CLIMATE CHANGE AND THE BIOPHYSICAL LANDSCAPE: THE INFLUENCE OF TOP-DOWN AND BOTTOM-UP CONTROLS ON SPATIOTEMPORAL PATTERNS OF FOREST EXPANSION AND TREE GROWTH IN DENALI NATIONAL PARK AND PRESERVE, ALASKA

A Dissertation in Geography

by

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Abstract

Increasingly rapid climate change at higher latitudes and altitudes are altering the spatial pattern and distribution of terrestrial vegetation leading to an ecosystem shift at the boreal-forest ecotone. Since 1900, in Denali National Park and Preserve, Alaska (Denali), average temperatures have increased approximately 3° C and total precipitation decreased approximately 150 mm. This change in climate has resulted in a steady encroachment and replacement of tundra vegetation by woody species. White spruce (Picea glauca) trees, an important species within the park, are particularly successful invaders into tundra. However, biological and physical site factors can influence the magnitude of the response of tree establishment and growth to climate change. Influential site factors may include elevation, soil temperature, total incoming solar radiation, aspect, permafrost presence, and adjacency to existing mature trees. The broad focus of this research explored variations in tree establishment and growth at the local and regional levels as a function of climate change and biophysical site factors using dendroecological, statistical, GIS, and remote sensing techniques. With this research, I wanted to determine: 1) Where is an increase in tree establishment and growth occurring and where is it not? 2) If there is an increase in tree establishment and growth, when is this change occurring? 3) In locations where increases in tree establishment and growth occur, why are they occurring in those locations? A total of 619 tree cores were collected at three sites along transects placed on north- and south-facing aspects within the closed canopy forest and treeline zone. Dendroecological analyses show, that though initial increases in temperature increased tree establishment in Denali around 1915, a pulse in establishment beginning in the 1950s corresponded with a negative shift in total...
precipitation with this relationship primarily evident on south-facing aspects. The relationship between tree growth and climate also strengthened after the 1950s with the strongest relationships occurring on south-facings aspects. Remotely sensed imagery shows a 10% parkwide average increase of tree invasion into tundra dominated locations and 11% increase in infilling within pre-existing 1950s forested locations since the 1950s with the exception of the easternmost site which experienced an approximately 30% increase in infilling. Elevation, topographic position, and proximity to existing trees, which provide a seed source and protection from extreme climatic conditions, were the most important biophysical variables promoting new seedling establishment, growth, and survival since the mid-1950s. This research highlights the need to assess the influence of multiple governing climatic and biophysical controls over time influencing heterogeneous spatial patterns of tree establishment and growth.
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DEDICATION

This dissertation is dedicated to Kirk Stueve who not only introduced me to the research possibilities in Denali in 2008, but also encouraged me to get the Ph.D.
Chapter 1 – Introduction

The Influence of Top-Down and Bottom-Up Controls on the Spatial and Temporal Patterns of Forest Expansion and Tree Growth at Higher Latitudes and Altitudes
Introduction

*Top-down (climatic) controls and effects on vegetation*

Rapid climate change in the 20th century has been magnified at high latitudes and altitudes, which have warmed at twice the global average (Chapin et al., 2010; Harsch et al., 2009; IPCC, 2007; Burkett et al., 2005). These continuing trends of climate change are expected to result in the creation of no-analog climates, no longer representative of current climatic conditions (Fox, 2007; Williams and Jackson, 2007). However, the timing of the creation of no-analog climates and the magnitude of their impact to ecosystems is difficult to predict (Scheffer et al., 2009), particularly in light of the high degree of spatiotemporal climatic variability observed globally (Kreyling et al., 2014). Observations of ecosystem responses to climatic regime shifts include the transitioning of dominant plant functional types and shifting species communities (Walther et al., 2002). However, individual species have thermal and moisture thresholds delimiting their response to rapid climate change (Jackson et al., 2009). For instance, at higher latitudes and altitudes, extirpation or a transition from conifer-dominated forests to deciduous-dominated forests is expected to occur with a continued increase in temperature (Johnstone et al., 2010; Chapin et al., 2006; Rupp, et al., 2001). Alternatively, within these higher latitudes and altitudes, geographic regions of increased precipitation may offset negative impacts from increased temperatures providing a refuge to otherwise stressed forest species (D’Orangeville et al., 2016).

Ecosystems undergoing species compositional transitions that reflect impacts from climate change most readily are at ecotonal boundaries or at the extreme limits of an
ecosystem’s range (Beck et al., 2011; Suarez et al., 1999). The clearest evidence of these impacts include shifts in the spatial distribution of vegetation like the steady encroachment of woody species upslope and towards the poles invading the tundra biome (Dial et al., 2016; Myers-Smith, 2015; Roland et al., 2013; Stueve et al., 2011; Sullivan and Sveinbjörnsson, 2010; Chapin et al., 2006; Burkett et al., 2005; Sturm et al., 2005; Sturm et al., 2001). However, geographic heterogeneity can result in widely variable ecological responses at different geographic locations, as well as at different spatial and temporal scales (Ju and Masek, 2016; Renard et al., 2016; Andersen et al., 2009; Jackson et al., 2009; Holtmeier and Broll, 2005; Wilmking et al., 2004; Scheffer and Carpenter, 2003; Smith et al., 2003). This is particularly true in mountainous terrain where topography strongly influences local climatic variability which can influence patterns of tree establishment and growth (Frey et al., 2016; Case and Duncan, 2015; Roland et al., 2013; Stueve et al., 2011; Johnstone et al., 2010; Daniels and Veblen, 2004; Rupp et al., 2001). While some species may experience increases in establishment and growth rates, other species will experience increased rates of mortality. Highly variable warming patterns, moisture availability, timing of snowpack melt, wind desiccation, and biological competition at the regional scale partially explains this divergence (Renard et al., 2016; Burkett et al., 2005).

**Bottom-up (biophysical) controls and effects on vegetation**

Numerous biophysical variables have been found to influence the spatiotemporal patterns of tree establishment and growth in the boreal-tundra ecotone (Sullivan and Sveinbjörnsson, 2010; Holtmeier and Broll, 2007; Resler, 2006, Daniels and Veblen,
The boreal-tundra ecotonal boundary represents the transition in tree cover density from closed-canopy forest through the treeline zone, an area comprised of a combination of forest and tundra species, to tundra (Ranson et al., 2011; Sveinbjörnsson, et al., 2002).

Physical site factors can promote or inhibit tree establishment and growth under changing climatic conditions (Pyatt et al., 2016; Treml and Chuman, 2015; Butler et al., 2007, Resler, 2006; Lookingbill and Urban, 2003; Smith et al. 2003; Cooper, 1986). Minimum temperature and permafrost are thought to be the predominant limiting factors controlling where the boreal forest can successfully establish and persist at its northern and high elevation limits (Helbig et al., 2016; Danby, 2011; Schrag et al., 2008; Chapin et al., 2006; Lloyd, 2005; Daniels and Veblen, 2004). Warmer temperatures and thawing permafrost can trigger an increase in tree establishment and tree density (Helbig et al., 2016; Wang et al., 2016; Lloyd, 2005; Camarero and Gutiérrez, 2004). However, in mountainous regions, discontinuous permafrost, and thermal modification related to terrain properties such as slope, aspect, elevation, or topographic position (Lookingbill and Urban, 2003), may limit tree establishment and movement of forests into tundra systems.

Previous research has demonstrated a strong correlation between tree establishment and growth, and physical site conditions including elevation, permafrost, aspect, solar radiation, topographic position, soils, and slope angle (Danby and Hik 2007; Rupp et al. 2001). In the northern hemisphere, north-facing aspects receive less incoming solar radiation and are therefore generally cooler than south-facing aspects (Harsch, et al., 2009; Lookingbill and Urban, 2003). Consequently, tree establishment is often observed at lower elevations on north-facing aspects (Stueve et al., 2011; Danby
and Hik, 2007), with trees growing at a much slower rate. Moreover, the total amount of solar insolation received at a location is influenced by solar angle, slope angle, and aspect which can favor or inhibiting tree establishment and growth. For instance, as the solar angle decreases during the transition from summer to winter, the photoperiod will shorten more rapidly on north-facing aspects or flatter slope angles (Bonan and Shugart, 1989).

Topographic position can influence whether an area is exposed or protected from more extreme climatic conditions and facilitate tree establishment and growth. A more protected area may increase both atmospheric and soil temperatures as well as reduce the influence of wind. Related to incoming solar radiation, moderately exposed slopes may favor establishment in the summer as a result of the expanded growing season length (Viereck, 1979). Alternatively, too much exposure may increase stress (e.g. drought stress and large diurnal to nocturnal temperature ranges) that prevents or suppresses tree establishment and growth (Brownlee et al., 2016; Wilmking et al., 2004, Cui and Smith, 1991). Considering the influence of prevailing wind direction combined with elevation, aspect, and slope angle, these factors might increase or reduce the amount of snow accumulation. For example, those sites located at higher elevations, leeward aspects, shallower slope angles, and had a higher degree of concavity, are expected to retain snow for the longest period of time and receive the greatest amount of accumulation.

Tree establishment and growth may also be strongly influenced by soil moisture conditions. Increased rates of tree establishment and tree growth have frequently been observed at locations associated with higher soil moisture retention (Stueve, et al., 2011; Calef et al., 2005). In addition, soil porosity and soil depth to the bedrock or permafrost layer can dictate the soil moisture storage capacity limiting water availability to trees.
(Resler, 2006). Moisture has an additional concurrent influence on soil temperature. The high latent heat of water has an ameliorating effect on soil temperatures in close proximity to streams. This trend is evident with the observation of higher rates of tree establishment and growth, and an increased density of trees adjacent to streams (Andersen and Baker, 2005; Viereck, 1970). Those areas receiving moderate amounts of snow not only produce an insulating effect increasing soil temperature, but also increase soil moisture which may enhance the rates of tree establishment and growth (Viereck, 1970; Geddes et al., 2005). However, a large seasonal snowpack may decrease the length of the growing season and photosynthesis, and in turn, inhibit tree establishment and growth (Alftine et al, 2003; Geddes et al., 2005).

Observations from historical landscape photography, aerial photography, and satellite imagery have shown tree seedlings often establish adjacent to existing forest edges and isolated patches of established trees or “tree islands” (Stueve, et al., 2011; Roush, et al., 2007; Zier and Baker, 2006; Smith et al. 2003; Kullman, 1993). Existing trees can modify microtopography and provide a seed source as well as protection against extreme temperature fluctuations and strong winds, and influence snowpack depth, which can facilitate tree expansion into tundra due to climate change (Pyatt, et al., 2016; Renard et al., 2016; Harsch et al., 2009; Germino, et al., 2002). Successful reproduction, and subsequent establishment and persistence of seedlings decrease with increasing altitude (Wardle, 1968). White spruce (*Picea glauca*), assessed in this research, produce winged wind-dispersed seeds that can travel large distances (Ritchie and MacDonald, 1986). Seed rain can range anywhere from 60-300 m away dependent on factors like nearby
topographic obstructions and wind strength with seed rain decreasing with increasing
distance from the seed source (Cooper, 1986).

The shrub layer may shelter seedlings from extreme climatic fluctuations at
higher altitudes while also providing a layer of insulation increasing temperatures near
the ground surface (Grace, et al., 2002). However, shrubs are also known to inhibit tree
seedling establishment and persistence through competition for resources like light,
water, nutrients, and space (Dial et al., 2016; Lloyd and Fastie, 2002; Germino, et al.,
2002; Grace, et al., 2002). Hobbie and Chapin (1998), for example, determined that
seedling growth and persistence were limited by water and nutrient (e.g. phosphate,
ammonium, nitrate) availability, decreasing with increased below-ground competition for
resources. Once seedlings are able to grow above the shrub layer, they not only have to
contend with the competition for resources, but also exposure to more extreme climatic
conditions (Grace, et al., 2002). These extreme conditions include mortality from cold
temperature stress, wind induced desiccation, and structural damage from snow or ice
accumulation (Harsch and Bader, 2011).

Study Area

Regional: Denali National Park and Preserve

In Denali National Park and Preserve, Alaska (Denali) (Figure 1), the Alaska
Range encompasses around 60% of the park and greatly influences local climate because
of orographic effects (Clark and Duffy, 2006). The Alaska Range bisects the park into
two climate zones. Compared to the areas south of the Range, the northern Interior
climate is colder in winter, warmer in summer, and drier due to the rain shadow effect on
weather patterns moving north and resulting in precipitation on or south of the mountain ridges (Hooge et al., 2006). The Gulf of Alaska produces a more maritime continental climate on the south side of the Alaska Range where the high peaks of the range limit moisture availability on the north side of the range.

Denali is comprised of five physiographic regions with glacial-fed braided streams flow throughout the park (Clark and Duffy, 2006). The study area for this research takes place in the Alaska Mountains physiographic region, part of the Alaska Range. In the Alaska Mountains region, soils are comprised of three main materials including gravelly colluvium, drift, and loamy and gravelly alluvium (Clark and Duffy, 2006). Major soils orders in the study locations include Inceptisols and Spodosols (Clark and Duffy, 2006).

**Average site-level descriptions**

Climatic and biophysical site factor influences on tree establishment and tree growth were assessed at three treeline study sites (Figure 1). These locations were restricted north of the Alaska Range to limit confounding influences of regional climate from the Alaska Range. The distance between Cabin Divide and Healy is approximately 50 km (30 miles). Healy has the least internannual variability of the three sites, and is warmer and drier on average (Table 1). The study sites vary in elevation from about 400 m to 1400 m. Soils are moderately to well drained and range from gravelly till, scree, or talus to silty eolian deposits from schist (Clark and Duffy, 2006). Within Denali, permafrost occurs mainly north of the Alaska Range (Yocum et al. 2007). The spatial distribution of permafrost, considered a primary limiting factor controlling tree establishment (Chapin et al., 2006), is classified as discontinuous (50-90% of area
comprised of permafrost) at the East Fork and Cabin Divide sites, and sporadic (10-50% of area comprised of permafrost) at the Healy site (Panda, et al., 2014; Osterkamp and Jorgenson, 2009).

The dominant tree species at all three sites were white spruce (*Picea glauca*), a species that comprises approximately 26% (12.1 million ha) of the boreal forest in Alaska (Juday et al., 2003). A variety of shrubs are present in and near the forest-tundra ecotone and include resin birch (*Betula glandulosa*) and dwarf arctic birch (*Betula nana*), *Vaccinium* spp. (e.g. blueberry, huckleberry, mountain-cranberry), and willow spp. (*Salix* spp.) (Stevens et al. 2001). There is a large diversity of forbs and graminoids in the park. Common forbs observed in the field included fireweed (*Epilobium* spp), crowberry (*Empetrum nigrum*), and Labrador tea (*Rhododendron tomentosum*) as well as variety of *Poaceae* spp and *Cyperaceae* spp. The most common bryophytes observed included peat moss (*Sphagnum* spp.) and navel lichen (*Umbilicaria proboscidea*) and Arctic finger (*Dactylina arctica*) lichen species. Black spruce (*Picea mariana*) is present and can be locally abundant on cool wet north-facing aspects, and on sites underlain by permafrost.

The observed elevation of upper tree limit in the forest-tundra ecotone at the East Fork Toklat study site is approximately 1100 m on both south-facing and north-facing aspects, approximately 1100 m and 1000 m on south- and north-facing aspects respectively at the Cabin Divide site, and approximately 700 m and 1100 m on south- and north facing aspects at the Healy site.
A Century of Climate Change

Annual Climate Change

In Denali National Park and Preserve, Alaska (Denali) (Figure 1), temperature has increased approximately 3 °C over the last century (Figure 2A). During this same period, there has also been a decrease in total precipitation of around 150 mm (Figure 2B). Between 1950-2009, the increase of 1.9° C in average annual temperature has led to an increase of 0.9 °C in average permafrost temperature and a decrease in the area of near-surface permafrost from 75% to 50% within the park (Panda, et al., 2014).

Though the data are limited, instrumental climate records from the center of the park at Wonder Lake and Eilson, and at the park entrance (near Healy) show Healy may receive 100 mm less precipitation than the Cabin Divide and East Fork sites, and may be 6 °C warmer. In addition, between 1910-2009, downscaled gridded historical climate data (771 m spatial resolution) reveals variable rates of increase in temperature (Figure 3A) and decrease in precipitation at each site (Figure 3B). Average temperature increased approximately 1.6 °C at Cabin Divide and East Fork and 1.4 °C at Healy. Total precipitation decreased approximately 93 mm at Cabin Divide, 89 mm at East Fork, and 73 mm at Healy.

