CLIMATE AND REGENERATION AT UPPER TREELINE EAST AND WEST OF THE CONTINENTAL DIVIDE IN THE NORTHERN AND SOUTHERN ROCKY MOUNTAINS: DO LANDSCAPE- AND LOCAL-SCALE MOISTURE GRADIENTS IMPACT THE BIOGEOGRAPHIC EXPRESSION OF CLIMATE CANGE?

A Thesis presented to

the Faculty at the University of Missouri-Columbia

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

By

CHRISTOPHER A. PETRUCCELLI

Dr. Grant Elliott, Thesis Supervisor

MAY 2015

The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

CLIMATE AND REGENERATION AT UPPER TREELINE EAST AND WEST OF THE CONTINETNAL DIVIDE IN THE NORTHERN AND SOUTHERN ROCKY MOUNTAINS: DO LANDSCAPE- AND LOCAL-SCALE MOISTURE GRADIENTS IMPACT THE BIOGEOGRAPHIC EXPRESSION OF CLIMATE CHANGE?

Presented by Christopher A. Petruccelli,

a candidate for the degree of Master of Arts

and hereby certify that, in their opinion, it is worthy of acceptance.

Professor Grant Elliott

Professor Soren Larsen

Professor Ricardo Holdo

ACKNOWLEDGEMENTS

Many and much thanks to Dr. Grant Elliott for taking me on as his first graduate student. I am eternally grateful to have been a part of his lab and would not have achieved such amazing accomplishments without his tutelage (BGSG award, baby! Oh, and this thesis). Dr. Elliott is an incredible mentor and scholar, but an even greater friend. I appreciate his effort in assisting me complete not only this research, but this program at large.

I would also like to thank Dr. Larsen for serving as a committee member as well as Dr. Holdo who took up the outside committee member position on wildly short notice. Both provided thoughtful feedback and recommendations on early drafts of this manuscript.

Thank you to my family for ongoing support and thanks to my academic family—Emma, Lebo, Jared, Dave, Anna and the rest of the room 2 crew.

Thanks to Becca Moss who helped process a huge amount of data—I could not have completed this thesis in a timely manner without her!

I would like to lastly, but not leastly, acknowledge Lily Cole for making the study area maps used in chapters 2 & 3. If I could thank everyone the way I'd like to this page would go on forever just like Sublime's "Thanks Dub" so I won't do that.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

Chapter 1. Introduction

The scientific community at large contClinues to provide evidence for increased global mean temperatures and a growing consensus on anthropogenic induced global climate change particularly in the 20th century (IPCC 2014). Boundaries of timberline ecotones—identified as an area of transition where closed canopy forests from lower elevations begin to give way to a more sparse, open forest at higher elevations—are expected to advance in altitude in response to climate warming (Daniels and Veblen 2004, Danby and Hik 2007). This theory is supported by the relationship between growing-season temperature and tree establishment and growth in this particular environment (Tranquillini 1979, Körner 1998). Yet, a recent global meta-analysis highlights the mixed results in treeline studies—displaying that although trees within the upper treeline ecotone are indeed sensitive to climate warming, there appear to be a multitude of factors at play (Harsch et al. 2009).

Accumulating evidence suggests that rates of successful regeneration at upper treeline are not only dictated by temperature, but also through temperature-precipitation interactions (Hessl and Baker 1997, Lloyd and Gramulich 1997, Daniels and Veblen 2004, Elliott 2012a). Furthermore, without appropriate changes in precipitation regimes, the ameliorative effects of warmer temperatures may be lost through heat-induced moisture stress (Hessl and Baker 1997, Daniels and Veblen 2004). Cool season snow typically delivers most of the moisture available for trees at upper treeline, although the biogeographical impacts of this vary by slope aspect. In the Front Range Mountains of Colorado, for example, the facilitative effect of less snow is confined to trees on north-facing slopes (Elliott and Kipfmueller 2011), while years with heavy snow appear to favor sharp increases in tree establishment on more xeric south-facing slopes (Elliott and Cowell, manuscript in review). The slope aspect mediation of tree establishment acts to not only reinforce the likely importance of both temperature and moisture, but how local-scale site conditions can modify broad-scale climate inputs (Elliott 2011, Harsch and Bader 2011).

Recent studies show that broad-scale warming has led to abrupt increases in successful establishment and corresponding treeline advance across both south- and north-facing slopes along a latitudinal gradient in the southern and central Rockies (Elliott 2012b), but it remains unknown whether climate has triggered similar pulses in the northern Rockies and southern Rockies west of the Continental Divide. Some researchers underscore the importance of local and landscape scale dynamics and suggest that temperature is not always the dominant factor at some sites (Holtmeier and Broll 2007). This result suggests a need for future research to consider fine scale conditions and feedbacks—especially those of increasing tree population in modulating climate driven change. Specifically, the elucidation of increasingly complex climate-vegetation interactions at upper treeline underscores the usefulness of studying these high-elevation ecotones at multiple spatial scales and within different climatic regions. For example, while temperatures are expected to rise uniformly at large scales, changes in precipitation patterns are projected to be less uniform (New et al. 2001, Walther et al. 2002). A north-south seesaw of precipitation pivots around 40°N in western North America with opposite moisture conditions existing simultaneously to the north and south of this parallel, and offers a novel opportunity to study the effects of precipitation on forest ecology (Dettinger et al. 1998). Additionally, this phenomenon offers unique insight on the biogeographic effects of anthropogenic climate change on forest ecosystems in the Rocky Mountains.

This thesis seeks to address three main questions: 1) Does the importance of temperature and precipitation vary in facilitating tree recruitment east and west of the Continental Divide? (2) Are these interactions further modified by slope aspect? 3) What differences, if any, exist between the northern and southern Rocky Mountains? We utilized dendroecological techniques to examine the relationship between climate and vegetation at study sites located in Colorado, Idaho and Montana.

Chapter 2 addresses the first two research questions in eastern Idaho and western Montana where we examined tree line advance, density and utilized regime shift analysis to quantify rates of tree establishment. In the northern Rocky Mountains we find numerous lines of evidence that suggest broad-scale climate patterns of primary influence on tree demography and those climatic inputs are nuanced by slope aspect. Such variations are further modified with respect to site orientation (east or west) around the Continental Divide and we conclude that future climate projections for the Intermountain West do not bode well for tree establishment.

Chapter 3 also addresses the first two aforementioned research questions, but in this chapter we are examining tree regeneration in southwest Colorado in the San Juan Mountains. Our study from the southern Rockies showcases vast amounts of nuance brought on by orientation around the Continental Divide, indicating potentially overriding landscape- and local-scale effects that sufficiently modify vegetative response to changes in broad-scale climate. Of particular interest in this study is the presence of spruce beetle (*Dendroctonus rufipennis*) at upper treeline. Beetle kill taken together with observed changes in altered precipitation and snowmelt patterns, as well projected changes in climate, may be causing the retrogression of treeline.

The final chapter, chapter 4, briefly reviews the conclusions from both chapters and considers the third research question of: what differences, if any, exist between the northern and southern Rocky Mountains?

Chapter 2.

INTRODUCTION

Boundaries of treeline ecotones—identified as an area of transition where closed canopy forests from lower elevations begin to give way to more sparse, open forests at higher elevations—are expected to advance in altitude in response to climate warming (Grace et al. 2002). This theory is supported by the relationship between temperature, tree reproduction, and establishment in this particular environment (Tranquillini 1979; Korner 2012). Numerous studies have found strong linkages between increased tree establishment and treeline advance with warmer temperatures. For instance, treeline advance has been identified in the Canadian Rockies (Danby and Hik 2007; Luckman, 1998), Alaska (Lloyd and Fastie 2002; Lloyd 2005), the Southern Rocky Mountains (Elliott and Kipfmueller 2011), and the Swedish Scandes (Kullman 1997, 2001, 2002; Kullman 2007; Kullman and Oberg 2009), all reportedly resulting from increases in temperature during the latter half of the 20th century. Despite these studies that lend further credence to the temperature-limited nature of upper treeline ecotonal dynamics, one of the hallmarks of high-elevation mountain environments is sharp environmental gradients, which typically confound a simple climate-vegetation interaction narrative (Bensiton 2003; Huber et al. 2005).

In a global meta-analysis, Harsch et al. (2009) state that 87 of 166 (52%) examined treeline studies reported advance, while 77 remained stable and 2 receded. Given the nearly ubiquitous rise in temperature worldwide since the middle of the 20th century, such pronounced variation in treeline advance during this time underscores the importance of other controlling factors on tree demography in these ecotones. For example, studies have found that tree establishment suffers under a warming climate without congruent increases in precipitation to lessen heat-induced moisture stress (e.g., Hessl and Baker 1997, Daniels and Veblen 2004). The primary mode of precipitation delivery at upper treeline is in the form of snow, which can singularly govern regeneration dynamics or act in tandem with warming temperatures to facilitate treeline advance (Holtmeier and Broll 2005; Kirdyanov et al. 2011). Topographic variability impacts the effectiveness of snow, in that depending on local conditions and how much snow commonly persists on the landscape, rates of successful tree regeneration can be accelerated or limited. For instance, drought conditions appear to favor abrupt increases in tree establishment on more snow-heavy north-facing slopes, whereas temperature-snowpack dynamics are more variable on south-facing slopes and contingent on local hydroclimate regimes (Elliott and Cowell, in review). Thus, it is not only important to understand the role of temperature and moisture in driving changes in tree establishment at upper treeline, but to also consider finer scale gradients like slope aspect because of how strongly it can mediate broad-scale climate (Danby and Hik 2007; Elliott and Kipfmueller 2010; Dang et al. in press). Questions remain, however, with respect to whether slope aspect is uniformly effective in modifying climate across ecologically-influential moisture gradients, such as the Continental Divide in the U.S. Rocky Mountains.

Between 1950 and 1999, the western United States experienced a shift towards increased rates of precipitation falling as rain instead of snow and earlier snow melt (Barnett et al. 2008). Additionally, annual and seasonal changes in maximum and minimum temperature represent rapid warming in the Rocky Mountains of western Montana. The region has experienced a +1.33C° rise in annual average temperature from 1900-2006. This increase is 1.8 times greater than the +0.74C° (1900-2005) rise in Global temperatures (Pederson et al. 2010). Furthermore, western Montana has been shown to track global and hemispheric temperature patterns which suggest that local- and regional-scale climate forcings do not strongly counteract global-scale influence (Pederson et al. 2010). Superimposed across this abrupt warming trend in the northern Rocky Mountains is an unprecedented reduction in snowpack (Pederson et al. 2011). Taken together, it is conceivable that these changes in temperature and moisture have strongly impacted regeneration dynamics at upper treeline in this region of the Northern Rocky Mountains, but research is lacking.

Regime shifts are abrupt changes on several trophic levels that lead to the rapid reorganization of an ecosystem between alternative states. Such shifts are often thought to be primarily driven by climatic thresholds, but the exact influence of change is often unknown (Andersen *et al*., 2008). Due to the complexity of ecosystem controls, they can appear relatively stable when subjected to extrinsic forces, such as climate, until a biological threshold is surpassed—resulting in a regime shift (Williams *et al*., 2011). More recently, studies show that broad-scale warming and abrupt decreases in snow led to abrupt increases in successful establishment and corresponding treeline advance across both north- and south-facing slopes along a latitudinal gradient in the southern and central Rockies (Elliott, 2012a), but it remains unknown whether climate has triggered similar pulses in the northern U.S. Rockies and more mesic environments west of the Continental Divide.

The primary objective of this study is to compare climate-vegetation interactions at upper treeline between sites in the Northern Rocky Mountains east and west of the Continental Divide. We seek to discern whether notable ecological differences exist among spatiotemporal patterns of tree establishment and treeline advance across this distinct bioclimatic gradient. Specifically, we address the following research questions: (1) Does the importance of temperature and precipitation vary in facilitating tree recruitment east and west of the Continental Divide? (2) Are these interactions further modified by slope aspect?

METHODS

Study area

The study area is in the Northern Rocky Mountains (NRM) of east-central Idaho and southwest Montana (Fig. 1.1). NRM zonation is the consequence of storm tracking along which maritime Pacific air penetrates to the Rockies between northwestern Oregon and southwestern British Columbia during winter, but otherwise remains under the predominant influence of continental air during the summer (Mitchell 1976). Pacific winter systems cause most of the precipitation in the area to be released during winter, while convective thunderstorms are the main source of precipitation in the summer (Knapp, 1997). The Northern Rockies are a topographically complex region in which small-scale controls produce large amounts of heterogeneity in climatic patterns (Mock, 1996).

Two study sites are located west of the Continental Divide at Double Springs Pass (ca. 44°N) in the Lost River Range of Idaho and two are east of the Divide at Sugarloaf Mountain in the Pioneer Range (ca. 45°N) of Montana (Fig. 1.1). The Lost River Range forms NW-SE trending mountains while the Pioneer Range predominantly trends N-S. The Lost River Range is mostly composed of Precambrian and Paleozoic metasediments (Cluer, 1989). The Pioneer Mountains are within the Cordilleran fold and the eastern portion of the range is primarily occupied by the Pioneer batholith (Pearson et al 1988). Sedimentary and metamorphosed rocks are common in western Montana and most of the alpine area in the Pioneers is composed of granite although high peaks form a contact between igneous and Paleozoic limestone and dolomites (Cooper et al. 1997). Elevation of treeline throughout our study sites varied, ranging from 2539m in Montana to 2995m in Idaho with mostly geologic treeline ecotones in this region where subalpine forests abut sheer rock. The dominant tree species at our sites were whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*), with fewer Engelmann spruce (*Picea engelmannii*) and Douglas fir (*Pseudotsuga menziesii*) confined to the south-facing slope east of the Divide in Montana.

Field methods

In order to stratify the influence of temperature-moisture interactions we used dendroecological techniques to sample trees on a mountain peak east and west of the Continental Divide with climatic upper treelines on both north- and south-facing slopes. Climatic treelines refer to environments where tree establishment and eventual treeline advance beyond the current ecotone boundary are unimpeded by local topography or geomorphological conditions, such as steep and rocky slopes, absence of soil development, or frequently-disturbed avalanche tracks (see Holtmeier and Broll 2005; Butler et al. 2007). Sampling solely on north- and south-facing slopes with opposing soil moisture regimes allows us to make inferences regarding the importance of slope aspect and corresponding temperature-moisture interactions in driving ecotonal dynamics at upper treeline (Daniels and Veblen, 2004; Elliott and Kipfmueller 2010). Study sites (n = 4) were selected *a priori* through the use of satellite imagery, topographic maps and extensive field reconnaissance owing to the relative dearth of climatic treelines, particularly along multiple aspects on the same mountain peak, compared to areas in the Southern Rocky Mountains.

At each site, we placed a nested-belt transect through the upper treeline ecotone. Transects began at the outpost tree (term after Paulsen et al. 2000), which was classified as the furthest upright tree or sapling existing within the treeline ecotone and then descended downslope perpendicular to slope contours, through the timberline boundary and 40-m into relatively closed-canopy subalpine forest. Here treeline is defined as the uppermost limit of individuals having an upright growth form and timberline as the elevational limit of closed-canopy forest with the treeline ecotone existing between them (Malanson et al. 2007). Krummholz were not sampled because they operate in a different microclimate than that experienced by upright growing individuals and thus may not reflect suitable conditions for tree establishment within the treeline ecotone (Holtmeier 2009). Transects were divided into two parts to ensure an adequate number of saplings were collected to analyze regeneration patterns. Above timberline (ATL), we sampled all trees and saplings within a 20-m wide belt on each side of the transect. Below timberline (BTL), the widths were half as wide at each site (saplings and trees collected within 10m) to account for increasing stand density downslope. The only exception to this was on the north-facing slope of Sugarloaf Mountain, where the uppermost slope terminated at 39 m downslope from the outpost tree because we could not traverse the steep terrain, punctuated by talus and sheer rock faces. As a result of variations in tree density and elevation of the outpost tree, overall transect length varied at each site.

Local site conditions were recorded at each site including elevation and GPS coordinates of the outpost tree, slope aspect, slope steepness, and distance from the outpost tree to timberline (length of the ecotone). Additionally, we recorded detailed notes for each tree such as diameter at breast heigh (dbh) (diameter at ground level [dgl] if applicable), coring height, local microtopography, and *x* and *y* coordinates to the nearest 0.1m along the transect relative to the outpost tree. We recorded local microtopgoraphy within a 1 m radius of each tree to examine whether tree establishment was predominantly confined to sheltered microsites and more common on concave, convex, or relatively uniform slopes (cf. Elliott 2012b). Furthermore, evidence of tree mortality, disturbance and a general site description were also recorded.

