ANNUAL EVIDENCE OF MOISTURE LIMITATIONS AT TREELINE

IN THE SANGRE DE CRISTO MOUNTAINS

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by

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

thesis entitled

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TREELINE IN THE SANGRE DE CRISTO MOUNTAINS

presented by Sydney Bailey,

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

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ACKNOWLEDGMENTS

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ABSTRACT

This study is focused on capturing a recent regeneration patterns on an annual level over the landscape of the Sangre de Cristo (SDC) mountain range. Modern temperature trends (post-1945) of this area are dominated by sharp rises in minimum temperature during the warm and cool seasons. Coincidentally, the onset of heat-induced drought stress is impacting trees throughout the mountain forest belt, though research is lacking across broad spatial scales at treeline. I used dendroecological techniques to destructively sample seedlings on contrasting north and south facing slopes at upper treeline in the SDC to investigate moisture interactions at treeline. I hypothesized that if patterns of tree regeneration are primarily driven by temperature, then I would expect seedling establishment to be more abundant on south-facing slopes. Alternatively, if heat-induced drought stress is an important driver, I would expect seedling establishment to be more confined to north-facing slopes. Results show that seedling establishment is significantly ($p < 0.01$) favored on north-facing slopes (n=169) verses south-facing slopes ($n = 66$). These seedlings are also significantly younger ($p < 0.05$) and smaller ($p < 0.01$) than their counterparts on south-facing slopes. The relationship between climate and annual establishment patters were investigated to identify any important drivers. Results show that there is a negative relationship between drought conditions and establishment events. Across all sites (n=6) and slope aspects, there was no establishment found after 2009, possibly indicating a minimum threshold has been surpassed and conditions are no longer suitable to regeneration above treeline. This indicates the possibility of moisture limitations at treeline and brings into question the future structure and extent of the upper forest border under a warmer and drier climate.

1. INTRODUCTION

Climate exerts fundamental control over natural ecological processes from a top-down perspective and the changes that have happened to the global climate system since the 1950's are unprecedented within the past several millennia (IPCC 2014). Due to human-caused emissions, for example, greenhouse gas levels are higher than they have been for the past 800,000 years, which has led to an overall increase in global temperature (IPCC 2014). In fact, amplified rates of warming during recent decades produced the highest mean temperature for any century (1917–2016) of the past 11,000 years (Marsicek et al. 2018). A temperature regime increasingly outside the natural range of variability for the Holocene raises the likelihood of threshold-induced regime shifts affecting key ecological processes (Anderson et al. 2009). This is especially true for mountain regions because they are warming faster than lowland environments and this is expected to continue through the 21st century (Nogués-Bravo et al. 2007, Pepin et al. 2015). Across Colorado, for instance, observations since the 1950's indicate that temperatures are rising twice as fast in the mountains compared to the rest of the state (ca. 1.0°C vs. 0.4°C per decade; Rangwala & Miller 2012). It seems likely that this accelerated warming will impact the structure and extent of the mountain forest belt, yet future changes are particularly challenging to predict across topographically complex mountain ranges (Villalba & Veblen 1994, Mensing et al. 2012).

To attempt to understand what impacts these climatic changes will have on the Earth's forests, changes at alpine treeline are commonly used as a proxy for future forest extent. The alpine treeline ecotone is the elevational transition zone from subalpine forests to alpine tundra and results from environmental gradients (Elliott 2017). Trees

here are growing at the furthest extent of their ecological limit, which lead to them being sensitive to critical climate thresholds that affect the pattern and process of establishment (Lloyd & Graumlich 1997, Millar et al. 2004, Danby & Hik 2007, Kullman 2007). The sensitivity of these climatic treelines and the fact they can be relatively narrow ecotones makes them a favorable location to observe the effects of climate change on the forested mountain landscape (Elliott 2017). Temperature is believed to be the classic limiting factor in treeline advance (Körner 2012), so warming temperature would be expected to allow for an increase in regeneration at treeline and an expansion of the mountain forest belt (Broderson et al. 2019). A global meta-analysis by Harsch et al. (2009) found that only 52% of treelines have advanced in elevation since 1900 A.D. A majority of studies worldwide have found a densification in treeline between 1950 and 1995 as response to warming temperatures (e.g. Lloyd & Fastie 2003, Danby & Hik 2007, Kharuk et al. 2010, Liang et al. 2016). Despite global observations of warming, treeline response is not ubiquitous and therefore establishment may now be limited by other factors such as moisture (e.g. Hessl & Baker 1997, Lloyd & Graumlich 1997, Harsch et al. 2009, Malanson et al. 2019).

Rising temperatures without accompanied rise in precipitation have created "hotter drought" conditions (Allen et al. 2015) and these conditions have reached unprecedented severity in recent years, which could alter the ecological processes in the ecosystem (Millar & Stephenson 2015). High elevation areas, while not more susceptible to drought, are more susceptible to increase evapotranspiration rates which leads to increased drought stress on vegetation (Lloyd & Graumlich 1997). Drought stress would also be more relevant in shallow-rooted seedlings, rather than mature trees who have

roots that can reach water deeper in the soil (Smithers et al. 2018). As a result, moisture

limitations could now be more important that temperature limitations for potential

establishment at or above treeline (Moyes et al. 2015, Loranger et al. 2016, Kueppers et

al 2017), but a broad scale examination is non-existent in the U.S. Rocky Mountains. Past

climate reconstructions have shown that paleo-treelines have descended in response to

extreme drought during the Holocene (Lloyd & Graumlich 1997, Morgan et al. 2014,

Bunn et al. 2018). Mountain forests have already seen changes in processes and increased

mortality associated with the shifting climatic controls (Allen & Breshears 1998,

Mantgem et al. 2009, Smith et al. 2015, Davis et al. 2019). Growing season moisture has

been found as an important beneficial factor of establishment at treeline (Weisberg &

Baker 1995, Hessl & Baker 1997, Lloyd & Graumlich 1997, Elliott & Cowell 2015), but

the impact of moisture limitations in the context of regeneration during hotter drought is

lesser known (Martínez-Vilalta & Lloret 2016). Water stress is more likely at treeline due

to greater sun exposure and relatively thin soils, and even more likely on south-facing

slopes because of the typically less developed soils (Sveinbjörnsson 2000, Shickoff

2005). There has already been decadal evidence of drought affecting the regeneration of

seedlings at treeline in the 1950's-1960 in northern Patagonia (Villalba & Veblen 1997).

Multiple other studies across the Himalayas (Liang et al. 2012, Sidgel et al. 2018, Lu et

al. 2019), Rocky Mountains (Kueppers et al. 2017), and Patagonia (Daniels and Veblen

2004) suggest that hotter drought may already be causing a decline in establishment

along these historically temperature-limited treelines.