Seasonal Climate Change

To visualize the change in seasonal climatic patterns in Denali, a hythergraph was created of ten-year averages for average monthly temperature and total monthly precipitation to show average climatic conditions at the beginning of the century, mid-
century, and through 2010 (data from KNMI Explorer) (Figure 4). On average, average monthly temperatures were coolest and total monthly precipitation highest during the growing season months (May through September) in the early 1900s. Around the middle of the century, growing season average monthly temperatures had increased by approximately 1.5 °C and total monthly precipitation had decreased by approximately 5 mm per month. By 2010, growing season average monthly temperatures had increased by another approximately 1.3 °C and total monthly precipitation decreased approximately 17 mm per month. The winter months of December, January, and February also became warmer and drier since the beginning of the century. Between the beginning of the century and mid-century, average monthly temperatures increased around 1.48 °C and another 1.85 °C by 2010. February average monthly temperature increased the most by approximately 5.8 °C between the beginning of the century and 2010. Total monthly precipitation was more variable. Between the beginning of the century and mid-century, total monthly precipitation increased approximately 6.7 mm per month. By 2010, total monthly precipitation decreased approximately 7.5 mm per month.

In general, there was a more statistically significant shift in average monthly temperature versus total monthly precipitation between the early 1900s and 2010 (Table 2). A significant increase in average monthly temperatures occurred in every month with the only exceptions of March and November. Alternatively, while there was an overall trend of decrease in total monthly precipitation, the only statistically significant decreases occurred in March, May, and June.
Introduction to the Research Chapters

White spruce trees are considered a dominant and keystone species comprising the boreal forest (Barber et al., 2000). This dissertation identifies the impacts of climate change on the spatiotemporal patterns of white spruce (Picea glauca) tree establishment and growth in Denali National Park and Preserve, Alaska (Denali) where average temperatures have increased approximately 3 °C and total precipitation decreased approximately 150 mm between 1900-2010. An approximately 1.9° C increase in average annual temperature since 1950, has led to an increase of 0.9° C in average permafrost temperature and a decrease in the area of near-surface permafrost from 75% to 50% within the park (Panda, et al., 2014). There were also seasonal variations in climate change. During the growing season (May through September), between 1900-2010, average monthly temperatures increased 2-4 ° C and total precipitation decreased 13-31 mm. Average winter (December, January, February) temperatures were more variable with an average increase of around 3.3 ° C and February experiencing the highest increase around 5.8 ° C. The change in total winter precipitation was also more variable since 1900. Between the beginning of the century and mid-century, total precipitation increased approximately 6.7 mm per month. By 2010, total precipitation decreased approximately 7.5 mm per month.

In chapter 2, I explore the spatiotemporal variability of climate change induced regime shifts on tree establishment within the treeline zone since 1900. Alpine treeline (treeline) is defined as the transition between closed montane forest and the uppermost limit that can sustain the tree life form (Holtmeier and Broll, 2005). Tree core age data
were collected on north- and south-facing aspects at three sites in Denali. Regime shift analyses were used to determine timing of regime shifts in climate and tree establishment. Correlation analyses were performed to assess the relationship of climate variables to tree establishment. I demonstrate the importance of spatial extent and site location on the timing of regime shifts and the strength of the influence of specific climate variables. These influences were assessed by analyzing the data at different levels: (1) all site data combined (regional); (2) between-site differences (three sites assessed individually); and (3) north- and south-facing aspect differences.

In chapter 3, I assess the spatiotemporal variability of climate change on tree growth in Denali since 1900. A correlation function analysis assessed the strength of the relationship of tree growth to monthly climate data. A cross-correlation function analysis assessed the strength of the relationship of tree growth to annual climate data. Again, I demonstrate the importance of spatial extent and site location on observed patterns of tree growth over space and time. These relationships were examined at the regional, site, and aspect levels to determine if geographic heterogeneity influenced local climate conditions which would in turn produce higher rates of tree growth in certain locations. Temporal relationships were examined to determine whether a shift in the strength of the relationship between tree growth and climate has been occurring since 1900. Three timeframes were examined to assess the strength of the impacts from climate change on tree growth: (1) the entire timeframe (1900-2010), and pre- and post- the 1950s tree establishment regime shift discovered in chapter 2 (2) 1900-1950, and (3) 1950-2010.

In chapter 4, I explore broader scale changes in tree cover in Denali since the mid-1950s using panchromatic aerial photography taken in 1953/4 and IKONOS satellite imaging.
images captured in 2004/5. Land cover classes were manually classified in the imagery at three locations where field data had previously been collected, and the types of land cover change were identified. Random Forest analyses were used to determine predominant biophysical variables influencing patterns of land cover change in the park between the mid-1950s and the mid-2000s with a focus on areas of infilling within the established forest in the 1950s and new establishment into the tundra zones. The random forest statistical method was chosen as this method often produces higher classification accuracy than linear statistical models (Cutler et al. 2007). Tree age and tree growth data were used determine more precisely the timing of changes in tree establishment and growth patterns within the park.
References


Table 1 Average study site composition. Elevation and slope data from digital elevation model. Climate data from NCDC COOP climate stations. Frost free days from USDA NRCS soils survey report (Clark and Duffy, 2006).

<table>
<thead>
<tr>
<th>Study Sites (west to east)</th>
<th>Average Temperature (°C)</th>
<th>Total Precipitation (mm)</th>
<th>Slope (%)</th>
<th>Frost Free Days</th>
<th>Permafrost Classification</th>
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<td>25-70%</td>
<td>50-70</td>
<td>Discontinuous</td>
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<td>East Fork</td>
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<td>Discontinuous</td>
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<td>450-870</td>
<td>10-50%</td>
<td>50-70</td>
<td>Sporadic</td>
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**Table 2** T-Test of the difference in means between 10-year average climate conditions in 1900-1910 and 2000-2010 (p < 0.05).
**Figure 1** Study area map of Denali National Park and Preserve, Alaska, U.S. Black triangles indicate field work locations at the Cabin Divide, East Fork, and Healy study sites (from west to east).
Figure 2 (A) Average annual temperature (°C); and (B) total precipitation (mm) from 1900-2010. Data were obtained from KNMI Explorer (https://climexp.knmi.nl).
Figure 3 Ten-year averages of (A) average temperature(°C) and (B) total precipitation (mm) values obtained from SNAP downscaled gridded historical climate data (771 m spatial resolution) (https://www.snap.uaf.edu/; 2012) for the three study sites in Denali.
Figure 4 Ten-year average of the annual cycle of average temperature (°C) and total precipitation for Denali, Alaska to visualize the change in climate before, during, and after the 1950s tree establishment regime shift identified in chapter 2. Data were obtained from KNMI Explorer (https://climexp.knmi.nl).
Chapter 2:

Spatiotemporal Patterns of Climate Change Induced Regime Shifts in Tree Establishment at the Forest-Tundra Ecotone in Denali National Park and Preserve,

Alaska, USA
Abstract
In Denali National Park and Preserve (Denali), a 3°C increase in average annual temperature and 150 mm decrease in total annual precipitation beginning in 1900, have resulted in a steady invasion of white spruce trees into tundra zones at treeline. In this study we examine the spatiotemporal variability of tree establishment at treeline. Tree cores were collected from white spruce trees on north- and south-facing aspects at three sites. Tree establishment was positively correlated with spring and summer temperatures, with an increase in temperature initiating increases in tree establishment beginning around 1915. However, a park-wide positive regime shift in tree establishment was observed in the 1950s, corresponding with a negative shift in total precipitation. Most variability was observed when comparing tree establishment on different aspects with shifts ranging from 1945-1980. Regime shifts on north-facing aspects appeared to be a function of shifts in precipitation at East Fork and Cabin Divide. A combination of a shift in spring temperatures and adjacency to the forest edge and tree islands seemed to initiate the shift at Healy. A shift in tree establishment on south-facing aspects was a function of precipitation. There also was an east to west longitudinal gradient on south-facing aspects with shifts in tree establishment initiating earliest on the warmer and drier east end of the park, and last in the cooler and wetter park interior. In general, colder temperatures and too much precipitation was a limiting factor to tree establishment prior to 1950. After 1950, decreasing precipitation and increasing temperatures decreased snowpack depth, triggered earlier snowpack melt, and increased the length of the growing season, initiating an increase in the establishment and persistence of seedlings into tundra zones.

**Key Words:** climate change, tree establishment, regime shift, threshold, treeline, Alaska
Introduction

Temperature increases of two times the global average have occurred at higher altitudes and latitudes (Serreze and Barry, 2011; Harsch et al., 2009; IPCC, 2007; Burkett et al., 2005). These trends of climate change have triggered climate regime shifts and are expected to result in the creation of no-analog or “novel” climates, no longer representative of current climatic conditions (Fox, 2007; Williams and Jackson, 2007). A regime shift occurs when a threshold is surpassed initiating a shift or transition from one stable state to another (Elliot, 2012; Rodionov, 2006). However, the timing of these climatic regime shifts and the magnitude of the impact to ecosystems is difficult to predict (Scheffer et al., 2009) and there has been considerable debate about the potential implications to ecosystems, particularly in light of the high degree of spatiotemporal climatic variability observed globally (Kreyling et al., 2014).

Observations of ecosystem responses to climatic regime shifts include the transitioning of dominant plant functional types and shifting species communities (Walther et al., 2002). For example, climatic shifts in the last century in Alaska have resulted in the encroachment and replacement of tundra vegetation with woody species (Dial et al., 2016; Myers-Smith, 2015; Roland et al., 2013; Stueve et al., 2011; Sullivan and Sveinbjörnsson, 2010; Chapin et al., 2006; Sturm et al., 2005; Suarez et al., 1999; Hobbie and Chapin, 1998). These climatic regime shifts may also exceed physiological thresholds controlling current species distributions, resulting in varying ecological responses at different geographic locations, as well as at different spatial and temporal scales (Renard et al., 2016; Beck et al., 2011; Andersen et al., 2009; Jackson et al., 2009; Holtmeier and Broll, 2005; Wilmking et al., 2004; Scheffer and Carpenter, 2003).
instance, at higher latitudes and altitudes, extirpation or a transition from conifer-dominated forests to deciduous-dominated forests is expected to occur with a continued increase in temperature (Chapin et al., 2006). Positive feedbacks associated with the interactions between these climatic and ecosystem changes at northern and higher latitudes include increased fire activity (van Lierop et al., 2015; Beck et al. 2011), decreased albedo and snow cover (Foley et al., 1994; Bonan, et al., 1992), and increasing rates of permafrost thawing (Panda, et al., 2014; Jafarov et al. 2012).

Ecosystem sensitivity to climatic change is most frequently observed at ecotonal boundaries at the extreme limits of an ecosystem’s range (Beck et al., 2011; Allen and Breshears, 1998). Changes in the spatial pattern (i.e. infilling) and location (i.e. upslope and northward) of ecotone boundaries between temperate forest, alpine treeline, and tundra, are frequently cited as indicators of a recent warming (Beck et al., 2011). Alpine treeline (treeline) is defined as the transition between closed montane forest and the uppermost limit that can sustain the tree life form (Holtmeier and Broll, 2005). Temperature is thought to be the predominant limiting factor controlling where trees can successfully establish and persist at treeline (Danby, 2011; Schrag et al., 2008; Daniels and Veblen, 2004), and hence, natural treelines are thought to predominantly be climatically controlled (Harsch et al., 2009; Körner, 1998). Yet, some treelines have not recently expanded with warming temperatures and some have even shifted to lower elevations (Holtmeier and Broll, 2007; Smith et al., 2003).

Numerous local site conditions have been found to influence the timing and spatial pattern of recent tree establishment at treeline (Holtmeier and Broll, 2007; Resler, 2006; Daniels and Veblen, 2004; Wilmking et al., 2004). Research on tree establishment
at treeline has demonstrated a strong correlation between treeline and physical variables including elevation, aspect, solar radiation, and slope angle (Rupp et al. 2001, Danby and Hik 2007a), which can promote or inhibit tree establishment under changing climatic conditions (Lookingbill and Urban, 2003). In the northern hemisphere, north-facing aspects receive less incoming solar radiation and are therefore generally cooler than south-facing aspects (Harsch, et al., 2009; Lookingbill and Urban, 2003). In Alaska, this results in an increase in permafrost and a decrease in the length of the growing season on north-facing aspects (Danby and Hik, 2007b). Following this trend, treeline is often observed at lower elevations on north-facing aspects (Stueve et al., 2011; Danby and Hik, 2007b). Furthermore, the total annual insolation on a site can fluctuate dramatically throughout the year favoring or inhibiting tree establishment as a consequence of solar angle, slope angle, and aspect. For example, as the solar angle decreases during the summer to winter transition, the photoperiod is shorter on north-facing aspects and flatter slope angles (Bonan and Shugart, 1989).

Species-specific life history characteristics can also contribute to the rate of treeline expansion (Smith et al., 2003). Tree adaptability at treeline in light of short growing seasons and cold soil moisture conditions, may influence which tree species are able to successfully establish and persist in a location (Harsch and Bader, 2011). At which age a species is able to reproduce and how frequently a tree can produce viable seeds may influence its competitive capacity at a specific location (Juday et al., 2003; Noble and Slatyer, 1980). Favorable climatic conditions from the previous year may trigger episodic seed masting events at treeline in an attempt to maximize the likelihood of seedling survivability when climatic conditions are most favorable for reproduction.
Tree seedlings often establish and persist adjacent to existing forest edges and isolated patches of established trees or “tree islands” (Stueve, et al., 2011; Roush, et al., 2007; Zier and Baker, 2006; Smith et al. 2003; Kullman, 1993), with survivability commonly decreasing with increasing elevation (Wardle, 1968). Moreover, while shrubs can shelter seedlings from extreme climatic conditions (Grace, et al., 2002), once seedlings grow above the shrub layer, they compete for light and nutrient resources, as well as space (Dial et al., 2016; Germino, et al., 2002; Grace, et al., 2002).

This research will explore spatial and temporal patterns tree establishment at treeline as a function of climate change from 1900 to present. We address the following questions: (1) Do regime shifts in tree establishment at treeline vary regionally (all sites), at different site locations (each individual site), and on different aspects in Denali (north vs. south)? We hypothesize that regime shifts in tree establishment occur at similar times when all trees are included in the analysis, but experience a lag effect on cooler, wetter north-facing aspects. (2) Does tree establishment correlate with annual temperature and precipitation variables? We hypothesize that tree establishment at each site and aspect will correlate with temperature variables, but not with precipitation. (2) Are the regime shifts in tree establishment synchronous with regime shifts of annual temperature and precipitation variables? We hypothesize that tree establishment at each site and on south-facing aspects are synchronous with annual temperature variables.
Methods

Field Methods

To quantify tree establishment patterns within the forest-tundra ecotone, tree cores were extracted along elevational transects extending from closed montane forest to the location of the uppermost seedling (Lloyd, 2005, Daniels and Veblen, 2004, Wilmking et al., 2004, Grace and Norton, 1990). At each study site, one transect was placed on a north-facing aspect and one on a south-facing aspect as these aspects typically produce more contrasting and distinctive spatial patterns of tree establishment. Transect length varied among the three study sites as a result of contrasting distances between the closed montane forest and the uppermost seedling limits at each site.

Sample points were placed at 15 m intervals along each transect. The random pairs distance method (Mueller-Dombois and Ellenberg, 1974) was used to select trees along each transect providing an efficient way to observe trends in establishment at each site. This method assumes a random distribution of trees across each site location (Mueller-Dombois and Ellenberg, 1974). At each sample point, the nearest mature spruce tree, sapling, and seedling were located. From that tree, a 180° angle perpendicular to the sampled tree was established to create an “exclusion” zone to ensure the sample collected from the second or “paired” tree was located in the adjacent region. Because the distance between sampled points might result in the same “nearest” spruce sampled at some of the sample point locations, only the “nearest” non-duplicated spruce was sampled. At each sample point, random pairs were determined for mature trees, saplings, and seedlings. A seedling was defined as a tree < 1 m in height, a sapling as a tree at least 1 m height and <
2 cm diameter at breast height (dbh), and mature trees defined as trees larger than 2 cm dbh.

Tree cores for mature trees and saplings were extracted at 20 cm height above the ground. The average age of the seedlings along each transect was estimated by counting the total number of branch whorl nodes to account for the approximate number of years to grow to 20 cm in height. The branch whorl node count method is frequently used to date seedlings (Millar, et al., 2004; Zackrisson, et al., 1995). The accuracy of this method was evaluated by counting the total number of branch whorl nodes and comparing these to basal cross sections taken from 18 seedlings at each study site location (mean = 22.58, standard deviation = 13.9).

Data Processing

Each tree core sample was glued to a slotted mounting board and sanded with 120 – 400 grit sand paper to aid in identification of the tree rings. Samples were then visually cross-dated using marker years (i.e. wide or narrow tree rings) to determine each ring’s year of growth (Stokes and Smiley, 1968; Yamaguchi, 1991). Dating accuracy of marker rings was verified by comparing marker rings to tree ring data collected in and around Denali via data obtained from the International Tree-Ring Data Bank (ITRDB) (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring). For tree cores with missing piths, a pith estimator was used to identify the number of rings missing from the core based on the sizes of rings near the pith. The number of rings identified from the pith location was then added to estimate the date of the inner most ring from the missing cores. All seedling whorl counts were averaged to estimate the
number of years needed for a tree or sapling to grow to a height of 20 cm. The number of years needed for seedlings to grow to a height of 20 cm was then added to the core data for mature trees and sapling to estimate dates of tree establishment.