Age structure

We collected age-structure data by extracting increment cores as close to the base of each tree as possible to minimize error when assigning calendar dates of establishment. Every sapling was harvested at ground level and seedlings were inventoried by species and position relative to timberline (above or below) along the entire transect. All cores and cross sections were processed following standard dendrochronological procedures (Stokes and Smiley 1996). All tree-ring samples were visually crossdated by identifying individual marker rings under a stereo microscope (Yamaguchi 1991). Pith estimators were used to geometrically determine the number of rings to center when the pith was not obtained during field sampling (Applequist, 1958). Considering the uncertainty involved in assigning an annual value for tree establishment, we combined our age-structure data into more conservative five-year age classes for the period 1900 to 2000.

Climate data

To analyze climate-vegetation interactions at each site and between mountain peaks, we used Precipitation-elevation Regression on Independent Slopes Model (PRISM) climate data (PRISM Group, Oregon State University, http://www.primsclaimte.org, created 5 May 2014). We used PRISM data because the nearest weather stations are situated in low-elevation valleys that do not experience comparable conditions to upper treeline ecotones. In addition, PRISM data accounts for physiographic variation and in the topographically complex western United States, these data, in turn, more accurately represents mountain climate (Daly et al. 2008). In the event that one site drew form a different PRISM grid (4 km resolution) than the site with an opposite slope aspect, the transect drawing from the highest elevation PRISM grid was used to more accurately represent climatic conditions at upper treeline (Elliott and Kipfmueller 2011). Precipitation, maximum temperature (T_{max}) and minimum temperature (T_{min}) were used to calculate the following seasonal mean values: (1) spring (March-May); (2) summer (June-August); (3) fall (September-November); and (4) cool season (November-April). Cool season data were used in lieu of winter data to more accurately capture the period of snowfall in this region. All climate variables were averaged into five-year bins to match the minimum resolution of the age-structure data.

Data analyses

Outpost tree advancement was reconstructed to document the change in elevation of treeline during the twentieth century. Upslope advancement (m) and increases in stand density above and below timberline (trees ha^{-1}) were reconstructed for 5 year periods throughout the 20^{th} century. Density data was normalized using a natural-log transformation to account for differences in ecotone area between study sites (Elliott and Kipfmueller 2011). Examining advance and density together is useful in determining whether outpost tree advance is a single random event or part of more widespread changes indicative of a switch to favorable climatic conditions. Mann-Whitney U Tests were used to test for statistically significant differences between median tree ages on contrasting slope aspects, as well as ages east and west of the Continental Divide

To assess the influence of climate on tree establishment during the twentieth century, we employed three statistical techniques. First, we compared age-structure data to climate pentads using Spearman's rank correlation coefficients (r_s). Correlation analysis was used to compare all trees within a transect and stratified by slope aspect to evaluate the contrasting influences of climate that might be caused by variations in local topography. Second, in an attempt to gain a more holistic understanding from statistical correlations, we follow Anderesen et al. (2008), who highlight a gap between the prominence of theoretical frameworks discussing ecological thresholds and regime shifts, and the dearth of simple tests and quantitative inferences on the actual appearance of this phenomena in ecological data. Previous research in the Southern and Central Rockies (Elliott 2012a) addresses this gap by utilizing a sequential algorithm developed Rodionov (2004) to test for regime shifts in regional-scale tree establishment. This assessment quantifies deviations in time-series data that can signify a threshold-induced regime shift change in either climate or ecological systems. This test was used in our study to further assess the relationship between climate and tree establishment in the Northern Rockies.

This data-driven method does not require an *a priori* hypothesis and sequential *t*-tests are conducted on time-series data to detect regime shift changes (Rodionov 2004). A regime shift change is identified when the cumulative sum of normalized deviations from the mean value of a potential new regime is significantly different from the mean of the current regime (Rodionov and Overland 2005). For this analysis, we used a 0.05 significance level to test for the shifts in the mean value of the time series and a cutoff length of ten years due to considerable decadal variability present in the Western United States (McCabe et al. 2004). Our final statistical analysis included chi-square goodness-of-fit tests to determine if rates of tree establishment coincided more with dry or wet conditions based on the proportion of each pentad during the 20th century. Annual cool season precipitation values were standardized relative to the 1900–1999 mean and averaged into five-year bins to match the temporal resolution of the age-structure data. Wet years were classified as a positive z-score anomaly and dry years as a negative z-score anomaly.

RESULTS

West of the Divide

Tree demography

All of the trees we sampled west of the Divide in Idaho are relatively young with 90% (n=82/90) establishing since 1955 (Fig. 1.2). Trees on the north-facing slope at Double Springs are also significantly younger than those on the south slope ($P < 0.01$). Establishment above timberline (ATL) began in 1925 on the south-facing slope and in 1955 on the north-facing slope. Trees ATL are significantly younger than those below timberline (BTL) on the north-facing slope ($P < 0.01$), but there is no such distinction on the south-facing slope ($p = 0.09$). Seedling establishment was recorded at both slopes with one seedling BTL each. Seedling establishment ATL was only present at WNF-1 with eleven recorded individuals. No seedling mortality was recorded at either site.

Upslope advancement of treeline occurred on both aspects during the latter half of the 20th century. The greatest upslope migration of treeline occurred on the north-facing slope (71m). The contrasting south-facing slope only migrated 8.3m (Fig. 1.3). Outpost trees established in the 1960 age class at WSF-1 and in 1985 for WNF-1. Tree density on the north-facing slope of Double Springs was zero prior to 1950 indicating that there was little to no regeneration throughout treeline ecotone until an abrupt shift towards widespread density increases in 1955 below timberline and 1975 above timberline (Fig. 1.4). The opposite is true on the south-facing slope where tree establishment was present throughout the transect since 1925 both above and below timberline. Regime shifts in tree density were indicated in 1925 and 1955 ATL and in 1935 BTL (Fig. 1.4).

Climate

Each seasonal climate variable was tested for correlation with tree establishment using Spearman's rank correlation coefficient, but only statistically significant correlations (p value < 0.05) are discussed hereafter. Significantly correlated variables with increased rates of tree regeneration were confined to north-facing slopes and include (1) cool season precipitation, (2) cool season T_{min}, (3) cool season T_{max}, (4) spring precipitation, (5) summer T_{min}, (6) fall T_{min}, and (7) fall T_{max}. The strongest positive correlation on the north-facing slope was with minimum summer temperatures while the strongest negative correlation was with maximum fall temperatures (Fig. 1.5).

Additionally, a significant inverse correlation exist between tree recruitment and cool season maximum temperatures. Tree establishment on north-facing slopes appears to be favored by increased summer minimum temperatures as well as spring precipitation (Fig 1.5).

Synchronicity exists between regime shifts in tree establishment and corresponding step changes in the most strongly correlated climate variables (Fig. 1.2). Two shifts were documented in tree establishment in Idaho—one in 1960 and one in 1980. The earlier shift occurred on the southern slope and is congruent with a step-wise increase in minimum summer temperature. Prior to increasing summer temperatures, only 19% (n = 3/16) of current trees were growing above timberline. The north slope experienced the later shift in tandem with decreasing fall maximum temperatures (Fig. 1.2). Prior to the decrease in temperature there was only a single tree (n = 1/34) above timberline.

Overall, significantly more trees established during wet winter ($\chi^2 = 4.67$, $p = 0.03$) and wet spring pentads ($\chi^2 = 92.32$, $p = 0.00$) compared to dry pentads on north-facing slopes than would be expected given the prevalence of dry pentads. Similar patterns of increased establishment during wet spring periods were found on the south-facing slope ($\chi^2 = 12.64$, $p = 0.00$). Contrastingly, significant patterns were not found on the southern aspect during the cool season ($\chi^2 = 0.01$, $p = 0.93$).

East of the Divide

Tree demography

Establishment within the treeline ecotone at Sugarloaf (SL) is a relatively recent phenomenon as all trees within our transects have established since 1955 and approximately 75% (n = 44/59) of trees established since 1980 or later (Fig. 1.2). Tree ages above and below timberline were not significantly different on the south-facing slope (p = 0.23 Mann Whitney U-Tests). There was also no significant difference in age between trees growing ATL on the north or south slope (p = 0.34). Due to slope steepness and inability to traverse difficult terrain at Sugarloaf's north-facing slope, no data was collected BTL and thus not available for comparison.

The greatest amount of total upslope tree migration was 12.9 m on the north-facing slope. On the contrasting south slope, treeline only advanced by 5 m (Fig. 1.3). Outpost trees established in 1980 (ENF-1) and 1985 (ESF-1). Tree density above timberline was zero on both slopes prior to 1950 and zero below timberline at ESF-1. A sudden, unprecedented increase in tree density occurred on the south-facing slope in 1970. Increases in tree density above timberline began earlier on the north-facing slope in 1955 (Fig. 1.4). No seedlings were observed at Sugarloaf south, but regeneration was prolific on the northern aspect with a total of 25 seedlings above timberline (Table 1).

Climate

Unlike west of the Divide, tree establishment on Sugarloaf Mountain is significantly correlated with climate on both north-facing and south-facing slopes. Establishment on south-facing slopes showed significant inverse correlations with cool season and fall minimum temperatures. Cool season and spring precipitation correlated positively and significantly with tree regeneration on north-facing slopes. The strongest climate correlation for ENF-1 was spring precipitation. On the south-facing slope, the strongest correlation was with fall T_{min}. ESF-1 also exhibited a relationship with cool season T_{min} (Fig. 1.3).

Two regime shifts in establishment occurred in Montana—one in 1955 and the other in 1975. The increase in establishment in 1955 occurred on the northern slope in tandem with a step-wise increase in spring precipitation. The south-facing slope's 1975 shift was synchronous with decreasing fall minimum temperatures. Within the transect at ENF-1, no tree establishment predates the 1955 shift in increased spring precipitation while the same is true on the south-facing slope, but in regards to the 1975 shift in decreased fall minimum temperatures (Fig. 1.2).

Patterns of establishment in relation to dry and wet pentads were similar to results found at Double Springs. A surprisingly high amount of regeneration occurred during spring wet periods as opposed to more prevalent dry periods on north ($\chi^2 = 15.30$, $p = 0.00$) and south slopes ($\chi^2 = 6.16$, $p = 0.01$). A similar relationship between increased establishment during wet cool season periods was confined to the north-facing slope ($\chi^2 = 10.12$, $p = 0.00$).

DISCUSSION

Our study shows that climatic thresholds have been surpassed and are synchronous with increased rates of tree regeneration above timberline. Furthermore, these threshold regime shifts are not biased in regards to slope aspect or orientation about the Continental Divide. Thus, it appears that broad-scale regional climate is the primary influencer on tree establishment at the treeline ecotone in the Northern Rocky Mountains. However, this does not override nor negate the importance of slope aspect or fine-scale conditions in modifying the expression of tree demography. Distinctions among and within study sites exist and hint at the ability that site-specific characteristics have on modulating the impact of broad-scale climate (*cf.* Malanson 2007; Kullman & Oberg 2009; Elliott 2011).

Recent tree regeneration ATL is evident on south- and north-facing slopes at each site east and west of the Continental Divide. Additionally, much of the establishment BTL is recent as well, with 85% (n = 34/40) of trees establishing BTL at DS since 1955 and 100% of trees at SL establishing BTL since 1975 (n = 18/18)—displaying widespread regeneration as a recent phenomenon. Furthermore, there is no significant difference in tree ages between Idaho and Montana (Mann-Whitney Tests, $P = .3658$). However, in Idaho, trees growing on the northern aspect are significantly younger than those growing on the south-facing slope and higher rates of seedlings were documented on the northern aspect as compared to the south-facing aspect. This contrasts with previous research where tree regeneration ATL is typically reserved to south-facing slopes while stable treeline positions are recorded at northern-facing slopes in the Canadian Rockies (Luckman and Kavanagh 2000; Danby and Hik 2007) and the Swedish Scandes (Kullman, 1998).

Similar patterns of establishment on contrasting slope aspects have been found in the Southern Rocky Mountains (Elliott & Kipfmueller 2010; Elliott 2012a; Elliott 2012b). These patterns are attributed to water stress that is common at upper treeline due to increased solar radiation in environments with typically shallow soils and low water carrying capacity (Kupfer and Cairns 1996; Sveinbjörnsson, 2000). In the southern and central Rocky Mountains, such conditions are expected to be found on the more sun exposed south-facing slopes (Weisberg and Baker 1995; Germino *et al.,* 2002), and thus increased moisture stress may indicate why fewer seedlings were found ATL on southern aspects east and west of the Divide.

Shifts in tree establishment occurred in tandem with regime shifts in climate at WNF-1 and WSF-1. Despite this, only WNF-1 reports significant correlations with climate variables, chief among them are maximum fall temperature followed by minimum summer temperature. This is surprising given that previous research identifies south-facing slopes as xeric and more prone to treeline advance when exposed to ameliorative climatic conditions (Kullman, 2002). Thus, it would be expected that south-facing slopes be more responsive to temperature-precipitation interactions, yet this does not appear to be the case when considering seedling establishment. Previous treeline research shows that establishment is significantly correlated with warmer conditions throughout the year (Elliott and Kipfmeuller 2011) and it is suggested that treeline advance will occur only if long-term warming stimulates growth in the absence of extreme cold events that may prevent establishment (Körner 2000). Such conditions were found in the Swedish Scandes (Kullman 2007; Kullman and Öberg 2009) and in the Front Range of Colorado on north-facing slopes (Elliott and Kipfmeuller 2011). In a global meta-analysis conducted by Harsch et al. (2009), treelines appear to be widely responsive to overall warming. Results from Double Springs appear to be in partial-agreement in regards to such relationships given significant inverse correlations with cool season and fall maximum temperatures and positive correlations with summer minimum temperatures. The importance of cooler temperatures in Idaho may represent the reliance of tree establishment on year round moisture availability.

Contemporary studies suggest that facilitative effects of warmer temperatures on upper treeline vegetation could be negated without a simultaneous increase in precipitation to counteract heat-induced moisture stress (Weisberg and Baker 1995; Daniels and Veblen, 2004; Elliott and Cowell, in review). We propose the relationship between cooler fall/wintertemperatures and warm summer minimum temperatures indicate such a necessary facilitative abiotic change. It is understood that earlier snow free conditions have the potential to induce enhanced regeneration throughout treeline ecotones and some studies document the facilitative effects of higher T_{min} throughout the year on tree establishment in the Pyrenees and throughout the Iberian Peninsula (Camarero and Gutiérrez, 2004; 2007), in the Swedish Scandes (Kullman,2002; 2007), in the central and southern Rocky Mountains (Elliott, 2012), and in the Urals (Wilmking et al. 2012). Despite earlier snow free conditions ameliorating harsh winter effects elsewhere, it is possible that reduced snowpack cover can leave young growth vulnerable to abrasive ice crystals that have the potential to cause damage to trees and as a result, retard the rate of establishment in the Northern Rocky Mountains (Hadley and Smith 1983; 1986). Furthermore, decreasing fall and winter temperature may act in concert to induce earlier snowfall and prolong potential snowcover. Hagedorn et al. (2014) suggests that increases in snowfall may be the primary causal mechanism for forest advance in the Ural Mountains due in part to protection from frost wind damage and abrasion as well as soil insulation. Similarly, Kirdyanov et al. (2011) found that increased winter precipitation coincided with increased larch recruitment in the remote Putorana Mountains. Rather than temperature being the primary influencer on establishment, it is possible that increased precipitation in the form of snow and subsequent snowpack can be more ameliorative to winter stress than temperature (Holtmeier 2003).

It has also been reported that summer soil moisture is influenced mainly by snow accumulation during winter (Oberbauer and Billings 1981; Hättenschwiler and Smith 1999). Average cool season precipitation was positively, although not significantly correlated, with tree establishment at WNF-1 and WSF-1. However, it is worth noting that at Double Springs average cool season precipitation increased by 53.69 mm in 1950 and that spring precipitation, which predominantly falls as snow and is significantly correlated with establishment, increased by 30.54 mm in 1955. These increases in precipitation preceded warming summer minimum temperatures in 1960 and thus indicate the importance of winter precipitation in the treeline ecotone in regards to tree regeneration.

AT ENF-1, our study found that tree establishment was significantly correlated with cool season and spring precipitation. Furthermore, synchronous regime shifts occurred between tree establishment and spring precipitation in 1955. Previous research in Rocky Mountain National Park found that establishment of *Abies lasiocarpa* and *Picea engelmanii* increased substantially during warm, higher than usual snow pack periods, in which regeneration is attributed to meltwater alleviating moisture stress in continental areas (Hessl and Baker 1997; Peterson 1998; Holtmeier and Broll 2005). Snowpack not only has the ability to alleviate moisture stress, but also provides protective cover from wind and warmer soil temperatures. Closer relationships between establishment and winter precipitation than with summer temperatures have been documented in the Ural

Mountains of Russia (Hagedorn et al. 2014). Our findings east of the Continental Divide suggest a similar relationship. Spring precipitation, which falls predominantly as snow, was the highest correlating climate variable on the north-facing slope of Sugarloaf Mountain and the highest seedling counts (n = 25) were also found at this site. Significant correlations between establishment at ENF-1 and cool season precipitation also suggests that snow fall, and the associated protection from snow cover, may be of primary influence in this particular treeline ecotone.