  A large factor in patterns of tree establishment interactions is slope aspect and

differences between north and south slope aspects have been shown to cause a variation

between temperature and moisture and should be examined separately from each other (Bell et al. 2014, Salzer et al. 2014, Elliott & Cowell 2015, Bunn et al. 2018, Kambo & Danby 2018). Slope aspect creates differences in soil moisture conditions that have been shown to constrain success in establishment at treeline (Weisberg & Baker 1995, Hessl & Baker 1997, Lloyd & Fastie 2003, Daniels & Veblen 2004, Danby & Hik 2007, Salzer et al. 2014, Davis & Gedalof 2018). South-facing slopes are typically drier and hotter than north-facing slopes on the same peak (Barry 2008). The tradition paradigm would suggest that, in response to rising temperatures, establishment would first happen on south facing slopes due to the already warmer environment (Elliott & Kipfmueller 2010). With the surpassing of a temperature threshold to a moisture limited environment, these south-facing slopes would be expected to first show signs of drought stress when compared with corresponding north-facing slopes (Germino et al. 2002, Salzer et al. 2014). These dry south-facing slopes could be the first indicators that treelines are no longer temperature dependent but instead drought limited (Daniels & Veblen 2004, Danby & Hik 2007, Salzer et al. 2014, Lu et al. 2019). The rise in temperature and decrease moisture availability would be expected to lead to a favoring of tree recruitment on mesic north-facing slopes as opposed to more xeric south-facing slopes (Elliott & Cowell 2015). This shows that while the focus is normally on top-down controls in treeline research, there is also a factor of fine scale, bottom-up controls taking place across broad scales that can have an even bigger impact on the ability for regeneration to happen at treeline. This collectively demonstrates the importance of considering local scale interactions of factors such as geomorphic processes, moisture availability, or topography (e.g. Elliott & Cowell 2015, Sidgel et al. 2018, Malanson et al. 2019). What

remains unknown, however, is how fine-scale moisture gradients produced by differences in slope aspect regulate the ecological expression of broad-scale drought conditions across upper treeline ecotones in the Rocky Mountains (Elliott & Cowell 2015).

Past research on treeline analysis has been on a relatively coarse timescale, with many being on the millennial timescale (e.g. Fall 1997, Lloyd & Graumlich 1997, Mensing et al. 2011, Carrara & McGeehin 2015). As shown by multiple studies (i.e. Elliott 2012, Camarero et al. 2015, Kueppers et al. 2017, Kullman 2018) changes are now happening at a timescale of decades since the 1950's rather than centuries. Tree survival has been shown to be correlated with climate variation on an approximate decadal scale (Villalba & Veblen 1997, Danby & Hik 2007, IPCC 2014). Short term (decadal) predictions are difficult to establish due to the lack of fine scale data, so now there is a need for annual studies to look at these changes on a finer scale (Lloyd 2005). There are many uncertainties in extrapolation decadal-scale predictions from millennial-scale studies, which calls in the need for more fine scale studies (Lloyd 2005). Seedlings give the opportunity to see establishment changes at an annual resolution unlike older growth, which annual establishment dating is near impossible because of the susceptibility to missing inner rings (Germino et al. 2002). Few studies (Smith et al. 2009, Andrus et al. 2018, Malanson et al. 2019) have looked at annual variability in seedling establishment, even less have looked in relation to slope aspect-drought relationships, and annual variability in seedling establishment could be the key to being able to understand climate variability (Germino et al. 2002). Recent histories could lead to conclusions about what the most plausible scenario might be for the not so distant future of the forests (Lloyd 2005).

The specific objectives of this study were to (a) obtain an annual resolution of seedling regeneration above treeline at sites in the Southern Rocky Mountains and (b) analyze annual climate variables and determine the role of drought on temporal seedling regeneration patterns. Based on the evidence of increasing drought conditions in Western North America, I hypothesized that the influence of drought conditions would be meditated by topoclimate with north-facing slopes showing a higher rate of regeneration. I also hypothesized that south-facing sloped would show a slowed regeneration as moisture constrains overtake temperature constrains as the limiting factor for treeline regeneration. It is the hope that reconstruction of tree regeneration patterns at treelines along short timescales could lead to better understanding of the effects of a changing climate on the future forest dynamics.

2. METHODS

2.1 Study Area

The Sangre de Cristo (SDC) mountains form a long, narrow range that extend approximately 389 km along the eastern front of the Rocky Mountains, forming the southeastern extent of the Southern Rocky Mountain massif in western North America (Fig. 1). As a region, the Southern Rocky Mountains rise abruptly from the Great Plains with vast expanses of alpine tundra on peaks rising to 3800–4280 m. Compared to the Northern Rocky Mountains, this region contains more climatically-sensitive treeline ecotones to study the influence of climate change (Butler et al. 2007, Elliott & Petruccelli 2018). The ice ages largely shaped the SDC mountains visible today. Glaciers have advanced at least three times into the SDC range and shaped many of the peaks during the last advance 30,000–12,000 years ago (Lindsay 2010). Soils across the SDC range are complex and can vary widely over short distances (Allen & Peet 1990). In general. pedogenic processes create shallow, infertile soils with a course texture, although higher elevations tend to have a deeper soil profile from more weathering (Peet 2000).

Opposite south-facing and north-facing slope aspects were used for this study to contrast opposing temperature-moisture regimes (Barry 2008). North-facing slopes are generally more mesic with denser vegetation, while south facing slopes are more xeric. In the low moisture region of the SDC range, vegetation is strongly related to elevation and site-specific moisture availability (Allen & Peet 1990) and can vary across slope aspects. Engelmann spruce (*Picea engelmannii*) dominate across north-facing slopes, while Rocky Mountain bristlecone pine (*Pinus aristata*) is more common on south-facing

slopes, with both species often forming monospecific stands at treeline (Elliott &

Kipfmueller 2010).

The precipitation regime of the SDC is bimodal, with both warm season and cool

season regimes controlled by separate mechanisms (Coats et al. 2015). Cool season

precipitation falls mainly as snow while the warm season precipitation falls as rain and is

brought on by the North American Monsoon (NAM) in July/August. The summer

monsoon season provides on average 57.1% of annual precipitation (Elliott & Cowell

2015). It has been found that these two seasons of precipitation are inversely related (Lo

& Clark 2002). There has been a trend of decreasing snowpack since 1978 and the

summer monsoon season provides critical moisture to compensate for persistent cool

season droughts (Clow 2010, Coats et al. 2015). Climate trends from PRISM

(precipitation–elevation regressions on independent slopes model) data show that while

annual maximum temperatures (T_{max}) has been relatively stable in the past, it has been

consistently above the 20th-Century average since c.a. 2000. Minimum temperature (T_{min})

has increased dramatically since the early 1990's (Fig. 2a). Annual precipitation,

however, has fluctuated with an increase in the late 20th century before a swift decrease

at the turn of the 21st century (Fig. 2b).

2.2 Field Methods

During summer 2019, I re-visited six study sites at upper treeline in the SDC range to

examine decadal-scale changes wrought by increasingly warm and dry conditions (Fig.

1). These sites were originally sampled in 2007 (see Elliott & Kipfmueller 2010, 2011).

These sites were selected for study based on the presence of a climatic treeline to avoid

human or natural disturbances, such as grazing, fire, and/or avalanches (Butler et al.

2007). I placed paired nested-belt transects on contrasting south-facing (azimuth 135° to 225°) and north-facing (azimuth 315° to 45°) slopes on three mountain peaks in the SDC (n = 6 transects). Transects were attempted to be repeated from Elliott & Kipfmueller (2010) on each of these peaks, but if the ecotone had shifted or the transect could not be found a new transect was placed. Transects began at an outpost tree (term after Paulsen et al. 2000), which was defined as the furthest upright seedling (<1m in height) within the ecotone. At each site, a rectangular plot [40m wide to timberline (maximum length of 150m)] was created on each of the six slopes. Timberline, or the forest line, was used to demarcate the uppermost extent of closed-canopy subalpine forest. I recorded detailed information for each of the transects including elevation, GPS coordinates of the outpost tree, slope aspect, and slope steepness (°). All seedlings inside the plots were sampled and detailed conditions were collected for each one including height, diameter at ground level, and species.