**Climate Data**

Climate data was downloaded from KNMI explorer (www.climexp.knmi.nl) (1900 to 2010) for the Denali region to assess the influence of average temperature and total precipitation on tree establishment. Temperature variables examined include mean, maximum, and minimum annual temperature, as well as seasonal temperature variables. Seasons were divided into three month blocks: 1) spring = March, April, and May (MAM), 2) summer = June, July, and August (JJA), 3) fall = September, October, and November (SOM), and 4) winter = December, January, and February (DJF). The Fairbanks, Alaska instrumental temperature and precipitation climate record is commonly used to represent climatic conditions for the region because this station has the longest, continuous record starting in 1906, and have been used in previous tree establishment and growth studies for the area (see Wilmking et al., 2004; Barber et al., 2000). However, we used the gridded data from KNMI to capture more local Denali climate and this record also extends back to 1900. To assess the similarity of the KNMI and Fairbanks data, a correlation analysis was performed between Fairbanks and KNMI generated temperature \((r = 0.78)\) (Figure 1) and precipitation data \((r = 0.43)\) (Figure 2).

**Correlation and Regime Shift Analyses**

To determine if there was a significant relationship between tree establishment and climate, a Spearman’s rank correlation coefficient was calculated between tree age
data and climate variables (Elliot and Kipfmueller, 2011). Tree establishment data was partitioned for analysis: (1) all tree data collected in Denali (all sites pooled) (2) the pooled data divided between north- and south-facing aspects; (3) all trees at each individual site location; and (4) all trees divided between north- and south-facing aspects at each individual site location. This breakdown of the data was intended to determine whether aspect and site location resulted in lag in tree establishment in cooler and wetter locations. All correlation analyses were performed in R 3.1.2 (R Core Team, 2014) on five-year bins of mean tree age and climate data (Elliot and Kipfmueller, 2011). A Bonferroni adjustment was applied to the data to reduce the chances of obtaining a Type-I error and improve statistical power (Rice, 1989).

Though correlation analyses can assess the strength of the relationship between climate variables and tree establishment, this analysis is unable to provide a link in time series datasets to identify whether the timing of regime shift events occurred at similar times. Therefore, a regime shift analysis was performed to determine whether climatic and tree establishment regime shifts were synchronous with each other. A sequential t test analysis of regime shifts (STARS) was performed on all significantly correlated climate variables and tree establishment to identify abrupt regimes shifts in the time-series data. This analysis was chosen because unlike classical intervention analysis, the regime shift analysis can identify abrupt regime shifts in time series without \textit{a priori} known timing of the event (Andersen et al., 2009; Rodionov, 2004). Unlike classical methods, STARS can also be performed on shorter time series data sets (Rodionov and Overland, 2005). Regime shifts are identified when the cumulative sum of normalized anomalies from the mean were significantly different (p < 0.05) from the mean of the current regime.
(Rodionov, 2004). This data was used to determine whether a corresponding shift in climate variables, and tree establishment had occurred (Elliot, 2011). A 30-year cut-off length was chosen to reflect long-term trends in climatic variables and the “lag effect” between tree establishment response and changing climatic conditions (Stueve et al., 2011).

Results

**Treeline Establishment Regime Shifts**

**1) All Trees Pooled From All Treeline Sites in Denali**

A total of 373 tree cores from live white spruce trees were collected within the treeline zone at the three study sites in Denali. Peak establishment of mature trees at treeline occurred in the mid-1960s, in the 1970s for saplings, and in the mid-1990s for seedlings (Figure 3). When grouped together, the peak establishment of all trees occurred in the mid-1970s (Figure 4). Tree establishment at treeline began as early as 1915. A regime shift to a period of high tree establishment at treeline occurred around 1950.

Similar temporal shifts were noted when tree core data were also included from closed canopy sites at all three study locations (Figure 5). The first detected regime shift after 1900 occurred around 1940. Prior to 1900, a statistically significant increase in tree establishment occurred in the 1820s with a subsequent decrease in the 1890s.

**2) All trees: north- vs. south-facing aspects**

There was not a significant difference between the first detected regime shift date between north- and south-facing aspects (Figures 6 A and B). Similar to the grouped data, a regime shift in tree establishment began around 1950 on north-facing aspects, and 1955
on south-facing aspects. Peak establishment occurred around 1980 on north-facing aspects, and around 1995 on south-facing aspects.

(3) Individual Sites

The timing of regime shift events became more asynchronous when examining each of the three sites within the park (Figures 7 A-C). While the East Fork site (Figure 7B) corresponded to park wide trends with the regime shift in tree establishment occurring in 1950, the Cabin Divide (Figure 7A) and Healy (Figure 7C) sites experienced a lag in tree establishment at treeline. The regime shift in tree establishment at treeline at the Cabin Divide site occurred in 1960 and at the Healy site in 1965.

(4) Individual Sites: north- vs. south-facing aspects

Timing of regime shift events became even more variable when examining each aspect within the three site locations within the park (Figures 8 A-F). While the regime shift on south-facing aspects at the Cabin Divide site (Figure 8D) occurred in 1960, the regime shift on these north-facing aspects did not occur until 1980 (Figure 8A). Aspect did not have an impact on the timing of the regime shift in tree establishment at treeline at the East Fork site (Figure 8 B and E). The regime shift in tree establishment on the north- and south-facing aspects occurred around 1950 and 1955 respectively, and corresponded with park-wide trends when all tree establishment data were pooled together. The timing of regime shifts on different aspects was also varied at the Healy site (Figures 8C and F). The regime shift in tree establishment occurred in 1975 on north-facing aspects, and 1945 on south-facing aspects. The most variation in the timing of regime shift events occurred when comparing north-facing aspects at each site (Figures
8A-C) with a 30-year lag between the earliest regime shift around 1950 and the latest around 1980.

**Correlation Analyses**

*Tree establishment and Climate: Grouped tree data*

Correlation analysis of tree establishment and temperature variables determined regional treeline establishment and tree establishment on south-facing slopes was positively correlated with spring temperatures (Table 1). Tree establishment on south-facing aspects was also positively correlated with summer temperatures. Regional tree establishment and tree establishment on south-facing slopes was found to have a significant negative correlation with total precipitation with the strongest correlation on south-facing aspects. There were no significant correlations between any of the climate variables and tree establishment on north-facing aspects.

*Tree establishment and Climate: Site and aspect*

When tree establishment data was further divided into the three individual sites, and north- and south-facing aspects within each site, similar trends were observed as compared to the regional data (Tables 2). Spring temperatures were positively correlated with all tree establishment data at Cabin Divide and Healy. Spring temperatures were also positively correlated with tree establishment on south-facing aspects at all sites. Total precipitation was negatively correlated with tree establishment on south-facing aspects at East Fork and Cabin Divide, as well as all tree establishment at Cabin Divide. No climate variables were significantly correlated with tree establishment on any north-facing aspects.
Climate Regime Shifts

Though positively correlated with tree establishment, synchronous regime shifts between spring and summer temperatures and the initial regime shift in tree establishment were not evident (Figure 9). The initial regime shifts in spring temperatures occurred in 1932 and in 1925 in summer temperature. A second regime shift in spring temperatures occurred in the mid-1978 while the second shift in summer temperatures occurred in 1993. The second regime shift in summer temperatures and precipitation occurred in the early 1990s is synchronous with peak establishment of seedlings, and shortly thereafter, an overall decline in tree establishment. The initial negative regime shift in total precipitation around 1950 seems to have been the most influential cause of a shift in tree establishment within the park.

Discussion

Regional

The influence of change in spring and summer temperature regimes, as well as total precipitation on tree establishment was apparent at the treeline ecotone in Denali. These regime shifts have triggered a regime shift in tree establishment patterns. While colder temperatures and greater precipitation were limiting factors to tree establishment prior to 1950, a shift to more optimal climatic tree establishment conditions arose after the 1950s regime shift in tree establishment (Figure 9). Between 1900 and the 1950s regime shift in tree establishment, spring temperatures increased by approximately 0.5 °C and summer temperatures by approximately 1.5 °C, while precipitation decreased approximately 50 mm. Initial increases in tree establishment around 1915 appear to be
related to increasing temperatures in general over the last century likely allowing for increased seed germination in previously thermally regulated locations (Hobbie and Chapin; 1998). However, the climatic variable triggering the larger demographic shift in tree establishment occurred with a corresponding shift in total precipitation in the 1950s. In other words, the precipitation regime shift in the 1950s likely triggered a threshold response and the expansion and establishment of trees at treeline beginning in the 1950s. The importance of precipitation in triggering a shift in tree establishment patterns at treeline runs counter to most studies which find that temperature is the most predominant limiting factor (Korner, 2012; Harsch et al., 2009; Schrag et al., 2008; Lloyd, 2005; Daniels and Veblen, 2004). However, the importance of cool-season precipitation triggering a regime shift in tree establishment was noted in a similar study conducted in the Rocky Mountains, USA (Elliot, 2012).

After the 1950s regime shift in tree establishment, spring temperatures increased approximately 2 °C and summer temperatures approximately 1 °C. Precipitation, on the other hand, exhibited a more extreme post-1950s regime shift decrease of approximately 100 mm. Peak establishment of mature trees, saplings, and seedlings at treeline all occurred after this shift. Large white spruce seed crop years are often initiated by favorable cooler and wetter climatic conditions during the growing season increasing radial growth following more stressful warmer and drier years (Juday et al., 2003). During these years, the trees store growth hormone and carbohydrates used in later years for tree growth (Jacoby and D’Arrigo, 1995) and cone crop production (Juday et al., 2003). Suarez et al. (1999) found a positive correlation between favorable climatic conditions, tree growth, and increased tree establishment into tundra. In addition,
continuing decreases in precipitation and warmer temperatures may have also decreased snowpack depth, initiated earlier snowpack melt, and increased the length of the growing season. This has likely allowed for increased rates of establishment and survivability of seedlings (Elliott and Cowell, 2015; Roland et al. 2013; Barbeito et al., 2012; Geddes et al., 2005; Hobbie and Chapin, 1998; Alftine et al, 2003; Taylor, 1995) after a good seed crop year. Once established, as found in previous studies trees can modify microtopographic conditions that promote new establishment and survival (Renard et al., 2016; Stueve et al., 2011; Harsch, et al., 2009; Alftine and Malanson, 2004).

**Individual sites and aspects**

Surprisingly, there was not a significant lag in tree establishment on north-facing aspects when data were pooled together for all site locations. This was surprising because this hypothesis was developed based on the fact that in the northern hemisphere, north-facing aspects receive less incoming solar radiation and are therefore generally cooler and wetter than south-facing aspects resulting in disparate rates and patterns of tree establishment (Körner, 2012; Harsch, et al., 2009; Lookingbill and Urban, 2003). These cooler and wetter north-facing aspects commonly result in an increase in permafrost and a decrease in the length of the growing season (Danby and Hik, 2007; Bonan and Shugart, 1989) decreasing soil temperatures and ground water storage capacity (Panda et al., 2014; Juday and Alix, 2012; Körner, 2012).

An east to west longitudinal lag appears to develop on south-facing aspects within sites (Figure 10). On south-facing aspects at Cabin Divide and East Fork, precipitation appears to be the main driver initiating a regime shift in tree establishment. South-facing
aspects are warmer and drier so are likely more susceptible to moisture-related deficits influencing these spatiotemporal rates of tree establishment (Elliot and Cowell, 2015). An experiment by Danby and Hik (2007) found that warming on south-facing aspects increased soil temperatures and lengthened the snow-free period which increased the growth and photosynthetic rate of white spruce seedlings. Moreover, there appears to be an east to west longitudinal lag with the regime shift on the south-facing aspect at Healy beginning approximately 10 and 15 years earlier than at the East Fork and Cabin Divide sites respectively. On average, Healy is warmer and drier so may have been more susceptible to the effects from moisture-related deficits earlier in the century and in turn, decreased snowpack depths and increased rates of seedling establishment and survivability.

Surprisingly, there was no real discernible difference between shifts in tree establishment on north- and south-facing aspects at the East Fork site. The long delay before a regime shift was triggered on the north-facing aspect at the Cabin Divide site may more be a function of the circumstantial sampling along this elevational transect as there were no individuals in the 1975 5-year age bin. This could also be a function of dating errors from tree cores with missing piths which resulted in establishment dates in the 1980s bin. Had there been establishment of individuals during that 5-year time frame, the most likely initiation of a regime shift would have occurred in the 1960s corresponding to the regime shift on Cabin Divide’s south-facing aspect. If that is the case, this is again counter to our hypothesis of a lag in establishment on north-facing aspects.
The biggest difference in timing of events occurs on the north-facing aspect at the Healy site around 1975 and is the only location to correspond with our north-facing aspect lag hypothesis. Unlike the other locations, this regime shift may have been triggered by the second shift to warmer spring temperatures and more favorable local site conditions occurring in the mid-1970s. Seedling recruitment and survivability is often highest adjacent to the existing forest edge and tree islands (Renard et al., 2016) with survivability increasing if seedlings establish adjacent to mature trees (Maher and Germino, 2006; Germino et al., 2002). This particular location had the least observed closed canopy forest cover and the fewest tree islands of all of the site locations. This may have led to an increase in seedling mortality until a threshold in initial tree establishment had been surpassed to initiate a more rapid rate of tree establishment on that particular aspect.

The Second Regime Shift

Lastly, there was a second regime shift to warmer summer temperatures and reduced precipitation beginning in the mid-1990s (Figure 9). Shortly thereafter, there was a second shift to reduced tree establishment observed in almost all of the analyses at the region, individual site, and aspect levels (11 out of 13). If climatic conditions were still conducive to increased tree establishment, principally among seedlings, then there should still be evidence of a continued increase in seedling establishment. However, this decline in establishment may be an indication of a possible surpassing of the temperature-related drought stress threshold initiating seedling die-off at treeline (McGuire et al., 2010). Warmer temperatures, decreasing precipitation, and a lengthening of the growing season
are triggering earlier snowpack melt and decreasing available soil moisture (Körner, 2012).

Conclusions

White spruce trees are considered a dominant and keystone species comprising the boreal forest (Barber et al., 2000). Climate change since 1900 has allowed for increased rates of white spruce establishment in Denali. The increase in temperature and a regime shift in precipitation triggered a positive response in tree establishment likely as a function of reduced snowpack depth. In fact, experimental studies performed by Hobbie and Chapin (1998) have shown that as compared to other species, white spruce seedlings are more likely than any other northern tree species to establish and survive as they invade into tundra in northern latitudes and high altitudes locations in Alaska. Modeling of suitable locations for white spruce establishment show a 20km northward latitudinal shift and a 91m upslope elevational shift since the 1960s, with those numbers doubling in by the 2020 (Gray and Hamann, 2013). In Denali, average upslope advancement of trees ranged between 100m to 290m, much higher than the modeled averages. This ecological shift is expected to result in cascading positive feedbacks. Based on paleoecological records (Bigelow and Edwards, 2001; Billings 1987), an increase in boreal forest cover is expected to drastically change the landscape. This is of concern because during the middle Holocene (approximately 6 thousand years ago), growing season temperatures were approximately 3° C warmer in the northern hemisphere with feedbacks from increased boreal forest coverage at higher latitudes accounting for around 1° C of that warming by reducing albedo and snow cover (Ganopolski, et al., 1998; Foley et al.,...
Moreover, warming is expected to increase permafrost thaw and decrease soil moisture (Panda et al., 2014). Along with the expected ecological shift in vegetative species coverage, the increased fuels and drier soils are expected to increase fire activity (Young et al., 2016) leading to additional permafrost thaw and further ecosystem shifts (Brown et al., 2015).

However, the spatiotemporal variability of temperature and precipitation across a mountainous landscape will likely lead to varying rates and degrees of tree establishment throughout the park with trees on warmer and drier sites becoming more vulnerable to temperature-induced drought stress earlier than those on cooler and wetter sites. Further, with continued increases in temperature and decreases in precipitation, white spruce will likely encounter thermal and moisture related physiological thresholds causing increased mortality in interior Alaska. Temperatures greater than 12° C are becoming more common during the summer months, which are critical growing season periods for white spruce. Long-term drought stress from a decrease in soil moisture availability is expected to negatively impact white spruce tree establishment. Moreover, drought-stressed trees are more susceptible to widespread mortality from insect outbreaks (Csank et al., 2016; Roland et al., 2013). These cascading ecological feedbacks are expected to transform the region from a carbon sink to a carbon source (Young et al., 2016; Brown et al., 2015; Beck et al., 2011; Barber et al., 2000).

With increasing temperatures and decreasing precipitation and snowpack expected to continue, future research should examine moisture-limiting thresholds for seedling establishment at treeline on north- and south-facing aspects. This experimentation would help elucidate whether seedlings on warmer and drier south-
facing aspects are more vulnerable to temperature-related drought stress versus north-facing aspects and what these temperature and precipitation thresholds might be. Moreover, this experimentation could be used to determine whether cooler and wetter north-facing aspects might truly become climate refuges for seedling survival and persistence in the future. Plots with white spruce seedlings could be distributed between north- and south-facing slope aspects with varying rates of increased temperatures and decreased precipitation and snowpack dependent on the slope aspect. For instance, increases in air and soil temperatures would be higher with lower amounts of water added to seedling plots on south-facing slopes as opposed to north-facing slopes.