The south-facing slope of Sugarloaf Mountain did not exhibit as strong a relationship with precipitation variables, but rather with fall and cool season minimum temperatures. Such a relationship contrasts with aforementioned research (Camarero and Gutiérrez, 2004; 2007; Kullman 2002; 2007; Elliott, 2012; Wilmking et al. 2012) where generally warmer temperatures are thought to be a prerequisite for successful tree establishment. It has been shown that a lack of snow cover during fall can yield high rates of seedling mortality due to exposure to hard frosts and high sunlight (Germino et al. 2002). However, decreasing fall temperatures may provide relief from heat-induced moisture stress late in the growing season. Furthermore, a tight coupling between decreasing fall minimum temperatures and increasing establishment may indicate earlier snowfall while a strong association between establishment and cool season minimum temperatures may indicate the ameliorative effect of snowcover. Although not significantly correlated, spring precipitation was positively associated with tree establishment and may indicate the persistence of snowcover later into the year. Such thermal relationships taken together with cool season and spring precipitation highlight the seemingly overriding importance of cool season and spring climate.

CONCLUSION

This study finds evidence that climatic thresholds have been surpassed and are synchronous with increased rates of tree regeneration above timberline. Numerous facets of evidence exist that suggest broad-scale climate patterns are of primary influence in moderating expressions of tree demography. However, the effects of broad-scale climate are nuanced by slope aspect and corresponding temperature-precipitation interactions which modify successful tree establishment and tree advancement upslope. This is especially apparent west of the divide in Idaho where establishment significantly correlated with climate variables on only the north-facing slope of Double Springs. Synchronous shifts in establishment and decreasing fall temperatures in 1980 were preceded by increases in cool season (1950) and spring precipitation (1955) suggesting an overriding importance of temperature-precipitation interactions at upper treeline. Furthermore, when these effects are examined in tandem with increased summer minimum temperatures, we can see the process of increased moisture availability ameliorating the potential harmful effects of warmer growing season temperatures thus increasing both establishment and density and promoting upslope advance of treeline on the northern slope. Establishment on the south-facing slope increased abruptly, although to a much lesser extent, in conjunction with a regime shift in summer minimum temperatures in 1960. This may serve to indicate that previous increases in precipitation were not substantial enough to induce consistent, long term regeneration at the more xeric sites found on southern-aspects as north-facing slopes experienced greater rates of regeneration, increases in stand density and upslope advance of treeline in the latter half of the 20th century.

These climate-vegetation interactions further showcase the dictatorial nature of broad-scale climate as similar processes were found governing treeline dynamics east of the Continental Divide. In Montana, trees responded to similar variables and only the north-facing slope significantly correlated with precipitation. Synchronicity between establishment and spring precipitation in 1955 on the northern aspect further suggests the pivotal role of snowfall and moisture availability in the Northern Rocky Mountain treeline ecotone. However, unlike Idaho, establishment on both slope aspects was responsive to climate and tree regeneration on the south-facing slope solely correlated with minimum cool season and fall temperatures. Despite cold weather being potentially harmful to plants, shifts towards increased establishment were concomitant with a regime shift in decreasing fall minimum temperatures. Colder fall and winter temperatures are often harmful to plant life, and thus unconducive to establishment, yet the opposite appears true across our study sites. We attribute such relationships to the possibility of cooler temperatures in fall alleviating heat-induced moisture stress in the late growing season. Additionally, cooler falls and winters may induce earlier snowpack and increase snowcover—protecting young establishment from abrasion, frost, and wind damage (Holtmeier, 2003).

Future projections for the intermountain west foretell annual temperature increases of 2-5°C over the course of the 21st Century (Mote et al., 2005). It is expected that winter moisture would increase north of 40°N (Wise 2012), but that rising temperatures may offset these gains via greater evaporation resulting in overall net drying (Giorgi and Bi, 2005; Gutzler and Robbins, 2011 Stonefelt et al., 2000; Wise 2012). In addition to these forecasts, it is also predicted that snowpack will decrease across the

Western United States and that snow season length will decline (Leung et al., 2004). Such predictions are foreboding for treeline regeneration at Double Springs and Sugarloaf given the apparent reliance on precipitation falling as snow and dependence on cool temperatures throughout much of the year.

Table 1. Study site characteristics for upper treeline sites in Idaho (Double Springs) and Montana (Sugarloaf).

Site Name	Elevation (m)	Aspect (°)	Slope (°)	Trees dated (*n*)	Trees establ. Post- 1950 (*n*)	Seedlings (
Double Springs North (WNF-1)	2863	350	22	52	52	12
Double Springs South (WSF-1)	2995	172	24	38	30	1
Sugarloaf North (ENF-1)	2700	0	26	24	24	25
Sugarloaf South (ESF-1)	2539	220	10	35	35	0

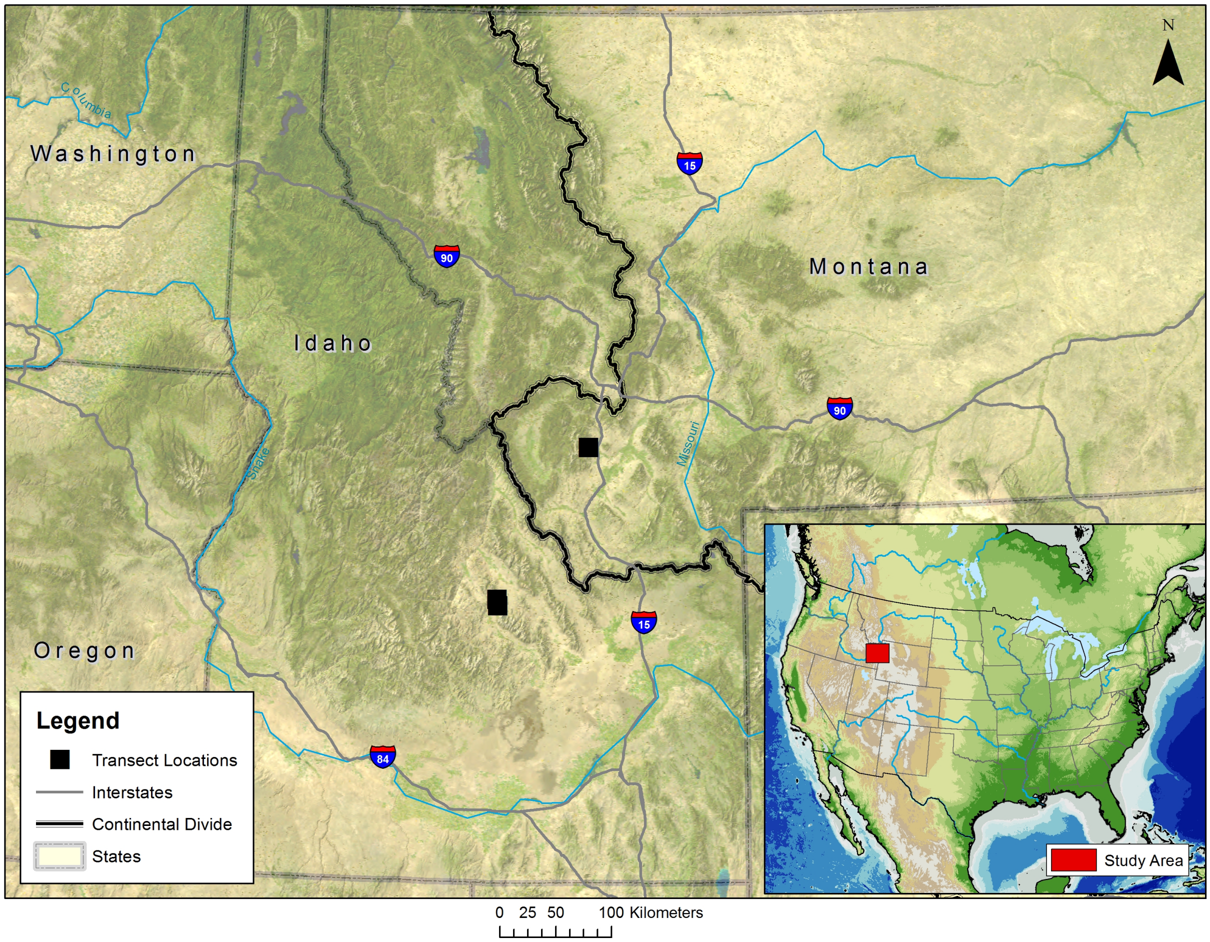

Figure 1.1. Study area and transect locations west and east of the Continental Divide.

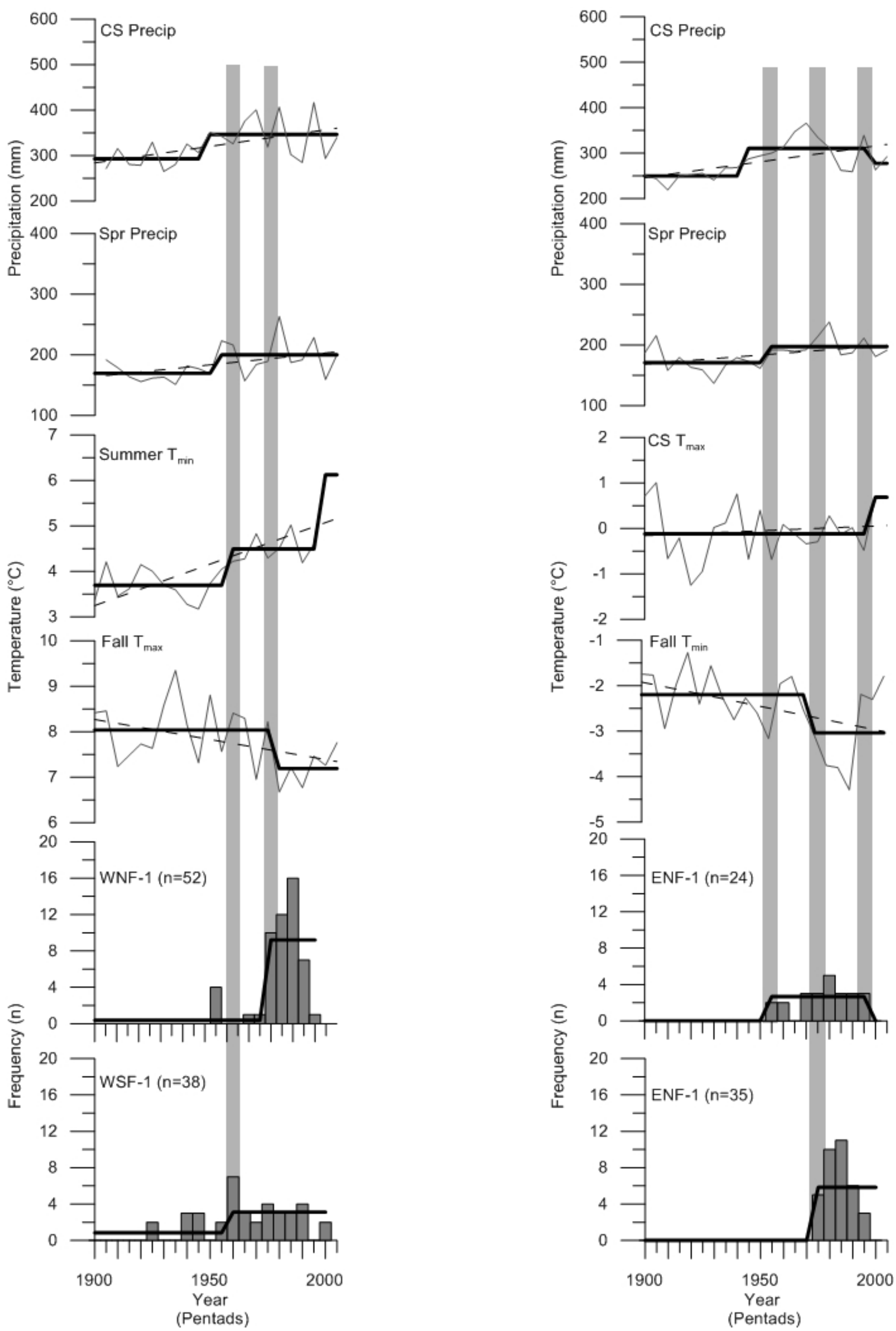

Figure 1.2. Age structure data (1900-2000) in pentads for each study site. WNF-1 = Double Springs North-facing; WSF-1 = Double Springs South-facing; ENF-1 = Sugarloaf North-facing; ESF-1 = Sugarloaf South-facing. Significantly correlating climate variables are depicted above the age structure graphs and bold lines indicate the

value derived from regime shift analysis ($p < 0.05$). Regime shift analysis detects abrupt, sudden changes towards a new climatological or ecological regime. Grey boxes display synchronous regime shifts in climate and establishment, highlighting climate-vegetation interactions. Note the presence of different axes for climate variables.

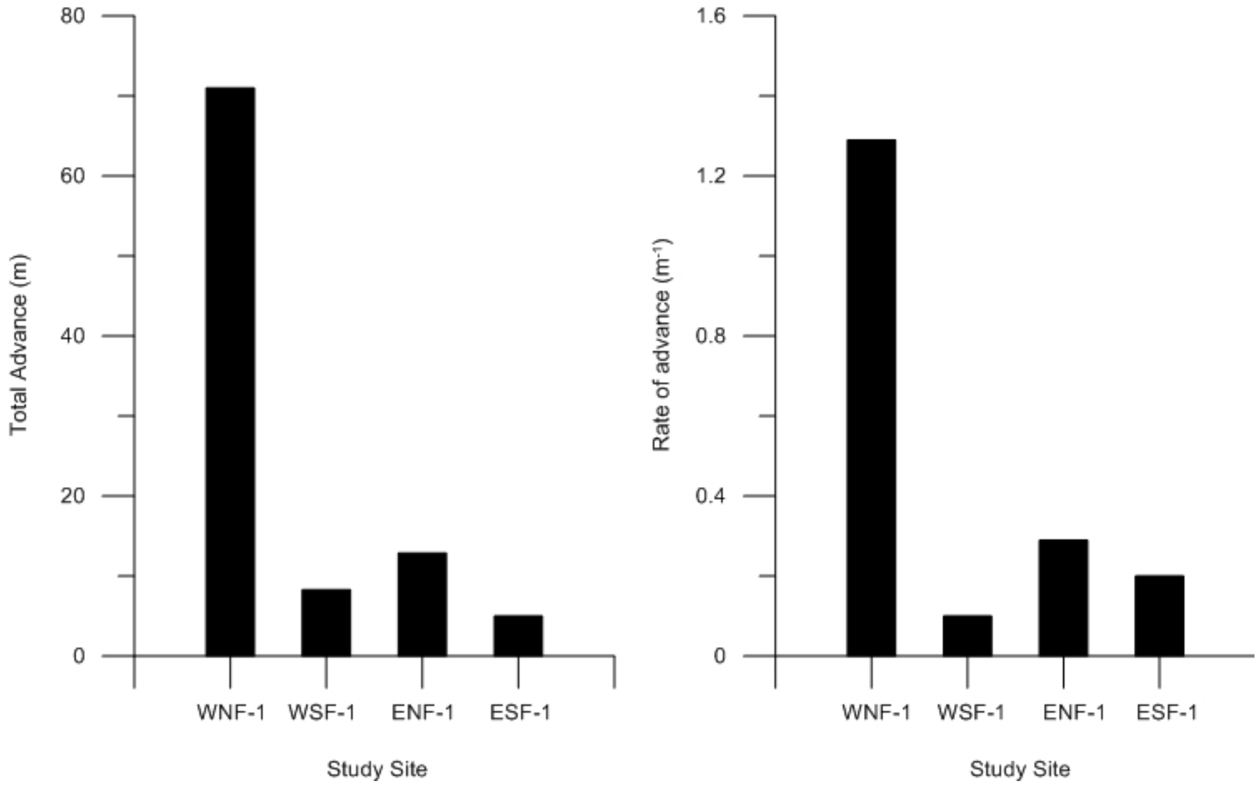

Figure 1.3. Total advance (a) and rate of advance (b) of treeline at individual study sites.