2.3 Dendrochronology Methods

To obtain annual resolution for the year of establishment, seedlings were destructively sampled and uprooted by removing the surrounding soil with a gardening shovel and retrieving the section of the stem containing the root-shoot boundary. Larger samples were cut to extend at least 10cm above and below the root-shoot boundary (Davis et al. 2019), while seedlings that were smaller were kept whole until I returned to the lab. In the lab, I cut the samples into four 1 cm successive cross sections from the root upward or until the pith appeared (League & Veblen 2006). The pith is apparent in the stem, but not the root, so method was used to ensure that the cross sections spanned the critical root-shoot boundary (Telewski 1993). The cross sections were glued to wooden mounts and

then sanded with progressively finer grit sandpaper. Annual rings were counted under a binocular microscope along at least two radii to account for the possible influence of partial or damaged rings (Andrus et al. 2018). The segment with the largest number of rings that also contained the pith was interpreted to signify the transition zone at the root-collar and was then used to denote the year of establishment (Davis et al. 2019). In addition, for a segment to be accepted as the annual date of establishment, it had to be bracketed by cross sections with fewer annual rings above and below. If the ring boundaries were too indistinct to be confidently counted or a segment with a smaller number of rings above and below the root shoot boundary could not be identified, the sample was excluded from the final age structure (n = 12). Abnormal features, such as narrow rings or scars, were identified and recorded, but the seedlings were too young to allow for quantitative cross- dating based off marker rings (Andrus et al. 2018).

2.4 Climate Data

Climate stations are rare at high elevations around the globe (Pepin et al. 2015) and stations do not exist in the SDC range. To obtain climate data for this study, I downloaded PRISM data (PRISM Group, Oregon State University, http:// www.prismclimate.org) for each mountain peak. These data have been shown to accurately represent precipitation and temperature values across remote mountain regions that are strongly influenced by elevation and complex topography (Daly et al. 2008). If the opposing transects fell within two different grids in the PRISM database (2.5′ resolution), the higher elevation one was chosen to more accurately represent conditions at upper treeline. The climate variables analyzed were as follows: (1) cool season (October-May) T_{min}; (2) cool season T_{max}; (3) warm season (June-September) T_{min}; (5)

warm season T_{max}; (6) Snow water equivalent (SWE) on April 1; and (7) warm season

Standardized Precipitation-Evapotranspiration Index (SPEI). Annual SWE data were

collected from the nearest high-elevation (3000–3390 m) SNOTEL station to each site.

(https://www.wcc.nrcs.usda.gov/snow/snow_map.html). SWE on April 1 was used as an

estimate of snowpack depth toward the end of the snow season and to indicate how much

moisture would be available at the beginning of the growing season and/or to understand

years when high snowpack accumulation could delay the onset of growth. I used SPEI

data to analyze the influence of drought on seedling establishment

(http://spei.csic.es/database.html). SPEI data combine temperature and precipitation

values to produce a multiscalar drought index based on the environmental water balance

(Vicente-Serrano et al. 2010). For each climate variable, data from the three mountain

peaks in the study area were combined to create a regional average that was used for

analyses.

2.5 Data Analysis

I used statistical analyses to quantify the differences in treeline structure across north and

south-facing slopes. A two-sample Kolmogorov-Smirnov test was used to quantify

differences in seedling age structure between slope aspects. A chi-square goodness-of-fit

test was used to test the proportional differences in the frequency of seedling

establishment. The expected value was half of the observed number of seedlings, which

assumes that establishment was not favored by a specific slope aspect. A Mann-Whitney

U-test was used to test for statistically significant differences in seedling height, diameter

at ground level (DGL), and age because data did not have a normal distribution.

To test for the relative importance of seasonal climate variables on annual seedling establishment, I used a Poisson family linear regression and stepwise regression. It is not known how many seedlings failed to establish in a given year so a binary output was not possible, therefore a Poisson regression was chosen because the results could be modeled as simply the count of events that occurred (Hardin & Hilbe 2012). Each seedling established in a year was classified as an individual event and establishment was modeled in R as number of events per year across the years 1994 to 2009 as a function of slope aspect and annual climate variables. The relative impact of each variable on seedling establishment was assessed using the coefficients and the p-value each variable in the model results.

I performed a regime shift-analysis using a sequential t-test method (Rodionov 2004) on the PRISM climate data to measure significant switches ($p < 0.05$) in warm season and cool season temperature and precipitation patterns. This method identifies a regime shift when the cumulative sums of normalized deviation from the mean differs significantly from the present regime (Rodionov & Overland, 2005). The analysis was done with a 10-year cut off to show the importance of decadal scale trends (Villalba & Veblen 1997, Elliott 2012). Only PRISM climate data was used because it contained a complete record from 1900 to 2019 to capture the true likelihood of regime shifts compared to past climate trends.

3. RESULTS

3.1 Treeline Structure

A total of 234 seedlings were collected from six treeline sites in the SDC range. Of these, there were significantly more ($p < 0.01$) seedlings found on north-facing slopes ($n = 169$) than south- facing slopes ($n = 66$; Fig. 3). There was also a higher density of regeneration on north-facing slopes ($\mu = 228.4$ seedlings/ha) compared to south-facing slopes ($\mu = 78.3$ seedlings/ha; Fig. 4). In addition, seedlings on north-facing slopes were significantly shorter ($p < 0.01$) and smaller in diameter ($p < 0.01$) than those on south-facing slopes (Fig. 5).

The year of establishment was successfully determined for 223 samples (95% of total). These seedlings were relatively young, with 93% ($n = 207$) established since 1994. The seedlings on north-facing slopes were significantly younger ($p < 0.05$) than those on south-facing slopes at a regional scale (Fig. 5). The annual patterns of establishment (Fig. 6) showed only moderate rates from 1994 to 1996 with relatively little establishment from 1997 to 2002. From 2003 to 2006 there was an abrupt peak that contained over 67% of seedling establishment. Following the peak, moderate establishment was seen again from 2007 to 2009 with no successful establishment recorded since 2010. Based on a two-sample Kolmogorov-Smirnov test, the overall age- structure patterns were not significantly different across slope aspects ($p > 0.05$).

3.2 Climate Interactions

Based on the regression results, the intercept modeled at a baseline of 12.5 seedlings established per year across all sites (Table 2), though this was exceeded in 31% of the modeled years. When including climate predictors, the model showed that patterns of

seedling establishment were driven mainly by cool season temperatures and growing

season drought stress. Seedling establishment showed a significant ($p < 0.001$) and

inverse relationship with drought stress, meaning a lower SPEI value led to higher rates

of establishment. Both cool season T_{min} ($p < 0.001$) and cool season T_{max} ($p < 0.01$) were

significant with maximum temperature having an inverse relationship with establishment.

Also, SWE was found to have a significant inverse relationship ($p < 0.01$). Establishment

was more likely to occur on both slope aspects in seasons with a lower SPEI index, less

variation in winter temperatures, and a lower snowpack at the start of the warm season.