Future research should also continue to monitor tree establishment to determine whether the decline beginning around 2000 is indicative of a long term trend related to climate change. And though this research took place in a topographically complex landscape, similar patterns at other boreal-tundra ecotones may arise. Even small differences in topography, edaphic conditions, soil moisture, and other site factors may result in heterogeneous rates of infilling and new tree establishment in other boreal-tundra locations and determine whether change occurred prior to or after 20th century warming trends (Appendix A). In these locations, we suspect the spatial patterns may become more visible over broader regions and undergo more extreme range expansion in locations that don’t have as many topographical limitations.
References


Table 1 Spearman’s rank correlation between climate variables and all tree establishment on all sites, as well as individuals on north- and south-facing aspects.

<table>
<thead>
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<th>Climate Variable</th>
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<td>0.31</td>
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<tr>
<td>Total Precipitation</td>
<td>-0.59*</td>
<td>-0.48</td>
<td>-0.64*</td>
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KNMI 20th Century Reanalysis Data (DENA) (1900 - 2010; n=22)
Bonferroni Adjusted P-Value: 0.006*
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<thead>
<tr>
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<th>Cabin Divide</th>
<th>Healy</th>
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<td>North</td>
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</tr>
<tr>
<td>Mean Temperature</td>
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<td>-0.58*</td>
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KNMI 20th Century Reanalysis Data (DENA) (1900 - 2010; n=22)
Bonferroni Adjusted P-Value: 0.006*

Table 2 Correlation analysis between climate variables and tree establishment in Denali for: (1) each site, (2) north-facing aspects on each site, and (3) south-facing aspects on each site.
Figure 1 The relationship between KNMI average annual temperature data for Denali and the Fairbanks, AK instrumental record.
Figure 2 The relationship between KNMI total annual precipitation data for Denali and the Fairbanks, AK instrumental record.
Figure 3 Tree establishment age-structure data for all treeline growth forms (tree, sapling, and seedling) in Denali, AK.
Figure 4 Regime shift analysis (P < 0.05) performed on all individuals at treeline. The dark gray rectangles indicate regime shifts and the black line is the mean value for the regime length. Regime-shift index (RSI) values: 1950 = 1.88 and 2000 = -1.2.
Figure 5 Regime shift analysis (p < 0.05) performed on all trees in the treeline and closed canopy zones. (RSI) values: 1820 = 0.24, 1890 = -0.46, 1940 = 0.41, and 2005 = -0.25. The dark gray rectangles indicate regime shifts and the black line is the mean value for the regime length.
Figure 6 Tree establishment age-structure data for all mature trees, saplings, and seedlings at treeline (A) only individuals on north-facing aspects (RSI values: 1950 = 1.83 and 2000 = -0.99), and (B) only individuals on south-facing aspects (RSI values: 1955 = 1.26 and 2000 = -0.59), in Denali, AK. Regime shift analysis (P < 0.05) performed on all individuals at treeline. The dark gray rectangles indicate regime shifts and the black line is the mean value for the regime length.
**Figure 7** Regime shift analysis (P < 0.05) performed on all individuals in the treeline zone at each site: (A) Cabin Divide (RSI values: 1960 = 0.92 and 2005 = -0.05), (B) East Fork (RSI values: 1950 = 1.9 and 2000 = -0.78), and (C) Healy (RSI values: 1965 = 0.99 and 2000 = -1.63). Dark gray rectangles indicate regime shifts and the black line is the mean value for the regime length.
Figure 8 Regime shift analysis (P < 0.05) performed on all tree form individuals in the treeline zone on north- and south-facing aspects within each site. North-facing aspects: (A) Cabin Divide (RSI values: 1980 = 0.19), (B) East Fork (RSI values: 1950 = 1.79 and 1985 = -0.69), and (C) Healy (RSI values: 1975 = 0.84 and 2000 = -1.29). South-facing aspects: (D) Cabin Divide (RSI values: 1960 = 1.04 and 2000 = -0.42), (E) East Fork (RSI values: 1955 = 0.57 and 2005 = -0.12), and (F) Healy (RSI values: 1945 = 0.21 and 2000 = -0.8). The gray rectangle indicates regime shifts and the black line is the mean value for the regime length.
Figure 9 Regime shift analysis results for significantly correlated variables (Bonferroni adjusted P < 0.006): spring temperature (°C) (RSI values: 1932 = 0.16 and 1978 = 0.26), summer temperature (°C) (RSI values: 1925 = 0.64 and 1993 = 0.23), total precipitation (mm) (RSI values: 1950 = -0.26 and 1994 = -0.25), and tree establishment data (RSI values: 1950 = 1.88 and 2000 = -1.2) between 1900-2010. The black lines indicate the mean value for the regime length. The gray rectangle highlights the tree establishment regime shift and the relationships with statistically significant climate variables.
Figure 10 West to east longitudinal gradient on south-facing aspects in Denali. Trees established earlier and grew larger on warmer and drier slopes at the east end of the park and established later and are smaller in size on cooler and wetter slopes in the park interior.
Appendix A: A sample of the average onset of North American treeline advance pre- and post- 20th century warming trends based on dendrochronological reconstructions.

<table>
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<th>Authors</th>
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<tbody>
<tr>
<td>Elliot, 2012</td>
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<td>Battlori and Gutiérrez, 2008</td>
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<td>x</td>
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<td>Danby and Hik, 2007</td>
<td>Yukon, Canada</td>
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<td>Esper and Schweingruber, 2004</td>
<td>Siberia</td>
<td>x</td>
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<tr>
<td>Kullman, 2002</td>
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<td>MacDonald, 1998</td>
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<td>Payette and Filion, 1985</td>
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<td>Scott, et al., 1987</td>
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Chapter 3:
Biogeographic and Temporal Variation in Tree Growth and Climate Relationships
in Denali National Park and Preserve, Alaska, USA
Abstract

Interior Alaska has experienced a rapid increase in temperature and decrease in precipitation over the last century. However, the response of tree growth at alpine treeline to changing climatic conditions has been more uncertain, likely a result of biogeographic and temporal variations. We examined tree growth and climate relationships at multiple spatial (regional, site, aspect) and temporal scales (1900-2010, 1900-1950, 1950-2010) to assess whether (1) tree growth would respond positively to climate change over the last century (1900-2012) or only during specific time periods, and (2) were significant tree growth-climate relationships dependent on the spatial extent of the study area or aspect.

Tree cores were collected from white spruce (*Picea glauca*) on north- and south-facing aspects at three sites. The strongest relationships between tree growth and climate occurred after the 1950s. As the spatial extent of the study area decreased from regional to aspect, the strength of the tree growth-climate relationship increased though these relationships were consistently weaker on trees on north-facing aspects. While north-facing aspects have had a relatively weak relationship with climate over the past century as compared to south-facing aspects, this relationship will likely strengthen as temperatures continue to increase and precipitation continues to decrease. North-facing aspects may become more climatically suitable refuges for white spruce trees as opposed to more xeric south-facing aspects. Tree growth-climate relationship on south-facing aspects will likely weaken with climate change trends as physiological thresholds are surpassed leading to an increase tree mortality in the future.

**Key Words:** climate change, threshold, treeline, dendrochronology, Denali, Alaska
Introduction

Interior Alaskan temperatures over the last century have increased at a rate
twofold greater than the global average (Harsch et al., 2009; IPCC, 2007; Burkett et al., 2005). During this period, there was also a concurrent decrease in precipitation (Juday et al., 2003). This has resulted in the steady encroachment of woody species upslope in mountainous regions and to higher latitudes (Dial et al., 2016; Myers-Smith, 2015; Chapin et al., 2006; Sturm et al., 2001). Positive feedbacks associated with this change in woody vegetation distribution include increasing fire activity (van Lierop et al., 2015; Beck et al. 2011a), decreasing albedo and in turn snow cover (Bonan, et al., 1992), increasing permafrost degradation (Panda, et al., 2014; Jafarov et al. 2012), and increasing carbon uptake (Beck et al., 2011b; Barber et al., 2000). However, there has been continued debate about the potential implications of climate change as geographic heterogeneity can result in highly variable ecological responses at different geographic locations, as well as at different spatial and temporal scales (Brownlee et al., 2016; Ju and Masek, 2016; Barbieto et al., 2012; Holtmeier and Broll, 2005; Scheffer and Carpenter, 2003; Smith et al., 2003). Additionally, biologically, individual woody species have different thermal and moisture limits which may constrain their response to rapid climate change (Jackson et al., 2009).

Ecosystems that reflect climate change most readily are at ecotonal boundaries or at the extreme limits of an ecosystem’s range (Beck et al., 2011; Allen and Breshears, 1998) making high-latitude and high-altitude treelines ideal locations to identify the response of species and ecosystems to climate change (Juday et al., 2003). Alpine treelines can broadly be defined as the transition between closed montane forest and the
uppermost limit that can sustain the tree life form (Holtmeier and Broll, 2005). These
treelines are frequently cited as sensitive ecological indicators of the trend in temperature
increase because temperature is presumed to be the predominant limiting factor
controlling radial tree growth (Beck et al., 2011; Kullman and Öberg, 2009; Schrag et al.,
2008; Daniels and Veblen, 2004). Radial tree growth may also be strongly influenced by
precipitation as a function of temperature induced moisture stress (D’Arrigo et al., 2008;
Barber et al., 2000).

Multiple studies, however, have identified inconsistencies in climate-tree growth
relationships during the 20th century (Helama, et al., 2016; Lloyd et al., 2013; Ohse et al.,
2012; Wilmking et al., 2004; Lloyd and Fastie, 2002; Briffa, et al., 1998). For example, the relationship between tree ring width and precipitation was weak through the entire 20th century in some studies (Wilmking et al., 2004). In contrast, tree ring width has both been positively and negatively correlated with precipitation during positive phases of the Pacific Decadal Oscillation (PDO) in the 20th century likely a function of differences in local site water availability between the two time periods (1925-1946 vs. 1977-1998) (Ohse et al., 2012). Similar inconsistencies between tree ring width and temperature have also been identified. For example, D’Arrigo et al. (2008) found that tree ring width strongly correlated with temperature trends from 1910 through 1950 when tree ring width sensitivity to temperature decreased beginning around 1950 through 2002. In contrast, Wilmking et al. (2004) determined that ring width sensitivity to temperature strengthened after 1950 through 2000. Furthermore, Paulsen et al. (2000) noted that while long-term temperature increases resulted in overall trends of increased tree growth, short-term
climatic fluctuations surpassing a temperature threshold resulted in decreased sensitivity of tree ring widths and subsequent tree growth from year-to-year.

Differences in climate-tree growth relationships among these studies may be related to variations in biophysical local site conditions (Sullivan et al., 2015; Ohse et al., 2012; Brubaker 1980). For example, elevation, edaphic conditions, snow pack, slope angle, incoming solar radiation, biological competition, and proximity to existing trees, are some factors that can influence the magnitude of the response of tree growth to the changing climate (Carnwath and Nelson, 2016; Yin et al., 2016; Helama et al., 2016; Barbieto et al., 2012; Ohse et al., 2012; Stueve et al., 2011; Daniels and Veblen, 2004, Paulsen et al., 2000; Villalba et al., 1994).

In the northern hemisphere, north-facing aspects receive less incoming solar radiation and are therefore generally cooler than south-facing aspects (Harsch, et al., 2009; Lookingbill and Urban, 2003). In Alaska, this results in the increased presence of permafrost and a decrease in the length of the growing season on north-facing aspects inhibiting tree growth (Danby and Hik, 2007). In general, tree growth is thought to be predominantly limited by drought on south-facing aspects and soil temperature on north-facing aspects (McGuire et al., 2010). Moreover, total annual solar insolation received at a location is also influenced by local topography and can fluctuate dramatically throughout the year favoring or inhibiting tree growth as a consequence of solar angle, slope angle, and aspect. For example, as solar angle decreases during the summer to winter transition, the photoperiod shortens more rapidly on north-facing aspects and/or flatter slope angles (Bonan and Shugart, 1989).
Beginning in the 1950s, an increase in temperature and decrease in precipitation resulted in an increase in tree establishment in Denali (Chapter 2). There were three main objectives of this research. (1) To analyze the spatial and temporal relationships between white spruce (*Picea glauca*) radial tree growth and monthly temperature and precipitation variables from 1900-2012. We hypothesized radial tree growth in Denali at all sites would respond positively to an increase in temperature and a decrease in precipitation over the 1900-2012 time period. (2) To assess between-site and within-site variability (i.e. north- vs. south-facing aspects) of tree growth sensitivity to average monthly temperature and total monthly precipitation. We hypothesized a strengthening of the relationship between tree growth and climate along a west to east longitudinal gradient from cooler and wetter conditions in the park interior to warmer and drier conditions at the eastern edge of the park. Further, we hypothesized this relationship would be strongest on warmer and drier south-facing aspects. (3) To link the tree growth analysis with the sudden increase in tree establishment in Denali after 1950, we examined climate-tree growth relationships before and after the 1950s increase in tree establishment. We hypothesized the positive relationship between tree growth and climate strengthened after the 1950s and reflects overall better conditions for tree regeneration and tree growth in ecotonal white spruce forests. Understanding the influence of climate change on radial tree growth across space and time is key to determining the response of tree growth to future modeled climate change scenarios.
Methods

Field Methods

The relationship between climate and tree growth was assessed in Denali using
tree cores from mature white spruce trees within the closed-canopy forest (Table 1). At
each site, two 70 m transects were placed parallel to the slope approximately 20 m
downslope from timberline. One transect was placed on a north-facing aspect and one on
a south-facing aspect. The random pairs distance method (Mueller-Dombois and
Ellenberg, 1974) was used to select trees for sampling along each transect. At each
sample point, the nearest white spruce was cored to the pith. From that tree, a 180º angle
perpendicular to the sampled tree was established to create an “exclusion” zone to ensure
the sample collected from the second or “paired” tree was located in the adjacent region.
Cores were extracted 20 cm above the ground. Mature trees were defined as trees > 10
cm diameter breast height (dbh) on north-facing aspects, and > 20 cm dbh on south-facing aspects. Different dbh were selected to account for the observed growth
differences of the trees on different aspects over the past 60 years.

Data Processing

Each core sample was glued to a slotted mounting board and sanded with 120 –
400 grit sand paper to aid in identification of the tree rings. Samples were then visually
cross-dated using marker years (i.e. wide or narrow tree rings) to determine each ring’s
year of growth (Stokes and Smiley, 1968). Dating accuracy of marker rings was verified
by comparing marker rings to tree ring data collected in and around Denali via data
obtained from the International Tree-Ring Data Bank (ITRDB)
Tree ring widths for each core were measured using a Velmex sliding stage to an accuracy of 0.001 mm from the pith, or the nearest discernible ring, to bark. These chronologies were statistically cross-dated in COFECHA (Grissino-Mayer, 2001).

The chronologies were standardized by detrending the data using 15- or 30-year cubic smoothing splines in ARSTAN to create a dimensionless ring width index to remove age-growth related effects (Holmes, 1986). Spline time periods were dependent on the age of individual cores. The residual chronology was used to analyze climate-tree growth relationships because this chronology has autocorrelation removed (i.e. the correlation of the current year’s growth with previous year(s) growth (Speer, 2010; Fritts, 1976). The expressed population signal (EPS > 0.85) was calculated for each chronology to ensure stand-level signal rather than individual tree noise (Speer, 2010) for the time period of interest (1900-2012). Analyses were performed on the residual chronology generated from all pooled tree core data from all three study sites, each individual study site, and each north- and south-facing aspect at each site to assess possible site and aspect-generated differences in responses to climate.

**Climate Data**

To identify the relationship between climate data and tree growth, climate data was downloaded from KNMI explorer (www.climexp.knmi.nl) (1900 to 2010) for the Denali region. Monthly average temperature and total precipitation climate variables were derived from twentieth century reanalysis data (V2) (www.esrl.noaa.gov/psd/data/gridded/data.20thC_ReanV2.html). Though the Fairbanks,
Alaska instrumental temperature and precipitation climate record is commonly used to represent climatic conditions for the region because this station has the longest, continuous record starting in 1906, and has been used in previous dendrological studies for the area (see Wilmking et al., 2004; Barber et al., 2000), we used the gridded data from KNMI to capture the more local Denali climate signal and extend the record back to 1900. To confirm the similarity of this data, a correlation analysis was performed between Fairbanks and KNMI generated temperature data ($r=0.78$) (Figure 1) and precipitation data ($r=0.43$) (Figure 2).

