pH = soil pH, measured from near surface mineral soil samples (3 points/site)

^d Ranking of site moisture: 1=xeric, 2=subxeric, 3=subxeric to mesic, 4=mesic, 5=submesic, 6=subhygric

Table A3.2 RDA results for the Steese, Taylor, Dalton, and Dempster Highways, explaining the proportion and cumulative variances for both constrained* and relative constrained** variances and relative contributions of each environmental variable attributed to each axis.

			RDA1	RDA2	RDA3	RDA4
Steese Highway	Constrained Variance	Proportion	0.055	0.019		
		Cumulative	0.055	0.077		
	Relative Variance	Proportion	0.790	0.209		
		Cumulative	0.790	1.000		
	Explanatory Variables	Insolation	0.930	0.368		
		Longitude	-0.829	0.559		
Taylor Highway	Constrained Variance	Proportion	0.034	0.027		
		Cumulative	0.034	0.061		
	Relative Variance	Proportion	0.561	0.439		
		Cumulative	0.561	1.000		
Explanatory Variables	BS Density	0.997	0.076			
	Moisture	-0.347	-0.938			
Dalton Highway	Constrained Variance	Proportion	0.043	0.022	0.017	0.008
		Cumulative	0.043	0.064	0.081	0.089
	Relative Variance	Proportion	0.480	0.243	0.186	0.090
		Cumulative	0.480	0.724	0.910	1.000
	Explanatory Variables	Latitude	0.418	0.831	-0.081	0.357
		Slope	0.432	-0.213	0.770	0.419
		Aspect	-0.450	-0.068	0.591	0.666
		BS Density	0.062	-0.895	-0.268	0.352
Dempster Highway	Constrained Variance	Proportion	0.039	0.024	0.009	
		Cumulative	0.039	0.063	0.071	
	Relative Variance	Proportion	0.545	0.334	0.121	
		Cumulative	0.545	0.879	1.000	
	Explanatory Variables	DBH	0.866	-0.346	0.360	
		Soil pH	-0.657	-0.478	0.584	
Elevation		0.866	-0.346	0.360		

*The constrained variance is all the variance that can be explained by the constrained analysis.

** The relative constrained variance is the amount of variance captured by each axis relative to the total constrained variance (ex. relative constrained variance for RDA1 on Steese Highway = $0.073/0.116=0.634$)