Slope aspect was found to be moderately significant ($p < 0.1$) with north facing slopes

showing a greater likelihood of establishment (coefficient of ~6.8) with all other

variables kept constant. A significant difference in individual climate-slope interactions

was not found, but warm season maximum temperature and its slope interaction were

included in the final model. The negative relationship means that warm season T_{max} limits

establishment to a greater extent on north facing slopes than south facing slopes. Though

there is no significant slope aspect difference for an individual climate factor, the

interaction term still affects the overall model.

Climate has been changing rapidly since the 1950's and the regime-shift analysis

captured many significant shifts away from the mean of the 20th century within the 25

years of this study. There were multiple regime shifts found for warm season minimum

temperature. The first regime shift was in 1998 with an increase in warm season

minimum temperature after 46 years of a continuous regime that started in 1952 (Fig. 7a).

The second shift was relatively quick to follow in 2007, with a third increase in 2019

(Fig. 7a). A similar pattern was found for cool season minimum temperature with the first

shift happening in 1999 after 55 years of the previous regime that began in 1944. The second shift was, again, relatively quick with another increase in the minimum temperature in 2006 and a third increase in 2015 (Fig. 7b). Cool season precipitation declined in 2000 after 26 years in the previous regime and declined again in 2018 (Fig. 7c). There was an increase in the warm season precipitation regime in 2018. Moving forward, these shifts show an overall trend towards increasingly warm and dry conditions relative to the 20th Century.

4. DISCUSSION

Over the past 25 years, annual patterns of seedling establishment at upper treeline in the SDC range have been driven by temperature-moisture interactions. To my knowledge, this study represents the first collection of annually-resolved data to examine the influence of climate on seedling establishment at upper treeline across a broad landscape scale. The results from this research show evidence for a top-down drought-mediated response of seedling establishment since 1994 as well as demonstrating the importance of bottom-up influences from differences in slope aspect. As hotter drought intensifies in the coming decades, this research suggests that a majority of successful seedling establishment will likely be increasingly confined to north-facing slopes. The lack of successful establishment over the past decade, however, could be evidence that a threshold has been exceeded, whereby conditions might be 'beyond the climate optimum' (after Lu et al. 2019) for successful seedling establishment and related treeline advance moving forward.

4.1 Moisture-Driven Changes in Treeline Structure

Under drought stress at treeline it would be expected for moisture limitations to emerge on south-facing slopes and establishment to become more confined to north-facing slopes with higher moisture availability (Weisberg & Baker 1995, Germino et al. 2002, Millar et al. 2015). Due to slope aspect dynamics, a transition from temperature limitations to moisture mediated limitations would first be seen on south facing slopes (Salzer et al. 2014, Elliott & Cowell 2015). In fact, younger and a greater number of seedlings were found on north-facing slopes as opposed to south-facing slopes across the landscape, demonstrating that conditions for establishment may not be as favorable on south-facing

slopes as they once were (Weisberg & Baker 1995). Younger seedlings on north-facing slopes suggest that moving forward, slope aspect will continue to modify the influence of hotter drought on seedling establishment at upper treeline (Dang et al. 2015, Elliott & Cowell 2015). As moisture limitations progress, it would be expected that south-facing slopes continue to become less favorable as establishment continues to become more confined to north-facing slopes. A continued increase in temperature across the SDC would eventually begin to impact seedlings on north-facing slopes as well. This widespread presence of moisture limitations could obstruct the advancement of treeline that was once expected with a temperature increase (Lloyd & Fastie 2002, Sigdel et al. 2018, Lu et al. 2019).

4.2 Climate-Species Interactions

Given that moisture-mediated changes would be anticipated to be highest on south-facing slopes, the model output was counterintuitive with respect to seedling establishment being more negatively impacted by increased warm season T_{max} on north-facing slopes. This can likely be explained by the idiosyncratic response of species to climate variables (Loranger et al. 2016). While bristlecone pine is more drought-tolerant and dominates on south-facing slopes (Bunn et al. 2018), Engelmann spruce are more susceptible to drought and therefore could be impacted more by swiftly rising temperatures (Gill et al. 2015, Buechling et al. 2016, Kueppers et al. 2017). Still, there is an overall favoritism for establishment on north-facing slopes, even with less drought-tolerant Engelmann spruce as the dominant species. Despite the contradiction of the model results, this expands on the idea that due to increased warming, establishment is moving away from more warmer south-facing slopes that contain more drought-tolerant species (Danby & Hik 2007, Bunn

et al. 2018), to more mesic north-facing sites after the increased warming in the 1950's

(Salzer et al. 2014, Elliott & Cowell 2015). With a continued increase in warm season

temperature, establishment would become more constrained to north facing slopes, and as

the present species reach their physiological moisture limitations, establishment of

seedlings could become restricted or disappear altogether.

4.3 Relationship of Snowpack and Growing Season Moisture

Moisture-limited seedling establishment at upper treeline can be explained by examining

the relationship between spring snowpack and summer precipitation. The longevity of

spring snowpack contributes to moisture availability for seedling establishment by

helping to shape the length of the growing season (Moir et al. 1999, Smith et al. 2003, Hu

et al. 2010, Elliott 2012). Early loss of snowpack has been shown to increase drought

stress during the growing season and leave seedlings without a protective cover which

makes them more susceptible to wind damage, frost damage, and moisture deficiencies

from harsh arctic winds (Camararo & Gutiérrez 2004, Hagedorn et al. 2014, Elliott &

Petruccelli 2018, Broderson et al. 2019, Malanson et al. 2019), though this was not the

case with my results. The lengthening of the growing season from early emergence is

beneficial until the point when emergence is too early and instead causes an exacerbation

of moisture stress during the summer months (Kueppers et al. 2017). Summer

precipitation has been shown to be at least as important as increase in temperature for the

upward movement of treeline (Moyes et al. 2015). Drought stress is more harmful in

shallow rooted seedings (Smithers et al. 2018), so early emergence would only be helpful

when the loss of spring snowmelt is countered with moisture availability from the

summer monsoon. Many studies have found the Southern Rocky Mountains are at risk

for a continued rise in drought during the 21st century (i.e. Jiang et al. 2013, Coats et al. 2015), and if the summer monsoon was to fail along with a decrease in snowpack, dual-season drought could result with dire ecological impacts for this region (Coats et al. 2015). Past failure of the summer monsoon in the 1950's led to an increase in warm season T_{max} and in tree establishment at upper treeline throughout the region (Elliott & Kipfmueller 2011), but this research suggests that a similar combination would impede seedling establishment; providing likely evidence for non-stationary climate-vegetation interactions since the 1950s (Daniels & Veblen 2004, Fajardo & McIntire 2012, Holtmeier & Broll 2015). So, an earlier loss of spring snowpack, paired with the negative correlation with summer drought stress, highlights the importance of moisture obtained by the regional summer monsoon to mitigate the negative impacts of drought stress during the growing season.

