DENDROCLIMATIC RESPONSE ALONG A MOISTURE GRADIENT IN THE SOUTHERN ROCKY MOUNTAINS

A Thesis

by

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ABSTRACT

The spatial distributions of all plant species are controlled by their tolerances to a range of environmental conditions. However, growth patterns within the range of tolerance can vary considerably depending on the set of abiotic and biotic factors present. Understanding the mechanisms that control distributional limits of trees across environmental gradients remains an important question in biogeography, especially as we try to predict the effects of climate change on forests. However, few studies have examined tree growth patterns at distributional limits to understand how trees are responding to climatic variability across a moisture gradient. A better understanding of growth patterns and growth-climate relationships is essential to understanding drivers of distributional limits and for improving predictions about those distributions under climate change. Here I used dendroecological analysis to quantify the influence of climate and specifically moisture stress on radial growth patterns of ponderosa pine and Douglas fir growing along a moisture gradient in the Santa Fe National Forest of the Southern Rocky Mountains. I also examined growth before, during, and after a severe drought period in the 1950s to assess recovery rates across the moisture gradient.

Using tree-ring analysis, I found growth to be slower and more sensitive to climate at the low moisture distributional limit than elsewhere within the spatial distribution. Trees at this site were more impacted by the 1950s drought and showed slower growth recovery in years following. Climate sensitivity declined across the gradient from xeric to mesic sites, while the pattern of growth rate increased from xeric to intermediate sites and then plateaued. Growth and sensitivity at the xeric site indicates that the distribution is limited by the trees' physiological intolerance to low moisture, while patterns at the mesic site suggest that this distributional limit is not related to intolerances to high moisture, but rather that biotic interactions (e.g. competition) may be the controlling factor. Therefore distributional limits at high and low moisture ends of the gradient are likely driven by different environmental factors and as a result will respond differently to future climate change.

DEDICATION

To my parents for their encouragement, support, and love. And for always reminding me to follow my dreams. To my grandparents for keeping me positive. And to the love of my life, Chuck, for his patience, kindness, and love through it all.

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Finally, I am incredibly grateful for my friends Brianna Hammond, Luci Pounders, and Jamie Turner. They shared this journey with me and reminded me of the important things in life. Their friendship means more to me than I could ever express.

NOMENCLATURE

PDSI	Palmer Drought Severity Index
BAI	Basal area increment
RWI	Ring width index

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Introduction

Every plant species thrives only within a certain range of environmental conditions. For every environmental condition, there are both minimum and maximum levels, or tolerance limits, beyond which a species can no longer survive (Shelford 1913). However, growth within this range of tolerance can vary considerably along environmental gradients depending on the set of abiotic and biotic factors present (e.g., competition, temperature, moisture-availability, soil nutrients, light). The fundamental principles that shape species distributions have thus been a focus of biogeographic and ecological research for over a century. The law of the minimum, principle of tolerance, and the ecological niche concept together form the basis of our understanding of spatial distributions (Leibig 1855, Shelford 1913, Grinnell 1917, Elton 1927, Hutchinson 1957). Despite this theoretical background, we still do not understand the mechanisms that are creating different distributional limits (i.e. low resource limit vs. high resource limit) and how those may change in response to environmental change (Holt et al. 2009, Zimmerman et al. 2009, Wiens 2011). Specifically, we have limited understanding of how tree growth varies under different site conditions and how moisture availability affects the distributional limits of trees (Orwig & Abrams 1997, Adams & Kolb 2005).

In the Southern Rocky Mountains, moisture stress is one of the most important limiting factors for forest growth. With projected global climate change, it is important to understand how tree growth responds to climate parameters along a moisture gradient because spatial distributions may shift as a result (Allen & Breshears 1998, Allen et al. 2010). As resource availability changes over time and across environmental gradients, the distributional limits of species will also change (Smith and Huston 1989). Recent studies have shown evidence of widespread mortality, rapid drought-induced forest ecotone shifts, and the particular sensitivity of forests in semiarid landscapes of the Southwestern U.S. (Allen & Breshears 1998, Breshears et al. 2009, Koepke et al. 2010).

Physiological intolerances to limited moisture, however, may not be the only factors driving distributional limits. If range limits of species were based only on the broad set of resource requirements in the absence of competition (e.g. fundamental niche), many species would likely have wider distributions. Instead, competition can displace species toward spaces that are still within their tolerance limits, but which may be closer to their physiological limits than to the optimum (i.e. realized niche). The degree to which climate variability (especially climate extremes) or competition drives distributional limits is still not understood (Zimmerman et al. 2009).

While some studies have addressed radial growth responses to drought across different site conditions, there still remains a dearth of research that explicitly focuses on tree growth-climate relationships along a moisture gradient and emphasizes mechanisms that drive distributional limits (Orwig & Abrams 1997, Fekedulegn et al. 2003). In this research, I use dendroecological techniques to examine the influence of climatic moisture on tree growth within the context of species' growth at their distributional limits. I also seek to gain a better understanding of how tree growth responds to severe drought by examining growth before, during, and after a severe drought period in the 1950s. This is of interest because a) frequent severe drought is expected to accompany climate change, and b) extended growth suppression following a drought might precondition trees for mortality. The objectives of this research are to: 1) measure the growth rate of ponderosa pine and Douglas fir across a moisture gradient, 2) evaluate the relationship between tree-ring growth and climate parameters over time, and 3) assess growth responses to a major drought event across the moisture gradient.

Research questions

1. Do trees grow more slowly at their distributional limits than elsewhere within their spatial distribution?
2. Are trees at the species' distributional limits more sensitive to climate variability (i.e. stronger correlation to climate variables) than trees near the center of the distribution?
3. How do trees at their distributional limit respond to a severe multi-year drought?

Literature review

Species tolerance limits

All plants respond to and are limited by a set of abiotic and biotic constraints, including competition, temperature, moisture availability, soil nutrients, light etc. These factors that control the spatial distribution of all plants exist and act together along environmental gradients (e.g. from little to excessive moisture, infertile to fertile soils). This complex interaction of gradients limits the spatial distribution of plants to a particular geographical range. Understanding how plants respond to and are limited by these factors is of critical importance for explaining spatial distributions and for evaluating how communities may change in response to a changing environment (Loehle 1998, Zimmerman et al. 2009, Hart et al. 2010).

The fundamental ecological principles that account for biogeographical distributions are Von Liebig’s law of the minimum, Shelford’s law of tolerance and the ecological niche concept. Liebig’s law states that growth is controlled not by the total available resources, but rather by the availability of the resource that is in shortest supply and in high demand (Liebig 1855). The species will only be abundant where the minimum limiting resource is plentiful. Shelford’s law of tolerance takes this proposal further to say that each resource or environmental factor has a minimum and maximum level, or tolerance limit, outside which a particular species cannot survive (Shelford 1913). Therefore every plant species is able to survive, grow, and reproduce successfully only within a certain range of environmental conditions. For every abiotic factor along a gradient, a species’ range can be broken down into regions of optimal conditions, stressful conditions, and conditions of intolerance (Figure 1). Species growth and abundance should be high in the range of optimal conditions. Growth, abundance, and productivity would taper off as either end of the environmental gradient is approached (Hengeveld 1990, Hart et al. 2010). Low growth and low abundance would be expected in the region of stressful conditions, and beyond the minimum and maximum levels of that factor the species would no longer be present.

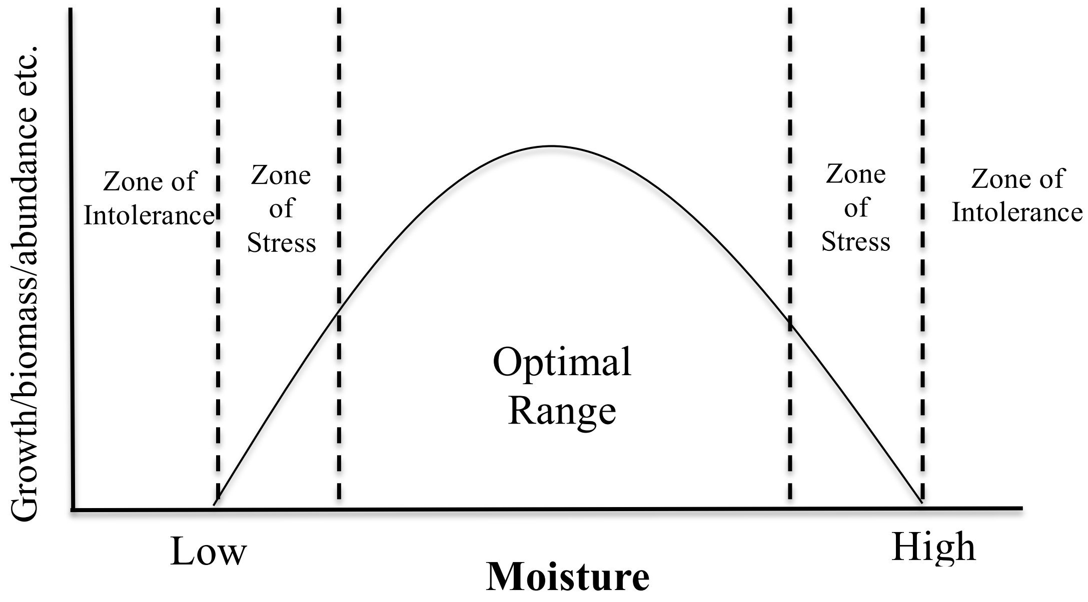


Figure 1. General model of growth across a moisture gradient based on the law of tolerance (adapted from Shelford 1913).

Models of tree growth based upon the law of tolerance suggest that growth will be reduced at the tolerance limits compared to elsewhere within the range (Figure 1) (Shelford 1913, Hengeveld 1990, Hart et al. 2010). Any abiotic factor (e.g. moisture, temperature, sunlight) could be placed along the x-axis in this model. It is important to note, however, that for any species there are a number of interacting factors that ultimately control species distributions.

The ecological niche concept is another fundamental concept in biogeography that structures our understanding of geographical distributions of species. The concept of niche was first used by J. Grinnell (1917) and C. Elton (1927) and refers to the way a species functions in its community and interacts with both the environment and other species. Grinnell emphasized the importance of resource requirements, behaviors that allow species to persist, and environmental limiting factors in his definition while Elton described niche as the specific and unique role that a species plays in its community. Thus the niche can be differentiated from the habitat, which is simply the spatial environment that a species occupies. G.E. Hutchinson (1957) further defined the niche as a multidimensional hyper-volume that accounts for resource requirements and environmental tolerances. His definition describes the set of biotic and abiotic conditions where a species can persist while also considering the impact of competition on niches. Many species can tolerate a wide range of abiotic conditions (e.g. climate) and yet we do not see species occupying such wide ranges on the landscape. Theoretically, no two species can occupy exactly the same niche resulting in spatial shift of species dominance. This is referred to as Gause's competitive exclusion principle (Gause 2003). Species can coexist and often have overlapping resource requirements, however it is still not well understood the degree of niche differentiation that is needed for coexistence (McDonald 2003,Silvertown 2004). The fundamental niche is the broad set of conditions under which a species can survive and flourish. However, if competition excludes a species from certain areas of potential niche space, this becomes the realized niche (Hutchinson 1957).

The fundamental and realized niches can further be explained in the context of the model of growth along an environmental gradient by breaking down the zone of tolerance into physiological and ecological categories. The physiological tolerance accounts for a species' potential range in the absence of competition, while the ecological tolerance accounts for species when exposed to competition (Crawford 2008).

The degree to which competition controls species distributions is still not well understood.

Species distributional limits are not only determined by abiotic and biotic conditions that are not fitting for growth, but also by the failure of the species to genetically adapt to those unsuitable conditions (Wiens 2011). Species can adapt to changing conditions over long periods of time, but based on the fact that every species does not occur everywhere, it is evident that limits do exist to create the range margins we see on the landscape. Niche conservatism is the idea that taxa tend to maintain similar ecological traits over time (Soberon & Nakamura 2009, Wiens 2011). Evidence supports that niches evolve slowly, however there have also been studies that show rapid shifts in climatically driven distributions (Soberon & Nakamura 2009, Wiens 2011). The term niche conservatism may be too vague and researchers should question what features or traits are being conserved and how some physical variables upon which niches are dependent may change faster than others (e.g. changes in moisture availability or changes in competitive ability) (Holt 2009, Soberon & Nakamura 2009). Some variables or axes within the hypervolume may vary at larger spatial scales, while others at smaller local scales (e.g. frost vs. soil acidity tolerances). Therefore it is important to understand the scale of the question at hand and how different edges of species' range can respond to different processes on the landscape.

In order to explain species distribution and succession patterns across environmental gradients, an individual-based model of plant competition for light and water was developed (Smith & Huston 1989). While it is generally understood that all plants will grow best with ample light and water, Smith and Huston showed that plants are seldom abundant under their physiologically optimal conditions due to competition from other species. For many species, the position of the ecological optimum along a resource gradient can be closer to their physiological limit than to their physiological optimum (Figure 2a) (Smith & Huston1989). Competition therefore displaces species toward spaces that are still within their tolerance limits, but may be closer to the limits than to the optimum (i.e. realized niche). The result is a pattern of species zonation on the landscape (Figure 2b). As resource availability changes over time and across environmental gradients, the distributional limits of species will also change (Smith & Huston 1989). While many models based on the ecological niche concept result in a Gaussian curve of species distributions across environmental gradients, Smith and Huston's model produced an asymmetrical curve. Here the distributions are skewed towards the low moisture end of the gradient where they are truncated by physiological limitations to low resources. The high resource end of the gradient consists of a longer "tail" of the curve where plants could potentially thrive, but are typically limited by competition. Therefore this model suggests that distributional limits are likely driven by a combination of biotic and abiotic factors.