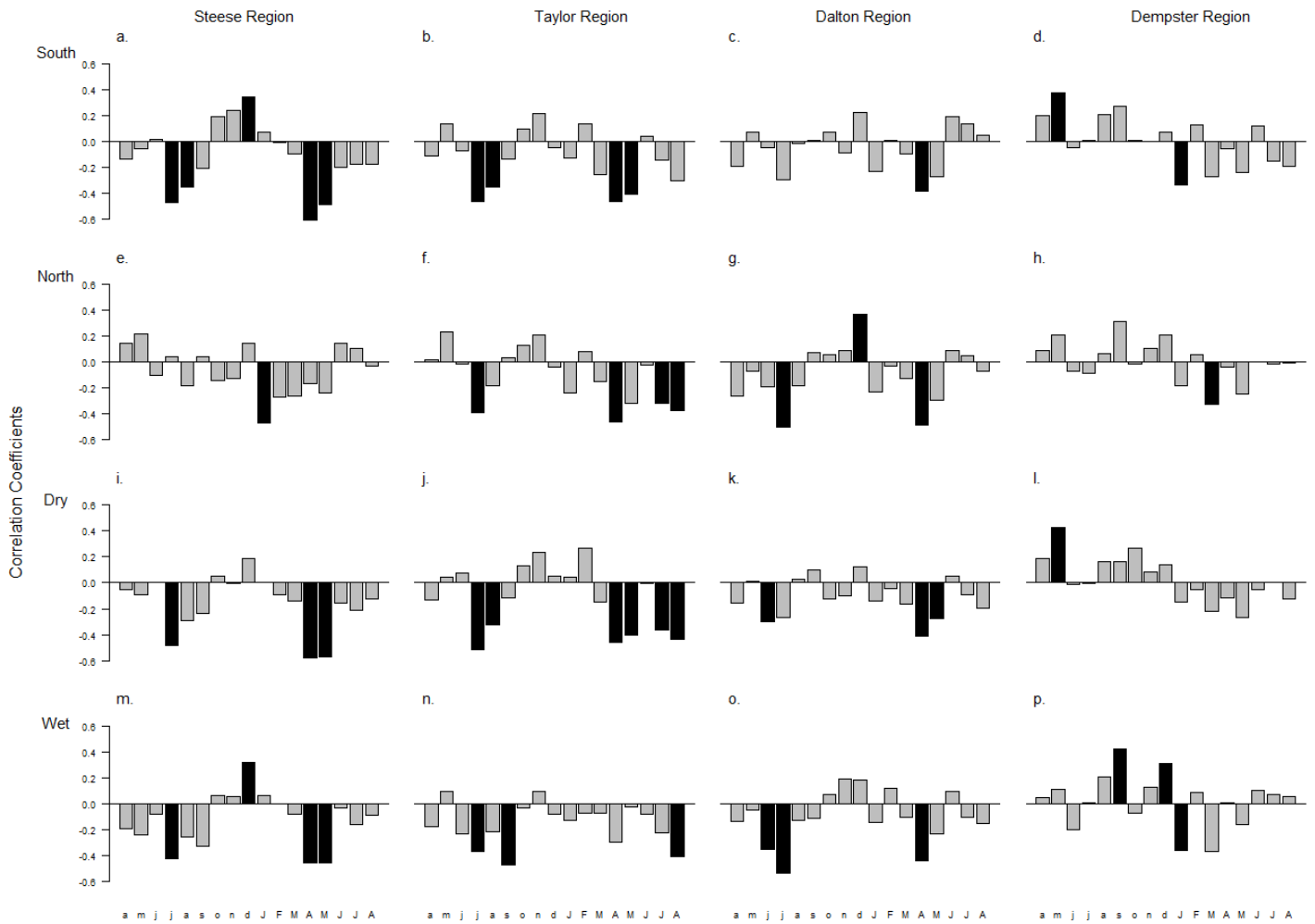


Figure A3.1 Correlations between ring width chronologies and mean monthly temperatures. Temperatures were obtained from SNAP climate data over a 17 month climatic window for the Steese (a,e,i,m), Taylor (b,f,j,n), Dalton (c,g,k,o), and Dempster (d,h,l,p) regions. Standard ring width chronologies were developed for south facing (a,b,c,d), north facing (e,f,g h), dry flat (i,j,k,l) and wet flat (m,n,o,p) sites. Y-axes represent correlation coefficients (black bars = significant correlations at $p < 0.05$), and X-axes represent months of the year (lower case = year prior to ring formation, uppercase = year of ring formation).