Tree Growth and Climate Analyses

Correlation function analyses were performed with the weather station data using the bootRes package in R (Zang and Biondi, 2012). This analysis identifies the correlation between tree ring width and average and monthly annual temperature and annual and monthly total precipitation for the current year and the previous year (Fritts, 1976). White spruce often exhibit a lag effect in which the tree ring width is more sensitive to climate from the previous year’s growing season (McGuire et al., 2010). We also performed analyses on the pre- and post-1950 timeframe to determine possible instabilities in tree growth relationships to climate at each site. The 1950s split was chosen because of a detected sudden increase in tree establishment in Denali at that time (Chapter 2).

Finally, mean annual temperature and total annual precipitation data were used to examine the ‘divergence problem’; or the weakening relationship between tree growth and climate evidenced at northern latitudes beginning in the middle of the twentieth century (D’Arrigo et al., 2008). A cross-correlation function (ccf) analysis in R 3.1.2 (R
Core Team, 2014) was used to identify the correlation between tree growth at each site and climate from current and 5 preceding years to capture the potential lag effect. Similar to the monthly assessment, these data were again divided into the two pre- and post-1950 periods examine the strengths of the correlations related to climate change.

**Results**

*Tree growth and monthly climate: Spatial Variability*

**Regional**

A total of 174 tree cores were used to assess the relationship between tree ring width and climate. There was a strong correlation between tree ring width and climate at the regional scale (Figures 3). Tree growth exhibited a negative response to previous year July and August temperature. The correlation between tree growth and winter (January and February) and spring (March, April, and May) temperatures was negative in the current year and positively correlated with July temperature of the current year. Trees exhibited a strong positive response to July precipitation, and a slightly weaker response to August precipitation from the previous year. Finally, trees exhibited a very weak negative correlation with the current year’s summer (July and August) precipitation.

*Between Site Variability*

Tree growth at all three sites was negatively correlated with July temperature from the previous year (Figure 4, A-C). While the Cabin Divide and Healy sites were negatively correlated with August temperature from the previous year, the East Fork site was not. East Fork and Healy responded negatively to the current year’s January and
spring (March and April) temperature, while Cabin Divide only responded to January temperature. Healy was the only site to respond positively to June temperature from the current year. Growth on all three sites exhibited a positive correlation to July precipitation from the previous year (Figure 4, D-F). A weaker, but still positive response to the previous year’s August precipitation was also observed at Cabin Divide and Healy. Healy had a weak negative response to the current year’s June precipitation.

**Within Site Variability: Aspect**

The largest difference between tree growth and climate were found within each sampled site (Figures 5 and 6). In general, relationships between tree growth and temperature on north-facing aspects were weaker than those on south-facing aspects (Figure 5). All north-facing aspects responded weakly, though were still negatively correlated with July temperature from the previous year, while all south-facing aspects exhibited a strong response to July and August temperatures. The south-facing aspects at East Fork and Healy were most reflective of regional-level January and spring (March, April, and May) temperature response patterns in the current year.

Similar to the temperature relationships, a stronger relationship between tree growth and precipitation was observed on south-facing versus north-facing aspects (Figure 6). Tree growth north-facing aspects on the East Fork and Healy sites responded positively to the previous year’s July precipitation and growth in Cabin Divide and East Fork responded negatively to the current year’s January and September precipitation respectively. Tree growth on all south-facing aspects responded positively to the previous year’s July precipitation. Cabin Divide and Healy also responded positively to the previous year’s August precipitation.
**Tree growth and monthly climate: Temporal Variability**

**Pre-1950**

Prior to the sudden increase in tree establishment in the 1950s, there were only five significant relationships between tree growth and temperature at each site (Figure 7, A-C). At Cabin Divide, tree growth responded positively to November and December temperature, East Fork tree growth responded negatively to the current year’s spring (April and May) temperature, and Healy tree growth, negatively to the previous year’s July temperature. There were also only five significant relationships between tree growth and precipitation prior to 1950 (Figure 8, A-C). Both East Fork and Healy responded positively to the previous year’s July precipitation. Cabin Divide and Healy were also negatively correlated with the current year’s July precipitation.

**Post-1950**

After the sudden increase in tree establishment in the 1950s, the strength and frequency of the relationship between tree growth and temperature increased from five (pre-1950) to fourteen (post-1950) significant relationships between tree growth and temperature (Figure 7, D-F). Each of the sites exhibited a negative response to summer (July and August) temperatures in the previous year and March temperature in the current year. Similar to temperature, the number of significant relationships between tree growth and precipitation increased from five (pre-1950) to eleven (post-1950). All sites responded positively to summer precipitation in the previous year, though they responded negatively to March precipitation in the current year (Figure 8, D-F).
Tree growth and annual climate: Temporal Variability

A high degree of variability was observed between tree growth and annual average temperature and total precipitation across all sites, as well as the pre- and post-1950s increase in tree establishment. No site in Denali reflected a significant correlation between tree growth and annual temperature when analyzing the entire period from 1900-2010 (Figure 9, A-C). Similarly, prior to the 1950s, tree growth was not significantly correlated with annual temperature (Figure 9, D-F). However, a positive correlation between tree growth and annual temperature was observed after the 1950s, with all sites exhibiting a lag effect of two years (Figure 9, G-I).

However, when analyzing the entire period from 1900-2010, the East Fork and Cabin Divide sites responded positively to annual precipitation experiencing a lag effect of 1-4 years, while the Healy site responded negatively to precipitation exhibiting a 3-year lag effect (Figure 10, A-C). Prior to the 1950s, only the East Fork site was correlated with annual precipitation (lag effect = 4 years) (Figure 10, D-F). After the 1950s, a negative correlation was observed between annual precipitation and tree growth at East Fork and Healy, and a positive correlation at Cabin Divide (Figure 10, G-I). The East Fork and Healy sites did not exhibit a lag effect, while the Cabin Divide site experienced a 1-year lag in response to precipitation.

Discussion

Tree growth and spatial variability

The significantly stronger relationships between tree growth and monthly temperature and precipitation on south-facing aspects influenced the strength of the signal observed at each of the three sites and across the region. In fact, by including trees
on the north-facing aspects in the analysis, the resultant site and regional tree growth sensitivity to both temperature and precipitation was reduced. Differences in the strength of the relationships between tree growth and climate when comparing regional, between-site, and within-site spatial extents, is strongly related to variations in local site conditions. Local site variations, even over relatively short distances, have been shown to have a significant impact on tree growth responses of the same species (Villalba et al., 1994).

Aspect in particular, along with incoming solar radiation, can influence air and soil temperatures over relatively short distances (Lookingbill and Urban, 2003). In Alaska, decreased amounts of incoming solar radiation, increased snowpack, and increased permafrost results in cooler north-facing aspects with shorter growing seasons (Harsch, et al., 2009; Danby and Hik, 2007; Lookingbill and Urban, 2003; Taylor, 1995). The shorter growing season can limit tree radial growth (Körner, 2012) and this was evident in the observed differences in tree growth on north- and south-facing aspects. On north-facing aspects, individual tree-ring width was on average narrower and almost half the width of individual rings on south-facing aspects at all sites. The dbh of trees on south-facing aspects were frequently almost twice that of trees on north-facing aspects (Regional: south = 37 cm dbh vs. north = 21 cm dbh).

Aspect and edaphic conditions can also influence the magnitude of tree growth response to climate (D’Arrigo, et al., 2008; Alftine et al., 2003). The limited growing season on north-facing aspects combined with increased prevalence of permafrost can impact ground temperature, water storage capacity, and ultimately tree growth (Panda et al., 2014; Juday and Alix, 2012; Körner, 2012). Soil porosity and soil depth to the
permafrost layer can dictate the soil moisture storage capacity limiting water availability for tree growth (Resler, 2006). Increased tree growth has frequently been observed at locations associated with higher soil moisture retention (Calef et al., 2005).

An increase in soil moisture during the spring and early summer months with snowmelt, associated with areas receiving moderate amounts of snow during the winter months, may enhance the rates of tree growth (Geddes et al., 2005; Viereck, 1970). Available moisture also has a concurrent influence on soil temperature. The high specific heat of water has an ameliorating effect on soil temperatures in close proximity to streams. This effect is suggested by the observation of higher rates of tree growth adjacent to streams (Juday and Alix, 2012; Viereck, 1970) lengthening the growing season and increasing water availability.

Tree growth and temporal variability

There were evident time-generated differences in the strength of the relationships between tree growth and temperature and precipitation variables. At each site, a consistent trend between increased tree growth sensitivity and climate variables began after 1950. Wilmking et al. (2004) similarly found a strengthening of this relationship after 1950 and hypothesized these trends were related to a warmer growing season. These trends may also be related to a regime shift in precipitation beginning in the 1950s (see chapter 2). Of the approximately 150 mm decrease in total annual precipitation since 1900, approximately 100 mm of the decrease occurred after the 1950s regime shift in total annual precipitation. The start of tree growth is initiated by an increase in soil and air temperature, as well as snowpack melt (Rossi, et al., 2006; Vaganov et al., 1999). Tree
growth extends through a portion of the growing season barring a high temperature threshold is surpassed (Vaganov et al., 1999). In Alaska, high temperature physiological thresholds were observed to be between 12-14° C (Lloyd et al., 2013; Beck et al., 2011). Tree growth does not continue through the length of the growing season, but rather white spruce store growth hormones and carbohydrates to be used in later years (Jacoby and D’Arrigo, 1995). Accumulation of growth hormones and carbohydrates during the previous growing season have a strong influence on tree growth during the current year (Barber et al., 2000).

The observed lag in response between tree growth and climate variables may be related to increased cambial activity during years when conditions were cooler and wetter during the growing season (Lloyd et al., 2013). In particular, after 1950, tree growth exhibited a significant negative response to temperature and positive response to precipitation respectively in July and August of the previous year. In other words, these results may be indicative of the strength of the influence of temperature-related drought stress on tree growth (McGuire et al., 2010). These temporal variations in tree growth and climate relationships have been observed in previous studies and hypothesized to be a result of combined climatic influences, particularly drought-related stress (Lloyd, et al., 2013; Ohse, et al., 2012; McGuire et al., 2010; Juday et al., 2003; Lloyd and Fastie, 2002; Barber, et al., 2000). Warmer temperatures and decreasing precipitation after 1950 are decreasing snowpack depth and triggering earlier snowpack melt in the growing season decreasing available moisture later in the season (Körner, 2012). The combined lengthening of the growing season and the increase in annual temperature, particularly
during the growing season (see chapter 2, Figure 4), can decrease soil moisture and increase drought stress.

*Geography and Climate Data*

Another possible component adding to some of the temporal variation in the sensitivity of tree ring growth to climate change, relates to the location of the climatic data. The Fairbanks, Alaska instrumental temperature and precipitation climate record is commonly used to represent climatic conditions for the region because this station has the longest, continuous record (Wilmking, 2004; Lloyd and Fastie, 2002; Barber, et al., 2000). However, a switch to using gridded modeled (Parameter-elevation Regressions on Independent Slopes Model (PRISM)) climatic data interpolated from weather stations in the region, is becoming more common (Lloyd, et al., 2013; Ohse, et al., 2012). This data reflects more of the regional climatic variability generated by the complex terrain of mountainous environments (Daly, 2006; Daly et al., 2002). This may contribute to the higher variability in observed tree-ring growth-climate relationships when comparing studies using instrumental versus modeled gridded data in the studies cited above. This includes variability of tree-ring growth sensitivity to precipitation, positive versus negative relationships with climate, and time-period sensitivity to climate.

To determine whether the selection of climate data for analysis might be a contributing factor, tree-ring growth and monthly average temperature and total monthly precipitation instrumental data from Fairbanks and regional Denali data values interpolated from PRISM were compared at the regional, site, and aspect levels (Appendix A, Tables 1-7). At the regional, site, and aspect levels, overall trends in
significant relationships between tree growth and monthly average temperature were similar, though the strength of the relationship was consistently stronger using the regional gridded data. These relationships were weakest on north-facing aspects. These similar trends were not unexpected considering the strong correlation between the gridded and Fairbanks instrumental temperature data. The differences between tree growth and the source of the precipitation data were more variable. For example, while the gridded data had a strong, positive correlation between tree growth and July precipitation from the previous year, there were no significant relationships found when using the Fairbanks instrumental record at the regional, site, and aspect levels. This is important in the interpretation of results from dendroclimatological studies. In this research, there is every indication that both temperature and precipitation are limiting factors to white spruce tree growth. Moreover, the strengthening of the climate and tree growth relationship after 1950 demonstrates trees are exhibiting temperature-related drought stress associated with increasing temperatures and decreasing precipitation. Further, these results are also concerning when considering the implications to long-term climate reconstructions and future climate modeling which may not take into account white spruce tree growth relationships with precipitation.

**Conclusion**

Though initial positive responses to warming temperatures and decreased precipitation may currently increase radial tree growth and carbon uptake, as temperatures continue to rise and precipitation continues to decrease, drought-related stress may turn white spruce dominated areas in Denali into carbon sources as tree
mortality is expected to increase (Peng et al., 2016; D’Arrigo et al., 2004; Barber et al., 2000). Additionally, trees experiencing drought-related stress are more susceptible to spruce beetle outbreaks and more likely to be killed (Csank et al., 2016). Trends over the last century, particularly after 1950, have thus far reflected a strong coherence between tree growth sensitivity and climate on warmer, drier south-facing aspects, though this may change with continued anthropogenic climate change. Lloyd et al. (2013) and Barber et al. (2000) hypothesize that variations in tree growth sensitivity may decrease, particularly as temperatures continue to increase and surpass high temperature stress-induced physiological thresholds. Temperatures greater than 12° C are becoming more common during the summer months, which is the critical season for white spruce radial growth. The combined effect of temperatures exceeding 12° C as well as decreased moisture have been found to have a negative impact on tree growth (Wilmking et al., 2004). With continued concurrent decreases in precipitation, these climatic conditions will likely exceed physiological thermal and moisture stress thresholds, and with higher frequency and more rapidly on south-facing aspects. The impacts of increasing temperatures at the regional level are likely to have a delayed detrimental impact to tree growth on cooler, more mesic north-facing aspects. These variations in more xeric south-facing aspect versus mesic north-facing aspects site conditions will likely greatly influence tree growth sensitivity with climate change trends. In fact, the strength of the relationship between tree growth and climate may increase on north-facing aspects as sites that most frequently exhibited a positive response to temperature were in cooler, and wetter locations (McGuire et al., 2010). Expected warmer and drier growing season conditions may create climate refuges for white spruce on north-facing aspects without
exceeding physiological thresholds, as well as by increasing the depth of permafrost thaw and decreasing the depth of snowpack.

Species responses to changing climate are difficult to predict. Impacts to an ecosystem, particularly keystone species like white spruce, can result in synergistic effects potentially reducing a biological community’s resilience and adaptive capacity to climate change and other natural disturbances (Folke et al., 2004). Climatic influences on white spruce trees in particular, a dominant and keystone species comprising the boreal forest biome, are expected to heavily impact rates of carbon sequestration (Barber et al., 2000). As the second largest biome on Earth, the boreal forest is estimated to store approximately 35-50% of the total carbon stored in all forested ecosystems (Bhatti et al., 2012; Malhi et al., 1999). A more thorough understanding of the underlying complexities controlling tree growth patterns will aid in a more accurate modeling of the future impacts of climate change to this ecosystem.
References


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<th>Total</th>
</tr>
</thead>
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</tr>
<tr>
<td></td>
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<td></td>
</tr>
<tr>
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</tr>
<tr>
<td></td>
<td>South</td>
<td>32</td>
<td></td>
</tr>
<tr>
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</tr>
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<td></td>
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<td></td>
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</table>

*Table 1* Total number of mature white spruce trees collected at each study site and each aspect.
**Figure 1** The relationship between KNMI average annual temperature data for Denali and the Fairbanks, AK instrumental record.
Figure 2 The relationship between KNMI total annual precipitation data for Denali and the Fairbanks, AK instrumental record.
Figure 3 Correlation coefficient values of tree ring width in Denali and (A) monthly average temperature (°C) and (B) monthly total precipitation (mm) for the year of growth and the previous year’s growth (p < 0.05*).
**Figure 4** Correlation coefficient values of tree ring width for three sites in Denali and (A-C) monthly average temperature (°C) and monthly total precipitation (mm) (D-F) for the year of growth and the previous year’s growth (p < 0.05*).
Figure 5 Correlation coefficient values of tree ring width for each site aspect in Denali and monthly average temperature (°C) for the year of growth and the previous year’s growth (p < 0.05*).
Figure 6 Correlation coefficient values of tree ring width for each site aspect in Denali and monthly total precipitation (mm) for the year of growth and the previous year's growth (p < 0.05*).
Figure 7 Correlation coefficient values of tree ring width for each site in Denali prior to and after the 1950s tree establishment regime shift and monthly average temperature (°C) for the year of growth and the previous year’s growth (p < 0.05*).
Figure 8 Correlation coefficient values of tree ring width for each site in Denali prior to and after the 1950s tree establishment regime shift and monthly total precipitation (mm) for the year of growth and the previous year’s growth (p < 0.05*).
Figure 9 Cross-correlation function analysis between annual tree growth and annual temperature (°C) for each site in Denali (p<0.05).
Figure 10 Cross-correlation function analysis between annual tree growth and annual precipitation (mm) for each site in Denali (p<0.05).
## Appendix A - Correlation coefficient values of tree growth-climate comparisons between Fairbanks instrumental data and KNMI interpolated data

Table 1 Regional data comparisons using all tree growth data collected in Denali.