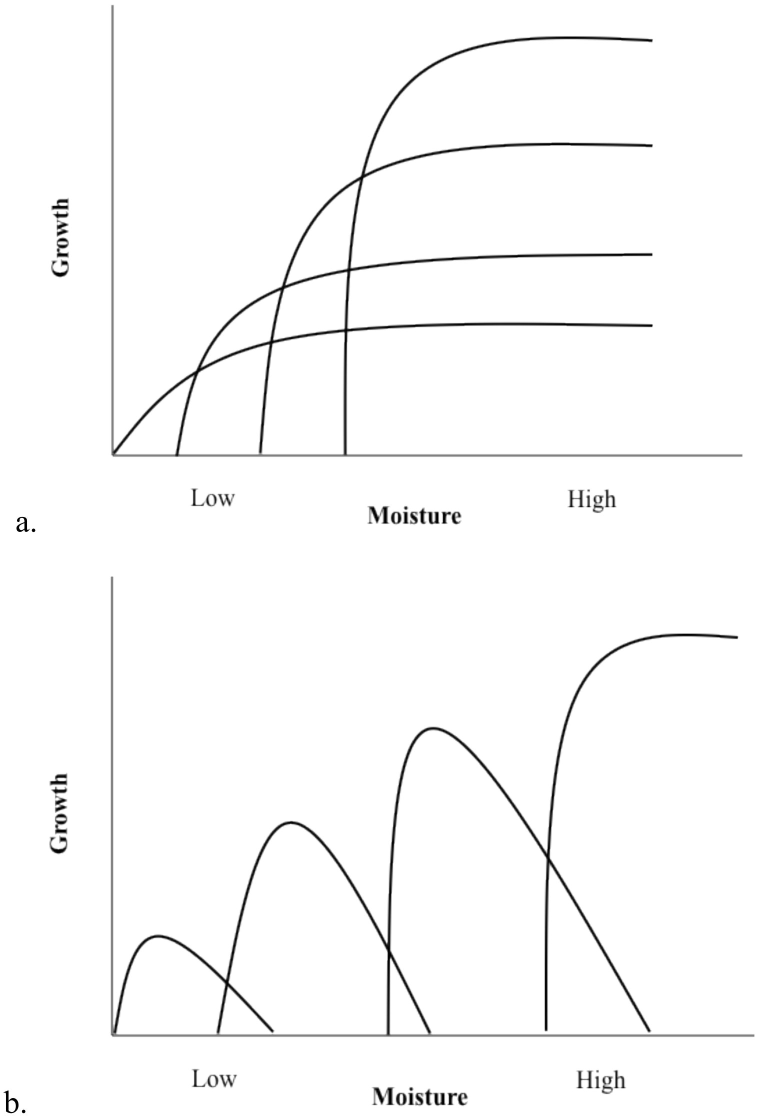


Figure 2. Modified from Smith & Huston (1989). Simulated patterns of plant growth along a moisture gradient. a) The response of plants of different functional types showing similar physiological optima. b) The response of plants in competition resulting in zonation (i.e. species with different ecological optima).

The combination of factors driving distributional limits and how they evolve may also vary depending on which end of the resource gradient is being examined. Zimmerman et al. (2009) stressed the importance of including climatic variability (i.e.

climate extremes rather than climate means) to improve species distribution modeling. They further suggest that climate extremes may have a stronger effect on species distributional limits where trees are closer to their physiological limits. In contrast, competition may be a more important driver of change at distributional limits with more abundant resources. This study emphasizes the importance of using both climatic means and extremes to analyze species distribution patterns.

Vegetation response to climate change

Climate has changed significantly over the last century and is projected to continue to do so as a result of increased greenhouse gasses (IPCC 2007). Climate models predict that temperatures will continue to increase, and many semi-arid regions of the world, including the U.S. Southwest, will experience more frequent and more intense droughts (Hanson & Weltzin 2000, Breshears et al. 2005, Seager et al. 2007, Breshears et al. 2009). The potential ecological effects of droughts due to climate change are numerous: plant mortality, dieback, ecotone shifts, and changes in vegetation structure from woodland to shrubland with reduced canopy cover.

Moisture stress due to prolonged drought is one of the greatest limiting factors for tree growth and establishment in the Southwest U.S.(Fritts et al. 1965, Fritts 1976, Dettinger et al. 1998, Swetnam & Betancourt 1998). Drought is defined as the absence of precipitation for a period long enough to deplete soil moisture and stress vegetation (Kramer 1983, Kramer & Kozlowski 1979). According to Hanson & Weltzin (2000), forest vegetation exhibits a strong physiological response and strong growth response to the “annual drought regime”, or wet/dry seasonality, in the Southwest. In general, low moisture and high temperatures associated with drought periods causes a reduction in growth. In addition to growth reduction, "global climate change type drought" is the primary causes of tree mortality in this region. Breshears et al. (2009) found that piñon pine mortality was a direct result of water stress leading to carbon starvation in their study near Los Alamos, NM during the drought of 2002-2003 in the Southwest. Compared to the 1950s drought which was the most severe continuous drought since the 1700s (Swetnam & Betancourt 1998), the 2000-2003 drought period was similarly dry, but much higher in temperature (Breashears et al. 2009). The timing of high temperatures and reduced precipitation led to dry soil water conditions, which contributed to high mortality of piñon pine. Mortality was greater than 90% which was observed by changes in foliar water content and spectral conditions reflected in reduced NDVI values. Furthermore, bark beetle infestations contributed to high mortality rate of overstory tree species. Regional scale die-off results in major changes to vegetation structure and provides insights into how vegetation responds to severe climatic events. Moisture stress and drought can also cause mature trees to become susceptible to other forests disturbances like insect outbreaks, wildfires, and disease (Allen & Breshears 1998, Hanson & Weltzin 2000, Breshears et al. 2009). Furthermore, changes in drought regimes are expected to affect the frequency of these disturbances.

Increases in the frequency and magnitude of droughts may also cause broad ecotone shifts. Allen & Breshears's (1998) study in northern New Mexico provides evidence of a rapid drought-induced ecotone shift. Focusing on the ponderosa pine and piñon-juniper woodland ecotone, they quantified changes in the semiarid ecotone over a span of 40 years following the 1950s drought period. Widespread die-off of ponderosa pine at the lower forest-woodland ecotone resulted in an ecotone shift of 2km or more in fewer than five years. Infestations of bark beetles coincided with drought conditions contributing to mortality. Trees under drought stress are more susceptible to biotic disturbances because survival efforts are allocated elsewhere. Evidence of piñon pine die-off not associated with bark beetle attacks poses strong evidence that the pattern of mortality is primarily driven by drought. Furthermore, ponderosa pine mortality directly corresponds to moisture and elevation gradients. Subsequently, mortality was more widespread on drier, low-elevation sites than on wetter, high-elevation sites. There has been little evidence of ponderosa pine reestablishment at the lower sites in the decades following the severe drought. Therefore, semiarid forests are considered to be most sensitive to climate variation, especially at ecotones. Similar patterns of growth sensitivity at drier sites have been observed (Adams & Kolb 2005). The consequences of large-scale die-off include forest fragmentation, changes in carbon stores, and shifts in near-ground solar exposure, soil erosion, runoff and changes in the genetic structure of dominant tree species. The complex dynamics illustrated here underline the need to assess tree growth at ecotones and distributional limits in the context of global climate change. Climate change is expected to continue to cause shifts in vegetation distribution because it is responsible for shifting the zone of physiological tolerance for many species. As the environmental gradients shift in space, we must understand how growth at the distributional limits will be affected.

Tree growth-climate relationships

Understanding the relationship between tree growth and climate can elucidate important limitations on growth imposed by climate (Fritts 1966, Orwig & Abrams 1997). These relationships can be used to create models to both reconstruct the past climate and predict future growth response under a changing climate. Dendrochronology is employed in order to understand tree growth over time. Dendrochronology, or tree ring analysis, is a discipline of study used to interpret the record of environmental variability captured in tree rings. It involves the measurement of ring-widths to determine patterns of annual growth for a tree. Trees of seasonal climates generally add one ring of growth each growing season, allowing us to determine the age of the tree. The width of a ring, other markings, or the lack of a ring for a particular year can indicate to the dendrochronologist whether the environmental conditions for a particular year were favorable for tree growth or not. A wide ring, for example, indicates that conditions were favorable for growth while a narrow year may be associated with a drought or perhaps a late frost. Multiple tree core samples from different trees in an area can be compared to develop a chronology of environmental factors, which influence tree growth. Crossdating is the process of matching growth patterns of tree cores in order to ultimately assign a calendar year to each ring, thus dating the tree (Fritts 1976). Narrow rings, indicative of a year in which environmental factors limit growth, can be used as marker rings when comparing core samples. This technique is fundamental to dendrochronological analysis. When correlated with temperature, precipitation, fire, insect outbreak, and/or drought pattern data, tree ring data can be used to lengthen the record of such events beyond observational measurements.

Tree rings have been shown to serve as an important measure of growth response to interannual moisture variability (Orwig & Abrams 1997,Adams & Kolb 2005, Eilmann & Rigling 2012). Semiarid regions, and especially semiarid ecotones, are considered to be among the most sensitive to climate variation (Fritts et al. 1965). In theory, optimal climate conditions for a particular species are found closer to the center of the distribution and as the physiological tolerance limits are approached species growth becomes increasingly more sensitive to climate. Dendrochronological analysis should reveal these patterns of growth. While this theory has been discussed in the literature, few studies have analyzed radial growth patterns for sensitivity to climate at distributional limits (Hart et al. 2010). Analyzing mean sensitivity– a measurement that quantifies the interannual variability in ring width–across a species range may indicate which regions or distributional limits are more vulnerable to climate change. (Fritts et al.1965, Mäkinen et al. 2002, Speer 2010). Dendroecological studies that quantify the response of tree growth to environmental changes are valuable for clarifying climate driven limitations on growth (Dolnac et al. 2013). Even though growth rate does not directly correspond to shifts in species distribution, both growth rate and distributional limits are related to climate; and trends in radial growth show a relationship with survival or mortality.

CHAPTER II

STUDY AREA

Santa Fe National Forest

The study area includes four sites within the east side of the Santa Fe National Forest on the Sangre de Cristo mountain range, which extends from Salida, CO in the north to Santa Fe, NM in the south. The forest covers 6306 km², ranging from 1600 meters to 3993 meters at the summit of Truchas Peak (Figure 3) with the east side centered approx. at 35º49’20” N, 105º41’22”W (USDA FS 2012).

Figure 3. Photo of Truchas Peak.

Figure 4. Photo from atop Elk Mountain.

The Santa Fe National Forest was chosen as a study region for the following reasons: a) the variety of western North American tree species present in that region b) the ability to sample at multiple sites with different moisture conditions due to the mountainous topography (Figure 4) and c) public land ownership.

The Rocky Mountain terrain provides strong environmental gradients and significant tree species diversity. According to broad patterns, species richness tends to increase with decreasing latitude (Allen, Peet, & Baker 1991). Previous intensive gradient analysis conducted by Peet (1978) (Figure 5) shows forest types relative to elevation and moisture gradients present at this site. The target species of this study, Ponderosa pine and Douglas fir, are present here as seen in the USGS species range maps (Figure 6) (Little 1971).

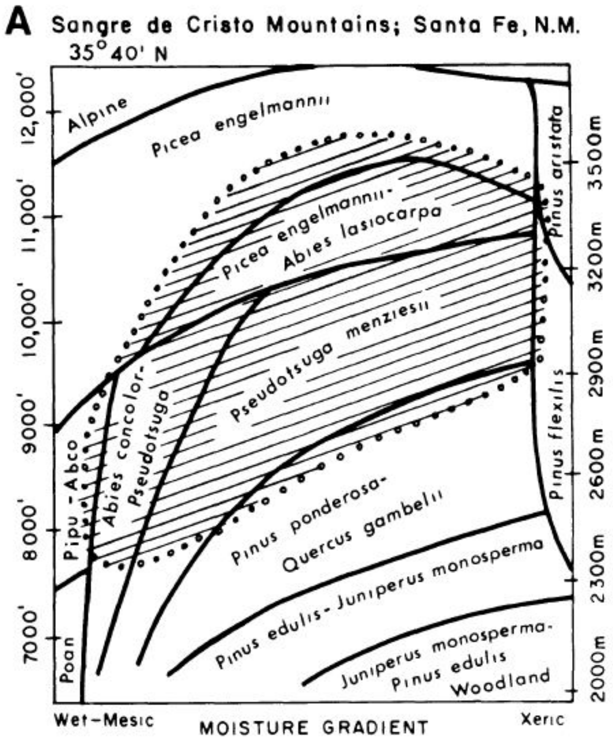
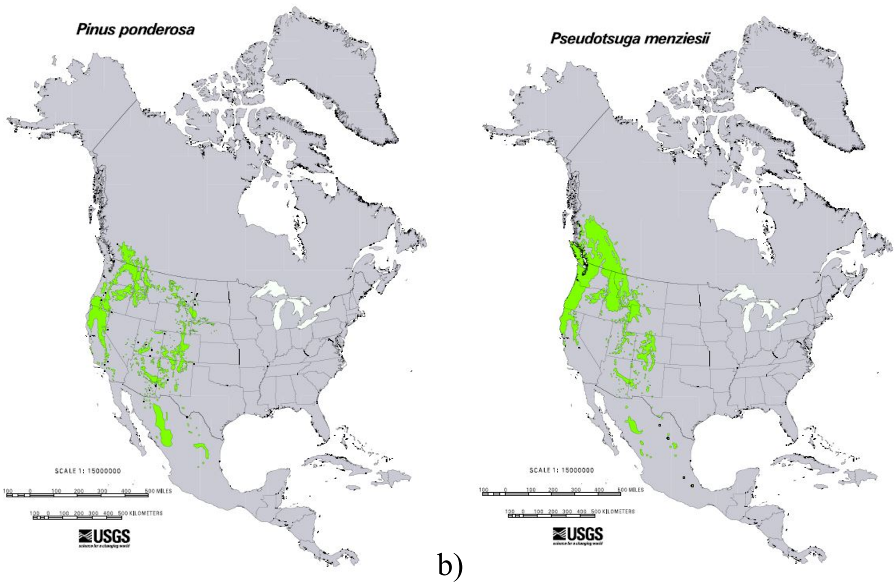


Figure 5. Vegetation diagram indicating the distribution of forest types relative to elevation and moisture gradients (Peet 1978).



a) b)

Figure 6. Species range maps for a) ponderosa pine and b) Douglas fir (Little 1971).