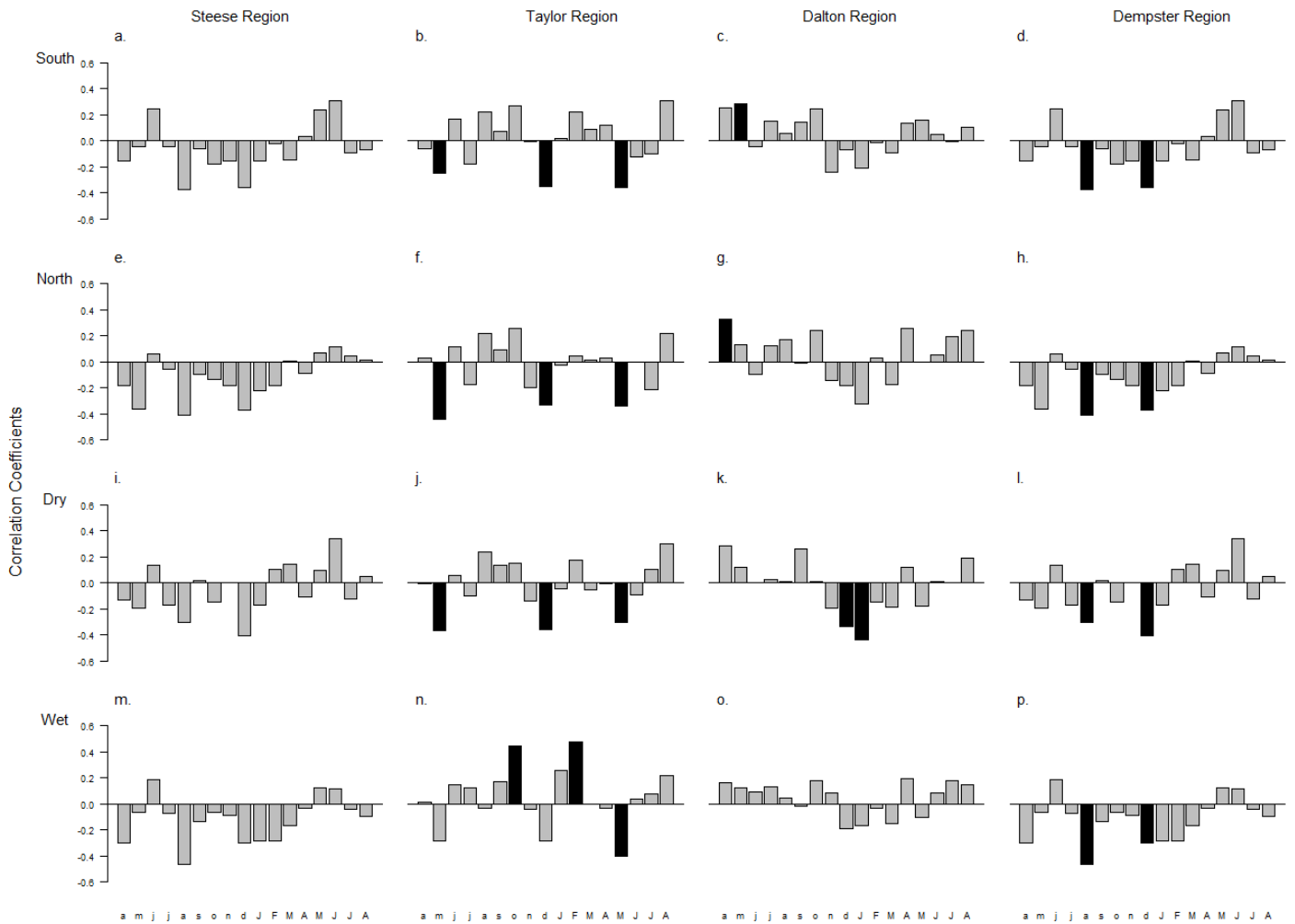


Figure A3.2 Correlations between ring width chronologies and total monthly precipitation. Precipitations were obtained from SNAP climate data over a 17 month climatic window for the Steese (a,e,i,m), Taylor (b,f,j,n), Dalton (c,g,k,o), and Dempster (d,h,l,p) regions. Standard ring width chronologies were developed for south facing (a,b,c,d), north facing (e,f,g,h), dry flat (i,j,k,l) and wet flat (m,n,o,p) sites. Y-axes represent correlation coefficients (black bars = significant correlations at $p < 0.05$), and X-axes represent months of the year (lower case = year prior to ring formation, uppercase = year of ring formation).

APPENDIX 4: ANALYSIS OF WOOD COMPONENT FOR STABLE ISOTOPE COMPOSITION

Background

Despite the relatively straightforward interpretation of dendroisotopic analysis, there is considerable debate regarding which wood component to isolate for determining $\delta^{13}\text{C}$ (McCarroll and Loader 2004). Wood is comprised of various chemical components, including cellulose, lignins, hemicelluloses, resins, and tannins. Variations in the proportions of these components, both among trees and even within the same ring, can introduce error in the analysis of stable isotopes from wholewood (WW) (Helle and Schleser 2004). Early work used WW (e.g. Craig 1954, Libby et al. 1976), but as different wood components differ isotopically, most studies have used either holocellulose (HC) or α -cellulose (AC). Cellulose is the most easily isolated component of wood (Leavitt and Danzer 1993, Van de Water 2002) and is the only wood component that retains its carbon isotopic composition from the time of formation (McCarroll and Loader 2004). Cellulose is therefore widely accepted as the standard in dendroisotopic analysis (Leavitt and Danzer 1993, Harlow et al. 2006). However, the extensive chemical processing needed to isolate cellulose is a potential source of error and is typically the rate-limiting step. Furthermore, isotope analysis on cellulose compared to WW requires significantly more sample material, which is often limited, particularly for trees producing very narrow annual rings. Numerous studies have shown significant similarity in carbon isotopes of cellulose and WW, supporting the use of WW for dendroisotopic analysis (e.g Borella et al. 1999, Barbour et al. 2001, Loader et al. 2004, Au and Tradiff 2009). However, the effects of chemical processing on $\delta^{13}\text{C}$ values need to be evaluated on the particular tree species and the local conditions of interest to ensure accuracy and reliability of results. Here we assess $\delta^{13}\text{C}$ in replicate samples of wholewood (WW), extractive-free wood (EF), holocellulose (HC), or α -cellulose (AC), to determine which wood component provides the most reliable results.