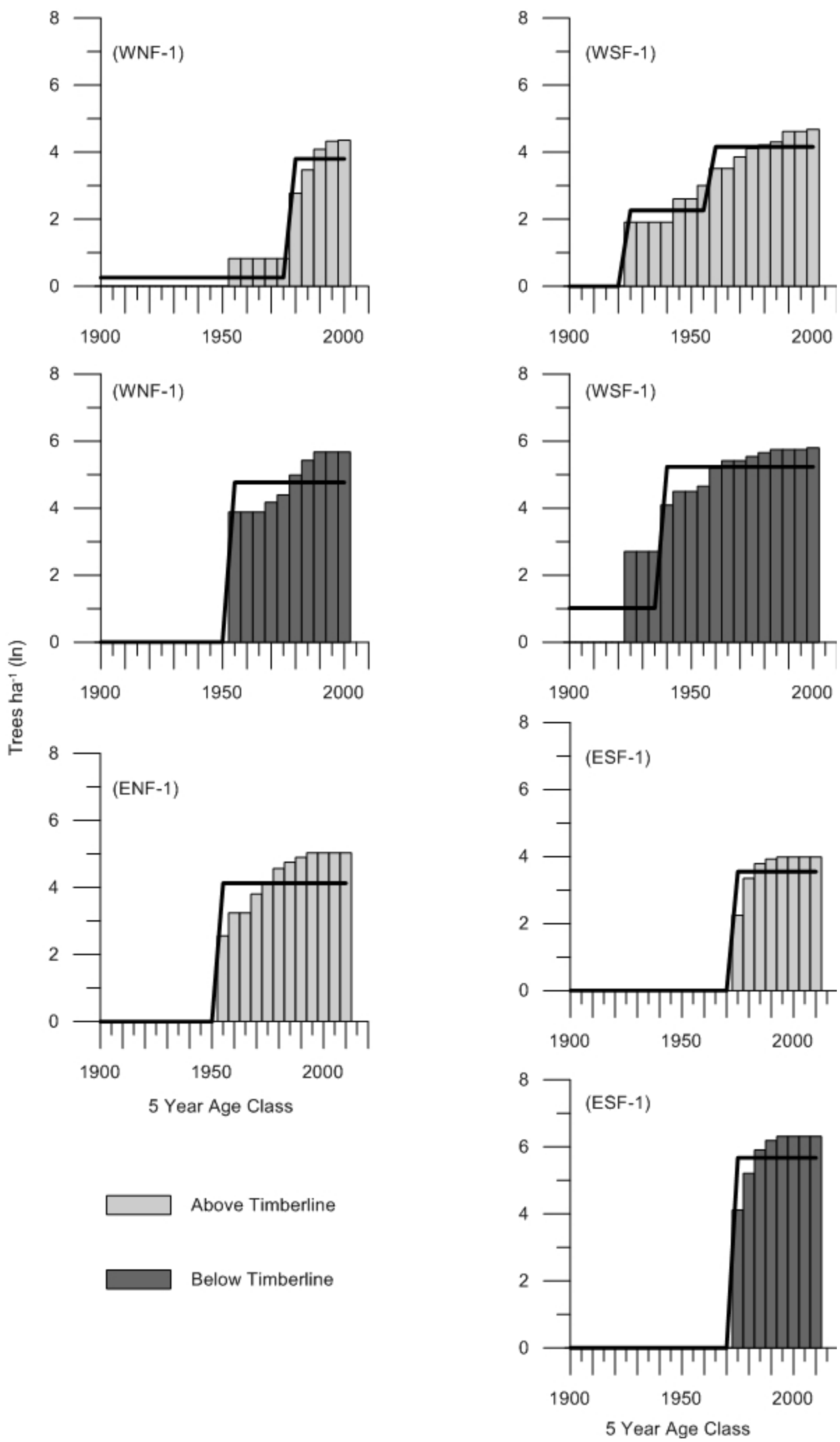

Figure 1.4. Natural log reconstruction of tree density (trees ha^{-1}) above and below timberline at each site. Natural log transformation was used to account for variation in

transect area among study sites. The bold line shows the value generated by regime shift analysis which indicates an abrupt change towards a new ecological regime.

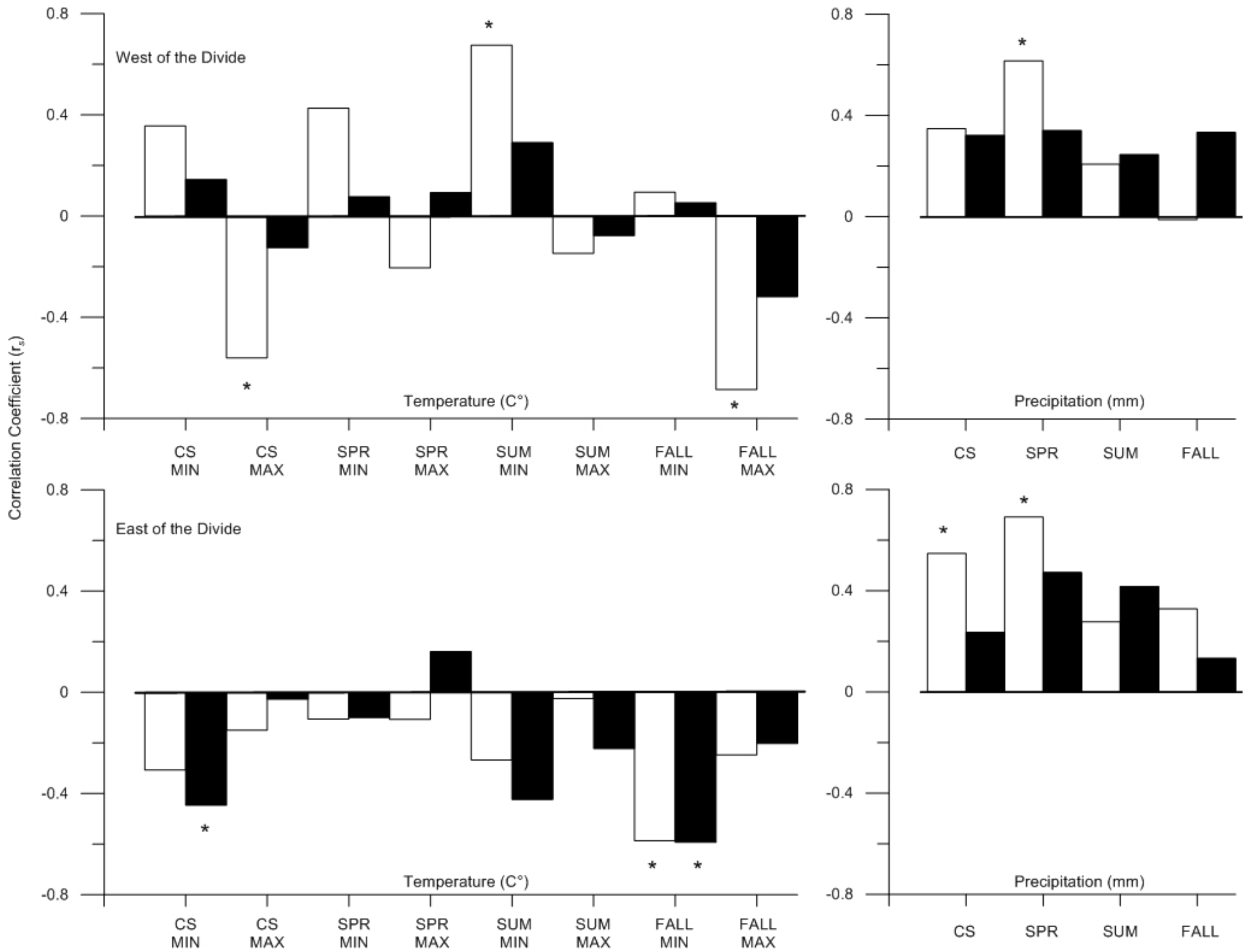

Figure 1.5. Spearman rank correlation coefficients (r_s) comparing tree establishment with seasonal temperature and precipitation data from 1900 to 2000. * = $p < 0.05$. MAX = maximum temperature; MIN = minimum temperature; CS = cool season; SPR = spring; SUM = summer.

Chapter 3.

INTRODUCTION

Boundaries of timberline ecotones—areas of transition where closed canopy forests from lower elevations begin to give way to more open forests with increasing elevation—are expected to advance in altitude in response to warming climates (Grace et al. 2002). This theory is supported by the relationship between temperature, tree reproduction, and establishment in this particular environment (Tranquillini 1979; Korner 2012). Numerous studies have found strong linkages between increased tree establishment and warmer temperatures. For instance, the altitudinal shift of treeline has been identified in several locations including the Canadian Rockies (Danby and Hik 2007; Luckman, 1998), Alaska (Lloyd and Fastie 2002; Lloyd 2005), the Front Range of Colorado (Elliott and Kipfemueller, 2011), and the Swedish Scandes (Kullman 1997, 2001, 2002; Kullman 2007; Kullman and Oberg 2009) all reportedly resulting from 20th century climate changes, particularly warming temperatures.

Elsewhere, the altitudinal extent of trees has experienced no significant change (Butler et al. 1994; Cullen et al. 2001; Cuevas 2002; Liang et al. 2011). In a global meta-analysis, Harsch et al. (2009) state that 87 of 166 (52%) examined treeline studies report advance, while 77 had remained stable and 2 receded. At the global scale, it appears that warming will facilitate treeline advance into greater elevations. However, it is important to understand the role of regional topography and site specific conditions which can mediate treeline response to climate changes (Holtmeier and Broll 2005; Elliott and Kipfmueller 2010).

Other studies have found that tree establishment suffers under a warming climate without congruent increases in precipitation to lessen heat-induced moisture stress (Hessl and Baker 1997, Daniels and Veblen 2004) but this relationship varies by slope aspect. Indeed, climatic variability resulting from topographic influence confounds a simple climate-vegetation interaction narrative (Bensiton 2003; Huber et al. 2005). Luckman and Kavanagh (2000) report similar disparate climate-vegetation interactions on contrasting north- and south-facing slopes where northern aspects experienced less rates of advance than their south-facing counterpart.

Between 1950 and 1999, the western United States experienced a shift towards increased rates of precipitation falling as rain instead of snow and earlier snow melt (Barnett et al. 2008). This is seen in the San Juan Mountains where, between 1895 and 2005, Rangwala and Miller (2010) found a net warming of 1°C with the majority of warming occurring between 1990 and 2005. The rapid warming in the region is due to large increases in T_{max} during spring and summer which may have led to earlier snowmelt in spring and reduced soil moisture in summer. Furthermore, the trend found in the San Juan's was greater than the trend for western Colorado (Rangwala and Miller 2010). Both linear and nonlinear changes in climate are expected to induce crossings of bioclimatic thresholds and lead to abrupt ecological regime shifts (Groffman et al. 2006; Andersen et al. 2008).

Regime shifts are abrupt changes on several trophic levels that lead to the rapid reorganization of an ecosystem between alternative states. Such shifts are often thought to be primarily driven by climatic thresholds, but the exact influence of change is often unknown (Andersen *et al*., 2008). Due to the complexity of ecosystem controls, they can appear relatively stable when subjected to extrinsic forces, such as climate, until a biological threshold is surpassed—resulting in a regime shift (Williams *et al*., 2011). Despite the complexity of studying regime shifts, they have been documented in a range of ecosystems from open oceans to savannas (e.g. Scheffer and Carpenter, 2003). More recently, studies show that broad-scale warming and abrupt decreases in snow have led to abrupt increases in successful establishment and corresponding treeline advance across both north- and south-facing slopes along a latitudinal gradient in the southern and central Rockies (Elliott, 2012), but it remains unknown if climate-vegetation interactions change in regards to orientation east and west of the Divide.

The primary objective of this study is to compare climate-vegetation interactions at upper treeline between sites in the San Juan Mountains east and west of the Continental Divide. We seek to discern whether notable, ecological differences exist among spatiotemporal patterns of tree establishment and treeline advance across this distinct bioclimatic gradient. Specifically, we address the following research questions: (1) Does the importance of temperature and precipitation vary in facilitating tree recruitment east and west of the Continental Divide? (2) Are these interactions further modified by slope aspect?

METHODS

Study Area

Our study sites are located in the Southern Rocky Mountains (SRM) of southwestern Colorado (Fig. 2.1). Two study sites are located east of the Continental Divide in the San Juan Mountains (ca. 37°N) and west of the Divide in the La Plata subrange (ca. 37°N). Volcanic rocks in the San Juan Mountains rest on older igneous, sedimentary and metamorphic rocks ranging in age from lower Tertiary to Precambrian (Ellingson, 1996). Prevolcanic rocks include gneiss, schist, quartzite and slate overlain in the south and west by Paleozoic and Mesozoic sandstone, shale and limestone. Intrusive rocks are resistant to erosion and are visible in locations throughout the region (Ellingson, 1996).

Climatically, Mitchell (1976) characterizes the region by infrequent intrusion of Pacific air in winter, and by its summer rainy season brought by monsoon air from the Gulfs of Mexico and California. The topographic variation in the San Juan Mountains alters large scale controls on precipitation—causing high spatial variability in moisture patterns (Wise, 2012). Most of the precipitation in the region falls as snow during winter and in the fall, high elevations west of the Divide receive increased precipitation from the penetration of maritime Pacific air masses inland (Mock, 1996). At upper elevations in the San Juan Mountains, subalpine forests are primarily composed of Engelmann spruce (*Picea engelmannii*),subalpine fir (*Abies lasiocarpa*) and interspersed with quaking aspen (*Populus tremuloides*) on south-facing slopes (Elliott and Baker 2004).

Field Methods

Study sites (n = 4) were systematically located in order to stratify the influence of temperature-moisture interactions. We used dendroecological techniques to sample trees on a mountain peak east and west of the Conintental Divide with climatic upper treelines on both north- and south-facing slopes. Climatic treelines refer to environments where tree establishment and eventual treeline advance beyond the current ecotone boundary are unimpeded by local topography or geomorphological conditions, such as steep and rocky slopes, absence of soil development, or frequently-disturbed avalanche tracks (see Holtmeier and Broll 2005; Butler et al. 2007). Sampling solely on north- and south-facing slopes with opposing soil moisture regimes allows us to make inferences regarding the importance of slope aspect and corresponding temperature-moisture interactions in driving ecotonal dynamics at upper treeline (Daniels and Veblen 2004; Elliott and Kipfmueller 2010). Sites were selected *a priori* through the use of satellite imagery, topographic maps and field reconnaissance.

We placed nested-belt transects through the upper treeline ecotone at each site. Transects began at the outpost tree (term after Paulsen et al. 2000), which was classified as the furthest upright tree or sapling existing within the treeline ecotone and then descended downslope perpendicular to slope contours, through the timberline boundary and 40-m into relatively closed canopy subalpine forest. Treeline is defined as the uppermost limit of individuals having an upright growth form and timberline as the elevational limit of closed-canopy forest with the treeline ecotone existing between them (Malanson et al. 2007). Krummholz were not sampled because they operate in a different microclimate than that experienced by upright growing individuals and thus may not reflect suitable conditions for tree establishment within the treeline ecotone (Holtmeier 2009). Transects were divided into two parts to ensure an adequate number of saplings were collected to analyze regeneration patterns. Above timberline (ATL), we sampled all trees and saplings within a 20-m wide belt on each side of the transect. Below timberline (BTL), the widths were half as wide at each site (saplings and trees collected within 10m) to account for increasing stand density downslope. As a result of variations in tree density and elevation of the outpost tree, overall transect lengths vary at each site.

We recorded local site conditions including elevation and GPS coordinates of the outpost tree, slope aspect, slope steepness and distance from outpost tree to timberline (length of the ecotone). Microtopography within a 1 m radius of each tree was recorder to examine whether tree establishment was predominantly confined to sheltered microsites and more common on concave, convex, or relatively uniform slopes (cf. Elliott 2012b). Furthermore, evidence of tree mortality, disturbance general site description and seedling abundance were also recorded.

Age Structure

Age structure data was collected by extracting increment cores as close to the base of each tree as possible to minimize error when assigning calendar dates of establishment. Every sapling was harvested at ground level and seedlings were inventoried by species and position relative to timberline (above or below) along the entire transect. Cores and cross sections were processed following standard dendrochronological procedures (Stokes and Smiley 1996). All tree-ring samples were visually crossdated by identifying individual marker rings under a stereo microscope (Yamaguchi 1991). Pith estimators were used to geometrically determine the number of rings to center when the pith was not obtained during field sampling (Applequist, 1958). Given the uncertainty involved in assigning an annual value for tree establishment, we combined our age structure data into more conservative five-year age classes for the period 1900 to 2000, and into 10 year age classes for the period from 1700 to 1890.

Climate Data

We used Precipitation-elevation Regression on Independent Slopes Model (PRISM) climate data to analyze climate-vegetation interactions at each site and between mountain peaks ((PRISM Group, Oregon State University, httip://www.primsclaimte.org, created 5 May 2014). Prism data was used because the data set accounts for physiographic variation and in the topographically complex western United States, these data, in turn, more accurately represents mountain climate (Daly et al. 2008). In the event that one site drew from a different PRISM grid (4km resolution) than the site with an opposite slope aspect, the transect drawing from the highest elevation PRISM grid was used in order to more accurately represent climatic conditions at upper treeline (Elliott and Kipfmueller 2011).