4.4 Role of Winter Temperature

Observed importance of winter temperature indicates that growing season climate is not the only important factor leading to successful regeneration. It has been found in other studies that winter temperatures play a significant role in annual seedling establishment and must also be accounted for (Kullman et al. 2007, Rickebusch et al. 2007, Harsh et al. 2009, Hagerdorn et al. 2014, Davis & Gedalof 2018). Unlike other studies, where sites that had more warming during the winter months were found to be more likely to have shown advancement (Kullman 2007, Rickebusch et al. 2007, Harsch et al. 2009, Hagedorn et al. 2014), model results show establishment is negatively correlated with winter maximum temperatures but positively correlated with winter minimum temperatures. This implies that less winter variation is beneficial for seedling

establishment the following growing season. Less variability during cool-season months

has been shown elsewhere to increase the establishment of seedlings above treeline

(Camarero & Gutierrez 2004). With both minimum and maximum temperatures rising,

this could lead to a decrease in the stability of the snowpack leading to issues in both

micro-environment and moisture availability (Hagerdorn et al. 2014). Consistent

snowpack is needed to provide thermal and physical protection to new establishment

during freezing (Elliott & Petruccelli 2018) and this overall rise in winter temperature can

result in a melting and refreezing of the snowpack that leaves seedlings susceptible to

winter desiccation. The increase in temperature also increases the evapotranspiration

during the cool season, which further diminishes the snowpack and the available spring

and summer moisture (Millar & Stephenson 2015, Sigdel et al. 2018).

4.5. Evidence of Moisture Threshold Surpassed

The observed decade (2009-2019) with no regeneration could be evidence that moisture

limitation thresholds have been surpassed and there are no longer appropriate conditions

for successful establishment above treeline in the SDC. In past studies, there has been an

overall increase of establishment at these sites since the onset of rapid warming around

the 1950's (Elliott 2012), but this study has shown an abrupt transition in establishment

patterns. Other studies have shown that if moisture availability were to surpass a

minimum threshold it would lead to the decline of treeline in the 21st century (Conlisk et

al. 2017, Sigdel et al. 2018, Lu et al. 2019). This lack of seeding regeneration could be

one of the first observed responses of a minimum threshold for moisture availability

being surpassed for successful regeneration. There has been as observed slowing of

regeneration on south facing sites above treeline (Weisberg & Baker 1995, Lloyd &

Fastie 2002), providing evidence that climate may already not be as favorable for establishment as it once was. The regime shifts that have happened within the study period showed a continuation towards a warmer and drier climate in the SDC range with climate trends having shown a large deviation from the mean of the last half of the 20th century (1950-1999). In particular, the increase in warm season minimum temperatures coupled with a decrease in precipitation (Fig. 8a). An increase in seasonal temperatures without a coinciding increase in precipitation increases drought impacts and negatively affects seedling establishment, which could limit upward treeline expansion (Lloyd & Graumlich 1997, Daniels & Veblen 2004, Moyes et al. 2015, Conslik et al. 2017, Kueppers et al. 2017, Sigdel et al. 2018). While lower SWE has been shown to have a positive impact on seedling establishment, it has dropped far below the average (Fig. 8b) and could now be hindering the establishment of seedling by increasing moisture deficiency in the warm growing season (Elliott 2012, Kueppers et al. 2017). For seedlings to establish, multiple years of appropriate climate conditions are needed, especially high-water availability (Gill et al. 2015, Buechling et al. 2016) and the observed regime shifts in climate may now be limiting the number of years that fall into appropriate climate conditions. While more studies and monitoring of these sites are needed in the future, the compounded effects of the decrease in growing season water availability from the early loss of winter snowpack, rise in warm season temperatures, and low to stationary precipitation values could now be surpassing a moisture availability minimum threshold at treeline, possibly providing an explanation to the absence of establishment in the last decade.

Given the timescale of decades to centuries that is needed for these mountain forests to form, the results of this study could just be showing the natural fluctuations in establishment at treeline. Though, if the patterns seen in this most recent decade continue, the mountain forest belt will no longer be expanding with the rising temperatures, and instead be at risk of losing area (Hu et al. 2010, Jiang et al. 2013). Another possible explanation of absence of regeneration is the possibility of human-driven disturbance, such as grazing. Lastly there is a possibility of newly established seedlings having been overlooked, though most sites did not have lush vegetation and small seedlings were easily spotted. However, the consistency of establishment patterns across a landscape scale supports the conclusion that the absence of establishment was climatically related. Yet it is possible that the timescale of this study is just too short be able to clearly interpret the patterns behind observed regeneration, or lack thereof.

5. CONCLUSION

In conclusion, the Southern Rocky Mountain region has been experiencing drought conditions since the beginning of the 21st century and the effects have been widespread across elevations (Breshears et al. 2005, Smith et al. 2015, Davis et al. 2019). Drought impacts have been observed at treeline on a local scale (Moyes et al. 2015), but it was unknown if drought impacts have influenced establishment across a broader scale. These results indicate a possible future decrease in forest spatial extent due to the restriction of regeneration necessary for advance at alpine treeline combined with the increase mortality in lower elevation mountain forests (Allen & Breshears 1998, League & Veblen 2006, Jiang et al. 2013). The change of these areas away from a temperature-controlled environment could mean the loss of these ecotones as a proxy data source for temperature variability (*sensu* Bunn et al. 2018). As these treelines surpass climatic thresholds and already show signs of remaining static or declining, it is unknown what consequences are to come from the quickly changing climate in the next several decades. Recent histories could lead to conclusions about what the most plausible scenario might be for the not so distant future of the forests (Lloyd 2005) and this information gathered could be used as a proxy for other sites if the trend of warmer and drier conditions continues throughout the 21st century and across the globe. Future studies should monitor the establishment patterns of the Sangre de Cristo range to see if this pattern persists and should also expand the scope of this study to reveal if these drought responses are spreading to other susceptible treelines, throughout the Southern Rocky Mountain region.

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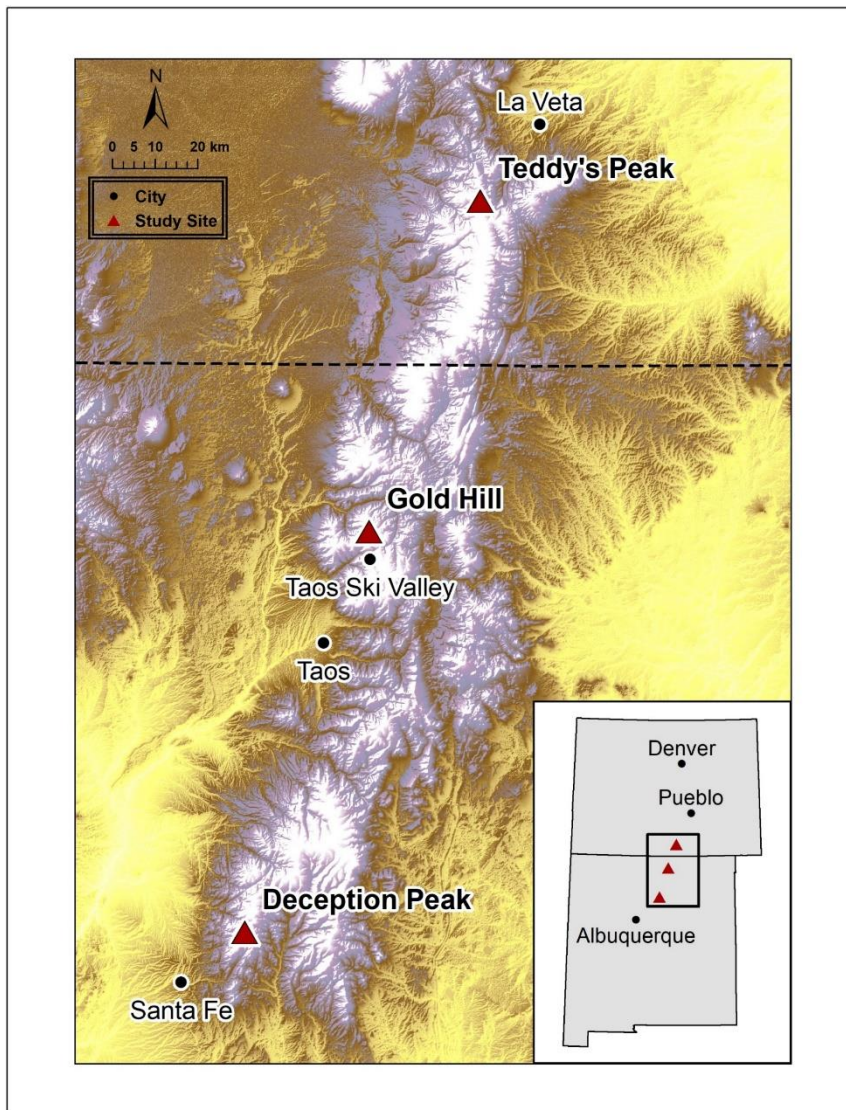   *Research*, *25*(8), 1326–1339. doi: 10.1139/x95-145.