<table>
<thead>
<tr>
<th>Month</th>
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<th>Total Precipitation (mm)</th>
</tr>
</thead>
<tbody>
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<td>Regional PRISM Data</td>
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</tr>
<tr>
<td>June</td>
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<td>-0.0528193</td>
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<td>July</td>
<td>-0.27238*</td>
<td>-0.36475*</td>
</tr>
<tr>
<td>August</td>
<td>-0.228761*</td>
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<tr>
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<td>-0.201702*</td>
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<td>June</td>
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Months beginning with lowercase letters denote the previous year (P <0.05*)
Table 2 Average monthly temperature and tree growth Cabin Divide data comparisons using pooled site and north- and south-facing aspect tree growth data collected in Denali.

<table>
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<tr>
<th>Month</th>
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<th>South</th>
<th>All</th>
<th>North</th>
<th>South</th>
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Months beginning with lowercase letters denote the previous year (P <0.05*)
### Table 3

Average monthly precipitation and tree growth Cabin Divide data comparisons using pooled site and north- and south-facing aspect tree growth data collected in Denali.

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Months beginning with lowercase letters denote the previous year (P <0.05*)
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**Table 4** Average monthly temperature and tree growth East Fork data comparisons using pooled site and north- and south-facing aspect tree growth data collected in Denali.
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Months beginning with lowercase letters denote the previous year (P <0.05*)

**Table 5** Average monthly precipitation and tree growth East Fork data comparisons using pooled site and north- and south-facing aspect tree growth data collected in Denali.
Table 6 Average monthly temperature and tree growth Healy data comparisons using pooled site and north- and south-facing aspect tree growth data collected in Denali.
Table 7 Average monthly precipitation and tree growth Healy data comparisons using pooled site and north- and south-facing aspect tree growth data collected in Denali.
Chapter 4:

Impacts from a Century of Climate Change on a Forested Landscape in Denali

National Park and Preserve, Alaska, USA
Abstract

Rapid climate change in northern latitudes has resulted in ecosystem shifts at the boreal-tundra ecotone. White spruce trees are particularly successful invaders into tundra. However, biophysical factors, particularly in mountainous terrain, can influence local climatic variability generating variations in tree establishment. This research explored spatiotemporal patterns of tree expansion in Denali National Park and Preserve, Alaska between 1900-2005 using a combination of mid-1950s aerial photography, mid-2000s IKONOS imagery, dendroecological methods, and random forest statistical analyses. Average temperatures in the park increased around 3 °C while total precipitation decreased around 150 mm. Climate data also revealed a longitudinal gradient with the park interior being cooler and wetter on average than the eastern edge of the park. Since the 1950s, climate change has resulted in an average 10% increase of new tree invasion into shrub/tundra dominated locations and an 11% increase in infilling within established 1950s forested areas. Most striking though, was a three-fold increase in infilling at the eastern edge of the park. Elevation, topographic position, and proximity to existing trees were the most important biophysical variables promoting new seedling establishment, growth, and survival since the mid-1950s. Of the 619 tree cores collected on north- and south-facing aspects, 423 individuals established after 1950 with peak establishment occurring between 1970-1980. Most forest-tundra ecotone studies focus on north- and south-facing aspects and consolidate data to report average conditions. This study highlights the need assess patterns along a longitudinal gradient and on lesser studied aspects as these areas can change more dramatically.

Key Words: climate change, white spruce, remote sensing, Denali, Alaska
Introduction

As the second largest biome on Earth (approximately 1.2 million hectares), the boreal forest dominates northern latitudes accounting for approximately 30% of the global forested area (FAO, 2015, Keenan et al., 2015). This biome is estimated to store approximately 35–50% of the total carbon stored in all forested ecosystems (Bhatti et al., 2012; Malhi et al., 1999). Rapid climate change in the 20th century has been magnified at high latitudes and altitudes, which have warmed at twice the global average (Chapin et al., 2010; Harsch et al., 2009; IPCC, 2007; Burkett et al., 2005). This has resulted in the steady encroachment of woody species upslope and towards the poles invading the tundra biome (Dial et al., 2016; Myers-Smith, 2015; Roland et al., 2013; Sullivan and Sveinbjörnsson, 2010; Chapin et al., 2006; Sturm et al., 2005; Sturm et al., 2001), which is a phenomena unique to the boreal-tundra ecotone. The boreal-tundra ecotone is defined as the transition in tree cover density from closed-canopy forest through the treeline zone to tundra (Ranson et al., 2011; Sveinbjörnsson, et al., 2002). The treeline zone is defined an area comprised of a combination of forest and tundra species to the uppermost limit that can sustain the tree life form (Holtmeier and Broll, 2005).

Positive feedbacks of increased warming in boreal forests also include the increased probability of fire at the boreal-tundra ecotone and tundra biome due to changes in fire weather and increases in area burned that will change the spatial distribution of these terrestrial ecosystems (Young et al., 2016; van Lierop et al., 2015; Beck et al. 2011a), and decreased albedo (Foley et al., 1994; Bonan, et al., 1992). Subsequently, this has led to decreases in snow cover further amplifying warming
(Bonan, et al., 1992) and increasing permafrost degradation (Panda, et al., 2014; Jafarov et al. 2012) opening up new areas to establishment by woody species. While increased coverage in woody species may initially account for an increase in carbon uptake at northern latitudes (Beck et al., 2011b; Barber et al., 2000), drought stress regulating woody species carbon uptake (Csank et al., 2016; D’Arrigo et al., 2008; Chapin et al., 2006) and thawing permafrost may release significant amounts of stored carbon into the atmosphere (Semenchuck et al., 2016; Brown et al., 2015; Schuur et al., 2008). In the boreal-tundra region, models estimate 0.5 to 1 petagram of carbon could be released into the atmosphere per year via permafrost thaw processes (Schuur et al., 2008).

The implications of climate change on tree establishment in the boreal-tundra system are uncertain in part because of environmental gradients observed at different spatial and temporal scales (Weiss et al., 2015; Lloyd et al., 2013; Ohse et al., 2012; Holtmeier and Broll, 2005; Wilmking et al., 2004; Smith et al., 2003; Bonan and Shugart, 1989). These biogeographic variations are a function of historical and spatial (i.e. location and scale) contingency which dictates all places are not created equal so generalizations about climatic and biophysical controls cannot be made, even within the same ecosystem or vicinity (Phillips, 2001). This is particularly true in mountainous terrain where topographic conditions strongly influence local climatic variability and create heterogeneous conditions that influence patterns of tree establishment (Frey et al., 2016; Case and Duncan, 2014; Roland et al., 2013; Stueve et al., 2011; Daniels and Veblen, 2004). For instance, physical site conditions like elevation, aspect, soils, and boulders, and biological facilitation from proximity to existing mature trees, are necessary to produce favorable microsite conditions for seedling recruitment and survival.
Temperature and permafrost are thought to be the predominant limiting factors controlling where trees can successfully establish and persist at the northernmost limit of the boreal forest (Helbig et al., 2016; Danby, 2011; Schrag et al., 2008; Chapin et al., 2006; Lloyd, 2005; Daniels and Veblen, 2004). Warmer temperatures and thawing permafrost can trigger an increase in tree establishment and tree density (Helbig et al., 2016; Wang et al., 2016; Lloyd, 2005; Camarero and Gutiérrez, 2004). However, in mountainous regions, discontinuous permafrost, and thermal modification related to terrain properties such as aspect, elevation, or slope (Lookingbill and Urban, 2003), may limit tree establishment and movement of forests into tundra systems. Furthermore, biological competition (e.g. with shrub species) may inhibit successful establishment even if temperatures are sufficiently warm for tree establishment causing a migration lag into tundra (Dial et al., 2016; Germino, et al., 2002; Grace, et al., 2002). However, this lag may not be observed around preexisting trees which can modify microtopography and provide a seed source as well as protection against extreme temperature fluctuations and strong winds, and influence snowpack depth, which can facilitate tree expansion into tundra due to increasing temperatures at higher latitudes and altitudes (Pyatt, et al., 2016; Renard et al., 2016; Harsch et al., 2009). Observations from historical landscape photography, aerial photography, and satellite imagery have shown tree seedlings often establish adjacent to existing forest edges and isolated patches of established trees or “tree islands” (Stueve, et al., 2011; Roush, et al., 2007; Zier and Baker, 2006; Smith et al. 2003; Kullman, 1993).
This research will explore the spatial and temporal patterns of infilling within established forests in the 1950s and new establishment in the treeline zone as a function of climate change from 1900 to present. The following questions will be addressed: (1) Has there been a consistent increase in tree establishment in the established forests and treeline zones at three sites in Denali between 1900-2005? We hypothesize that there will be an observable increase in infilling and new establishment in the established forest and treeline zones with the higher increase adjacent to established forests. (2) How do climatic and biophysical controls dictate the spatial patterns of tree establishment observed at the three sites in Denali? We hypothesize the highest rates of tree establishment and growth will predominantly be a function of two biophysical controls of elevation and adjacency to existing 1950s forested areas. This research uses observations and measurements from multiple scales to assess which biophysical controls generate spatial patterns of tree establishment over time in Denali.

**Study Area (extension from Chapter 1 Study Area description)**

For this study, these sites were chosen as an extension of previous dendroecological research conducted in the field at these locations. The intent for subsequent analyses was to focus on areas where trees were successfully infilling in the established 1950s forests and invading into tundra. Thus, the irregular shapes and sizes of the three sites (Table 1 and Figure 3) were the result of eliminating grid cells dominated by stream channels, non-vegetated rocky areas at the highest elevations, and restricted by the extent of the available topographic data (see Figure 1). Elevations for each site used in subsequent analyses range from 430-1196 m and slopes from 0-30 degrees (Table 1).
Methods

Imagery acquisition and processing

We identified the spatial patterns of tree establishment within forest and tundra using remotely sensed imagery that spans a period of tree establishment over an approximately 50 year period at each study site. 1.5 m panchromatic aerial photographs taken in 1953 and 1954 were acquired from the United States Geological Survey (USGS). Orthorectified pan-sharpened IKONOS satellite imagery from 2004 and 2005, as well as an IKONOS-derived 30m digital elevation model (DEM), were provided by the National Park Service (NPS). Bilinear interpolation was used to increase the pixel resolution of the IKONOS imagery from 1 m to 1.5 m to match the resolution of the aerial photographs. Georeferencing and orthorectification procedures were applied to the aerial photographs to ensure alignment with the IKONOS imagery and reduce spatial distortions inherent in mountainous terrain environments. We first roughly co-registered the aerial photographs with the IKONOS imagery using easily identifiable features visible in both sets of images like stream bends and large boulders to get the two images in similar projected space. Next, forty ground control points (GCPs) collected from the IKONOS image, were spread throughout each aerial photograph and more heavily concentrated in areas of steep terrain more prone to spatial distortion. A cubic convolution resampling method was applied to each of the aerial photographs though a subpixel resolution root mean square error (RMSE) was never achieved, particular in the steepest terrain on mountain slopes. To achieve a subpixel resolution RMSE and produce a more accurate land cover classification, small areas of similar terrain characteristics of each aerial photograph were
georeferenced to the IKONOS image. For example, approximately 10 GCPs would be used to georeference an approximately 2000 x 2000 m steep south-facing aspects.

Imagery analysis

The primary objective of the imagery analysis was to identify locations of tree infilling within the established forest and new tree establishment in the tundra zone within each study site in the mid-1950s and the mid-2000s (Figure 2). For the purposes of this study, the treeline zone is defined as the transition between the established forest in the 1950s and tundra. We overlaid a 200 x 200 m grid (4 ha) on the aerial photographs and IKONOS imagery in ArcGIS 10.1 to identify vegetation change between the mid-1950s and the mid-2000s (Figure 3). The grid cell size was chosen to capture patterns of change across the landscape that could be related to biophysical factors that affect tree establishment operating at multiple spatial scales without oversampling or too much resolution loss (Walsh et al., 1998). Each grid cell was assigned a land cover class for the two time periods. The classes were bare ground, shrub/tundra, and percentage of tree cover (1-33% = low tree cover, 33-67% = moderate tree cover, 67-100% = high tree cover). These land cover classes were then converted to categories of change over time from the 1950s to the mid-2000s including: 1) no change = no change in category class; 2) infilling = percentage increase in tree cover in established forest areas; 3) new establishment = conversion from no tree cover to percentage class of tree cover; and 4) forest loss = conversion from percentage class of tree cover to reduced cover and no tree cover observed.
Biophysical factors and statistical analysis

Trees establishment is often nonlinear and complex as a result of local site conditions. Topographic variables likely to influence tree establishment and growth were derived from the DEM for each site. The DEM pixel resolution was resampled from 30 m to 200 m using a bilinear interpolation to match the grid cell size of the land cover classification (Jensen, 2005). The topographic variables derived from the DEM included elevation, slope angle, topographic wetness index (TWI), topographic position index (TPI), northness, eastness, and annual and seasonal incoming solar radiation. TWI was calculated using a 3x3 rectangle neighborhood and TPI was calculated using a 5x5 rectangle neighborhood. TPI values range from negative (valley bottoms) to 0 (flat or mid-slope locations) to positive (mountaintops or ridges) values. Seasons were divided into Spring (March, April, May), Summer (June, July, August), Fall (September, October, November), and Winter (December, January, February). The biological variables representing the proximity to existing mature trees observed in the mid-1950s imagery, was calculated using Euclidean Distance from pixels identified as forest in the 1950s imagery (Stueve, et al., 2009). This variable was included to represent the increased likelihood of higher rates of establishment and survivability adjacent to mature trees present in the 1950s. White spruce produce winged, wind-dispersed seeds that can travel large distances (Ritchie and MacDonald, 1986) ranging anywhere from 60-300 m away dependent on factors like nearby topographic obstructions and wind strength (Cooper, 1986). Euclidean Distance was calculated from the moderate (33-67%) and high (67-100%) tree cover classes, as well as a combined moderate/high (33-100%) tree cover
class with the understanding there would be higher rates of seed rain, and seedling establishment and survival associated with these land cover classes.

Finally, we used the random forest classification method to identify the most important biophysical predictors of establishment as this method often produces higher classification accuracy than linear statistical models (Cutler et al. 2007). This statistical method is becoming a commonly used method for analysis in ecological research (Prasad et al. 2006). The random forest statistical method is a more advanced variation of the traditional classification and regression tree (CART) analysis in that it averages a large number of bootstrapped regression trees using resampled data with replacement for each iteration (Prasad et al., 2006). After testing various numbers of trees for averaging, we chose 4000 trees as this produced the lowest out-of-bag error (OOB error) with no measurable difference when choosing larger numbers of trees. The bootstrapped trees are randomly generated using a random subset of the predictor variables. The procedure randomly selects approximately two-thirds of the data to use as the training dataset, while the remaining one-third of the data is used to test the model’s accuracy (Liaw and Wiener, 2002). The OOB error demonstrates what proportion of the test did not fit the model’s classification. The influence of these variables was assessed by performing a random forest statistical analysis in R 3.1.2 using the randomForest package (Liaw and Wiener, 2002).

Field data collection and processing for imagery verification

The remotely sensed images are temporally restrictive, providing two snapshots in time from the 1950s and 2000s. To increase the temporal inference from the remotely
sensed imagery and verify the timing and spatial patterns of forest change, we collected tree age data from mature white spruce trees, saplings, and seedlings along transects in the closed canopy forest and treeline zone. These data were used to determine tree establishment dates at the three study sites and data were collected in 2011 and 2012. Because the three study sites were originally chosen for dendroecological work examining the predominant influences of aspect on tree establishment and growth, field data were only collected on north- and south-facing aspects and not east- and west-facing aspects. In the treeline zone, a seedling was defined as a tree < 1 m in height, a sapling as a tree at least 1 m height and < 2 cm diameter at breast height (dbh), and mature trees defined as trees larger than 2 cm dbh. In the established forest zones, only data from mature trees and seedlings were collected because the objectives of the original research was to examine the influences of aspect on tree growth and mature trees are considered most sensitive to climate signals. Seedlings were defined as a tree < 1 m in height. Mature trees were defined as trees > 10 cm diameter breast height (dbh) on north-facing aspects, and > 20 cm dbh on south-facing aspects. Different dbh were selected to account for the observed growth differences of the trees on different aspects over the past 60 years.