Precipitation, maximum temperature (T_{max}) and minimum temperature (T_{min}) were used to calculate the following seasonal mean values: (1) spring (March-May); (2) summer (June-August); (3) fall (September-November); and (4) cool season (November-April). Cool season data were used in lieu of winter data to more accurately capture the period of snowfall in this region. In order to further investigate the impact of precipitation on tree establishment, we also examined a monsoon (July-September) variable. All climate variables were averaged into five-year bins to match the minimum resolution of the age-structure data.

Data Analyses

Outpost tree advancement was reconstructed to document the change in elevation of treeline during the twentieth century. Upslope advancement (m) and increases in stand density above and below timberline (trees ha^{-1}) were reconstructed for 5 year periods throughout the 20th century. Density data was normalized using a natural-log transformation to account for differences in ecotone area between study sites (Elliott and Kipfmueller 2011). Examining advance and density together is useful in determining whether outpost tree advance is a single random event or part of more widespread changes indicative of a switch to favorable climatic conditions. Mann-Whitney U Tests were used to test for statistically significant differences between median tree ages on contrasting slope aspects, as well as ages east and west of the Continental Divide.

Second, in an attempt to gain a more holistic understanding from statistical correlations, we follow Anderesen et al. (2009), who highlight a gap between the prominence of theoretical frameworks discussing ecological thresholds and regime shifts, and the dearth of simple tests and quantitative inferences on the actual appearance of this phenomena in ecological data. Previous research in the Southern and Central Rockies (Elliott2012a) addresses this gap by utilizing a sequential algorithm developed Rodionov (2004) to test for regime shifts in regional-scale tree establishment. This assessment quantifies deviations in time-series data that can signify a threshold-induced regime shift change in either climate or ecological systems. This test was used in our study to further assess the relationship between climate and tree establishment in the Southern Rockies. This data-driven method does not require an *a priori* hypothesis and sequential *t*-tests are conducted on time-series data to detect regime shift changes (Rodionov 2004). A regime shift change is identified when the cumulative sum of normalized deviations from the mean value of a potential new regime is significantly different from the mean of the current regime (Rodionov and Overland 2005). For this analysis, we used a 0.05 significance level to test for the shifts in the mean value of the time series and a cutoff length of ten years due to considerable decadal variability present in the Western United States (McCabe et al. 2004).

Our final statistical analysis included chi-square goodness-of-fit tests to determine if rates of tree establishment coincided more with dry or wet conditions based on the proportion of each pentad during the 20^{th} century. Ecologically-significant precipitation variables (e.g. fall, monsoon, and annual) were standardized relative to the 1900–1999 mean and averaged into five-year bins to match the temporal resolution of the age-structure data. Wet years were classified as a positive z-score anomaly and dry years as a negative z-score anomaly.

RESULTS

West of the Divide

Tree Demography

All of the trees we sampled west of the Divide in the La Plata Mountains are relatively young with a majority (70%) of trees establishing since 1950 (Fig. 2.2). In fact, this trend in establishment is relatively uniform across space and over the reconstructed period of time (1780-2000), with no statistical difference in median tree age ($P = 0.58$) between the north- and south-facing slope in the La Plata Mountains (sites henceforth referred to as WNF-2 and WSF-2, respectively). In both cases, modest rates of establishment persisted for over 170 years until abrupt increases during the latter half of the 20^{th} century (Fig. 2.2). Initial colonization above timberline (ATL) began in 1810 on WNF-2 and in 1950 on WSF-2 (Fig. 2.2). Despite the existence of relatively old trees ATL at WNF-2, the median age is significantly younger ($P < 0.01$) than those below timberline (BTL). Seedlings were scarce at both sites, with four above the outpost tree on WNF-2 and only two above timberline on WSF-2 (Table 2).

Treeline advance upslope ranged from 61 m (0.3 m yr^{-1}) on WNF-2 to 114 m (0.7 m yr^{-1}),on WSF-2, with an average advance of 87 m (0.5 m yr^{-1}; Fig. 2.3). This advance began in the latter half of the 18^{th} century on WNF-2 and between 1800–1804 (1800 age-class) on WSF-2. Furthermore, the greatest upslope migration of treeline occurred at WSF-2 (113.8m). Outpost trees established in the 1995 and 1950 age classes at WNF-2 and WSF-2, respectively. Tree density BTL on the north-facing slope of the La Plata subrange appears to be fairly constant over time within our transect (Fig. 2.4). Contrastingly, density ATL experienced 3 abrupt shifts—1810, 1890 and 1960 (Fig. 2.4).

Climate

Each seasonal climate variable was tested for correlation with tree establishment using Spearman's rank correlation coefficient, but only statistically significant correlations (P-value < 0.05) are discussed hereafter. Tree regeneration west of the Divide is significantly correlated with climate on solely the north-facing slope (Fig. 2.5). At WNF-2 the greatest significant correlation was with annual T_{min} (r_s = 0.659) followed by fall T_{max} (r_s = -0.501). The importance of fall climate on north-facing slopes is further highlighted by the correlation with fall precipitation (r_s = 0.424; Fig. 2.5).

A regime shift in the rate of tree establishment occurred at WNF-2 between 1970–1974 (1970 age-class; Fig 2.2). This shift in tree regeneration occurred in tandem with a step-wise increase in annual minimum temperature (Fig. 2.2). Although not flagged by the regime-shift analysis, there are two peaks in establishment on the southern aspect in

1965 and 1980, the latter of which occurs in tandem with a step wise change in increasing fall precipitation, and decreasing fall T_{max} (Fig. 2.2).

Overall, significantly more trees established during wet fall pentads ($\chi^2 = 4.87$, $P = 0.03$) on south-facing slopes than would be expected given the divergence between observed and expected rates of regeneration. Establishment on south-facing slopes was also found to be more prevalent during wet monsoon years ($\chi^2 = 5.93$, $P = 0.01$). Chi-square analysis did not identify any significant crossover between tree regeneration and moisture regimes on the north-facing slope.

East of the Divide

Tree Demography

Similar to the west, spatiotemporal patterns of tree establishment were relatively uniform among sites (Fig. 2.6). For example, a majority (54%) of establishment within the ecotone at Bennett Peak occurred since 1950 and only 8% of establishment dates within our transect predate 1900. More than half (62%) of the trees on the north-facing slope (ENF-2) and approximately 43% of trees on the south-facing slope (ESF-2) have established since 1950 (Table 2). Tree ages above and below timberline were not significantly different on the north- ($P = 0.50$) or south-facing ($P = 0.69$) slopes. Furthermore, tree ages between slope aspects were not significantly different ($P = 0.44$).

Treeline advance upslope ranged from 68 m (0.5 m yr^{-1}) on ENF-2 to 48.5 m (0.8 m yr^{-1}), on ESF-2, with an average advance of 58 m (0.7 m yr^{-1}; Fig. 2.3). Upslope advance of treeline began in the first half of the 19^{th} century at ESF-2 where the highest elevational limit was reached in 1860 (total advance = 48.5 m; Fig. 2.3). Similarly, advance at ENF-2 began in the latter half of the 19^{th} century but continued until 1990

(Fig. 2.3). Density above timberline at ENF-2 was zero prior to 1900, when the first shift toward increased density occurred. Regime-shift analysis indicates two more abrupt changes in density ATL—one in 1925 and one in 1975. Two such shifts were documented BTL, one in 1860 and one in 1955 (Fig. 2.7). Documented density BTL extends further back on the south-facing slope with regime shifts in 1800 and 1920. Similarly, two shifts in stand density were documented on the northern aspect in 1860 and 1940 (Fig. 2.7). Five seedlings were observed at ENF-2 with four growing ATL and one BTL; only two seedlings, both growing BTL, were documented at ESF-2.

Climate

Unlike west of the Divide, tree establishment was not found to be significantly correlated with any climate variable (Fig. 2.5). Despite there being no significant correlations, synchronicity still exists between tree regeneration and climate (Fig. 2.6). For instance, ESF-2 experienced a decrease in establishment in 1975, synchronous with increasing cool season precipitation. Likewise, ENF-2 showcases decreasing establishment in tandem with decreasing fall T_{max} and increasing fall precipitation in 1980 (Fig. 2.6). Unlike on the western slope, chi-square analysis did not find significantly higher frequencies of establishment during dry or wet pentads on either aspect east of the Divide. In spite of the fact that these four sites are in close proximity to each other in the San Juan Mountains of southwest Colorado, notable ecological differences exist in the spatiotemporal patterns of tree establishment and in climate-vegetation interactions owing to the position relative to the Continental Divide.

DISCUSSION

We documented continual outpost tree advancement into the latter half of the 21st century at 3/4 of our study sites, suggesting the crossing of a bioclimatic threshold toward conditions favorable for treeline advance. These results align with similar studies throughout Europe (see Table 3 in Treml and Chuman 2015) and previous research in the Southern Rocky Mountains, where there was nearly ubiquitous upslope advance in the nearby Front Range and Sangre de Cristo Mountains since 1950 owing to overall summer warmth (Elliott and Kipfmueller 2011). However, notable differences exist when climate-vegetation interactions are observed at smaller landscape- and local-scales. For instance, advance at ESF-2 has been static since the 1860 age class (1860-1869), yet nearly all upslope advance at WSF-2 occurred between 1950 and 2000. Thus, although the elevational extent of treeline advanced upslope at all study sites throughout the San Juan Mountains by varying degrees, a straightforward climate-vegetation interaction narrative remains elusive across bioclimatic gradients east and west of the Continental Divide.

In an attempt to clarify the nature of climate-vegetation interactions, we examined changes in density above and below timberline and found increasing stand density across all sites further instilling the notion a bioclimatic threshold has indeed been crossed. Tree density increased both gradually and abruptly since the 19th century, with densities above timberline approaching densities found below timberline. Such increases are reported by a wealth of studies throughout the world (Szeicz and MacDonald 1995; MacDonald et al. 1998; Klasner and Fagre 2002; Lloyd and Fastie 2003; Camarero and Guitérrez 2004; Danby and Hik 2007; Batllori and Gutiérrez 2008; Elliott and Kipfmueller 2011; Elliott 2012b) and changes in density are suggested to be a more sensitive biomonitor to changes in climate than treeline position (Payette and Filion, 1985; Camarero and Gutiérrez 2004). Pairing increasing stand density with outpost tree advance bolsters the idea that a bioclimatic threshold was crossed, and implies that climate shifted towards more favorable growing conditions particularly during the 20th century. This is supported by the relatively young regeneration on both north- and south-facing slopes where 50% or more of all trees growing above timberline established after 1950, with the exception of ENF-2 (43%).

Our results suggest both north- and south-facing treelines are exhibiting biotic response to abiotic processes which contrasts with results from previous treeline dynamic studies where successful tree regeneration above timberline is confined to south-facing slopes while north-facing slopes remain relatively stable (Kullman 1998; Luckman and Kavanagh 2000; Danby and Hik 2007). While this suggests the overriding influence of broad-scale climate and minimal influence of slope aspect and orientation with respect to the Continental Divide, regimes shift analysis exposes various instances of nuance across study sites in the San Juan Mountains. For example, west of the divide it is the north-facing slope rather than the south-facing slope that exhibits a regime shift in establishment, while to the east both sites showcase abrupt stepwise changes in regeneration. Distinctions between sites become even more apparent when considering the timing and potential causal mechanism behind these altered regimes.

Traditional ecological theory characterizes the treeline ecotone as temperature limited (Jobbágy and Jackson 2000; Körner and Paulsen 2004) which is consistent with previous and more contemporary research that associates increases in tree density and treeline advance with general warming since the termination of the Little Ice Age (e.g.

LaMarche and Mooney 1967; Payette and Filion 1985; Hessl and Baker 1997; Lloyd and Fastie 2003; Danby and Hik 2007; Bittoz et al. 2008). Research elsewhere in the southern Rocky Mountains found significant positive correlations with summer T_{max} (Elliott and Baker 2004) and overall warmer conditions (Elliott and Kipfmueller 2011). Our results indicate a similar biotic response to warmer temperatures at WNF-2 via significant correlation between establishment and increasing annual minimum temperatures. However, the contrasting south-facing slope was not correlated with any climate variable. Similarly, establishment on both north- and south-facing slopes east of the Divide does not correlate with any climate variable suggesting considerable influence of slope aspect and orientation around the Continental Divide in moderating the effects of broad-scale climate.

Further distinctions among and within study sites exist when examining the role of fall climate. Significant correlations with increasing fall precipitation and decreasing maximum temperature are found solely at WNF-2 and may indicate facilitative effects of earlier snow fall and earlier snow cover. Recent studies throughout Russia (Kirdyanov et al. 2011; Hagedorn et al. 2014) found that increases in snowfall may be the primary causal mechanism for forest advance in the Putorana and Ural Mountains due to protection from wind damage and abrasion as well as providing soil insulation. It is possible that increased precipitation in the form of snow can be more ameliorative to winter stress than changes in temperature (Holtmeier 2009). It has also been reported that summer soil moisture is influenced mainly by snow accumulation during winter (Oberbauer and Billings 1981; Hättenschwiler and Smith 1999) and although cool season precipitation and temperature were not significantly correlated with tree establishment, it is recent increases in fall precipitation in the La Plata Mountains that may provide ample snowpack and, come summer, ample snowmelt, which may alleviate moisture stress.

Abrupt changes in the spatial and temporal dynamics of tree establishment during the 20th century coincide with similar step-wise changes in climate thus reinforcing the likelihood of climatic induced biotic response which appears to be associated with changes in annual minimum temperature, as well as fall climate east and west of the Continental Divide. Many studies conclude that upper treeline dynamics are likely to be influenced by the crossing of climate thresholds that produce nonlinear changes in vegetation with increasing frequency of such scenarios as the effects of global climate change materialize (Kupfer and Cairns 1996; Malanson 2001; Millar et al. 2004; Lloyd 2005; Camarero and Gutiérrez 2007; Danby and Hik 2007; Kullman 2007; Elliott and Kipfmueller 2011; Elliott 2012b). Results from the San Juan Mountains uphold the findings of those studies with the identification of synchronous regime shifts between climate and establishment both east and west of the Continental Divide.

Although there is widespread documentation of stepwise change interactions at our study sites, slope-specific nuance obscures a straightforward climate-vegetation narrative. For instance, annual minimum temperatures appear to play a crucial role in regeneration dynamics at WNF-2, but a likewise relationship is non-existent on the contrasting south-facing slope. A net warming of 1°C between 1990 and 2005 found by Rangwala and Miller (2010) in the San Juan Mountains is due in large part to increases in T_{max} during spring and summer. Such increases have the potential to induce earlier snowmelt (Rangwala and Miller 2010) which is shown to facilitate regeneration in treeline ecotones of the Canadian Rockies (Luckman and Kavanagh 2000) and increased establishment is also linked to higher T_{min} throughout the year in the Sierra Nevada (Millar et al. 2004). A potential reason for why a similar response is lacking at WSF-2 may be owed to the notion that south-facing slopes are proposed to be more xeric due to increased exposure to solar radiation (Weisberg and Baker 1995; Germino et al., 2002) and previous studies indicate that the facilitative effects of warmer temperatures on alpine vegetation may be negated without simultaneous increases in precipitation to counteract heat-induced moisture stress (Weisberg and Baker 1995; Daniels and Veblen, 2004; Elliott and Cowell, in review). Such alleviation may be seen in the recruitment pulse of 1985 at WSF-2 that occurs in tandem with increased fall precipitation—reinforcing the importance of fall climate west of the Divide.

Drastic differences in vegetative response to similar climate shifts at ENF-2 and ESF-2 continue to highlight intraregional variability further suggesting the importance of geographic orientation with respect to differences in climate brought on by the Continental Divide. The impact of climate on treeline dynamics at these sites is difficult to comprehend given that there are no significant correlations between tree establishment and any climate variable. Despite this lack of association, synchronous climate and ecological regime shifts occur—albeit negative shifts—in tree regeneration. Previous research utilizing regime shift analysis also found lower rates of establishment in the 20th century, but this was caused by the exclusion of seedling data in the age structure which, if included, would have resulted in substantial increases in late 20th century establishment (Elliott 2012a). However, at ENF-2 and ESF-2, seedlings were scarce and shifts towards a less regenerative regime began relatively early (1980 and 1975, respectively) even with continued establishment. These decreases occur in tandem with increasing cool season precipitation (1975) and increasing fall precipitation (1980). The implications of these interactions are confounding given that the same variables appear to facilitate regeneration on western side of the Continental Divide. Research further to the southeast in the Sangre de Cristo Mountains finds that tree establishment was favored by periods of reduced snowpack in spring and warm, dry summers (Elliott and Kipfmueller 2011) and similar relationships are found elsewhere (see Luckman and Kavanagh 2000; Camarero and Gutiérrez 2004; 2007). A similar relationship cannot be confirmed at ENF-2 and ESF-2, but we find evidence that an opposite relationship (increased snowpack and decreased temperatures) appears to retard tree regeneration and may lead to treeline retreat, supporting those previous studies documenting the ameliorative effects of warmer temperatures and reduced snowpack.