The two species targeted for this study are *Pinus ponderosa* var. *scopulorum* Dougl. Ex Laws. (Rocky Mountain ponderosa) and *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco (Rocky Mountain or blue douglas fir) (Burns & Honkala 1990). Both species are relatively widespread conifers across western North America and are valued for commercial timber, recreational use, and wildlife habitat. Douglas fir and ponderosa pine grow under a wide variety of climate conditions and elevations. In the Sangre de

Cristo range, ponderosa pine are generally found between 2000 and 3000 meters in elevation. Douglas fir ranges from about 2000 meters in mesic sites to as high as 3200 meters in elevation (Peet 1978). Both species are also known to crossdate well across a region which is important for studies using dendrochronology to assess growth (Grissino-Mayer 1993).

I initially identified potential study sites within the Santa Fe National Forest by examining vegetation cover maps, communicating with National Forest personnel, recognizing recent disturbances (i.e. fire, insect outbreak), and considering topographic characteristics before conducting field work.

In order to assess growth patterns and response to climate along a moisture gradient, final study sites were chosen in the field to represent the moisture gradient from xeric to mesic. Site moisture characteristics were based on a combination of slope aspect, topographic position, vegetation diversity, and field observation. Four sites were ultimately chosen; two sites at a xeric location, one in a moderately moist location, and one in a mesic location (Figure 7, Table 1).

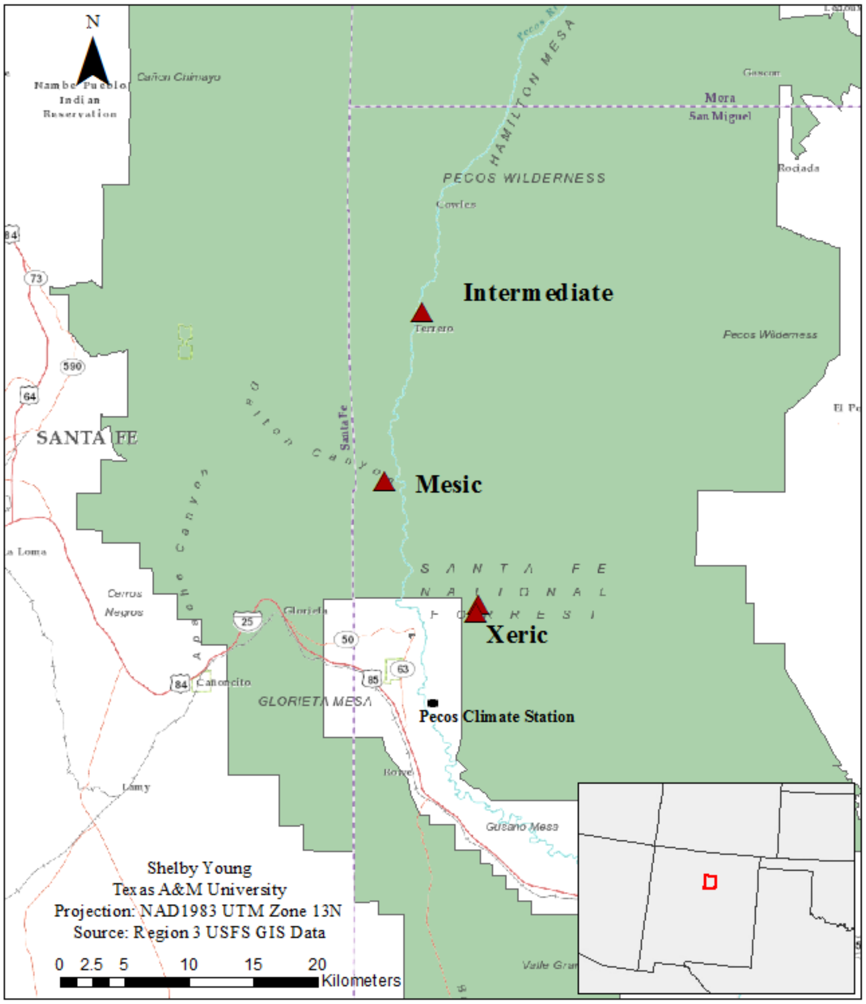


Figure 7. Map of study sites in the Santa Fe National Forest (shown in green). Created in ArcGIS using data from USFS region 3 GIS data.

Table 1. Study site information.

Site Type	Site Code	Brief description	Species Cored	No. trees	Elevation (m)	Latitude	Longitude
Xeric	EPA	dry rocky soils, bare ground	Ponderosa pine	10	2331	35.589	-105.631
Xeric	EPB	dry rocky soils, bare ground	Douglas Fir	10	2310	35.584	-105.633
Intermediate	ERC	gradual slope	Ponderosa pine, Douglas fir	20	2453	35.754	-105.670
Mesic	DCA	moist canyon bottom	Ponderosa pine, Douglas fir	20	2252	35.659	-105.696

Soil

The xeric sites are primarily composed of Typic Eutroboralfs and Typic Ustochrepts (USDA FS 1993) which are typical of semi-arid climates (Schaetzl & Anderson 2005). To be classified as ustic, the soil-moisture in a normal year is dry for more than 90 cumulative days, but moist for > 180 cumulative days or > 90 consecutive days. Soil at the intermediate site is composed of Eutric Glossoboralfs, which are characterized by high pH (alkaline) and generally fertile with a glossic horizon. The mesic site primarily contains Aquic Haploborolls soils which are considered to be periodically saturated. Furthrmore, the soil here is classified as deep (>100cm) with minimum horizonation (USDA FS 1993, Schaetzl & Anderson 2005).

Geology

The Sangre de Cristo Range is primarily underlain by Precambrian granites and gneisses with extrusions of phyolite and latite, as well as complex folded belts of sedimentary rock. Lower elevation sites are composed of exposed Tertiary sandstones, siltstones and conglomerates while higher elevations are largely composed of high silica content gneisses and schists. Through geomorphic and pedogenic processes, the high elevation rock forms acidic, infertile soils. (Allen, Peet, & Baker 1991). Additionally, the Southern Rocky Mountains were glaciated during the Pleistocene (Richmond 1972).

Climatology

In the spring and fall, moist air from the Gulf of Mexico brings precipitation to the eastern slopes, while summer precipitation is driven by convective thunderstorms. The El Niño Southern Oscillation and Pacific Decadal Oscillation cause interannual variation in precipitation as well (Swetnam & Betancourt 1998). The study region is also affected by the North American summer monsoon which initiates in July. The summer monsoon occurs when warm, moist air masses from the Gulfs of Mexico and California extend over the southwest due to the shifted position of the Bermuda high (Mitchell 1976). Winter precipitation is characterized by intrusions of Pacific air masses, which bring snowfall to the high peaks from November and into May. However, mountains significantly modify weather (temperature, precipitation) patterns at local sites, thus making broad uniform descriptions for a region difficult to generate. Figure 8 summarizes the climate for Santa Fe, New Mexico, which is less than 30km away from all three study sites.

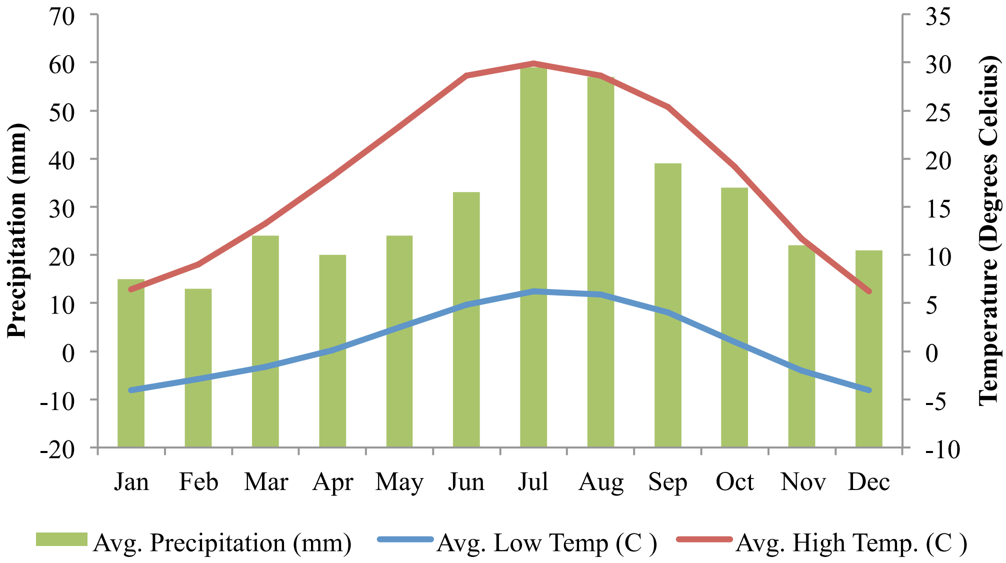


Figure 8. Santa Fe, New Mexico climograph (US Climate Data 2015).

Drought is one of the most important limiting factors for forest growth in the Southwest. According to Hanson & Weltzin (2000), the western U.S. is characterized by “periodic drought, in the form of chronic aridity, regular seasonal drought or stochastic drought occurring in seasons when water has historically not been limiting” (p. 206). The La Niña phase of ENSO lasts 1–3 years, typically brings drier winters, and is associated with severe droughts (Vankat 2013).

To understand long-term trends in climate over the study period and correlate those trends with tree growth, climate divisional data were obtained from National Climatic Data Center Global Historical Climatology Network (GHCND). These climate variables include Palmer Drought Severity Index (PDSI), precipitation, and temperature. PDSI is a measure of meteorological drought developed by Wayne Palmer (1965) that integrates precipitation, temperature, and soil moisture for a given region. Based on water supply and demand, PDSI values indicate the intensity of drought spells and can quantify long-term droughts as well (Dai 2004). The PDSI ranges from –6 to +6, with negative values indicating drought conditions and positive values indicating moist conditions (Palmer 1965). Some values may be +7 or –7 depending on the conditions. Values –2.0 to –3.0 indicate moderate drought, values –3.0 to –4.0 indicate severe drought, and values less than –4.0 indicates extreme drought (Figure 9). Precipitation index (Figure 10) and temperature index (Figure 11) are also divisional data sets that have been compiled from multiple climate stations within the climate division region. Each climate station within the climate division produces monthly precipitation totals and monthly temperature averages based on daily observations.

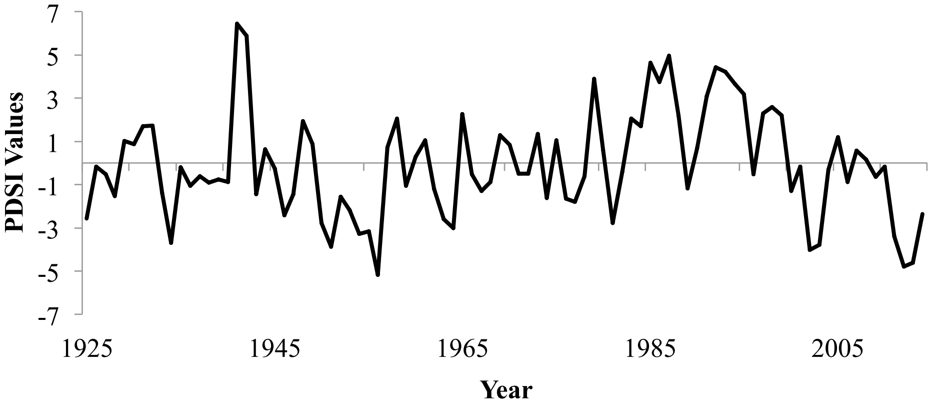


Figure 9. Average annual Palmer drought severity index values from 1925-2014

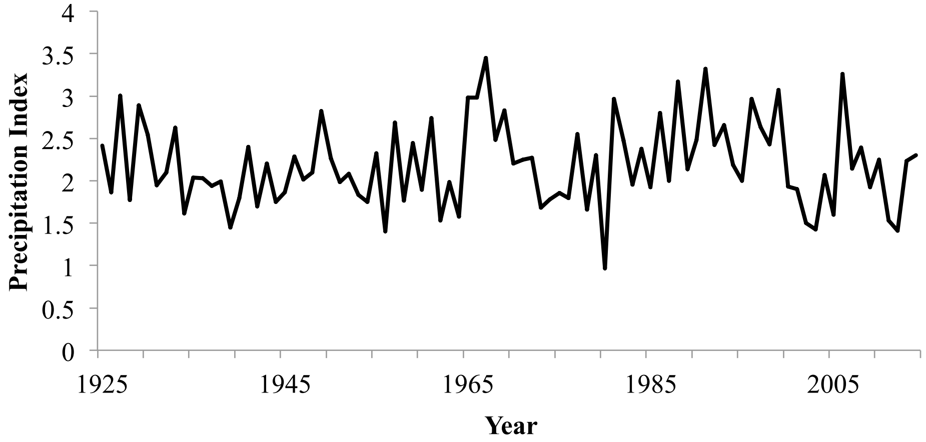


Figure 10. Average annual precipitation index values from 1925-2014.