At each site, transects were established on each of these north- and south-facing aspects. The random pairs distance method (Mueller-Dombois and Ellenberg, 1974) was used to select trees along each transect. At each sample point, the nearest mature white spruce tree and sapling were cored to the pith. Cores were extracted 20 cm above the ground, on the uphill side of the tree. To account for missing rings in mature trees and saplings below 20 cm, the average age of the seedlings along each transect was estimated
by counting the total number branch whorl nodes. The branch whorl node count method is frequently used to date seedlings (Millar, et al., 2004; Zackrisson, et al., 1995). The accuracy of this method was evaluated by counting the total number of branch whorl nodes and comparing these to cross sections taken from 18 seedlings at each study site location (mean = 22.58, standard deviation = 13.9).

Each core sample was glued to a slotted mounting board and sanded with 100 – 400 grit sand paper to aid in identification of the tree rings. Tree cores were then counted to determine age and year of establishment. The chronologies created from these cores were visually cross-dated to a master chronology from the International Tree-Ring Data Bank (ITRDB) using marker rings (Stokes and Smiley, 1968; Yamaguchi, 1991). For tree cores with missing piths, a pith estimator was used to determine the approximate pith location and the date of establishment. All seedling whorl counts were averaged to estimate the number of years needed for a mature tree or sapling to reach 20 cm height above the ground. Mature tree and sapling ages were adjusted by adding the age needed to grow to 20 cm height.

Finally, to determine the extent of upslope migration of trees between the 1950s and 2012, we used a combination of remotely sensed imagery and field data. The latitude, longitude, and elevation of the uppermost seedling observed at each site and on each north- and south-facing aspect were recorded in the field using a Garmin eTrex 20 GPS unit with a horizontal and vertical accuracy of +/- 3 m. The distance was then measured between the highest elevation of tree establishment observed during field collection and the nearest edge of the closed canopy forest in the mid-1950s aerial imagery.
**Results**

*Observations of forest change – Image Analysis*

Measurements between the nearest observed mature tree in the 1950s aerial photography and the highest seedling found during the 2011/2012 field seasons showed treeline advanced upslope around 150 m on north-facing aspects, and 200 m on south-facing aspects. On the north- and south-facing aspects respectively, the observed upper tree limit shifted 136 m and 212 m at the Cabin Divide site, 182 m and 113 m at East Fork, and 141 m and 289 m at Healy. The percentage of new tree establishment was similar at each of the three sites at around 10% though highest at the East Fork site (Table 2; Figure 3). Most of this change was the transition from shrub/tundra areas to new tree establishment rather than areas devoid of vegetation. The highest rates of new establishment occurred on east-facing aspects in East Fork and Healy, and marginally higher rates on west-facing aspects in Cabin Divide (Figure 4).

There were larger differences among sites of infilling in the established forest (Table 2; Figure 3). Infilling was three-fold higher at Healy than at Cabin Divide or East Fork. The highest tree cover class (67-100%) in the 1950s was typically found at lower elevations and adjacent to streams. Infilling at all sites was highest in areas that had high tree cover in the 1950s. The Cabin Divide and East Fork sites exhibited an increase in infilling of approximately 6% in highest tree cover class between the 1950s and 2000s, while the Healy exhibited 21% increase in the highest tree cover class. The highest rates of infilling occurred on west-facing aspects in Cabin Divide, south-facing aspects in East Fork, and east-facing aspects in Healy (Figure 4).
The influence of local site factors – Random Forest Analysis

A total of fourteen physical and biological variables were used to determine which local site conditions influenced spatial patterns of tree establishment at each site (infilling and new establishment) (Figures 5-9). RandomForest analysis indicated the highest rates of infilling and new establishment between the mid-1950s and mid-2000s occurred adjacent to the preexisting 1950s closed canopy forested areas (the combined moderate and high tree cover class) at the Cabin Divide site (n=195; OOB error = 15.46%) (Figure 5). In general, the tree cover class biological variables were the most important predictors of new tree establishment in Cabin Divide, while TPI became an important predictor for infilling. Elevation was the most important predictor of infilling and new tree establishment at East Fork (n=287; OOB error = 16.03%) (Figure 6). Proximity to existing trees was also an important predictor of infilling and new tree establishment at East Fork, though TPI became an important variable for infilling and fall (SON) incoming solar radiation an important predictor of new tree establishment. Elevation was the most important predictor of infilling, while TPI was the most important predictor for new tree establishment at Healy (n=336; OOB error = 8.93%) (Figure 7). TPI was also an important predictor of infilling at Healy, followed by winter (DJF) incoming solar radiation. Elevation and proximity to existing trees were important predictors of new tree establishment at Healy.

While the rank order of important variables controlling infilling and new tree establishment were similar at each site, how each of these variables dictated subsequent spatial patterns were the opposite of one another (Figures 8 and 9). At Cabin Divide and East Fork, the highest rates of infilling occurred at elevations between 750-900 m, and
450-550m at Healy. The highest rates of new tree establishment (i.e. within the treeline ecotone) occurred at elevations between 800-950 m at Cabin Divide, 850-1000 m at East Fork, and 600-800 m at Healy. In general, there was a higher probability of infilling at lower elevations and new tree establishment at higher elevations. Infilling had a higher probability of occurrence at slopes <15 degrees, while new tree establishment had a higher probability on slopes >20 degrees. On average, most infilling had a higher probability of occurrence within 300 m of the combined moderate/high tree cover class and new tree establishment a distances greater than 300 m. New tree establishment had a higher probability of occurrence in dry to slightly wet conditions, while infilling locations were wetter. Higher amounts of fall incoming solar radiation increased the probability of infilling and decreased the probability of new tree establishment. Infilling had a higher probability of occurring in flatter areas or midway up mountain slopes, while new establishment had a higher probability of occurrence higher up mountain slopes and in valley bottoms.

Observations of closed canopy and treeline change – Dendrochronological Analysis

While the remotely sensed imagery shows large change in tree cover over a 50-year period, dendrochronological analysis can increase the temporal resolution to more accurately identify the timing of change in tree establishment, as well as extend the record back to examine change over time since 1900. Tree age data from a total of 619 mature white spruce trees, saplings, and seedlings were collected within the established forest and treeline zones (Figure 8). Climate change has led to an increase in tree establishment into tundra on north- and south-facing aspects at all three sites within a decade or two of the 1950s imagery, and this increase has continued through to the 2012
field season. The highest rates of establishment at treeline occurred within the decade span of 1970-1980. A more bimodal distribution in the closed canopy forest at all three sites with a decrease in establishment during the 1970-1980 time span, is likely related to the lack of sapling size class tree age data collected in the established forest study areas. Though saplings were observed in the established forest regions on these aspects, there were fewer saplings observed in these locations as compared to the treeline zone. In addition, no tree age data were collected on east- and west-facing aspects which are clearly areas of substantial rates of new establishment and infilling (Figure 4) based on the image analyses.

Discussion

The influence of climate change on tree establishment in Denali was striking in both the remote sensing and dendrochronological records. An increase in infilling within the closed-canopy forest and encroachment upslope into tundra-dominated areas at all three study sites is indicative of regional scale climate change impacts, particularly after a regime shift in total annual precipitation 1950 (see Chapter 2). These changes in distribution were likely initiated by regional scale warmer temperatures and decreased precipitation since 1900. However, the lack of uniform replacement of tundra and shrub species across the landscape with trees is a clear indicator of historical and spatial contingent effects including variable rates of warming on different aspects, a longitudinal gradient in precipitation, the location and depth to permafrost, and the density of preexisting mature trees.

Widespread infilling and establishment of white spruce trees are indicative of the adaptive capacity of these trees to these variable environmental gradients across space
and time (Roland et al. 2013). Their ecological plasticity to a wide range of environmental conditions as well as their self-replacement successional strategies both within and adjacent to existing mature forest and around “tree islands”, have given white spruce a competitive edge in these higher latitudes and altitudes (Renard et al., 2016; Stueve, et al., 2011). Much of the increase in tree cover between the 1950s and 2000s imagery is an increase in tree establishment. This observation is based on dendrochronological data collected on north- and south-facing aspects (Figure 8) which shows an increase of more than two times the rate of establishment when examining the closed canopy and treeline zones over the last 60 years as compared to the previous 285 years of tree ring record. Between 1665-1950, 196 individuals established and survived at these three sites. Between 1950-2012, 423 individuals established. The magnitude of recent establishment is even more evident in the treeline zone where an approximate 20 times increase in establishment occurred over the last 60 years. Only 20 trees had established and survived prior to 1950, while 353 individuals established after 1950. This number becomes striking because more often, only two out of 100 white spruce seedlings will survive in treeline zones (Wilmking and Ibendorf, 2004). In other words, larger numbers of trees are establishing and surviving to produce and disseminate seeds.

Some of the infilling observed is also related to increased tree growth. Established smaller trees grew larger (increased basal diameter) and taller and therefore became visible in the IKONOS imagery. Dendroecological data from north- and south-facing aspects, however, show large radial tree growth differences between aspects (see Chapter 3). The dbh of trees on south-facing aspects at all sites combined, were frequently almost twice that of trees on north-facing aspects (south = 37 cm dbh vs. north = 21 cm dbh).
These radial growth differences may make observations of increased tree cover on south-facing aspects easier to discern in the imagery as trees grow larger than tundra and shrub species over time and therefore become more visible. For these reasons, increases in tree cover may be underestimated on north-facing aspects. Though there was no data collected on east- and west-facing aspects, I suspect that as compared to north-facing aspects and based on the increased infilling observed on these aspects (Figure 4), these aspects also exhibited increased rates of tree growth.

All three sites experienced a peak increase in establishment between 1970-1980 in the treeline zone. This is particularly relevant as seedlings in the treeline zone are often more susceptible to mortality than in the closed canopy forest (Hättenschwiler and Smith, 1999). This peak in establishment may relate to regime shifts to warmer spring temperatures (Chapter 3) as well as continued decreases in precipitation. Snowpack depth may also play an important role with too much snow shortening the growing season, and too little snow triggering drought stress related mortality (Renard et al., 2016; Barbeito et al., 2012; Wilmking and Ibendorf, 2004; Hättenschwiler and Smith, 1999). Warmer temperatures and decreased precipitation may have decreased snowpack depth in the treeline zone, initiated earlier snowpack melt, increased permafrost degradation, and increased the length of the growing season allowing for an increase in establishment.

Danby and Hik (2007) found that experimentally warmed plots at treeline increased tree seedling growth and photosynthetic rates by increasing soil temperature and the length of the snow-free period. These similar site conditions at each of the study areas likely allowed for increased encroachment and persistence of seedlings upslope into tundra-
dominated zones (Roland et al. 2013; Barbeito et al., 2012; Geddes et al., 2005; Alftine et al, 2003; Taylor, 1995).

The increase in infilling within the 1950s established forest and new tree establishment in the treeline zone, was determined predominantly by elevation, proximity to existing tree cover, and TPI at all three sites. Much of the infilling was at lower elevations while most of the new establishment occurred at middle elevations. This relationship is consistent with the temperature decrease with increasing elevation where tree establishment would be cold-limited and restricted at the highest elevations. Successful reproduction and subsequent establishment and persistence of seedlings decrease with increasing elevation (Wardle, 1968). High rates of tree cover change were also observed adjacent to streams, which occur primarily at the lower elevations and have an ameliorating effect on soil temperatures. This trend has been observed in other studies which observe higher rates of tree establishment and an increased density of trees adjacent to streams (Andersen and Baker, 2005; Viereck, 1970). High rates of infilling and new tree establishment also typically occurred within 300-500 m of existing moderate and high tree cover. White spruce produce wind-dispersed seeds that, with limited topographic obstructions and the presence of wind, can travel large distances (Cooper, 1986; Ritchie and MacDonald, 1986).

Established trees are often able to ameliorate conditions for new establishment in their vicinity by modifying microclimate, providing wind breaks, altering snow accumulation patterns and incoming solar radiation, and increasing soil moisture (Alftine and Malanson, 2004; Smith et al., 2003; Germino, et al., 2002; Hättenschwiler and Smith, 1999). This trend of increased rates of tree seedling establishment and persistence near
existing forest and tree islands has been observed in several studies (Stueve, et al., 2011; Roush, et al., 2007; Maher and Germino, 2006; Zier and Baker, 2006; Smith et al. 2003; Germino et al., 2002; Kullman, 1993). For example, Suarez et al. (1999) observed increasing stand density from time of initial patches of establishment of only a few trees in tundra locations. Further, seed rain will increase as more survive to maturity. These trees can also influence snow deposition. For instance, higher rates of successful seedling establishment have been observed on the leeward sides of tree islands where more snow was able to accumulate (Renard et al., 2016; Hättenschwiler and Smith, 1999).

Though similar rates of increase in new tree establishment upslope occurred at all three sites, spatially contingent effects (location and biophysical factors) (Phillips, 2001) influenced the rates of tree recruitment within the established forest. Among sites, infilling at Healy was three times greater than at Cabin Divide and East Fork (Table 2). This is likely a combination of local climatic differences and the increased importance of the influence of physical site controls that distinguish Healy from the other two sites. Healy is warmer and drier and has lower interannual temperature and precipitation variability (Table 1) so possibly experienced the effects from warming temperatures and decreased snowpack depths earlier allowing for infilling to occur in advance of the other two sites, particularly on east-facing aspects. This relationship is particularly evident with the increased probability of importance of fall (SON) and winter (DJF) incoming solar radiation (Figure 7). Moreover, infilling was able to occur across a wider elevational gradient at Healy. The 1950s established forest extended between 400-850 m at Healy with most of the infilling occurring at the lowest elevations. Trees were much better able to take advantage of the more moderate climatic and thermally regulated site conditions,
as compared to the established forests at the other two sites. In contrast, forests occupied elevations between 700-950m at Cabin Divide and 750-1000 m at East Fork. TPI also had a profound influence on tree infilling at Healy. The topographic position can influence whether an area is exposed or protected. Much of the infilling at Healy occurring in flatter locations (i.e. slopes < 15°), midway up mountain slopes, and on slopes with east-facing aspects. Flatter and moderately exposed slopes may favor establishment in the summer as a result of the expanded growing season length (Wilmking et al., 2004, Cui and Smith, 1991; Viereck, 1979) and an absence of topographic obstructions may allow white spruce seeds to travel greater distances (Cooper, 1986; Ritchie and MacDonald, 1986).

Finally, the influence of permafrost was most visibly evident at the East Fork site (Figure 11). We confirmed the presence of permafrost at this location by digging a hole to the permafrost layer. Warming of even a few degrees can lead to permafrost thawing and a restructuring of the underlying landscape (e.g. soil water holding capacity, soil temperature) and directly influences ecological processes (Panda et al., 2014). High rates of new establishment of trees observed in the remotely sensed imagery occurred at the edges of the permafrost-limited patches and adjacent to tree islands within the patches. The existing trees at the edges of the permafrost patch and early tree island colonizers can provide protection to nearby trees and younger trees against inclement weather conditions including strong winds and extreme temperature fluctuations facilitated new tree seedling establishment and survival (Sullivan and Sveinbjörnsson, 2010; Harsch et al., 2009). Tree encroachment into areas underlain by permafrost are a good indicator of sustained
permafrost thawing to greater depths as tree growth and establishment is thermally regulated by cold soil temperatures (Danby and Hik, 2007).

**Conclusion**

As the second largest biome on Earth, a more thorough understanding of environmental gradients controlling tree establishment patterns within the boreal forest will aid in more accurate modeling of the future impacts of climate change to this ecosystem. Positive feedbacks from increasing temperatures and decreasing precipitation since 1900 have led to park-wide increases in white spruce tree invasion into tundra in Denali. White spruce trees are more likely to invade and persist into tundra as compared to other northern tree species (Hobbie and Chapin, 1998). However, the heterogeneous nature of environmental gradients controlling vegetation distribution at different scales makes disentangling these effects particularly challenging. White spruce establishment was not uniform and likely related to differences in local climate and biophysical site characteristics.

Traditionally, forest-tundra ecotone studies focus on north- and south-facing aspects. Considering the high rates of tree cover change observed on east- and west-facing aspects, future studies should include dendroecological data from those aspects to further elucidate impacts from climate change. This study highlights the need to use multiple types of data collected at multiple scales (e.g. remote sensing, climate, dendroecological) to explore the historical and spatial contingency of a geographic location to quantify observed spatial patterns and distribution of vegetation related to climate change. These types of analyses are a particularly useful approach to exploring
the influences of environmental gradients operating at multiple temporal and spatial scales on vegetation distribution in topographically complex locations (Weiss et al., 2015; Case and Duncan, 2014; Cushman and Huettmann, 2010; Wu and Hobbs, 2002). Moreover, relatively complex spatial patterns were produced over relatively short distances. Though in a topographically complex landscape in Denali, similar patterns at other boreal-tundra ecotones may arise. Even small differences in topography, edaphic conditions, soil moisture, and other site factors may result in heterogeneous rates of infilling and new tree establishment in these other locations, though there may be more extreme range expansion in locations that don’t have as many topographical limitations. Further, this type of research could also aid in increasing the accuracy of regional or local predictive climate-vegetation interaction models, determining where white spruce trees are most likely to establish under future climate change scenarios and aid in forest management planning which transpires at these scales.