Research also suggests that treeline advance could only commence during warming trends with the absence of extreme cold events (Paulsen et al. 2000). Thus, periods of decreased establishment east of the Contintental Divide may be owed to rapid and drastic changes in annual minimum temperature. Prior to the 1975 and 1980 establishment shifts, annual T_{min} decreased by approximately 0.73°C in 1940 and this regime average prevailed until the mean returned to a warmer state in 1985 (ca. 0.75°C increase). During the cool period from 1940-1985, fall maximum temperatures also dropped by 0.63°C. These events taken together may serve to explain the lack of consistent establishment. Furthermore, although increases in fall and cool season precipitation may protect seedlings from harmful winter conditions (i.e. snow abrasion, winter dessication), decreased annual T_{min} may have reduced the longevity of the growing season and persistent snow cover into summer could have led to the development of snow fungi (Holtmeier & Broll 2010). At ESF-2, there was also the presence of a single snag above the outpost tree indicating that mortality may be common. In addition to adverse climate effects, ENF-2, and ESF-2 in particular, were marred by what appeared to be extensive spruce beetle (*Dendroctonus rufipennis*) induced mortality. Spruce beetle is known to attack recently downed wood and weakened trees which may cause widespread mortality in susceptible spruce stands (Hebertson and Jenkins 2008). Warm and dry conditions are shown to increase beetle population numbers (Hebertson and Jenkins) and these climate conditions have adverse effects on host trees as they are shown to make trees more susceptible to beetles (Hart et al. 2014). It is not clear, but perhaps increasing annual T_{min} (and T_{max} within San Juan Mountains at large) led to the stand being prone to beetle invasion and thus potential retrogression of treeline.

Another possible confounding variable is land-use legacies in the form of grazing during the 20th century which acted as the dominant disturbance agent at alpine treeline throughout the Rocky Mountains (Elliott, 2012a). For example, in the nearby Upper Rio Grande Valley, alpine areas were commonly grazed by sheep or cattle during the short growing season (deBuys 1985). These land-use practices are common throughout the Southwest and can create uncertainty in interpreting vegetation dynamics (Swetnam and Betancourt 1998). Impacts of grazing introduced by humans, as well as natural herbivory, was evident at ESF-2. Even low densities of grazers can limit seedling establishment at treeline—possibly causing misinterpretations regarding the role of climate over time (Speed, et al. 2010).

CONCLUSION

Treeline dynamics are incredibly nuanced and changes in treeline position may be affected by a range of environmental conditions at local, landscape and regional scales (e.g. Holtmeier and Broll 2005; Malanson et al. 2011). This research has important implications which raise questions as to the efficacy of examining regional treeline dynamics given the amount of intraregional variability found throughout the San Juan Mountains. Although much of the regeneration throughout our study sites appears to be fairly recent, only north-facing slopes west of the Divide are most directly influenced by climate—particularly fall variables, which we take to represent the importance of snowfall and subsequent protection provided by snowcover. Increased fall precipitation may also serve to alleviate moisture stress later in the year as snowmelt. Furthermore, cooling fall temperatures may also counteract heat-induced moisture stress brought about by increasing growing season temperatures.

Elsewhere in the San Juan Mountains a clear climate-vegetation interaction narrative is much less clear, indicating the potentially overriding landscape and local effects that are unexamined in this research. Changing abiotic components that facilitate tree establishment were reserved to a single site, and those same variables which appear to facilitate regeneration at WNF-2, appear to adversely affect rates of establishment east of the divide thus representing an aspect and orientation bias. Extreme cold events on the eastern side of the Divide and increasing fall and cool season precipitation have produced negative regime shifts in tree establishment on both north- and south-facing slopes. However, because climate variables were not significantly correlated, and due to the possible confounding nature of beetle kill and land-use legacies, these inferences are speculative and best taken *cum grano salis*.

Temperature in the San Juan Mountains increased by 1°C between 1895 and 1995 (Rangwala and Miller, 2010) and future projections for this region foretell continued annual temperature increases of 2-5°C by the middle of the 21st Century (Rangwala and Miller, 2011). It is expected that the southern Intermountain West region and the Upper Colorado River Basin will experience increased summer dryness and higher probability of drought under global warming scenarios (Seager et al., 2007). In addition to these forecasts, snowpack is decreasing across the Western United States and that snow season length is declining (Pederson et al. 2011). Current trends and future projections are foreboding for treeline regeneration at WNF-2 given the apparent reliance on precipitation falling as snow and the ameliorative effects of snowpack found at this site. To the contrary, the same projected future conditions may provide conditions that enhance regeneration at both ENF-2 and ESF-2 by alleviating pressures brought on by colder temperatures and higher amounts of snowfall. Ultimately, this research shows that regime shifts between climate and tree establishment occur in tandem, but biotic response to abiotic processes are nuanced by slope aspect and orientation around the Continental Divide.

Table 2. Study site characteristics for upper treeline sites in the eastern and western San Juan Mountains of Colorado. Slopes east of the divide are coded into ENF-2 (east north-facing) and ESF-2 (east south-facing). Western sites follow a similar scheme and are referred to as WNF-2 (west north-facing) and WSF-2 (west south-facing).

Site Name	Elevation (m)	Aspect (°)	Slope (°)	Trees dated (*n*)	Trees establ. Post- 1950 (*n*)	Seedlings (
Silver Mountain North (ENF-2)	3687	254	25	29	18	5
Bennett Peak South (ESF-2)	3706	288	13	21	9	2
La Plata North (WNF-2)	3602	276	20	32	20	4
La Plata South (WSF-2)	3563	231	27	30	24	2

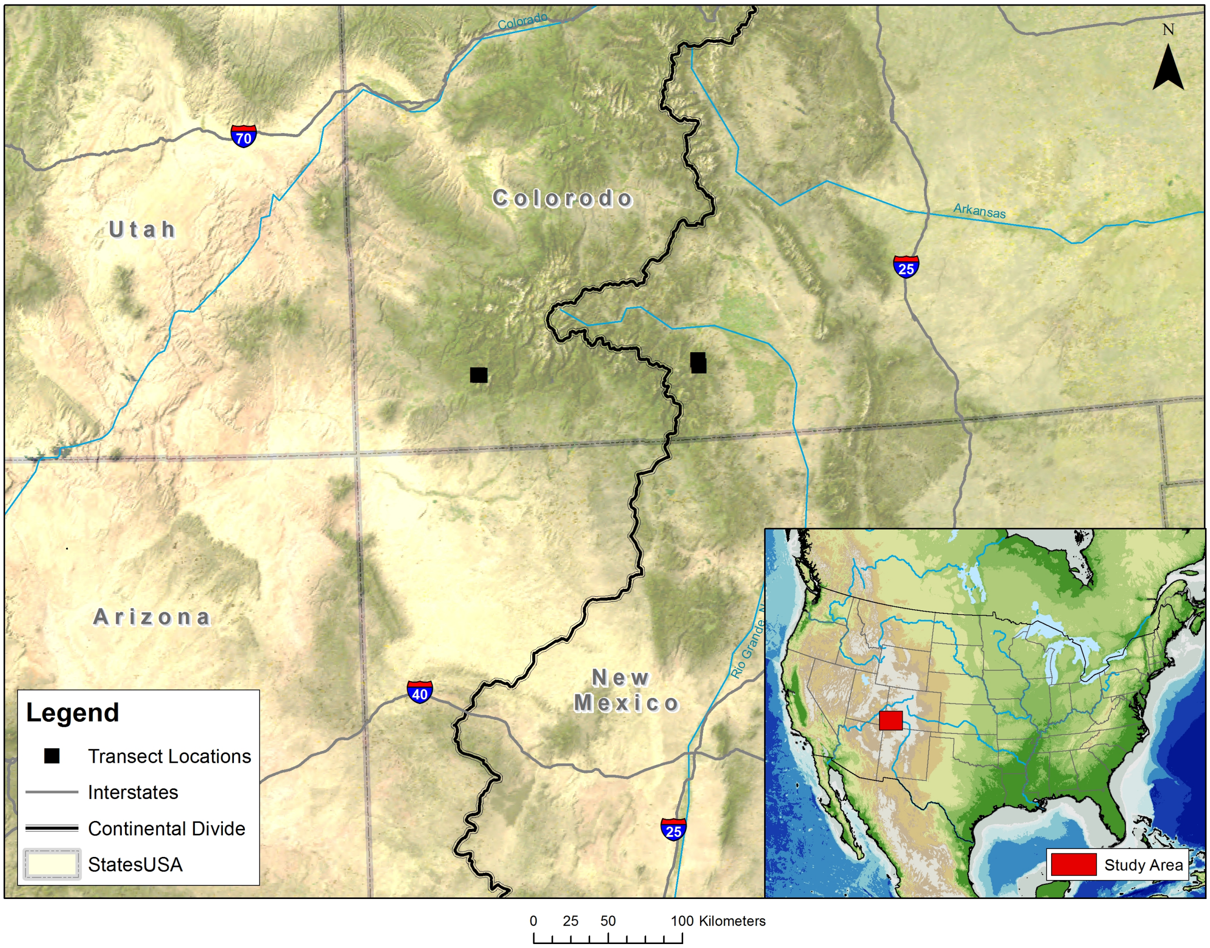

Figure 2.1. Study area map and transect locations east and west of the Continental Divide.

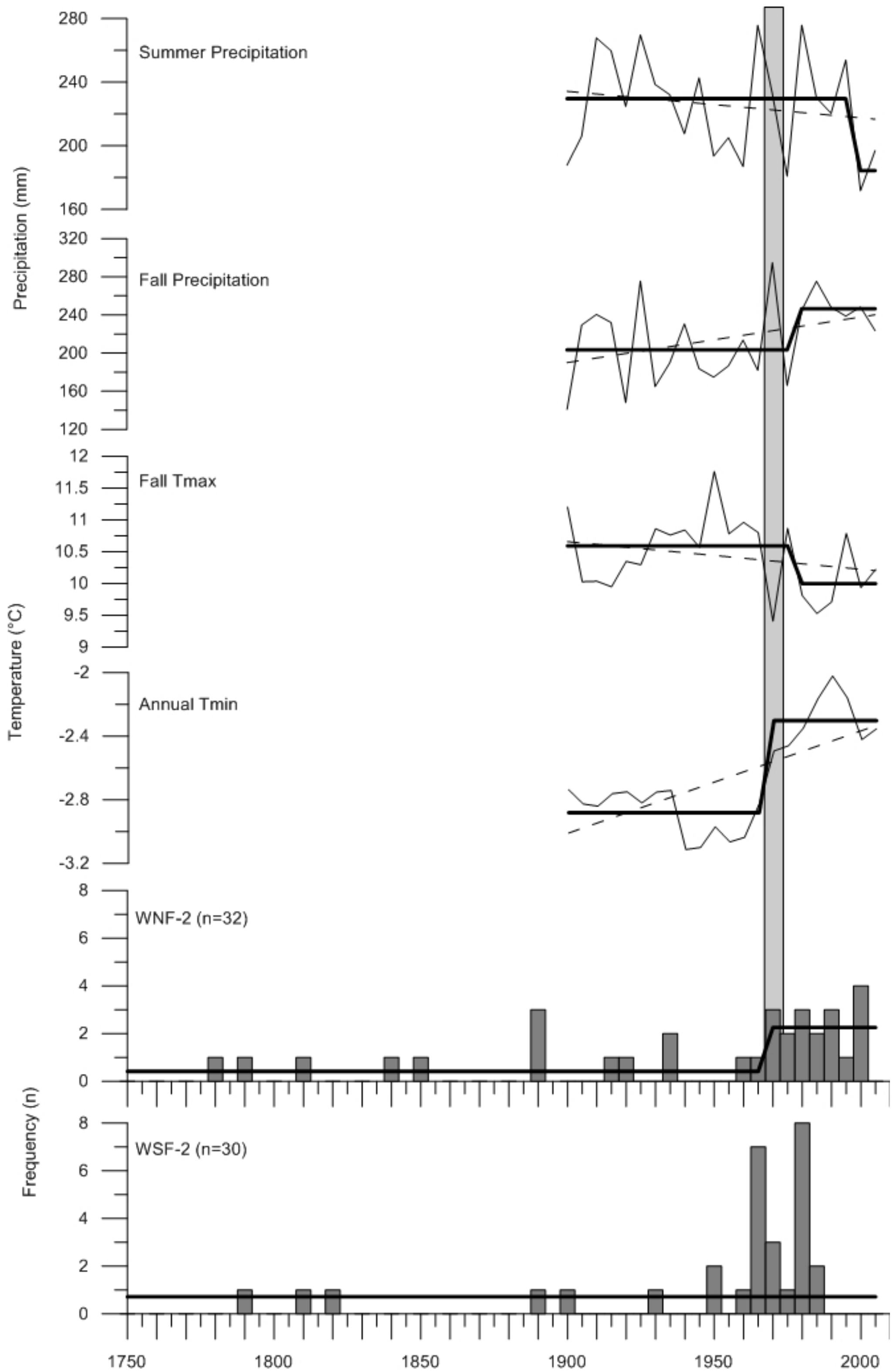

Figure 2.2. Age-structure data (1900-2000) in pentads for each study site west of the Divide. Select climate variables are depicted above the age structure graphs and bold lines indicate the value derived from regime-shift analysis ($P < 0.05$). Regime-shift

analysis quantifies abrupt, sudden changes toward a new climatological or ecological regime. Hashed lines depict the overall linear trend in each plot. The grey box highlights the synchronous regime shifts in climate and establishment between 1970-1974 (1970 age-class). Note the presence of different axes for climate variables.

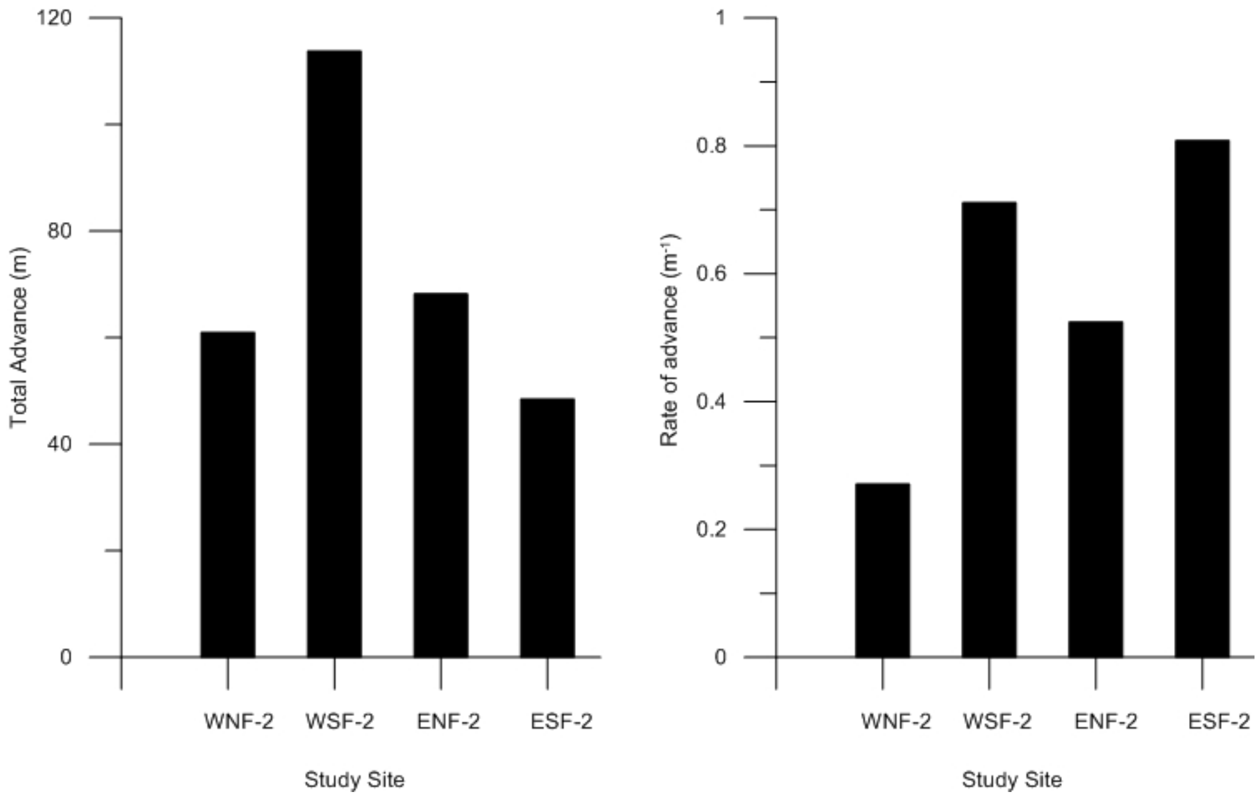

Figure 2.3. Total advance (a) and rate of advance (b) at individual study sites.