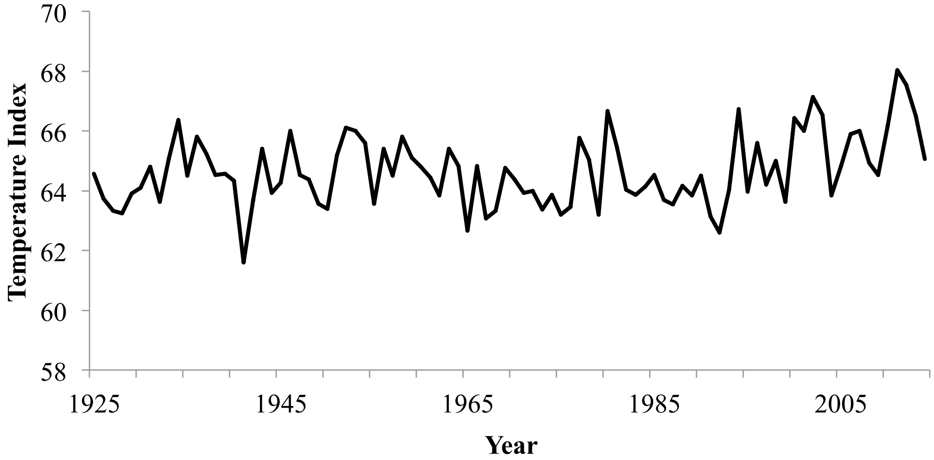


Figure 11. Average annual temperature index values for 1925-2014.

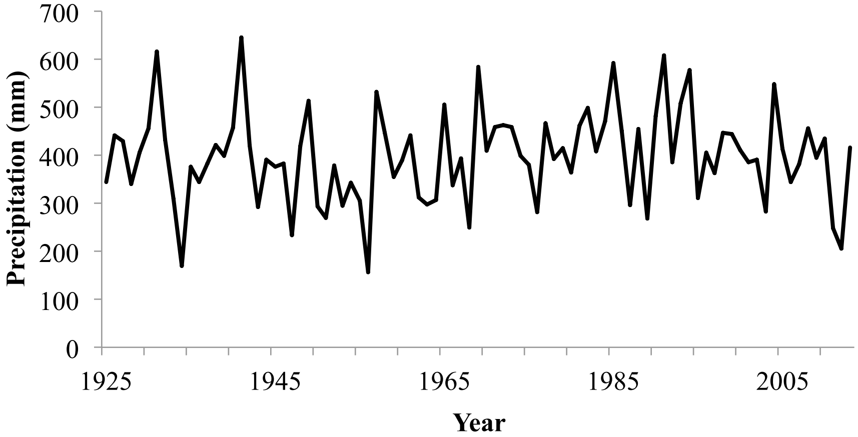


Figure 12. Total annual precipitation (mm) at Pecos, NM for 1925-2014.

In addition to the divisional data, the Pecos National Monument climate station within the vicinity of the study sites produced monthly precipitation data. This single climate station's data were included simply to support the climate data used in this study (Figure 12).

Human influence & disturbance history

The Santa Fe National Forest was established in 1915 and is managed by the U.S. Forest Service. Prior to establishment of the forest, the Southwest region has had a long history of human influence and disturbance. Evidence suggests the widespread presence of humans for thousands of years, with the exception of more limited presence at higher elevations. Permanent Spanish settlements in the valleys began in the 1500s and intensive livestock grazing and logging began in the 19th century. The targeted logging of ponderosa pine began in the 1870s (Finch et al. 1997). Fire exclusion began unintentionally with the increase of livestock grazing. By eliminating the herbaceous understory that carries fire, grazing began to exclude fire as a natural disturbance on the landscape (Vankat 2013). Active fire suppression practices were put in place by the U.S. Forest Service in the 1920s and 1930s and extended throughout much of the twentieth century. As a result, one of the major impacts has been the buildup of fuels that ultimately leads to large-scale crown fires. Without frequent small fires, leaf litter and dead branches and trees are able to build up on the forest floor over time. The next ignition, be it anthropogenic induced or by lightning, may ignite a much larger, more intense fire that will be more difficult to contain. In 1978, the U.S. Forest Service transitioned from exclusive fire prevention and suppression practices to more beneficial fire management practices, which include prescribed burns and managing lightning-ignited fires. The present day vegetation patterns exhibit the effects of fire. Large swaths of aspen (*Populus tremuloides)* reflect a post-fire landscape. As shade-intolerant, early successional species, aspen invade former ponderosa pine dominated stands after fire.

Study site descriptions

Xeric site: East Pecos A (EPA)

The xeric site at East Pecos A is a relatively lower-elevation site at 2331 meters in the southern region of the forest just east of Pecos, NM (Figure 13). EPA is located on a south-facing slope at the edge of the ponderosa pine forest. It is a transitional stand at the border of the Ponderosa pine distribution, where ponderosa pine mixes with the Pinyon-Juniper woodland. The associated vegetation at this site consists of pinyon pine (*Pinus edulis* Engelm.*)*, Rocky mountain juniper (*Juniperus scopulorum* Sarg.*)* and succulent plants. Much of the ground is bare at this site with few grasses and herbaceous species (Figure 14).

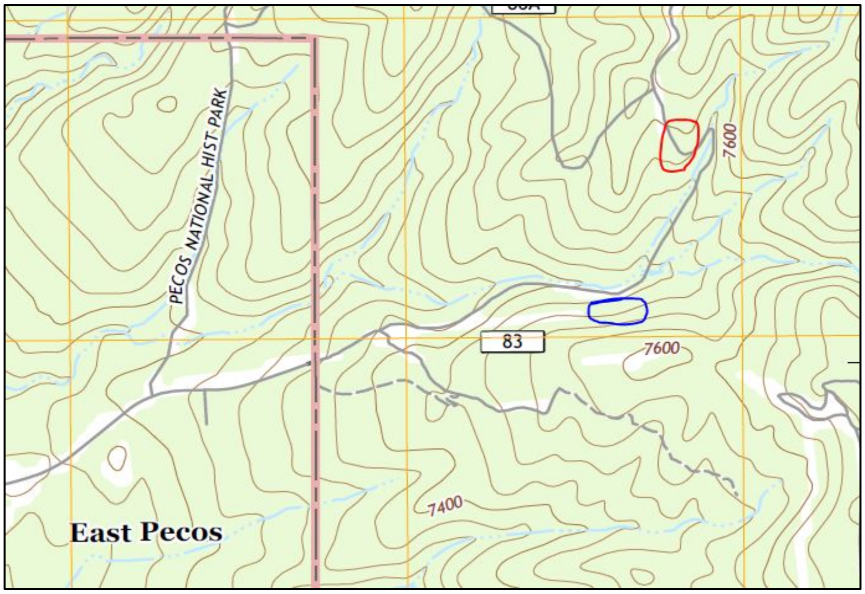


Figure 13. USGS topographic map of xeric sites. Pecos quadrangle. Red polygon indicates sampling area for EPA and the blue polygon indicates sampling area for EPB.

Figure 14. Xeric site at EPA.

Xeric site : East Pecos B (EPB)

The xeric site at East Pecos B sits at roughly 2310 meters on a steep north-facing slope (Figure 13). EPB is a xeric site for Douglas fir and is at the lower distributional limit for that species. The stand primarily consisted of Douglas fir and ponderosa pine with an open understory (Figure 15). Evidence of fire is present with fire scarred ponderosa pine. The Douglas fir appear to be encroaching on the ponderosa pine at this site.

Figure 15. Xeric site at EPB.

Intermediate site: Elk Road C (ERC)

The intermediate moisture site is positioned on a west-facing, gradual slope near the base of Elk Mountain (Figures 16 and 17). It falls on the east side of the valley carved by the Pecos River. At 2453 meters, ERC is a mid-elevation site for both ponderosa pine and Douglas fir. It is also relatively intermediate in its moisture, neither extremely wet nor dry. These two tree species form an old, even-aged stand and are the dominant vegetation at the site. The understory consists of grasses, a few saplings, and scattered shrubs including gambel oak (*Quercus gambelii* Nutt.).

Figure 16. Douglas fir and ponderosa pine at the intermediate site.

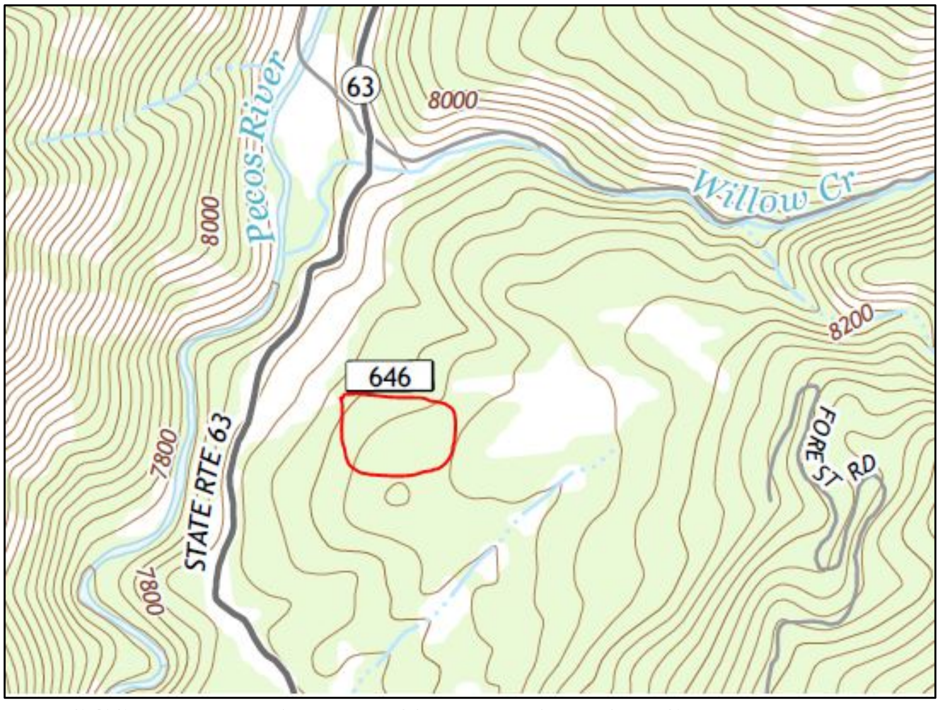


Figure 17. USGS topographic map of intermediate site. Cowles quadrangle. Red polygon indicates sampling area.

Mesic site: Dalton Canyon A (DCA)

The Dalton Canyon site is located along a creek at the bottom of the canyon (Figure 18). At a sampling elevation of about 2252 meters, DCA serves as a mesic site (Figure 19). The ponderosa pine trees cored at this site were on a steep, south-facing slope that is largely shaded by the opposite slope (Figure 20). These trees were larger in diameter than a stand of ponderosa pine upslope on a drier site.

Figure 18. USGS topographic map of mesic site. Rosillia Peak quadrangle. Red polygon indicates sampling area.

Figure 19. Dalton canyon creek at the mesic site. Photo by Andrew Evans.

Figure 20. Ponderosa pine at mesic site. Photo by Charles Lafon.

Figure 21. Douglas fir and associated species at the mesic site.

Douglas fir and ponderosa pine white fir were cored at this site along or near the canyon bottom which formed a flat area along the creek. Both white fir (*Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.)* and blue spruce (*Picea pungens* Engelm.*)* often dominate low slope areas along shaded drainages. The understory was dense with shrubs, herbaceous species, and diverse tree species. Associated species including gambel oak (*Quercus gambelii* Nutt.*),*oaks *(Quercus spp*.), and willow (*Salix spp.)*, were present along with Douglas fir in the wettest parts of the canyon (Figure 21).

CHAPTER III

METHODS

Field methods

With the help of four assistants, I cored a total of 80 canopy dominant trees across three sites within the east side of the Santa Fe National Forest. I sampled ponderosa pine and Douglas fir at each site across the moisture gradient. Additionally, white fir and blue spruce were sampled at the mesic DCA site to serve as a comparison with the target species and also provide context for the growth patterns at the extreme mesic end of the moisture gradient and distribution limit for the target species. At each sampling site, I identified a total of 10 live trees per species and marked them for sampling (Figure 22). Individual trees were selected for their dominance in order to avoid microenvironmental factors that trees in the subdominant canopy position might experience, weakening the climate signal (Speer 2010). Dominant trees rose above the crowns of surrounding trees and did not appear to have severe damage from fire or insects.


Figure 22. Identifying and flagging trees to be cored. Photo by Charles Lafon.

All trees were cored using an increment borer at breast height (1.4 m) (Figure 23). For each tree, my assistants and I took two cores samples, unless a core could be extracted which reached the pith and went through the entire diameter of the tree. For trees growing on a slope, cores were taken parallel to the contour in an effort to avoid reaction wood, or the compression of rings on the downhill side of the tree to maintain vertical orientation. I also measured diameter at breast height for each tree cored. Evidence of slight insect damage, rot and/or fire scars were noted. In addition, I documented any microsite conditions including evidence of tree mortality, general age structure and associated vegetation.

Figure 23. Using an increment borer to core a tree at breast height.

I recorded local site conditions including elevation, coordinates using a Global Positioning System, slope aspect, and slope steepness (degree). All cores were stored in paper straws and wrapped in newspaper to be transferred from the field to the lab.

Laboratory methods

I dried, mounted, and sanded all cores according to standard dendrochronological procedures (Stokes & Smiley 1968, Speer 2010). The cores were first allowed several days to air dry in their paper wrappings. Then I glued each core to a prefabricated wooden mount, secured them with string and left them to dry (Figure 24). Cores were sanded using a belt sander with increasingly finer grit sand paper from ANSI 80 to 400 grit until individual cells could be visible under a microscope (Figure 25) (Fritts 1976).

Cores were visually crossdated using skeleton plots, first invented by A.E. Douglass (Stokes & Smiley 1968), and the list method (Yamaguchi 1991) to create a master chronology.