Methods

Comparison of $\delta^{13}\text{C}$ in different wood components

Five trees were randomly selected for stable isotope analysis on the different wood components. Trees were both visually and statistically cross-dated and the outer ten rings on two perpendicular radii per tree were removed using a chisel and razor. As ring width was small, we did not differentiate earlywood versus latewood but used the entire ring. Wood from the two

radii were combined and ground into one homogenous sample using a Wiley Intermediate Mill to pass through a 20-mesh screen (*0.78 mm porosity). The ground wood sample from each tree was then separated into twelve equal portions, each of which was put into a vial. For each tree, three vials were left as is for WW analysis and the remaining nine vials were heat sealed in dried pre-weighed filter pouches (Ankom inc.). Three pouches were processed to each of EF, HC, and AC for each tree. In total, 60 samples were analyzed for $\delta^{13}\text{C}$.

Although there are numerous methods of cellulose extraction, we used the Jayme-Wise method (Green 1963) as modified by Leavitt and Danzer (1993), as it is known to yield the most reliable results (Gaudinski et al 2005) (Figure A2.1). Resins were extracted from treatments of EF, HC, and AC in a Soxhlet apparatus for 24 hours in 2:1 toluene:ethanol, then for 24 hours in 100% ethanol. The bags were then boiled in distilled deionized (DDI) water for 6 hours. Lastly, the EF samples were oven-dried at 70°C and their dry mass recorded. The second treatment consisted of taking the remaining 30 sample bags (6 bags/tree) and extracting HC by heating for 12 hours in a 1.5 litre flask of 1 ml of acetic acid, 6.7 g of sodium chlorite, and 700 ml of DDI water preheated 70°C. Four additions of the acidified sodium chlorite were made at 2 hour intervals, after which the samples were left in the solution for 12 hours at 70°C. Samples were then continuously rinsed with DDI water until conductivity reached <5 mmho/cm (~ 4hours), and lastly oven-dried at 70°C for 48 hours to result in HC. Half of these samples (15 in total – 3 bags/tree) were further processed to AC by separating the hemicelluloses from the HC. The samples were washed in 7.5% sodium hydroxide (NaOH) for one hour (Pettersen 1984), continuously rinsed with DDI water for 4 hours, placed in a 10% glacial acetic acid solution for one hour, and rinsed a final time with DDI water for 4 hours. The samples were then oven-dried at 60°C for 48 hrs and their dry mass recorded. Following the four preparation methods (WW, EF, HC, and AC), approximately 2.5 mg of each sample was encased in a tin cup for isotopic analysis.

All samples were measured for percent carbon (%C) and $\delta^{13}\text{C}$ using a continuous flow, stable-isotope mass spectrometer at the Light Stable Isotope Mass Spec Lab, Department of Geological Science, University of Florida. The $\delta^{13}\text{C}$ values are expressed relative to the Vienna PeeDee belemnite (VPDB) standard (Coplen 1995).

Data Analysis

The proportions of EF, HC, and AC, were determined by weighing the sample bags after extraction and calculating the ratio of dry mass remaining to that of WW. To determine the effects of removing extractives, lignin, and hemicelluloses, we correlated $\delta^{13}\text{C}$ values between each of the different wood components (WW, EF, HC, and AC). Additionally, we used a one-way analysis of variance (ANOVA) and post-hoc Tukey honestly significant different test (Tukey-HSD) to assess the difference in mean $\delta^{13}\text{C}$ values between the wood components.

Results

Comparison of $\delta^{13}\text{C}$ in wood components

With each successive chemical treatment the percent yield decreased relative to WW (EF, 89.1 ± 6.4 (mean \pm SD), HC, 57.3 ± 6.2 , AC 51.2 ± 12.7 ; fig A3.2(a)). The most pronounced decrease in %C occurred after processing from HC to AC (fig A3.2(b) and table A3.1). Enrichment of $\delta^{13}\text{C}$ was greatest after lignin removal to produce HC (fig A3.2(c) and table A3.1). Despite the enrichment of $\delta^{13}\text{C}$ in HC and AC compared to WW and EF, the $\delta^{13}\text{C}$ of all wood components were significantly correlated. The $\delta^{13}\text{C}$ values were significantly different between wood components (ANOVA, $F=12.298$, $df=3$, $p\text{-value}<0.001$). The post-hoc comparison revealed that $\delta^{13}\text{C}$ between WW and EF were not significantly different nor between HC and AC (fig A3.3). All other comparisons were significantly different.