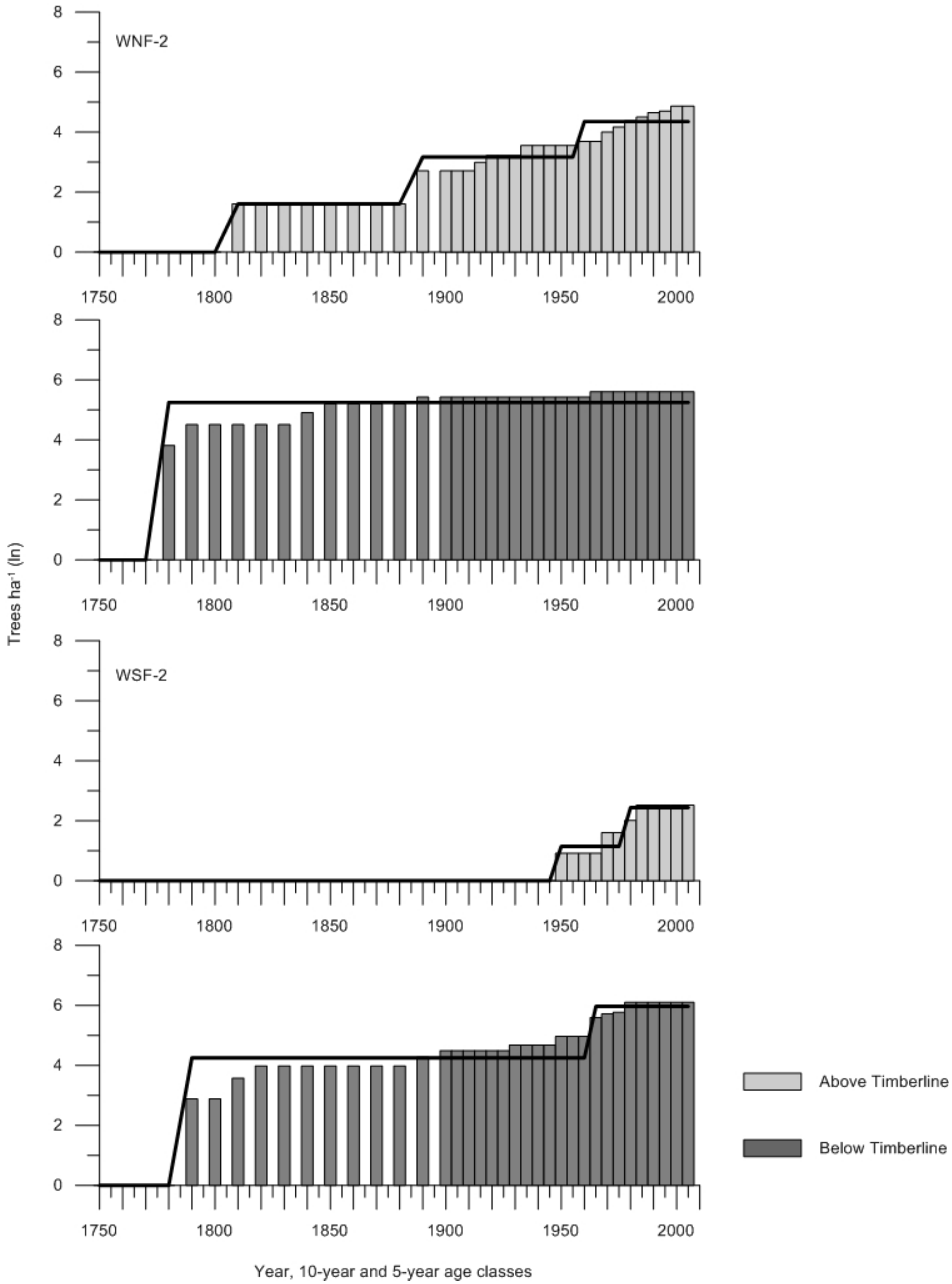

Figure 2.4. Natural log reconstructions of tree density (trees ha^{-1}) above and below timberline at each study site west of the Continental Divide. Natural log transformation was used to account for variation in transact area among study sites. The bold lines are

generated by regime shift analysis which indicates an abrupt change towards a new ecological regime.

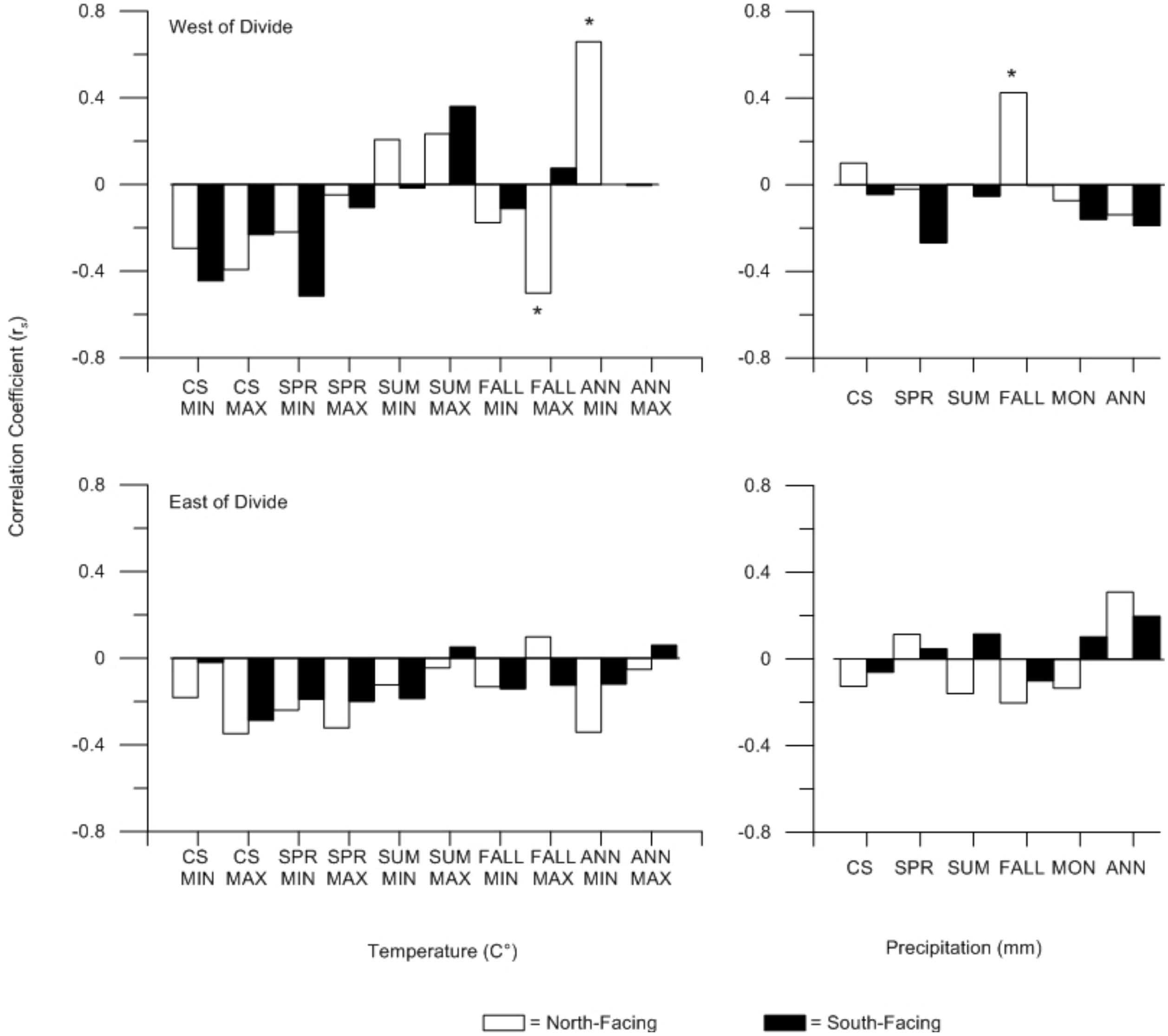

Figure 2.5. Spearman rank correlation coefficients (r_s) comparing tree establishment with seasonal temperature and precipitation data from 1900 to 2000. * = $p < 0.05$. MAX = maximum temperature; MIN = minimum temperature; CS = cool season; SPR = spring; SUM = summer; MON = Monsoon; ANN = Annual.

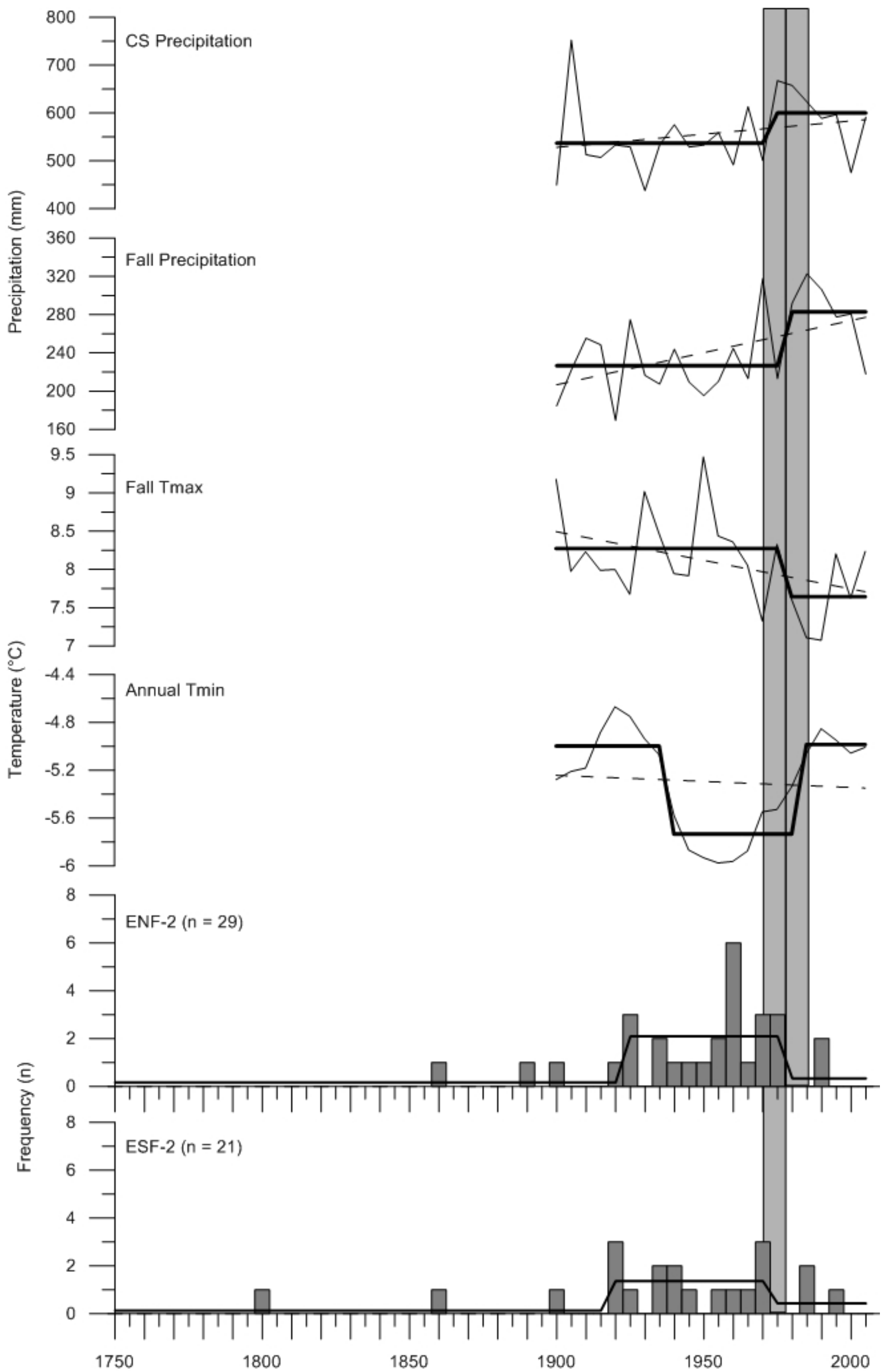

Figure 2.6. Age structure data (1900-2000) in pentads for each study site east of the Divide. Select climate variables are depicted above the age structure graphs and bold

lines indicate the value derived from regime shift analysis ($p < 0.05$). Regime shift analysis detects abrupt, sudden changes towards a new climatological or ecological regime. Hashed lines depict the overall linear trend in each plot. Grey boxes display synchronous regime shifts in climate and establishment, highlighting climate-vegetation interactions. Note the presence of different axes for climate variables.

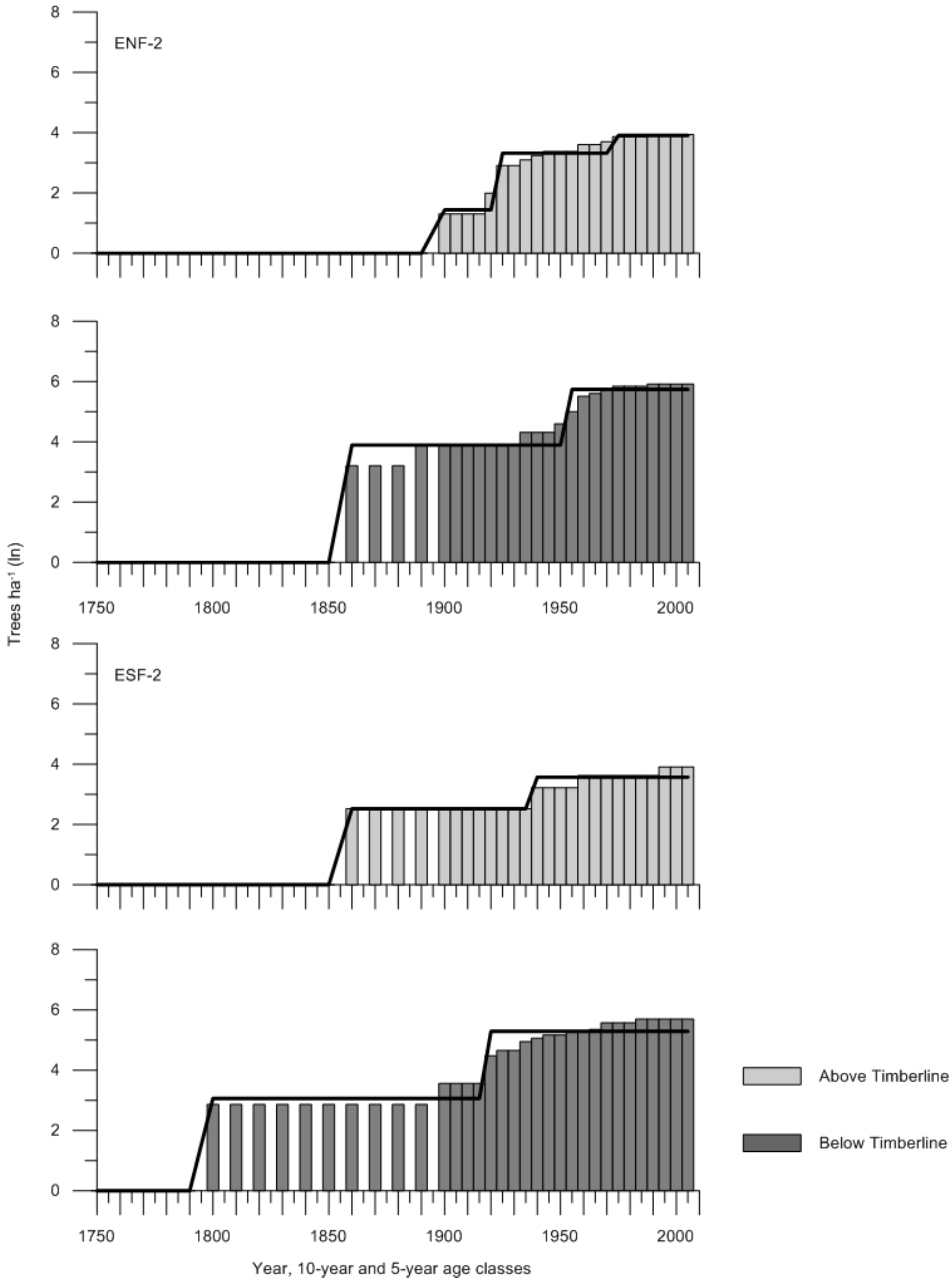

Figure 2.7. Natural log reconstructions of tree density (trees ha^{-1}) above and below timberline at each study site east of the Continental Divide. Natural log transformation

was used to account for variation in transact area among study sites. The bold lines are generated by regime shift analysis which indicates an abrupt change towards a new ecological regime.