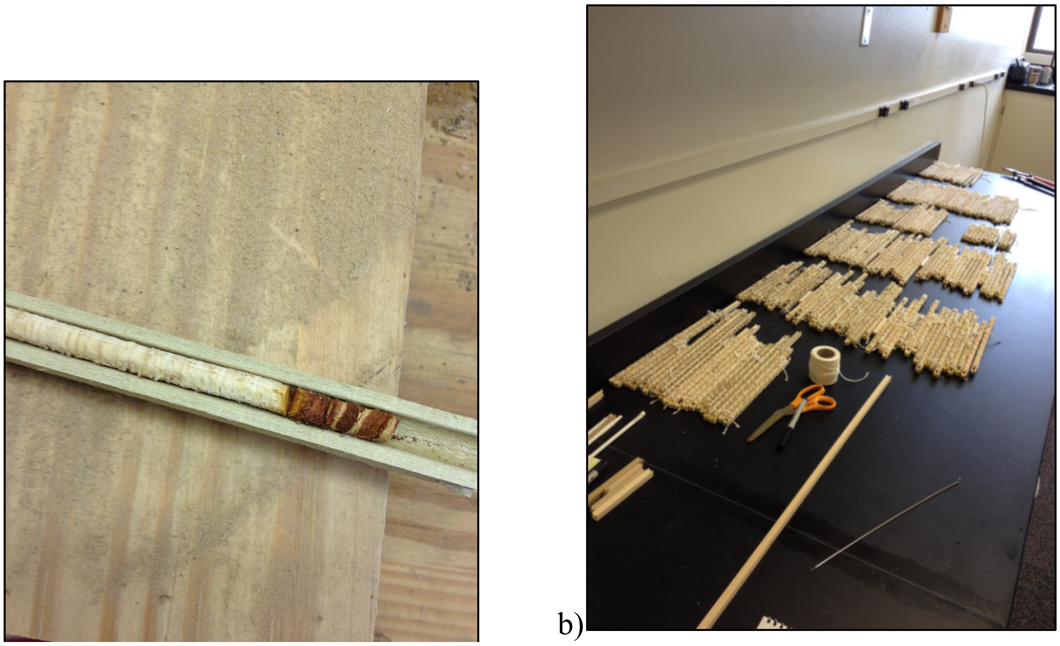


Figure 24. a) A raw tree core mounted in a prefabricated wooden mount. b) Mounted and glued raw cores.

Figure 25. A close up of a sanded ponderosa pine core.

Figure 26. Measuring a tree ring series using a stereomicroscope and Velmex system.

Ring widths were measured to the nearest 0.001mm using a stereomicroscope and Velmex measuring system with J2X software (Figure 26). The initial visual crossdating was then verified using COFECHA software, which statistically assesses the quality of crossdating and measurement accuracy of a tree ring series (Holmes 1983, Grissino-Mayer 2001). The program also identifies segments that have outliers, indicating an error in crossdating due to missing rings, false rings or human error. The default 32 year spline with a 50% frequency was used in the analysis because it has been shown to be the best spline size for detecting errors in the series (Grissino-Mayer 2001). Furthermore, segment lengths of 40 years with a 20 year overlap and 30 years with a 15 year overlap were used; each segment is correlated with the master chronology created from the other series in order to identify possible errors in dating. Any errors within the series that COFECHA flagged were re-examined under the microscope and re-dated when necessary. After making corrections, the measurements were run through COFECHA again and the processes repeated until all errors were addressed (Grissino-Mayer 2001). Cores that could not be crossdated due to indistinct rings or breakage were removed from the data set.

After completing the accuracy analysis in COFECHA, ARSTAN was used to build final stand-level chronologies. ARSTAN uses standardization techniques to remove long-term growth trends from the final chronology (Cook 1985, Cook & Holmes 1986). Since the aim of the study is to detect growth response to interannual climatic changes, long-term trends must be removed. This process involves creating a ring width index (RWI) so that all series can be compared to each other. The RWI is a unitless measure with a mean of one and constant variance over time (Fritts & Swetnam 1989). This index is important because trees younger in age tend to have faster and larger growth than when they approach older stages of life. The result is a general decline in ring width over time. Therefore, the ring widths must be standardized to permit me to composite the tree-ring series among trees of varying ages. Two detrending methods were used including a negative exponential curve and a 50-year cubic smoothing spline. The final six residual chronologies (one for each species at each of three sites) produced through ARSTAN are included in the appendix.

Raw ring width

Annual raw ring width data were organized by species and site. Two cores from the same tree were averaged together to create one raw ring width series for each tree. I then found the average annual raw ring width for each "tree series" for each species at each site across the gradient.

Basal area increment

Basal area increment is a measure of the two-dimensional growth added to the cross-sectional area of the tree in a given year. It is calculated by subtracting the area of a cross-section in year t-1 from the area in year t (Speer 2010). BAI is derived from radial growth (raw ring width) measurements, diameter at breast height, and estimations of bark thickness. BAI is a valuable dataset because it removes age-related trends in radial growth. Raw ring width in mature trees declines with age therefore it is difficult to compare the growth of multiple trees of different ages. A tree could add the same volume of growth each year; however, since this addition is to an "ever-increasing cylinder", the width of each new ring will decline over time (Speer 2010). BAI accounts for the total wood production in a given year and is able to capture any growth suppression due to forest disturbances such as drought or changes to the dynamics of the system (Speer 2010).

In order to calculate BAI for each year in a series, bark thickness must first be estimated and accounted for. Since bark thickness is difficult to measure in the field, only the total diameter (i.e. outside of the bark) was directly measured for each tree. Diameter at breast height (DBH) and diameter outside of the bark (DIAM*ob*) are equivalent for purposes of discussion. Miles & Smith (2009) developed an equation to estimate double bark thickness based on data collected by the Forest Inventory and Analysis (FIA) program of the U.S. Forest Service. Double bark thickness is calculated first so that it can then be subtracted from the diameter (outside the bark) in order to obtain the diameter of the tree without the bark (i.e. inside the bark). For example, if the thickness of the bark at any point around the tree equals x, double bark thickness is simply estimated as 2x (Figure 27). It is important to note that while tree bark thickness may vary on a single tree, this equation assumes that the thickness is equivalent throughout.

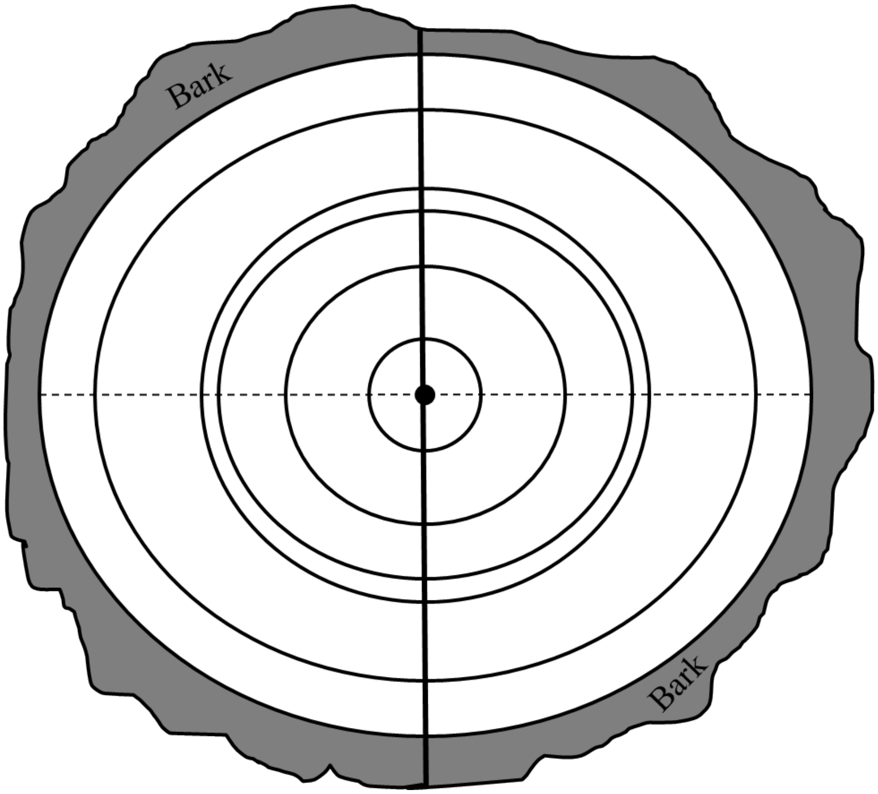


Figure 27. A simplification of a tree's cross-section where the grey area represents the bark thickness and the black concentric circles represent annual tree growth rings. The solid line indicates the diameter outside of the bark (DIAMob) which was measured in the field and includes bark thickness. The dashed line indicates the diameter inside the bark (DIAMib) which excludes bark thickness.

Double bark thickness (DBT) was calculated using the following equation (Equation 1) (Miles & Smith 2009):

(1) $\mathrm{DBT} = b0 + b1 * \mathrm{DIAM}ob$

DBT = double bark thickness in inches

$b0$ and $b1$ = regression coefficients (Table 2).

$\mathrm{DIAM}ob$ = diameter (inches) outside bark

Table 2. Species specific regression coefficients from (Miles & Smith 2009).

Tree Species	*b0*	*b1*
Ponderosa pine	0.21	0.1
Douglas Fir	-0.4	0.17

Once DBT is estimated for each individual tree, the DBT is subtracted from the DIAM*ob* in order to obtain the DIAM*ib* for each tree. BAI for each year for each individual tree is calculated in three steps. The first step is to calculate the unique DIAM*ib* for every year starting with the outermost year. Since the diameter for each year going back in time is smaller than the more recent year, I subtracted the raw ring width for each year in order to obtain the diameter (DIAM*ib*) for each year from 2014 to 1925. The second step is to then calculate the basal area for each year. Basal area is simple calculated as the area of a circle (Equation 2) where the calculated diameter for each year (from Step two) is used. The third step involves calculating the final BAI (Equation 3). The basal area of the inner year-for example, 2000- is subtracted from the next outer year- in this example, 2001. The BAI is the difference in total basal area from one year to the next. DIAM*ob*, double bark thickness estimates, DIAM*ib*, and outermost year basal area values for each individual tree are provided in the appendix.

Basal area increment for each year was calculated using the following equations:

(2) $BA= \pi * (DIAMib/2)^2$

(3) $BAI= BA_o – BA_i$

BAo = basal area of outer year

BAi= basal area of inner year

DIAM*ib*= diameter inside bark

Basal area increment (BAI) was calculated every year for each individual core or tree ring series. Two cores from the same tree were averaged together to create one BAI series for each tree (1925-2014). I then found the average annual BAI for each "tree series" for each species at each site.

Residual chronologies

Of the 120 cores acquired, 98 could be measured and crossdated accurately. I developed a total of six 89-year residual chronologies. The chronology development and standardization were carried out using COFECHA and ARSTAN (Holmes 1983, Gissino-Mayer 2001). Series intercorrelation for the raw ring widths (from COFECHA) ranged from 0.470 for ponderosa pine at the mesic site to 0.923 for Douglas fir at the xeric site (Table 3). Intercorrelation is a measure of the strength of the climate signal for all sampled trees at a site (Speer 2010). It is composed of the average correlations between each series and the master chronology developed from all the series. The highest intercorrelation values are associated with drought sensitive conifers. The standardized ring widths are presented as ring width indices (RWI) over the study period from 1925-2014 (Figure 28).

Table 3. Descriptive chronology statistics of the six residual chronologies. Unfiltered refers to the raw measurements, and filtered values reflect values after using a 32-yr. spline function to detrend and autoregressive modeling to remove autocorrelation.

Species	Site	No. dated series	Series intercorrelation	Standard Deviation (unfiltered)	Standard Deviation (Filtered)	First-order autocorrelation
Ponderosa pine	Xeric	16	0.512	0.771	0.402	0.039
	Intermediate	17	0.500	1.174	0.328	0.009
	Mesic	17	0.470	0.846	0.354	-0.023
		Total: 50				
Douglas fir	Xeric	13	0.923	0.801	0.411	-0.021
	Intermediate	16	0.828	0.957	0.377	-0.069
	Mesic	19	0.694	0.782	0.378	0.138
		Total: 48				

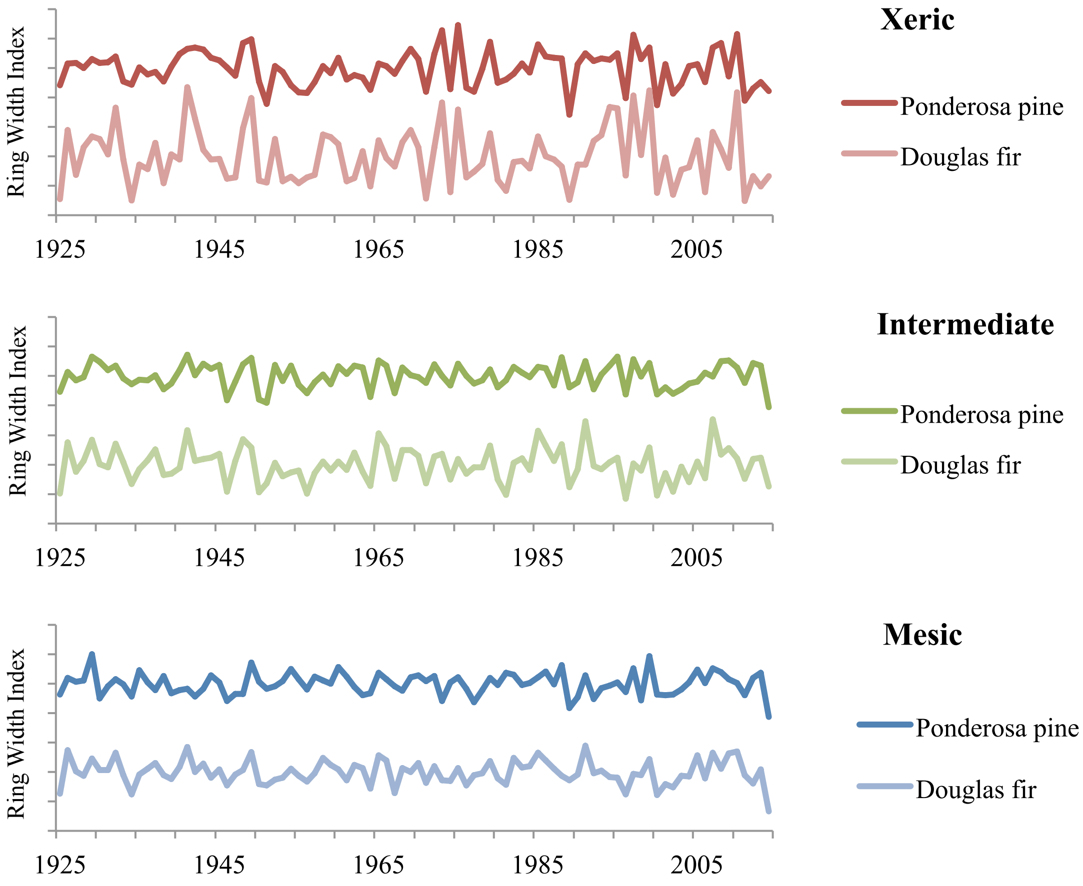


Figure 28. Residual ring width index chronologies for ponderosa pine (dark lines) and Douglas fir (lighter lines) for each site. Tic marks on the y-axis are in increments of 0.5 and therefore represent ring width index values +/- 0.5 relative to the mean.