Ultimately, continued climate change will lead to an ecological transition from tundra to forest and is expected to result in a cascade of positive feedbacks. Palynological records show an increase in boreal forest cover during the middle Holocene at higher latitudes reduced albedo and snow cover resulting in an approximately 1 °C increase in growing season temperatures (Ganopolski, et al., 1998; Foley et al., 1994). Additionally, Chapin et al. (2000) found that in the transition from tundra to forest, albedo decreased by almost 50% and local and regional atmospheric heating increased by at least 4.7-13.7 W m² during the growing season. Further, expected decreases in snow accumulation can create a water-limited environment that, in turn, increases seedling mortality (Hättenschwiler and Smith, 1999) and increases the susceptibility of mature white spruce
to drought-related stress. This, in turn, can impact seed quality and production (Ohse et al., 2012; Juday et al., 2003) and extend the interval between cone and seed crop years (Burns and Honkala, 1990).

Climatic influences on white spruce trees, a dominant and keystone species comprising the boreal forest biome, are also expected to heavily impact rates of carbon sequestration (Barber et al., 2000). As the boreal biome has shifted to higher latitudes and upslope into tundra-dominated systems as a function of climate change, models have shown increased carbon uptake is less than the carbon loss from fire activity and thawing permafrost releasing stored carbon into the atmosphere (Beck et al., 2011b). Though tree establishment is increasing at an exponential rate as a result of increasing temperatures and decreasing precipitation, intraspecific biological competition may limit positive feedbacks from more favorable climatic conditions (Wang et al., 2016) decreasing carbon uptake. Additional temperature-induced drought stress also reduces the resilience of white spruce to insect outbreaks making them more susceptible to widespread mortality (Csank et al., 2016; Roland et al., 2013) and a further carbon source. Furthermore, any offsets of increased carbon uptake from increased tree establishment are expected to be minimal. Tundra permafrost soils can store up to 10 times more C per m² than non-permafrost boreal forest soil leading to a large potential net loss in stored carbon (Schuur et al., 2008).
References


<table>
<thead>
<tr>
<th>Study Sites (west to east)</th>
<th>Study Area Size (ha)</th>
<th>Average Temperature (°C)</th>
<th>Total Precipitation (mm)</th>
<th>Elevation (m)</th>
<th>Slope (degrees)</th>
<th>Frost Free Days</th>
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<tr>
<td>Cabin Divide</td>
<td>4732</td>
<td>-11 - -2.5</td>
<td>550-2465</td>
<td>720-1086</td>
<td>0-27</td>
<td>50-70</td>
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<td>747-1196</td>
<td>0-30</td>
<td>50-70</td>
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<tr>
<td>Healy</td>
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<td>-5 - -2.5</td>
<td>450-870</td>
<td>430-1063</td>
<td>0-27</td>
<td>50-70</td>
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</tbody>
</table>

Table 1 Average study site composition. Elevation and slope data from digital elevation model. Climate data from NCDC COOP climate stations. Frost free days from USDA NRCS soils survey report (Clark and Duffy, 2006).
<table>
<thead>
<tr>
<th>Site</th>
<th>Infilling</th>
<th>New Establishment</th>
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<td>7%</td>
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<tr>
<td>East Fork</td>
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<td>13%</td>
</tr>
<tr>
<td>Healy</td>
<td>31%</td>
<td>9%</td>
</tr>
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</table>

Table 2 Percentage of tree cover infilling or new establishment observed at each site.
**Figure 1** Black triangles indicate field work locations at the Cabin Divide, East Fork, and Healy (from west to east). (A) Denali with inset rectangle zoomed in area of physical site conditions. Insets: (B) shaded relief map representing topography, (C) elevation (m), (D) slope (degrees), (E) aspect, and (F) modeled mean decadal ground temperature permafrost map from Panda et al. (2014).
Figure 2 Examples of infilling and new establishment within the established forest and treeline zone in the 1950s panchromatic aerial photography, the 2000s IKONOS satellite imagery, and fieldwork photographs in each study area.
Figure 3 Land cover classification in (A) the mid-1950s and (B) mid-2000s; and (C) land cover change classifications at the Cabin Divide, East Fork, and Healy sites in Denali, Alaska.
Figure 4 Spatial patterns of new tree establishment (dark grey bars) and tree infilling (light grey bars) on different aspects in (A) Cabin Divide, (B) East Fork, and (C) Healy between the 1950s-2000s.
**Figure 5** Rank order of variable importance plots from the randomForest analysis predicting spatial patterns of tree establishment (infilling and new establishment) at the **Cabin Divide** in Denali, Alaska. Variables include: (1) elevation (m), (2) slope (degrees), (3) TWI = topographic wetness index, (4) TPI = topographic position index, (5) Northness, (6) Eastness, and Incoming Solar Radiation (WH/m²), (7) Annual, (8) Spring, (9) Summer, (10) Fall, (11) Winter, and Euclidean distance calculations from (12) moderate, (13) high, and (14) combined moderate and high land cover classes.
Figure 6 Rank order of variable importance plots from the randomForest analysis predicting spatial patterns of tree establishment (infilling and new establishment) at the East Fork site. Variables include: (1) elevation (m), (2) slope (degrees), (3) TWI = topographic wetness index, (4) TPI = topographic position index, (5) Northness, (6) Eastness, and Incoming Solar Radiation (WH/m²), (7) Annual, (8) Spring, (9) Summer, (10) Fall, (11) Winter, and Euclidean distance calculations from (12) moderate, (13) high, and (14) combined moderate and high land cover classes.
Figure 7 Rank order of variable importance plots from the randomForest analysis predicting spatial patterns of tree establishment (infilling and new establishment) at the Healy site. Variables include: (1) elevation (m), (2) slope (degrees), (3) TWI = topographic wetness index, (4) TPI = topographic position index, (5) Northness, (6) Eastness, and Incoming Solar Radiation (WH/m²), (7) Annual, (8) Spring, (9) Summer, (10) Fall, (11) Winter, and Euclidean distance calculations from (12) moderate, (13) high, and (14) combined moderate and high land cover classes.
Figure 8 Partial dependence plots showing influential biophysical predictor variables as determined by the randomForest analysis of spatial patterns of infilling for each study site in Denali, Alaska. Variables include: (1) elevation (m), (2) slope (degrees), (3) Euclidean distance combined moderate and high land cover classes, (4) TWI = topographic wetness index, (5) Fall Insolation (WH/m²), and (6) TPI = topographic position index (Valley > Flat/Midslope > Mountaintops/Ridges).
Figure 9 Partial dependence plots showing influential biophysical predictor variables as determined by the randomForest analysis of spatial patterns of new tree establishment for each study site in Denali, Alaska. Variables include: (1) elevation (m), (2) slope (degrees), (3) Euclidean distance combined moderate and high land cover classes, (4) TWI = topographic wetness index, (5) Fall Insolation (WH/m$^2$), and (6) TPI = topographic position index (Valley > Flat/Midslope > Mountaintops/Ridges).
Figure 10 Total tree establishment in the established forest and treeline ecotone at (A) Cabin Divide, (B) East Fork, and (C) Healy in Denali, Alaska. Black bars represent the number of individuals in the established forest and grey bars, the number of individuals in the treeline zone.
Figure 11 Example of infilling of white spruce trees within a discontinuous permafrost area (white rectangle) on an east-facing aspect at the East Fork site (Photo taken by Kirk Stueve 2008).
Chapter 5 - Conclusions: Climate Change Impacts to Tree Establishment and Tree Growth, and Implications for the Future
Tree Establishment

In Denali National Park and Preserve, a 3°C increase in average annual temperature and 150 mm decrease in total annual precipitation beginning in 1900, have resulted in a steady invasion of white spruce trees into tundra zones at treeline. Much of this climate change has occurred during the growing season months. A park-wide positive regime shift in tree establishment was observed in the 1950s and corresponded with a negative shift in total precipitation. Most spatial and temporal variability in tree establishment was observed when comparing aspects within each site with positive shifts in tree establishment ranging over a period from 1945-1980. A positive shift in tree establishment on north-facing aspects appeared to be a function of shifts in precipitation at the westernmost sites. A combination of a positive shift in increased spring temperatures and more favorable local site conditions adjacent to the forest edge and tree islands initiated the shift at the easternmost site. Tree islands can facilitate greater seedling abundance through an amelioration of local environmental conditions enabling increased survival into new locations (Batllori and Gutiérrez, 2008; Smith et al., 2003). A regime shift in tree establishment on south-facing aspects was predominantly a function of decreasing precipitation with the timing of shift initiating the earliest in warmer and drier locations. Tree establishment had a positive association with spring and summer temperature variables with a temperature increase initiating the increase in tree establishment at treeline beginning around 1915. Overall, decreasing precipitation and increasing temperatures have likely decreased snowpack depth, triggered earlier snowpack melt, and increased the length of the growing season, likely allowing for increased establishment and persistence of seedlings into tundra zones.
Increases in white spruce tree infilling within the 1950s established forest and tree invasion into shrub and tundra locations were also observed in remotely sensed imagery. In Denali, average upslope advancement of trees ranged between 100 m to 290 m, much higher than modeled averages which have shown a 20 km northward latitudinal shift and a 91 m upslope elevational shift since the 1960s (Gray and Hamann, 2013). Most surprising was the east to west longitudinal gradient that became evident both with the timing of regime shifts in tree establishment at treeline, and broader spatial patterns of tree infilling and establishment. Tree establishment initiated earliest and infilling increased much more substantially in the warmer and drier locations at the eastern edge of the park. Moreover, biophysical local site conditions had an additional influence on the spatial patterns of tree cover change observed in the remotely sensed imagery. Much of the change occurred at lower elevations, flatter slope angles, midway up mountain slopes, and adjacent to established forest edge or tree islands. These settings produced a higher seed rain supply and more protection from extreme climatic fluctuations promoting seedling establishment and persistence over time.

**Tree Growth**

Similar to tree establishment patterns, the strongest relationships between tree growth and climate were found on south-facing aspects and after 1950. The strongest relationships between tree growth and climate occurred after the 1950s with a shift to warmer temperatures and decreased precipitation. As the spatial extent decreased from regional to aspect, the strength of the tree growth-climate increased. The tree growth-climate relationships were consistently weakest when trees on north-facing aspects were
included in the analysis. Though an initial positive response to climate change began in 1950, negative impacts to tree growth are being observed with these increasingly warmer and drier climatic conditions. The combination of an increase in temperature, decrease in precipitation, and a lengthening of the growing season, has likely decreased soil moisture and increased drought-related stress. White spruce trees grow best in cooler and moister environments. While north-facing aspects have had a relatively weak relationship with climate over the past century, this relationship will likely strengthen as climate continues to change, and these aspects become more climatically suitable refuges.

Trends over the last century, particularly after 1950, have thus far reflected a strong coherence between tree growth sensitivity and climate on warmer, drier south-facing aspects, though this is expected to shift with continued climate change. Lloyd et al. (2013) and Barber et al. (2000) hypothesize that variations in tree growth sensitivity may decrease, particularly as temperatures continue to increase and surpass high temperature stress-induced physiological thresholds. Temperatures greater than 12° C are becoming more common during the summer months, which are critical growing season periods for white spruce. The combined effect of temperatures exceeding 12° C as well as decreased moisture have been found to have a negative impact on tree growth (Wilmking et al., 2004). With continued concurrent decreases in precipitation, these climatic conditions will likely exceed physiological thermal and moisture stress thresholds, and with higher frequency and more rapidly on south-facing aspects. Additionally, variations in xeric versus mesic aspect site conditions will likely greatly influence tree growth sensitivity with climate change trends. The impacts of increasing temperatures at the regional level are likely to have a delayed detrimental impact to tree growth on cooler, more mesic
north-facing aspects. We expect in the future, climate change will result in significantly strengthened climate-tree growth relationships on north-facing aspects as these locations continue to become warmer and drier, while relationships on south-facing aspects become weaker as physiological thresholds are surpassed on a more consistent basis.

**Implications and Cascading Positive Feedbacks**

As the second largest biome on Earth (approximately 1.2 million hectares), the boreal forest dominates northern latitudes accounting for approximately 30% of the global forested area (FAO, 2015, Keenan et al., 2015). A more thorough understanding of environmental gradients controlling tree establishment patterns within the boreal forest will aid in more accurate modeling of the future impacts of climate change to this ecosystem. Positive feedbacks from increasing temperatures and decreasing precipitation since 1900 have led to park-wide increases in white spruce tree growth and tree invasion into tundra in Denali. White spruce trees are more likely to invade and persist into tundra as compared to other northern tree species (Hobbie and Chapin, 1998). However, the geographically heterogeneous nature of environmental gradients, particularly in mountainous environments, resulted in highly variable rates of tree expansion and growth in the park.

Ultimately, continued climate change will lead to an ecological shift from tundra to forest and is expected to result in a cascade of positive feedbacks. Palynological records show during the middle Holocene, an increase in boreal forest cover at higher latitudes reduced albedo and snow cover resulting in an approximately 1 °C increase in growing season temperatures (Ganopolski, et al., 1998; Foley et al., 1994). Additionally,
Chapin et al. (2000) found that in the transition from tundra to forest, albedo decreased by almost 50% and local and regional atmospheric heating increased by at least 4.7-13.7 W m² during the growing season. Further, expected decreases in snow accumulation can create a water-limited environment increasing seedling mortality (Hättenschwiler and Smith, 1999) and increasing the susceptibility of mature white spruce to drought-related stress, which, in turn, can impact seed quality and production (Ohse et al., 2012; Juday et al., 2003) and extending the interval between cone and seed crop years (Burns and Honkala, 1990). Positive feedbacks of increased warming in boreal forests also include the increased probability of fire at the boreal-tundra ecotone and tundra biome due to changes in fire weather and increases in area burned that will change the spatial distribution of these terrestrial ecosystems (Young et al., 2016; van Lierop et al., 2015; Beck et al. 2011a) and increasing permafrost degradation (Panda, et al., 2014; Jafarov et al. 2012) opening up new areas to establishment by woody species.

The boreal biome is estimated to store approximately 35-50% of the total carbon stored in all forested ecosystems (Bhatti et al., 2012; Malhi et al., 1999). While increased coverage in woody species may initially account for an increase in carbon uptake at northern latitudes (Beck et al., 2011b; Barber et al., 2000), drought stress regulating woody species carbon uptake (Csank et al., 2016; D’Arrigo et al., 2008; Chapin et al., 2006) and thawing permafrost may release significant amounts of stored carbon into the atmosphere (Semenchuck et al., 2016; Brown et al., 2015; Schuur et al., 2008). Furthermore, any offsets of increased carbon uptake from increased tree establishment are expected to be minimal. Tundra permafrost soils can store up to 10 times more C per m² than non-permafrost boreal forest soil leading to a large potential net loss in stored
carbon (Schuur et al., 2008). In the boreal-tundra region, models estimate 0.5 to 1 petagram of carbon could be released into the atmosphere per year via permafrost thaw processes (Schuur et al., 2008).

Scale

In general, when data were consolidated, tree establishment and tree growth relationships with climate evident at one scale were either not present or weakened at another scale. Often, the weakest relationships were found on north-facing aspects and when data from these aspects were included in the analyses, site and regional tree-climate trends were weaker. When examining the impacts of climate on tree establishment and growth, particularly in topographically complex landscapes, impacts should be assessed both at the site- and aspect-level rather than regionally. A similar impact was observed when data prior to the 1950s regime shift were included in the analyses (i.e. 1900-2010). Including pre-1950s data either weakened tree growth-climate relationships or eliminated them entirely. Rather than evaluate climate-tree growth and establishment relationships across an entire timeframe, timeframes in which to examine these relationships should be determined objectively. The temporal divisions to be assessed should be determined using statistically driven methodology like regime shift analyses. Ultimately, evaluating impacts at only one scale can impact results and conclusions drawn from this type of research in which processes and relationships observed at one scale are not evident at another. This can also influence management policy and practices which rely on this research to manage forest systems.
Future Research Directions

With warmer temperatures and decreasing precipitation, there is evidence of temperature-related drought stress on tree growth and tree establishment. Further, with the second regime shift in precipitation and summer temperatures, there is also evidence of seedling decline. As physiological thresholds of white spruce are surpassed, we may begin to observe widespread die-off, predominantly on south-facing aspects. However, north- and possibly east-facing aspects may become climatically suitable refuges for white spruce tree to survive and persist under more extreme climatic conditions. Future research should gather dendroecological data on white spruce trees on all aspects to determine whether the decline in individuals beginning around 2000 is a long-term trend related to climate change. Moreover, this type of research could also aid in increasing the accuracy of regional or local predictive climate-vegetation interaction models, determining where white spruce trees are most likely to establish under future climate change scenarios. However, the difference in results, specifically between the instrumental and the gridded precipitation data, highlights the potential influence on the interpretation of dendroclimatological studies. In this research, there was every indication that both temperature and precipitation are limiting factors to white spruce tree establishment and growth. The climate data chosen to model dendroecological data may influence the predictive accuracy of climate-vegetation models and influence forest management policies. Further tests comparing results from commonly used climate data sources should be tested in other locations.
References


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