7. TABLES AND FIGURES

Figure 1. Study area in the Sangre de Cristo Mountains of southern Colorado and northern New Mexico, within the Southern Rocky Mountain region. Each study site represents a mountain peak with a transect on opposite north- and south-facing slope.
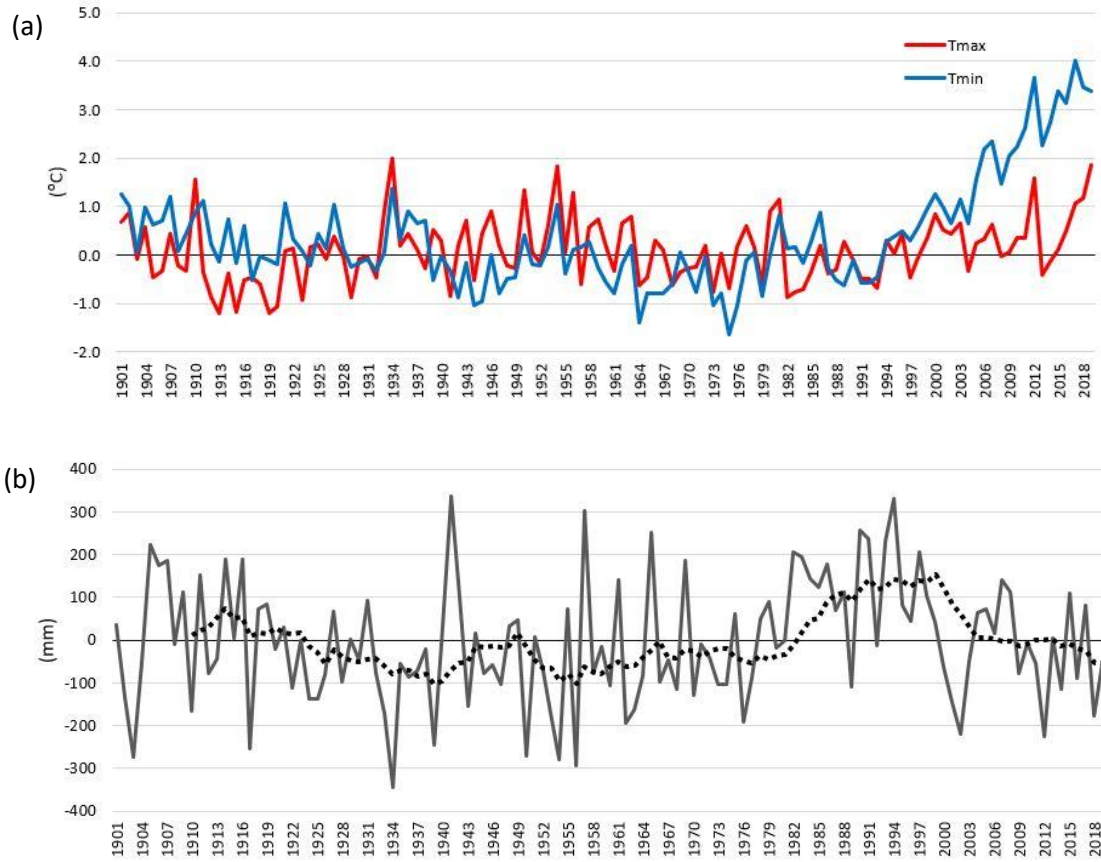
Figure 2. (a) Annual temperature data shown as deviations from the 20th century mean during the warm and cool seasons. (b) Annual precipitation for the entire year shown with a 10-year moving average (dotted line). Data is expressed as regional averages from the sites used in this study (n = 3) and calculated from PRISM data grids.
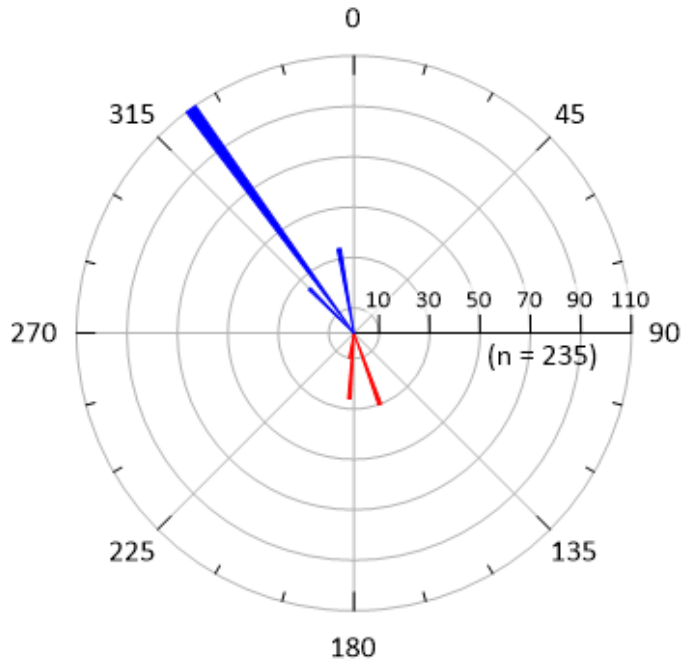
Figure 3. Polar bar charts of seedling establishment for north-facing slopes (plotted in blue) and south-facing slopes (plotted in red). Radius angle shows slope aspect in degrees and radius length denotes frequency (n). Based on chi-square goodness-of-fit test, significantly more seedlings ($p < 0.01$) found on north-facing slopes.
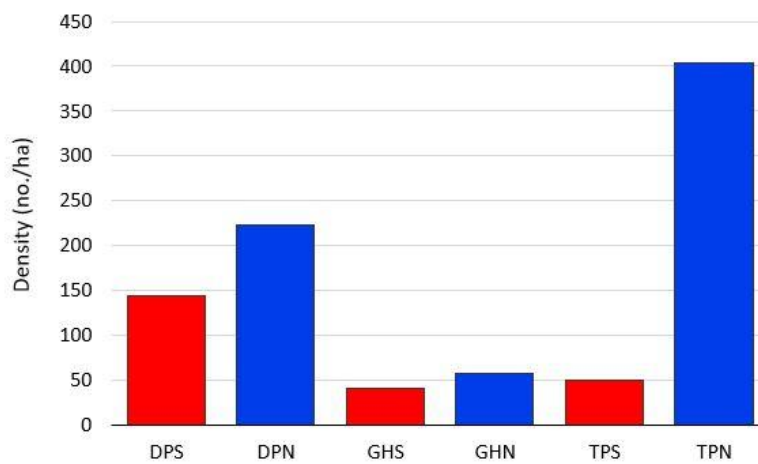