Climate data

Climate divisional data were obtained from National Climatic Data Center Global Historical Climatology Network (GHCND). Divisional data were used because the record extends from 1895 to the present, longer than individual climate stations in the area. The Santa Fe National Forest falls under New Mexico Climate Division 2: Northern Mountains. Climate variables analyzed included Palmer Drought Severity index (PDSI), temperature index and precipitation index. Previous studies have found that a stronger relationship exists between tree growth and climate when using regional climate data in the analysis instead of single climate stations (Blasing et al. 1981, Grissino-Mayer 1997, Hart et al. 2010). The result is most likely due to the fact that regional datasets are based on the combination of all local climate stations, thus reducing any local climatic effects (Grissino-Mayer 1997). Nevertheless, monthly precipitation data from the Pecos National Monument climate station was also analyzed. Monthly summary climate data were obtained in text (.txt) format and converted to an Excel document for manipulation. Previous to growing year climate data were analyzed in addition to current growing year data because current year tree growth still responds to previous year conditions. Since trees often allocate resources for use during the following year, it is important to analyze the effects of previous year climate on current year growth (Fritts 1976).

Analysis methods

Raw ring width and basal area increment

To learn if trees are growing more slowly at their tolerance limits compared to elsewhere within their spatial distribution, I performed a Kruskal-Wallis test. The Kruskal-Wallis test is a non-parametric test used in place of an ANOVA. While the ANOVA test is quite robust, it assumes a normal distribution of data in each group and homogeneity of variances in each group. Since the assumptions of ANOVA are not met, I decided to use the Kruskal-Wallis test to assess whether the BAI means and the annual raw ring width means for the xeric, intermediate and mesic sites were significantly different from one another. A Dunn post-hoc pairwise comparisons test was performed to reveal which sites were significantly different from each other (Zar 1999).

Mean sensitivity

In order to understand the variability in year-to-year growth for a tree ring series or for a stand of trees at a particular site, the program COFECHA calculated a mean sensitivity value for each series. Mean sensitivity is a measure that quantifies annual variability in raw ring width for a series and ranges from 0 to 1 (Equation 4). For a tree ring series in which every ring was the same width, the mean sensitivity would equal 0. Tree ring series that have mean sensitivity values closer to 1 indicate a stronger sensitivity or response to environmental factors like climate. As a result, mean sensitivity values vary by species and region. Understanding which climatic variables have the strongest impact on growth requires further investigation.

Mean sensitivity is calculated using the following equation:

$$(4)\quad MS_x = \frac{1}{n-1}\sum_{t=1}^{t=n-1} \left| \frac{2\left(x_{t+1} - x_t\right)}{x} \right._{t+1} - x_t$$

Where *x* is the width of a single ring, *t* is the year of a given ring, and *n* is the number of rings in the series (Fritts, 1976). I calculated the mean sensitivity values for all individual series and average values according to species and site to compare differences between each.

Correlating ring width index (RWI) and climate variables

To understand the nature of the relationship between tree growth and climate, a correlation analysis was performed, as is common in dendroclimatic research (e.g. Fritts et al. 1965, Briffa et al. 1990, Swetnam & Baisan 2003, Brown & Wu 2005) I calculated a series of Pearson's product-moment correlations (r) to identify relationships between annual ring width index and the following climate variables: monthly PDSI, monthly temperature and monthly precipitation. Additionally, I analyzed monthly precipitation from the Pecos National Monument climate station.

Ring width index is important to use when correlating growth with climate variables because it is a standardized dataset. The standardization procedure (outlined in the laboratory methods section of this chapter) removed nonclimatic trends from the raw ring width dataset. Raw ring width data would not be well suited to this particular analysis because they are not standardized.

Drought analysis

To learn how trees at their tolerance limit respond to major climatic events like severe drought, I analyzed the growth response of each species to the severe drought period of 1950-1956 for all sites. I chose this drought period because it was the longest and most intense drought period within my study period. The average summer (May through August) PDSI value for 1956 was -5.432, which is classified as an extreme event. The average summer PDSI value for 1950-1956 was -3.044. To understand the rate of recovery following a drought, I compared the mean growth for 5 years prior to the drought period to the mean growth for the drought period, and to the mean growth for 5 years following the drought. To determine if radial growth rate was suppressed following the drought period, I performed Friedmann's tests to compare the pre-drought, drought, and post-drought periods for each species by site (Fekedulegn et al. 2003). I performed Nemenyi post-hoc pairwise comparisons tests to determine which periods of time were significantly different from each other at each site (Zar 1999). This approach to analyzing drought events follows the study of Fekedulegn et al. (2003), where they compared mean growth in the drought years to the mean growth of the preceding and following five years for tree species in an Appalachian watershed in West Virginia. They found that growth generally declined for all tree species in drought years and the decline was greater at xeric sites. Growth recovery varied by species. In a different study, Eilmann and Rigling (2012) found that short-term analysis of tree growth response to drought is the best method for detecting drought tolerance. Here they analyzed changes in radial increment and the speed of recovery following drought periods. Using multiple comparison tests, they tested the growth in the four years prior to a drought year against growth in the drought years and the four years following the drought. These studies both support the short-term method of analyzing radial growth response to drought.

CHAPTER IV

RESULTS

Do trees grow more slowly at their distributional limits than elsewhere within their spatial distribution?

Raw ring width

Raw ring width varied among the sites along the moisture gradient for both tree species. The Kruskal-Wallis test performed for ponderosa pine revealed that the raw ring width for each site was significantly different at the $P < 0.05$ level ($\chi^2 = 7.23$, d.f.= 2, $P=0.027$) (Table 4). Post hoc comparisons using the Dunn test indicated that the mean raw ring width at the xeric site (mean = 0.213, SD = 0.059) was not significantly different than the mesic site (mean = 0.205, SD =0.107) or the intermediate site (mean= 0.320, SD= 0.098) (Table X). The BAI at the mesic and intermediate sites, however, were significantly different from one another at $P<0.05$ (Figure 29). For a Dunn post-hoc test the critical value of Q is as follows: Q=2.936 for $P<0.01$, Q=2.394 for $P<0.05$, and Q=2.128 for $P<0.1$.

Table 4. Post-hoc results for ponderosa pine raw ring width.* indicates P< 0.01, ** for P<0.05 & * for P<0.1.**

RW-Ponderosa Pine

Pair	Q	Significant?
Xeric vs. Intermediate	-1.670	
Xeric vs. Mesic	0.811	
Mesic vs. Intermediate	-2.776	**

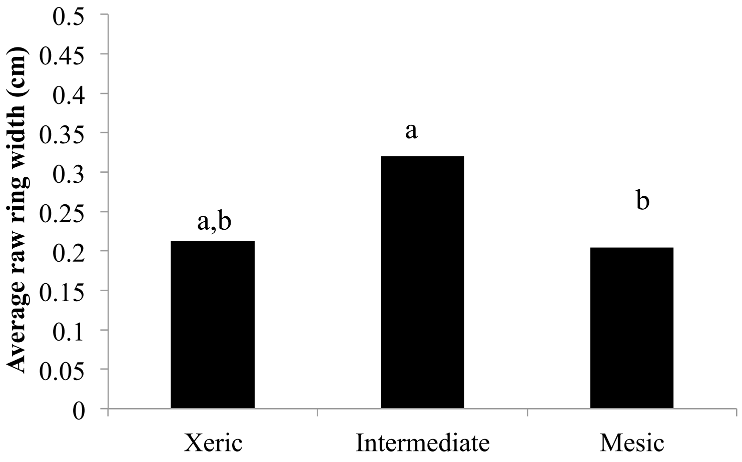


Figure 29. Average raw ring width by site for ponderosa pine. Sites labeled with different letters had significantly different means (P<0.05).

The Kruskal-Wallis test performed for Douglas fir revealed that the raw ring width for each site was significantly different at the $P< 0.05$ level ($\chi^2 = 12.27$, d.f.= 2, $P=0.002$) (Table 5). Post hoc comparisons using Dunn test indicated that the mean raw ring width at the xeric site (mean = 0.220, SD = 0.029) was not significantly different than the mesic site (mean = 0.303, SD =0.063). The xeric site growth was significantly different from the intermediate site (mean= 0.380, SD= 0.065) at $P<0.01$ (Table X). The raw ring width at the mesic and intermediate sites were not significantly different from one another at the $p<0.1$ level. This relationship is visually present in Figure 30.

Table 5. Post-hoc tests for Douglas fir raw ring width. * indicates P< 0.01, ** for P<0.05 & * for P<0.1.**

RW- Douglas Fir

Pair	Q	Significant?
Xeric vs. Intermediate	-3.496	***
Xeric vs. Mesic	-1.66	
Mesic vs. Intermediate	-1.7214	

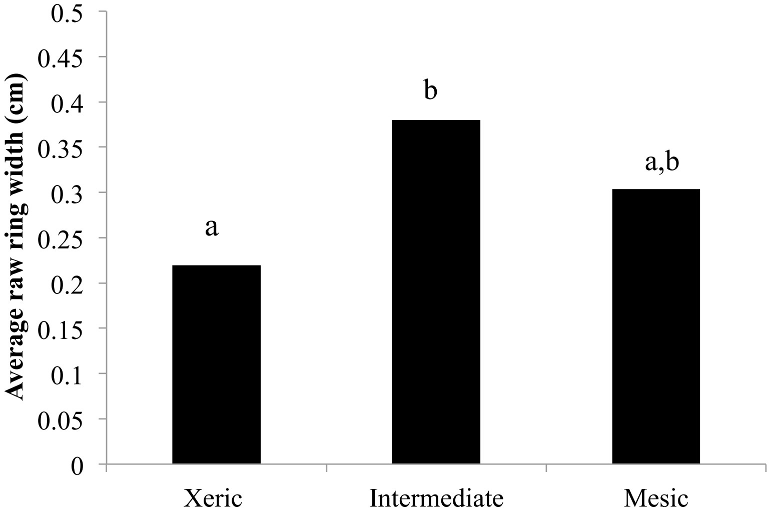


Figure 30. Average raw ring width by site for Douglas fir. Sites labeled with different letters had significantly different means (P<0.05).

Additionally, raw ring width was calculated for each year in every series and combined to create an average annual raw ring width dataset for each site for each species. Figures 31 and 32 show trends in average annual raw ring width during the study period from 1925-2014. For both species, the growth at the xeric site is generally the lowest, while growth at the intermediate site is the highest for the majority of the study period. This trend shifts in the year 2000 where raw ring width at the mesic site increases for both species. Additionally, Douglas fir growing at the xeric site shows a period of larger ring widths compared to the other sites in the 1990s. Growth appears to decline in the last year of the study period at all sites.

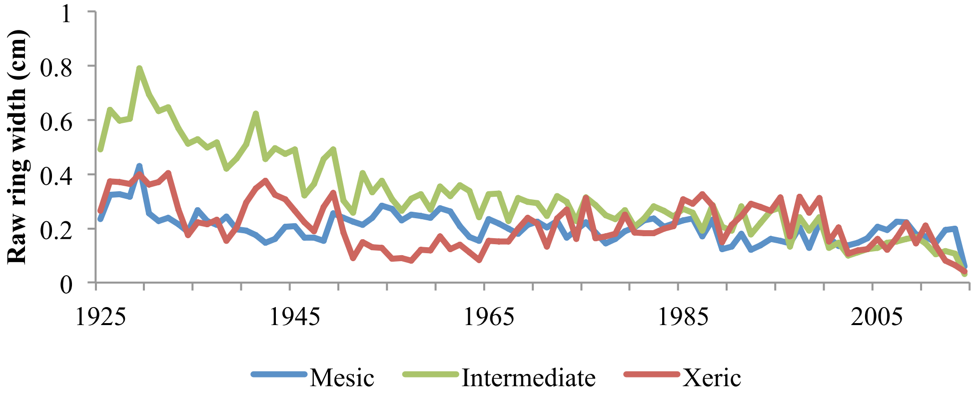


Figure 31. Annual raw ring width trends for ponderosa pine.

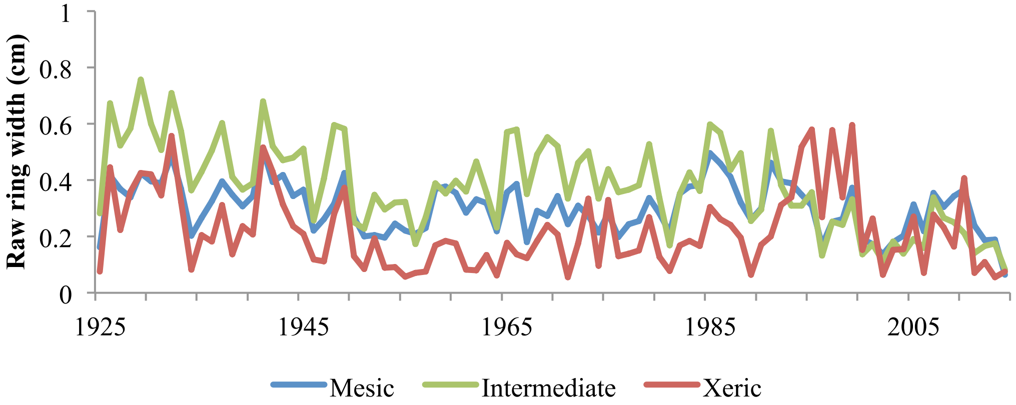


Figure 32. Annual raw ring width trends for Douglas fir.