Interpretation

Although cellulose is the standard used in tree-ring isotope analyses, the data we present here suggests that the isolation of cellulose from wholewood for black spruce samples is not necessary for $\delta^{13}\text{C}$ analysis. The high degree of correlation we detected between $\delta^{13}\text{C}$ in the different wood components taken from the same samples, indicates that the isotopic shift in cellulose was matched by an isotopic shift of similar magnitude in wholewood. Our finding that the isotopic composition of cellulose and wholewood are highly correlated is in agreement with other studies on different tree species (e.g. Borella et al. 1998, Harlow et al. 2005, Taylor et al. 2008). Given the observed high degree of correlation, and the significant sample size and preparation time required for processing wholewood to purified cellulose requires, we suggest that whole wood is suitable to work with when examining ecophysiological responses of black spruce to changing environmental conditions.

Table A4.1 The percent carbon (%C) and $\delta^{13}\text{C}$ (‰) values from five *P.mariana* trees with three replicate samples each of decadal wholewood (WW), extractive-free wood (EF), holocellulose (HC), and alphacellulose (AC).

Tree (site)	Wholewood (WW)		Extractive-free wood (EF)		Holocellulose (HC)		Alphacellulose (AC)	
	% C	$\delta^{13}\text{C}$ (‰)	% C	$\delta^{13}\text{C}$ (‰)	% C	$\delta^{13}\text{C}$ (‰)	% C	$\delta^{13}\text{C}$ (‰)
1 (N3)	46.00±1.71	-25.64±0.21	44.94±0.15	-25.52±0.10	44.94±0.15	-24.35±0.09	40.06±0.74	-24.38±0.22
2 (S3)	45.31±0.46	-25.10±0.07	45.16±0.21	-24.90±0.08	45.16±0.21	-23.87±0.10	40.66±0.34	-23.62±0.08
3 (N5)	45.43±0.43	-25.07±0.15	45.20±0.07	-25.01±0.26	45.20±0.07	-23.80±0.11	40.86±0.32	-23.77±0.16
4 (S1)	45.46±0.17	-26.35±0.08	45.82±0.57	-26.16±0.01	45.82±0.57	-24.79±0.14	40.98±0.68	-24.79±0.16
5 (S5)	45.24±0.31	-25.60±0.17	44.37±0.20	-25.43±0.09	44.37±0.20	-24.33±0.07	40.75±0.73	-24.22±0.15

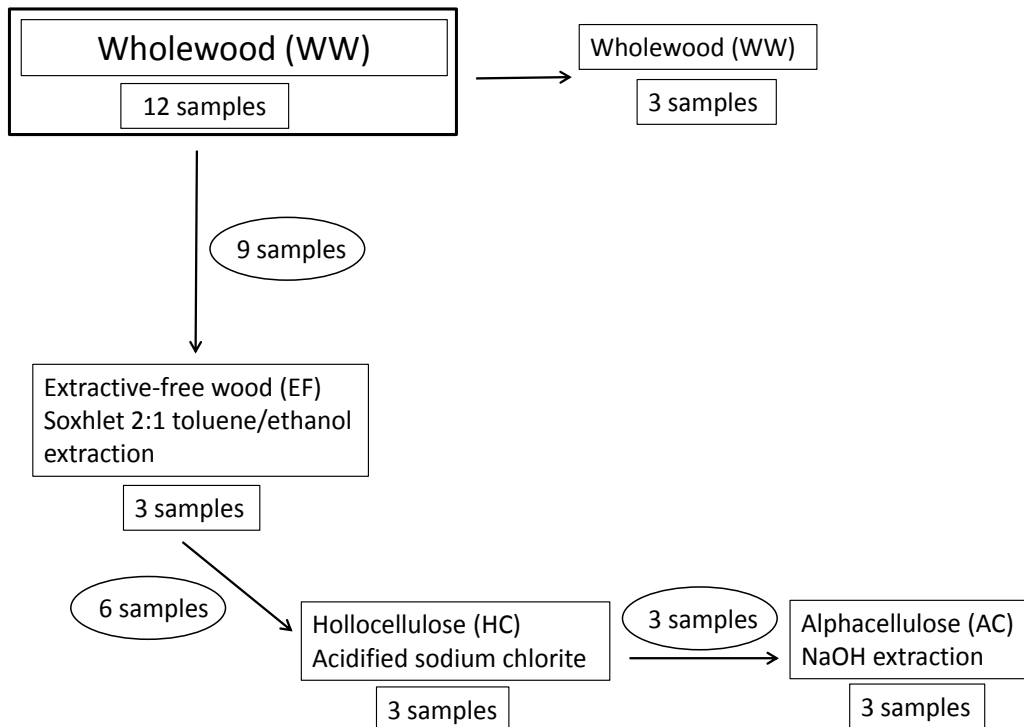


Figure A4.1 Resin, lignin, and hemicellulose removal for producing extractive free wood, holocellulose, and α cellulose, respectively. This procedure was completed on five randomly selected trees with three replicate sample bags per treatment per tree.