Figure 4. Density of seedlings at each site measured in number of seedlings per hectare. North-facing slopes are shown in red and south-facing slopes are shown as blue.
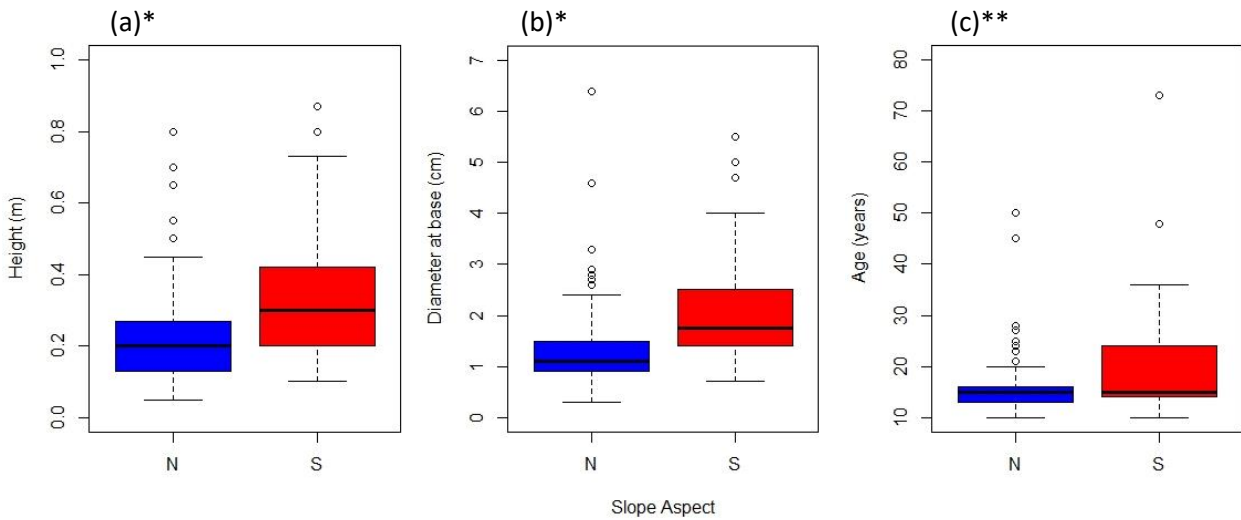
Figure 5. Boxplot-and-whisker plots showing distribution of (a) height and (b) diameter at base (c) age for seedlings collected (n=235) on north-facing slopes (n = 169) and south-facing slopes (n = 66). Circles denote outlier while (*) indicated significant differences ($p < 0.01$) and (**) signifies significant differences ($p < 0.05$) using Mann-Whitney U-Test.
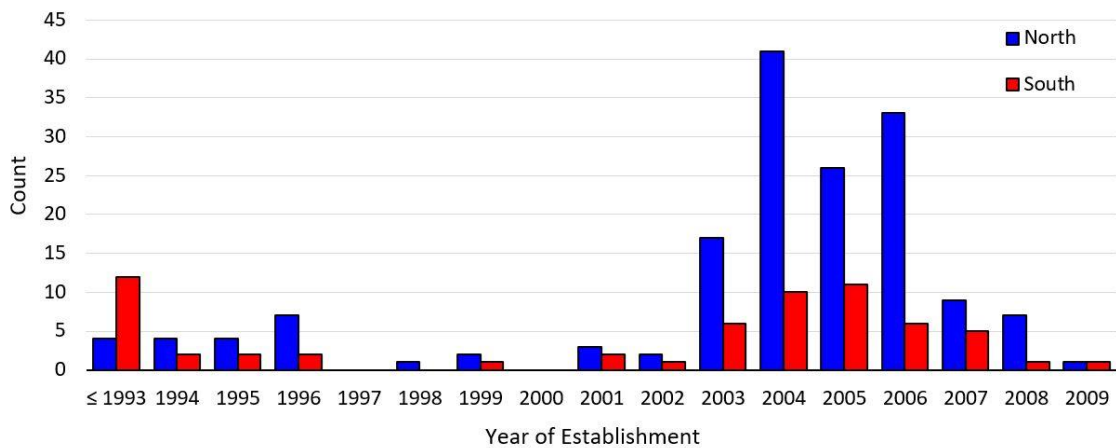