Chapter 4. Conclusion

Collectively, this research demonstrates the complexity and variability that is introduced into treeline dynamics vis-à-vis slope aspect and orientation with respect to the Continental Divide. Compared to previous research, these chapters highlight the importance of fall climate variables in driving the biogeographic expression of tree demography, which may become more important if temperatures continue to warm as predicted. Decreasing fall temperatures are conducive to tree regeneration at 3/4 of our study sites, possibly indicating the alleviation of moisture stress brought on by increasing temperatures during the growing season.

While our study sites share a few similarities, noticeable differences exist between the northern and southern Rocky Mountains—driven by differences east and west of the Divide. For instance, when comparing the northern Rocky Mountain climate-establishment correlations with the southern Rockies, slopes located in the northern Rocky Mountains appear to be more responsive to climate overall. Association between climate and vegetation is recorded both east and west of the divide in the northern Rocky Mountains with closely related variables (Fall T_{max} in the west; Fall T_{min} in the east). However, east of the Divide in the southern Rockies, not a single climate variable significantly correlates with establishment. This is surprising given the more xeric conditions thought to exist on the leeward side of the Divide. Furthermore, regime shift analysis recorded wholesale changes in rates of establishment at each site in the northern Rockies and that same consistency is missing from the southern Rockies given that no regime shift in establishment was recorded at WSF-2.

Snow has a more widespread impact on tree regeneration in the north as compared to the south. This is possibly owing to the North American Monsoon that delivers ample amounts of precipitation throughout the summer in the San Juan Mountains. This moisture provider may reduce the necessity of snowmelt, thus explaining the seeming reduction in the vitality of cool season, fall and spring precipitation in the southern Rockies. Also, extreme cold events on the eastern side of the Divide in the south and increasing fall and cool season precipitation produced negative regime shifts in tree establishment on both north- and south-facing slopes. These same climatic variables appear to be conducive to regeneration in the northern Rocky Mountains—further reinforcing the importance of subregional- (north and south of 40°N) landscape- (mountain range) and local-scale (slope aspect) variations and moisture gradients. Ultimately, this thesis demonstrates the value of examining tree regeneration at smaller scales. Intraregional and between site variability shows that a simple climate-vegetation interaction narrative can be heavily modified by slope aspect and orientation about the Continental Divide.

Literature Cited

Andersen, T., Cartensen, J., Hernández-García, E. and Duarte, C.M. (2008). Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology and Evolution*. 24 (1), 49-57.

Applequist, M. B. 1958. A simple pith locator for use with off center increment cores. *Journal of Forestry* 56, 141.

Barnett, T. P., Pierce, D. W., Hidalgo, H. G., Bonfils C., Santer B. D., Das, T., Bala, G., Wood, A.W., Nozawa, T., Mirin, A. A., Cayan, D. R., and Dettinger, M. D. (2008). Human induced changes in the hydrology of the western United States. *Science,* 319, 1080–1083.

Beniston, M. (2003). Climatic change in mountain regions: A review of possible impacts. *Climatic Change* 59, 5-31.

Butler, D. R., Malanson, G. P., and Cairns D. M. (1994). Stability of Alpine Treeline in Northern Montana, USA. *Phytocoenologia* 22, 485–500.

Butler, D. R., Malanson, G. P., Walsh, S. J., and Fagre, D. B. (2007). Influences of geomorphology and geology on alpine treeline in the American West—More important than climatic influences? *Physical Geography* 28 (5), 434–50.

Camarero, J.J. and Gutiérrez, E. (2004). Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyreness. *Climatic Change*. 63, 181-200.

———. (2007). Response of Pinus uncinata recruitment to climate warming and changes in grazing pressure in an isolated population of the Iberian system (NE Spain). *Arctic, Antarctic, and Alpine Research* 39 (2), 210–17.

Cluer, K. J. (1989). Surficial geology and geomorphology of the Doublespring Pass area, Lost River Range, east-central Idaho. *Contributions to Geology*. 27 (2), 55-62.

Cooper, S. V., Lesica, P. and Page-Dumroese, D. (1997). Plant Community Classification for Alpine Vegetation on the Beaverhead National Forest, Montana. US Department of Agriculture, Forest Service, Intermountain Research Station. Ogden, UT.

Cuevas, J. G. (2002). Episodic regeneration at the Nothofagus pumilio alpine timberline in Tierra del Fuego, Chile. *Journal of Ecology.* 90, 52-60.

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J. T., and Pasteris, P. A. (2008). Physiographically-sensitive mapping of temperature and precipitation across the conterminous United States. *International Journal of Climatology*. 28, 2031–64.

Danby, R. K., and Hik, D. S., (2007). Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology*, 95: 352-363.

Dang, H., Zhang, Y., Zhang, Y., Zhang, K., Zhang, W. (2015). Variability and rapid response of subalpine fire (*Abies fargesii*) to climate warming at upper altitudinal limits of north-central China. *Trees*. DOI: 10.1007/s00468-015-1156-9

Daniels, L. D., and Veblen, T. T. (2004). Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*. 85, 1284–1296.

Dettinger, M.D., Cayan, D.R., Diaz, H.F., Meko, D. M., (1998). North-south precipitation patterns in western North America on interannual-to-decadal timescales. *Journal of Climate.* 11, 3095-3111.

Elliott, G.P. (2011). Influences of 20th century warming at upper treeline contingent on local-scale interactions: evidence from a latitudinal gradient in the Rocky Mountains, USA. *Global Ecology and Biogeography.* 20, 46–57.

———. (2012a). Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. *Ecology*. 93(7), 1614-1625.

———. (2012b). The role of thresholds and fine-scale processes in driving upper treeline dynamics in the Bighorn Mountains, Wyoming. *Physical Geography*. 33, 129–145.

Elliott, G.P. and Kipfmueller, K.F. (2010). Multi-scale influences of slope aspect and spatial pattern on ecotonal dynamics at upper treeline in the Southern Rocky Mountains, USA. *Arctic, Antarctic, and Alpine Research*. 42, 45-56.

———. (2011). Multi-Scale Influences of Climate on Upper Treeline Dynamics in the Southern Rocky Mountains, USA: Evidence of Intra-Regional Variability and Bioclimatic Thresholds in Response to 20th Century Climate. *The Annals of the Association of American Geographers*. 101 (6), 1181-1203.

Germino, M. J., Smith, W. K., and Resor, A. C., (2002). Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology*. 162, 157–168.

Giorgi, F. and Bi, X. (2005). Updated regional precipitation and temperature changes for the 21st century from ensembles of recent AOGCM simulations. *Geophysical Research Letters*. 32, L21715, doi:10.1029/2005GL024288.

Grace, J., Berninger, F., and Nagy, L., (2002). Impacts of climate change on the tree line. *Annals of Botany*. 90, 537-544.

Groffman, P.M., Baron, J. S., Blett, T., Gold, A. J., Goodman, I., Gunderson, L. H., Levinson, B. M., Palmer, M. A., Paerl, H. W., Peterson, G. D., Poff, L. N., Rejeski, D. W., Reynolds, J. F., Turner, M. G., Weathers, K. C., and Wiens, J. (2006). Ecological thresholds: The key to successful environmental management or an important concept with no practical application? *Ecosystems*. 9, 1-13. DOI: 10.1007/s10021-003-0142-z

Gutzler, D. S. and Robbins, T. O. (2011). Climate variability and projected change in the western United States: regional downscaling and drought statistics. *Climate Dynamics*. 37, 835-849.

Hadley, J. L., and Smith, W. K. (1983). Influences of wind exposure on needle dessication and mortality for timberline conifers in Wyoming, USA. *Arctic and Alpine Research.* 15 (1), 127-135.

———. (1986). Wind effects on needles of timberline conifers: Seasonal influence on mortality. *Ecology*. 67 (1), 12–19.

Hagedorn, F., Shiyatov, S. G., Mazepa, V. S., Devi, N. M., Grigor'ev, A. A., Bartysh, A. A., Fomin, V. V., Kapralov, D. S., Terent'ev, M., Bugman, H., Rigling, A., Moiseev, P. A. (2014). Treeline advances along the Urals mountain range driven by improved winter conditions? *Global Change Biology.* 20 (11), 3530-3543.

Harsch M.A. & Bader, M. Y., (2011). Treeline form – a potential key to understanding treeline dynamics. *Global Ecology and Biogeography.* 20, 582-596.

Harsch, M.A., Hulme, P.E., McGlone, M.S. and Duncan, R.P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*. 12, 1040-1049.

Hättenschwiler, S. and Smith, W.K. (1999). Seedling occurrence in alpine treeline conifers: a case study from the Central Rocky Mountains, USA. *Acta Oecologica*, 20 (3), 219-224.

Hebertson E. G., and Jenkins M. J. (2008). Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environmental Entomology*. 37 (2), 281-292.

Hessl, A. E., and Baker, W. L. (1997). Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research* 29 (2), 173–183.

Holtmeier, F. K. (2005). Relocation of snow and its effects in the treeline ecotone. *Die Erde*. 136, 143-173.

———. (2009). Mountain timberlines: ecology, patchiness, and dynamics. Springer, London, UK.

Holtmeier, K.F. and Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*. 14, 395-410.

———, (2007). Treeline advance – driving processes and adverse factors. Landscape Online 1, 1-33. DOI: 10.3097/LO.200701

———. (2010). Altitudinal and polar treelines in the Northern Hemisphere – causes and response to climate change. *Polarforschung*. 79 (3), 139-153.

Huber, U.M., Bugmann, H.K.M. & Reasoner, M.A. (2005). Global Change and Mountain Regions: an Overview of Current Knowledge. Springer, Dordrecht.

IPCC, (2014). Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1132 pp.

Kirdyanov, A. V., Hagedorn, F., Knorre, A. A., Fedotova, E. V., Vaganov, E. A., Naurzbaev, M. M., Moiseev, P. A. and Rigling, A. (2011). 20^{th} century tree-line advance and vegetation changes along an altitudinal transect in the Putorana Mountains, northern Siberia. *Boreas*. 41, 56-67.

Knapp, P. A. (1997). Spatial characteristics of regional wildfire frequencies in intermountain west grass-dominated communities. *Professional Geographer.* 49 (1), 39-51.

Körner C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115, 445-459.

———. (2012). Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits. Springer, Basel.

Kullman, L. (1997). Tree-limit stress and disturbance. A 25-year survey of geoecological change in the Scandes Mountains of Sweden. *Geografiska Annaler*, 79A, 139-165.

———. (1998). Tree-limits and montane forests in the Swedish Scandes: Sensitive biomonitors of climate change and variability. *Ambio.* 27, 312–21.

———. (2001). 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. *Ambio*. 30, 72–80.

———. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*. 90, 68-77.

———. (2007). Tree line population monitoring of Pinus sylvestris in the Swedish Scandes, 1973–2005: Implications for tree line theory and climate change ecology. Journal of Ecology 95 (1), 41–52.

Kullman, L., and Öberg L. (2009). Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *Journal of Ecology,* 97, 415–429.

Kupfer, J. A., and Cairns D. M. (1996). The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography.* 20 (3), 253-272.

Leung, L. R., Qian, Y., Bian, X., Washington, W. M., Han, J. and Roads, J. O. (2004). Mid-century ensemble regional climate change scenarios for the western United States. *Climatic Change*. 62, 75-113.

Liang, E., Wang, Y., Eckstein, D., and Luo, T. (2011). Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytologist*. 190, 760-769.

Lloyd, A.H. (2005). Ecological histories from Alaskan tree lines provide insight into future change. *Ecology*. 86, 1687–1695.

Lloyd, A.H. & Fastie, C.L. (2002). Spatial and temporal variability in the growth and climate response of tree lines in Alaska. *Climatic Change*. 52, 481–509.

Lloyd, A.H., and Graumlich, L. J. (1997). Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology.* 78, 1199-1210.

Luckman, B.H. (1998). Landscape and climate change in the central Canadian Rockies during the 20th Century. *Canadian Geographer*. 42, 319-336.

Luckman, B.H., and Kavanagh, T. (2000). Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio* 29 (7), 371-380.

Malanson, G. P., Butler, D. R., Fagre, D. B., Walsh S. J., Tomback, D. F., Daniels, L. D, Resler, L. M., et al. 2007. Alpine treeline of western North America: Linking organism-to landscape dynamics. *Physical Geography* 28 (5), 378–396.

Malanson, G. P., Resler, L. M., Bader, M. Y., Holtmeier, F. K., Butler, D. R., Weiss, D. J., Daniels, L. D., and Fagre, D. B. (2011). Mountain treelines: a roadmap for research orientation. *Arctic, Antarctic and Alpine Research*. 43 (2), 167-177.

Mitchell, V. L. (1976). The regionalization of climate in the Western United States. *Journal of Applied Meteorology.* 15, 920–927.

McCabe, G. J., Palekci, M. A., and Betancourt, J. L. (2004). Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences* 101 (12), 4136–41.

Mock, C. J. (1996). Climate controls and spatial variations of precipitation in the western United States. *Journal of Climate*. 9, 1111-1125.

Mote, P. W., Hamlet, A. F., Clark, M. P., and Lettenmaier, D. P. (2005). Declining mountain snowpack in western North America. *Bulletin of the American Meterological Society*. 86, 39-49.

New, M., Todd, M., Hulme, M., and Jones, P. (2001). Precipitation measurements and trends in the twentieth century. *International Journal of Climatology*. 21,1899-1922.

Oberbauer, S. F. and Billings, W. D. (1981). Drought tolerance and water use by plants along an alpine topographic gradient. *Oceologia*. 50, 235-331.

Paulsen, J., Weber, U. M., and Körner, C. (2000). Tree growth near treeline: Abrupt or gradual reduction with altitude? *Arctic, Antarctic, and Alpine Research* 32 (1), 14–20.

Pederson, G. T., Graumlich, L. J., Fagre, D. B., Kipfer, T. and Muhlfeld C. C. (2010). A century of climate and ecosystem change in Western Montana: what do temperature trends portend? *Climatic Change*. 98, 133-154.

Pearson, R. C., Berger, B. R., Kaufmann, H. E., Hanna, W. F., and Zen, E. (1988). Mineral Resources of the Eastern Pioneer Mountains, Beaverhead County, Montana. Department of the Interior, U.S. Geological Survey.

Rangwala, I., and Miller, J. R. (2010). Twentieth century temperature trends in Colorado's San Juan Mountains. *Arctic, Antarctic, and Alpine Research*. 42 (1), 89-97.

Rodionov, S. N. (2004). A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31, L09204. DOI:10.1029/2004GL019448, 2004

Rodionov, S. N., and Overland, J. E. (2005). Application of a sequential regime shift detection method to the Bering Sea ecosystem. *Journal of Marine Science* 62, 328–32.

Scheffer, M. and Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*. 18 (12), 648-656.

Seager, R., Ting, M., Held., I., Kushmir, Y., Lu, J., Vecchi, G., Huang, H-P., Hamik, N., Leetmaa, A., Lau, N-Chueng, Li, C., Velez, J., Naik, N. (2007). Model projections of an inmminent transition to a more arid climate in southwestern North America. *Science*. 316, 1181-1184.

Speed, J. M., Austrheim, G., Hester, A. J., and Mysterud, A. (2010). Experimental evidence for herbivore limitation of the treeline. *Ecology*. 91, 3414-3420.

Stokes, M. A., and Smiley T. L. (1996). An introduction to treering dating. University of Arizona Press, Tucson, Arizona, USA.

Stonefelt, M.D., Fontaine, T. A. and Hotchkiss, R. H. (2000). Impacts of climate change on water yield in the upper wind river basin. *Journal of the American Water Resources Association.* 36 (2), 321-336.

Sveinbjörnsson, B. (2000). North American and European treelines: external forces and internal processes controlling position. *Ambio*. 29, 388–395.

Tranquillini, W. 1979. *Physiological ecology of the alpine timberline.* New York: Springer-Verlag.

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

Weisberg, P. J., and Baker, W. L. (1995). Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research*. 25, 1326–1339.

Williams, J.W., Blois, J.L. and Shuman, B.N. 2011. Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *Journal of Ecology*. 99, 664-677.

Wilmking, M., Samders, T. G. M., Zhang, Y., Kenter, S., Holzkämper, S. and Crittenden, P. D. 2012. Effects of climate, site conditions, and seed quality on recent treeline dynamics in NW Russia: permafrost and lack of reproductive success hamper treeline advance? *Ecosystems*. 15, 1053-1064.

Wise, E. K. 2012. Hydroclimatology of the US intermountain west. *Progress in Physical Geography.* 36 (4), 458-479.

Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research.* 21, 414–416.