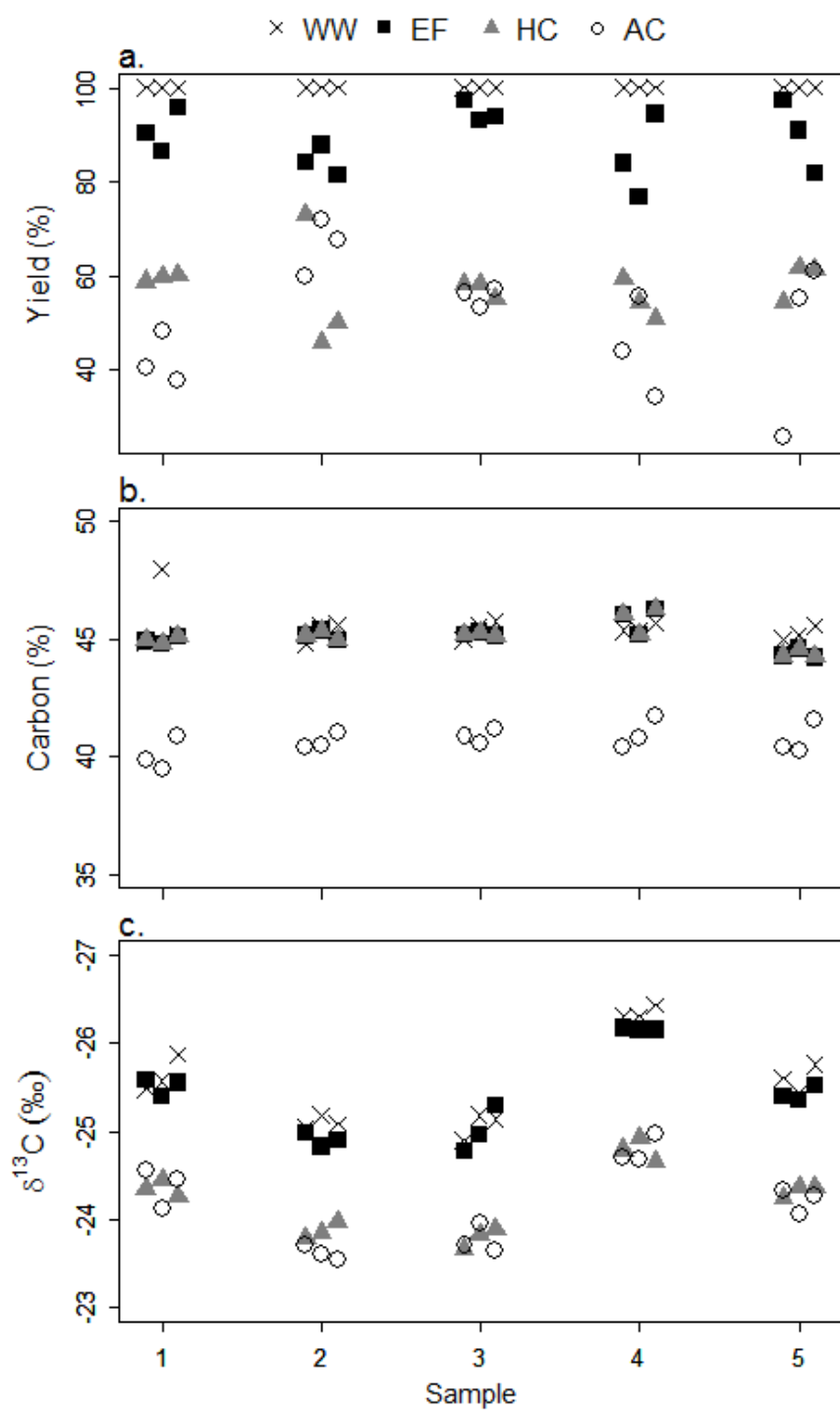


Figure A4.2 a) percent yield, b) percent carbon, and c) $\delta^{13}\text{C}$ values from five *P.mariana* trees with three replicate samples each of decadal wholewood (WW), extractivefree wood (EF), holocellulose (HC), and alphacellulose (AC).