Figure 6. Annual age-structure data (1994-2009) for all seedlings sampled. Seedlings that were established before 1994 are shown in the ≤ 1993 class. There were significantly more ($p < 0.01$) seedling on north-facing slopes (blue) than south-facing slopes (red).
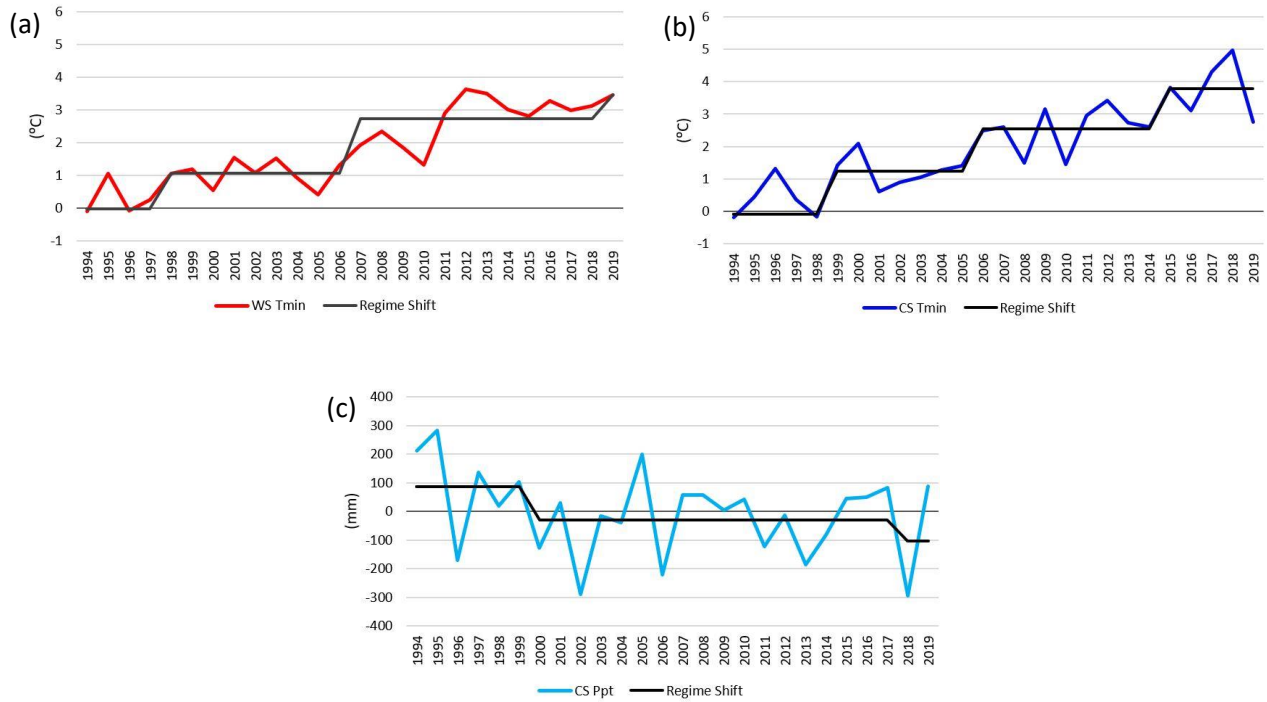
Figure 7. Annual climate data shown as deviation from the mean that contained regime-shifts for the study period (1994-2019). Regime-shifts found for (a) WS T_{min} (b) CS T_{min} and (c) CS Ppt. Bold line denotes value of respective regime-shift analysis and the abrupt change point in time reflects a significant positive or negative shift ($p < 0.05$) toward a new regime.
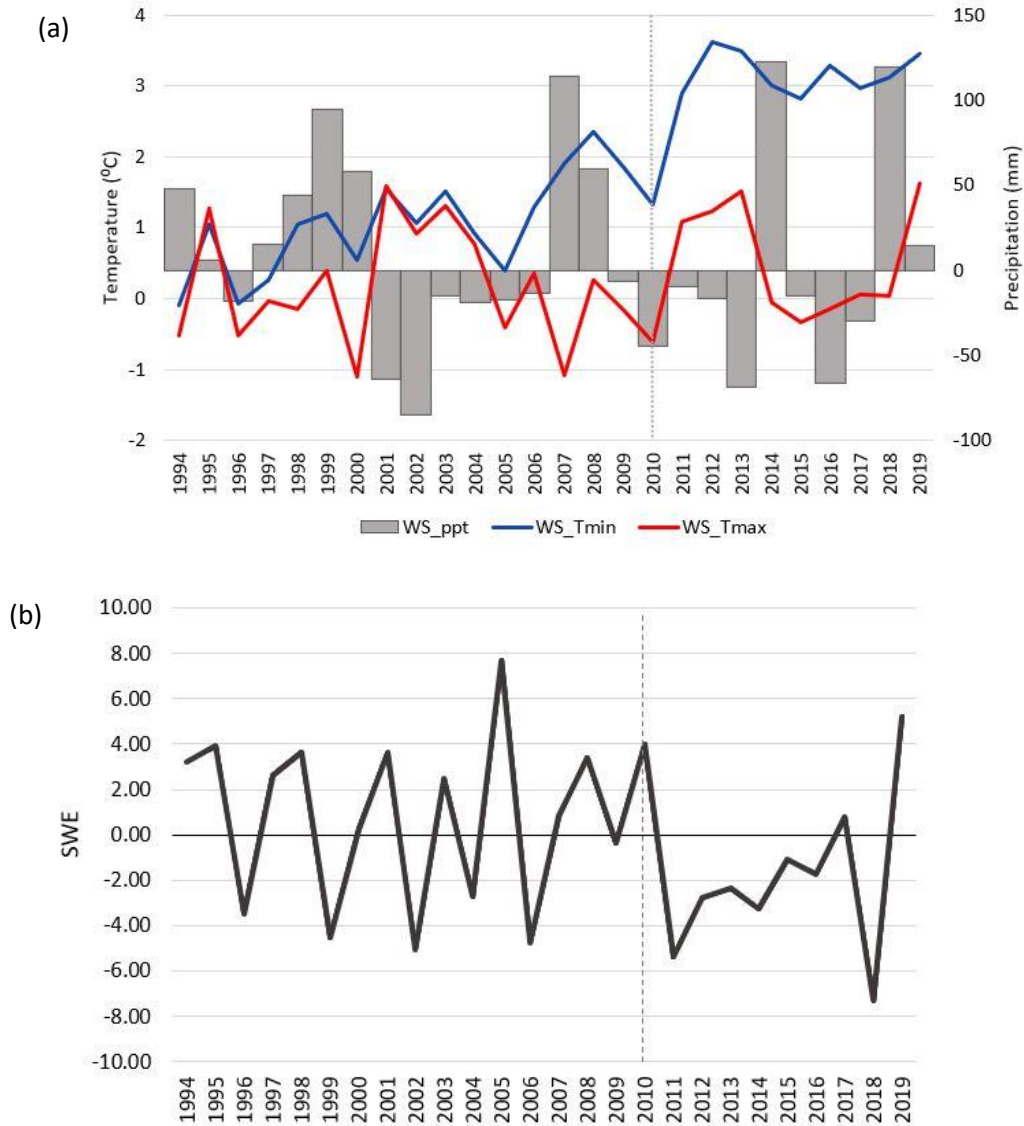
Figure 8. Annual climate data shown as deviations from the late half of the 20th century (1950-1999) mean for (a) warm season temperature-moisture interactions (precipitation, T$_{min}$, T$_{max}$) and (b) SWE to emphasize the rapid changes in the study period (1994-2019). Data is expressed as regional averages from the sites used in this study (n = 3) and calculated from PRISM data grids.

Site Code	Elevation (m)	Aspect (°)	Slope (°)	Distance to treeline (m)	No. seedlings sampled	Seedling density (no./ha)	Dominant Species
DNS	3,733	170	26	45	26	144.4	PIEN
DPN	3,716	313	21	28	25	223.2	PIEN
GHS	3,698	184	15	62	10	40.3	PIAR
GHN	3,680	340	10	148	34	57.4	PIEN
TPS	3,713	150	19	188	30	50.0	PIAR
TPN	3,660	310	23	68	110	404.4	PIEN

Table 1. Treeline study sites and characteristics in the Sangre de Cristo mountains. Abbreviations are given for each of the sites; Deception Peak (DP), Gold Hill (GH), and Teddy's Peak (TP) with their respective north (N) or south (S) slope aspect. Elevation (m) refers to the location of the outpost tree. Distance to treeline (m) refers to the distance of the outpost tree downslope to timberline.

Variable	Coef. Estimate	Std. Error	z-value	p-value
Intercept	12.528	3.561	3.518	< 0.001
Warm Season SPEI	-1.152	0.259	-4.445	< 0.001
Cold Season Tmin	0.667	0.160	4.174	< 0.001
Cold Season Tmax	-0.918	0.281	-3.265	0.001
SWE April 1	-0.105	0.036	-2.953	0.003
Slope Aspect	6.897	3.698	1.865	0.06
WS Tmax * Slope Aspect	-0.348	0.223	-1.561	0.12
Warm Season Tmax	-0.106	0.210	-0.505	0.61

Table 2. Results from the Poisson model after the stepwise selection was ran. Each factor in the model in shown with the estimated coefficient, standard error, z-value, and relative p-value. Listed in order from lowest to largest p-value. Slope aspect refers to the interaction term that was placed into the model and shows the effects on north-facing slopes. WS T_{max}*Slope Aspect refers to the interaction between slope aspect and the warm season temperature and shows the results on north-facing slopes.