Basal area increment

Basal area increment varied among the sites for both tree species. The analysis for ponderosa pine revealed that the average annual BAI varies among the sites along the moisture gradient at the *P*< 0.05 level (χ^2 = 11.78, d.f.= 2, *P*=0.003) (Table X). Post hoc comparisons using the Dunn test indicated that the mean BAI at the xeric site (mean = 6.801, SD = 1.829) was significantly different than the mesic site (mean = 13.460, SD =7.157) at a *P*<0.1 level and different from the intermediate site (mean= 17.336, SD= 4.927) at a *P*<0.01 (Table 6). The BAI at the mesic and intermediate sites, however, were not significantly different from one another. This relationship is visually present in Figure 33.

Table 6. Post-hoc test results for ponderosa pine. * indicates P< 0.01, ** for P<0.05 & * for P<0.1.**

BAI-Ponderosa Pine

Pair	Q	Significant?
Xeric vs. Intermediate	-3.419	***
Xeric vs. Mesic	-2.226	*
Mesic vs. Intermediate	-1.633	

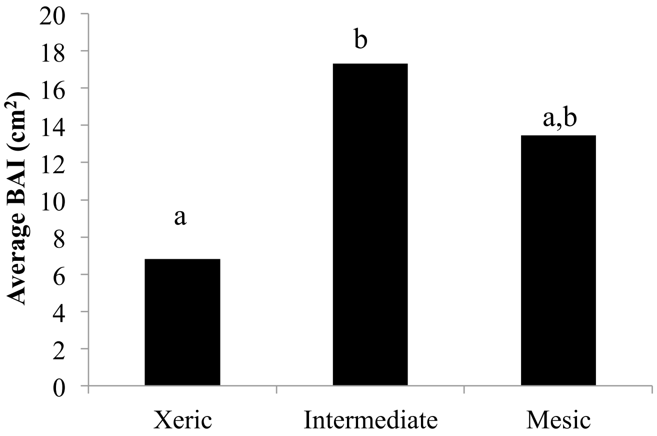


Figure 33. Average BAI by site for ponderosa pine. Sites labeled with different letters had significantly different means (P<0.05).

The Kruskal-Wallis test performed for Douglas fir revealed that the average annual BAI for each site was significantly different at the $P< 0.05$ ($\chi^2 = 12.00$, d.f.= 2, $P=0.002$) (Table 7). Post hoc comparisons using the Dunn test indicated that the mean BAI at the xeric site (mean = 6.762, SD = 1.301) was significantly different than the mesic site (mean = 14.137, SD = 3.033) at $P<0.05$ and different from the intermediate site (mean= 14.544, SD= 3.323) at $P<0.01$(Table X). The BAI at the mesic and intermediate sites, however, were not significantly different from one another. This relationship is visually present in Figure 34.

Table 7. Post-hoc test results for Douglas fir. * indicates P< 0.01, ** for P<0.05 & * for P<0.1.**

BAI-Douglas Fir

Pair	Q	Significant?
Xeric vs. Intermediate	-3.130	***
Xeric vs. Mesic	-2.928	**
Mesic vs. Intermediate	0.000	

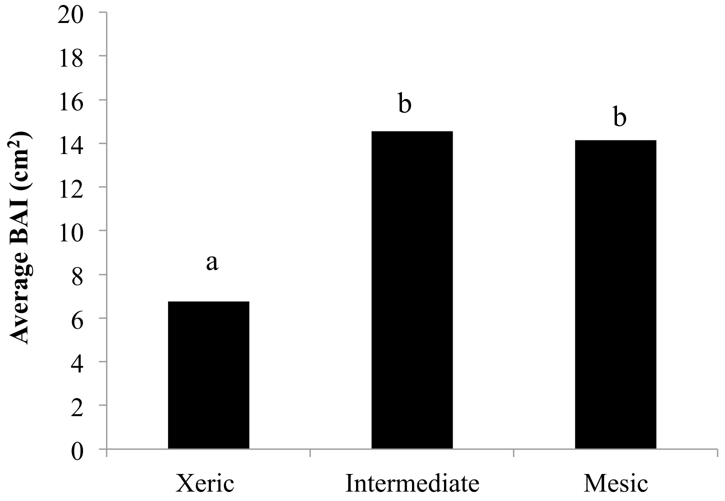


Figure 34. Average BAI by site for Douglas fir. Sites labeled with different letters had significantly different means (P<0.05).

Additionally, basal area increment was calculated for each year in every series and combined to create an average annual BAI dataset for each site for each species. Figures 35 and 36 show trends in average annual BAI during the study period from 1925-2014. For both species, the growth at the xeric site is the lowest, while growth at the intermediate site is the highest for the majority of the study period. This trend shifts in the year 2000, after which the mesic site for both species shows greater growth than both the intermediate and xeric sites. Growth at the intermediate site begins to show a decline around this time as well.

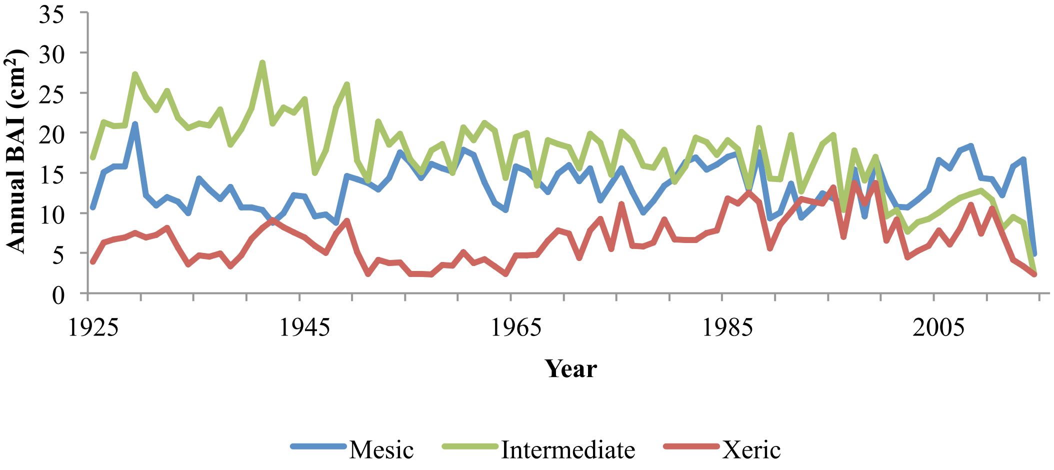


Figure 35. Annual BAI trends for ponderosa pine.

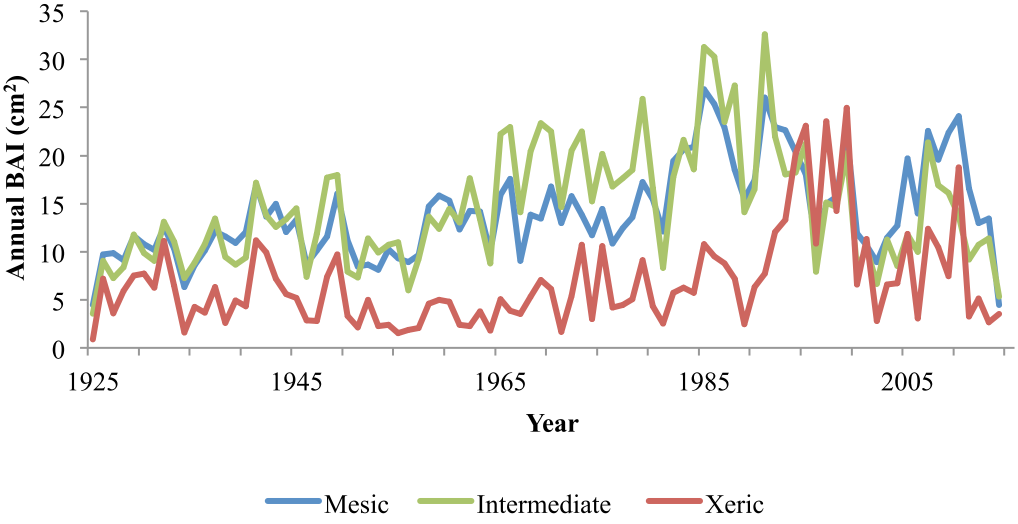


Figure 36. Annual BAI trends for Douglas fir.

Are trees at the distributional limit more sensitive to climate variability (i.e. stronger correlation to climate variables) than trees near the center of the distribution?

Mean sensitivity

The program COFECHA calculated the mean sensitivity for each tree ring series (Figure 37). For both species, the xeric site has the highest mean sensitivity values, followed by the intermediate site and mesic site. This pattern of sensitivity across sites corresponds to the variability in RWI seen in the residual chronologies. As for species difference, ponderosa pine is more sensitive than Douglas fir at the mesic and intermediate sites, but Douglas fir was the most sensitive at the xeric site.

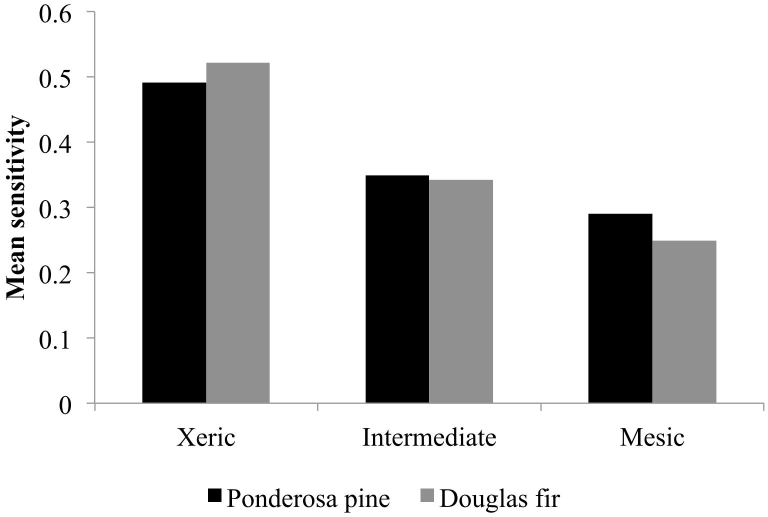


Figure 37. Mean sensitivity values for each species and site.

Tree growth-climate relationships

Ring width indices for all chronologies generally showed positive relationships with Palmer drought severity index (PDSI) and precipitation, and negative relationships with temperature. Common patterns across the moisture gradient emerged, however, the strength of the relationships varied among sites. To examine trends in climate variables and ring width during the study period from 1925-2014, I graphed annual trends for summer PDSI, precipitation index, and temperature index with ring width indices across the moisture gradient (Figure 38, 39, 40). I defined summer PDSI as an average of monthly PDSI for May through August (Figure 38). Trends in total annual precipitation come from the Pecos National Monument Climate station (Figure 39). Trends in average annual temperature reflect climate divisional data (Figure 40). Growth trends are represented as standardized ring width indices (RWI). Differences in RWI between ponderosa pine and Douglas fir can be attributed to differences in life history traits.

Among the annual trends for climate variables, summer PDSI exhibits the strongest relationship with growth during the study period compared to precipitation and tempertature for both species.

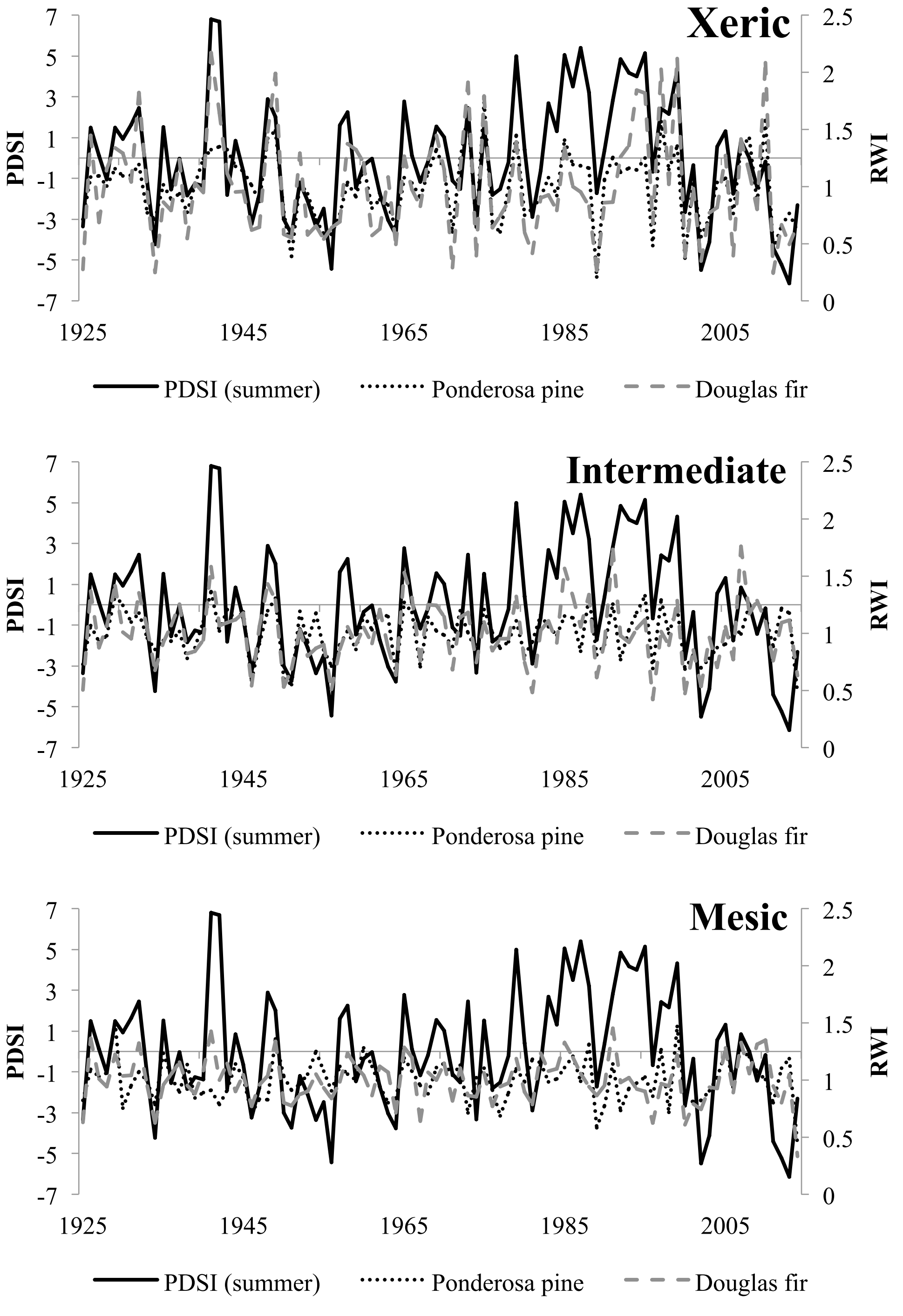


Figure 38. Average summer (May through August) PDSI and RWI over study period of 1925-2014.