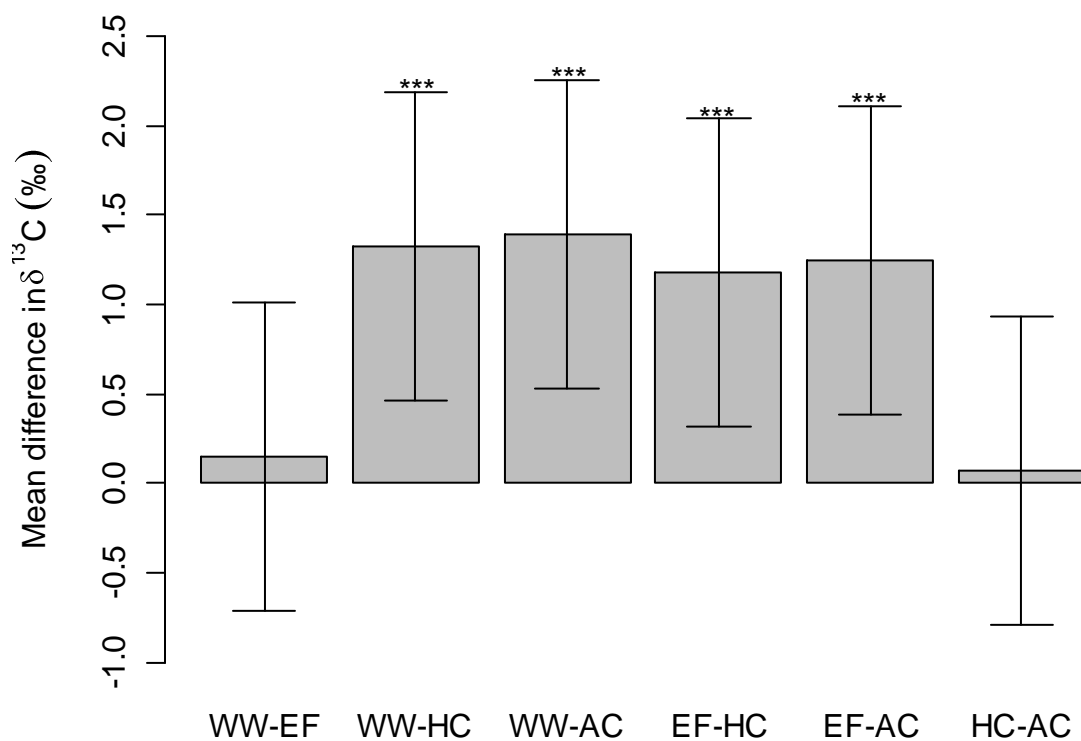


Figure A4.3 The mean difference, or offset in $\delta^{13}\text{C}$ values, between paired wood components of wholewood (WW), extractive-free wood (EF), holocellulose (HC), and alpha-cellulose (AC) as calculated by Tukey-HSD (see Table A3.1). Error bars represent 95% confidence intervals. Statistically significant comparisons ($p\text{-value} < 0.05$) are denoted with ***.

APPENDIX 5: SUPPORTING INFORMATION FOR CHAPTER 3.

Table A5.1 χ^2 test results of the difference in radial growth-climate response category proportions between northern and southern aspects within interior Alaska (n=180), the toposequence (n=60), and the subsampled trees within the toposequence (n=18). Response categories are defined as follows: positive (>67% of significant correlations were positive), negative (>67% of significant correlations were negative), mixed (between 33 and 67 % of significant correlations were negative) or none (no significant correlations).

		Temperature		Precipitation		Climate Moisture Index	
		North	South	North	South	North	South
Interior Alaska	Negative	0.526	0.544	0.333	0.304	0.154	0.114
	Positive	0.218	0.228	0.333	0.481	0.538	0.608
	Mixed	0.115	0.127	0.141	0.076	0.026	0.051
	None	0.141	0.101	0.192	0.139	0.282	0.228
	χ^2	0.596		4.409		1.888	
	p-value	0.897		0.22		0.5957	
Toposequence	Negative	0.536	0.793	0.179	0.345	0.036	0.034
	Positive	0.214	0.103	0.536	0.379	0.964	0.931
	Mixed	0.214	0.103	0.036	0.103	0	0.034
	None	0.036	0	0.25	0.172	0	0
	χ^2	4.668		3.599		0.983	
	p-value	0.197		0.308		0.612	
Subsample	Negative	0.889	0.889	0	0	0	0
	Positive	0	0	0.778	0.667	1	1
	Mixed	0.111	0	0.111	0	0	0
	None	0	0.11	0.111	0.333	0	0
	χ^2	2		2.077		0	
	p-value	0.368		0.354		1	

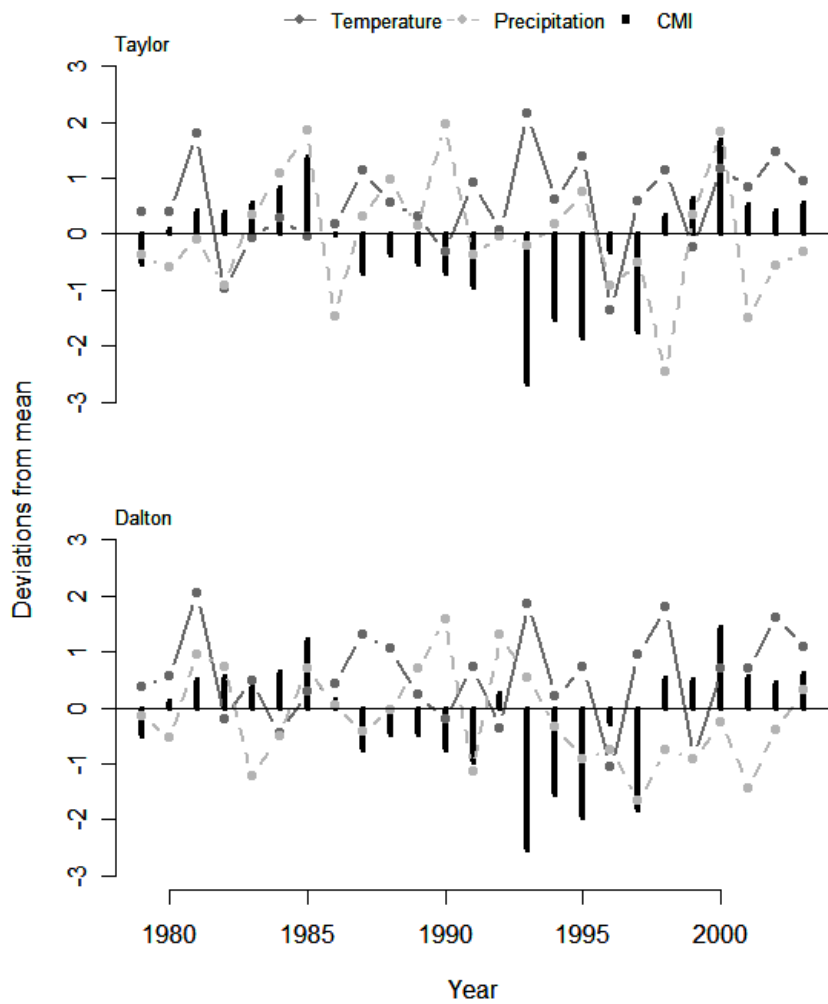


Figure A5.1 Temperature, Precipitation and Climate Moisture Index (CMI), deviations (1979-2003) from the historical mean (1950-2003) for the Taylor and Dalton regions. Temperature and Precipitation data was obtained from Scenarios Network for Alaska and Arctic Planning, and the CMI was calculated using the simplified Penman–Montieth method of Hogg (1997). Climate deviations for the Steese region are presented in main text (fig 3.2).

APPENDIX 6: SUPPORTING INFORMATION FOR CHAPTER 4

Table A6.1 Summary of dendroclimatic responses, showing the percentage of sites that were significantly correlated to monthly metrics of temperature, precipitation, and CMI and the average correlation of all sites to the same monthly climate metrics.

		Percentage of sites with significant correlations			Average correlation of all sites		
		Temperature	Precipitation	CMI	Temperature	Precipitation	CMI
Previous Year	April	1.4	8.3	8.3	-0.08	0.11	0.01
	May	4.2	4.2	6.9	0.07	-0.06	0.03
	June	5.6	2.8	12.5	-0.02	0.01	0.08
	July	40.3	0	36.1	-0.29	0.04	0.29
	August	26.4	2.8	43.1	-0.19	0.15	0.26
	September	5.6	2.8	0	-0.07	0.07	0.02
	October	2.8	6.9	2.8	0.04	0.15	0.04
	November	0.00	8.3	2.8	0.05	-0.06	-0.01
	December	12.5	9.7	1.4	0.12	-0.13	-0.09
Current Year	January	9.7	1.4	0	-0.14	-0.07	0.04
	February	1.4	11.1	4.2	0.02	0.16	-0.05
	March	0	0	0	-0.10	-0.03	0.08
	April	47.2	0	30.6	-0.32	0.07	0.28
	May	50.0	4.7	57.2	-0.30	-0.06	0.32
	June	8.3	1.4	8.3	0.00	-0.01	-0.02
	July	12.5	1.4	16.7	-0.12	0.03	0.15
	August	13.9	8.3	36.1	-0.17	0.16	0.25