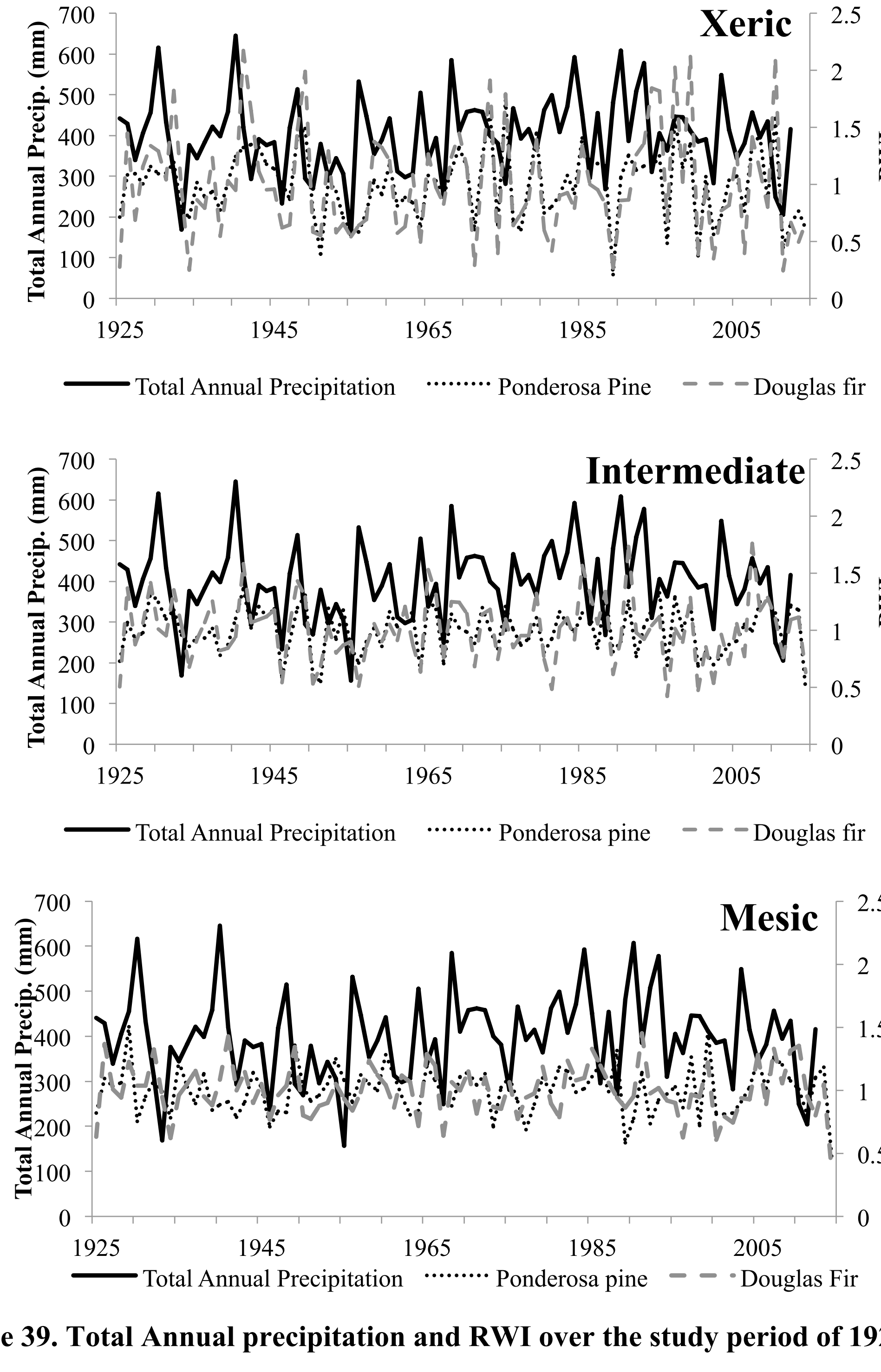


Figure 39. Total Annual precipitation and RWI over the study period of 1925-2014.

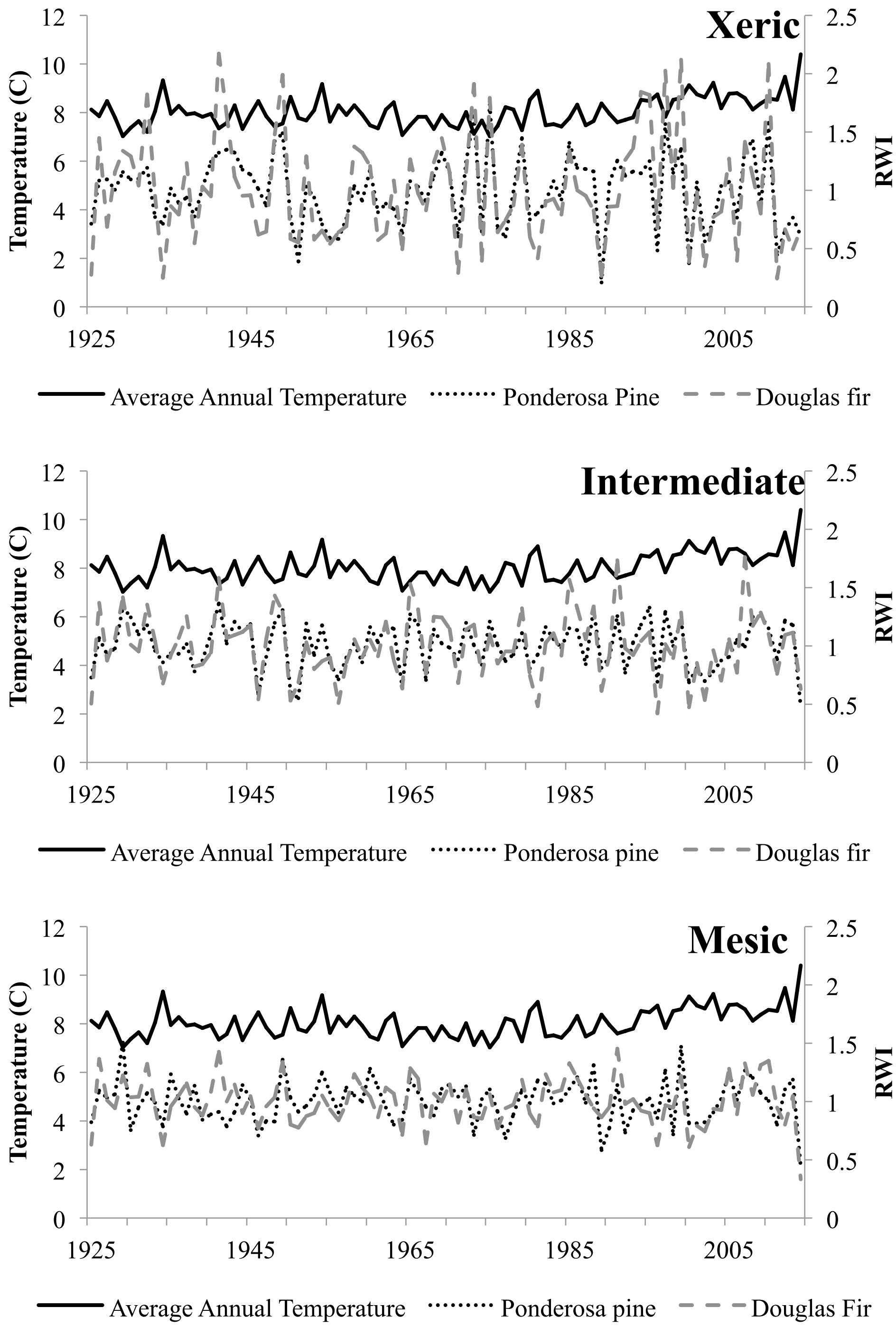


Figure 40. Average annual temperature and RWI over the study period 1925-2014.

Among the climate variables examined, monthly PDSI had the strongest correlation with growth for both species and across all sites. A statistically significant (*P*<0.05) positive correlation between tree growth and monthly PDSI is present from the previous year's autumn through the growing season at all sites with the exception of ponderosa pine at the mesic site (Figure 41). Here there is only a weak positive correlation between growth and PDSI for the current year growing season's summer months.

The average PDSI for the growing season's summer months of May through August was the climate variable with the strongest relationship to ring width index across the moisture gradient for both species. Significant positive relationships were found across all sites, but the variance in RWI explained by summer PDSI declines from the xeric site to the mesic site (Figure 42). About 50% of the variance is explained for both species at the xeric site, but only 5% for ponderosa pine and 25% for Douglas fir at the mesic site, suggesting some interspecific differences in drought tolerance.

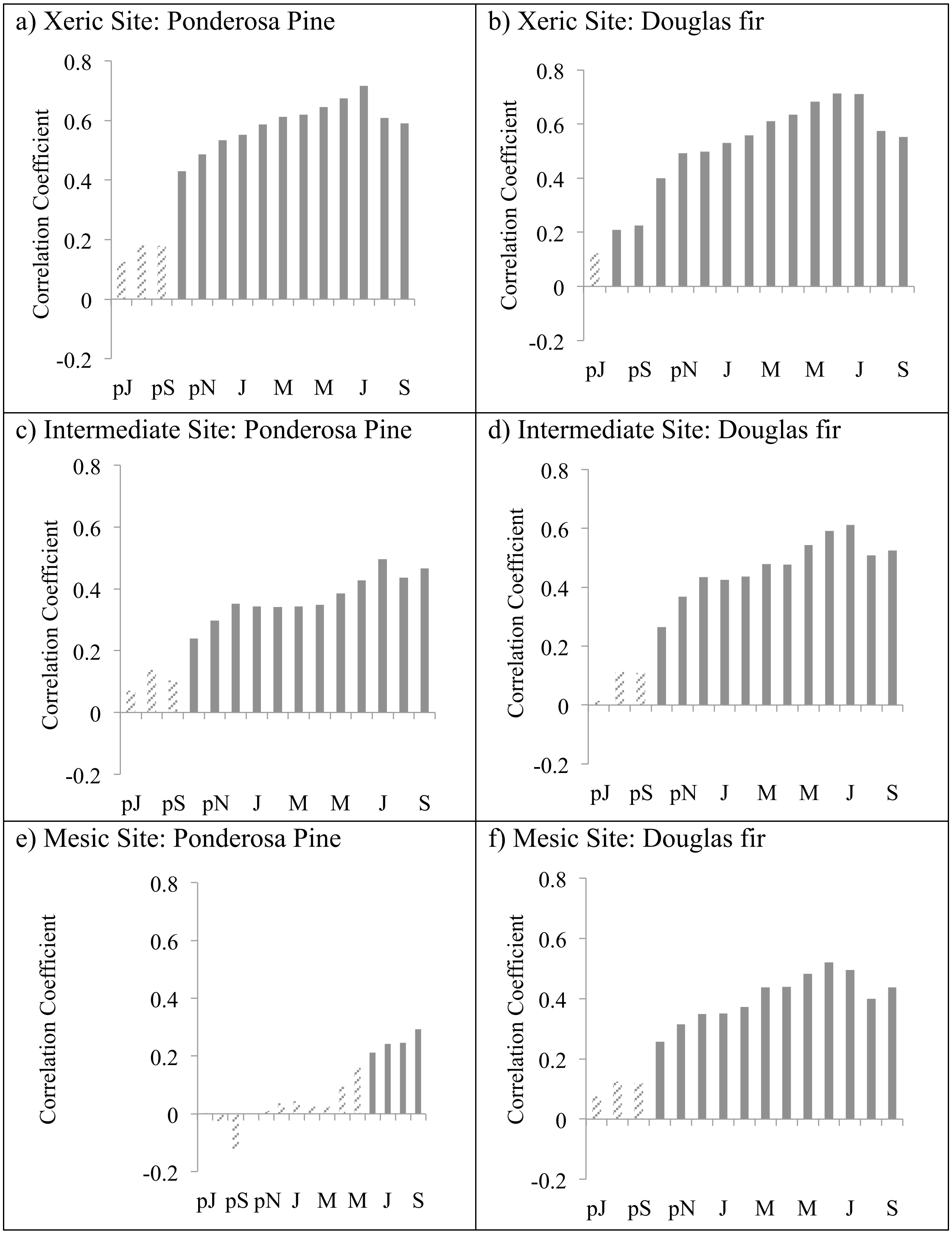
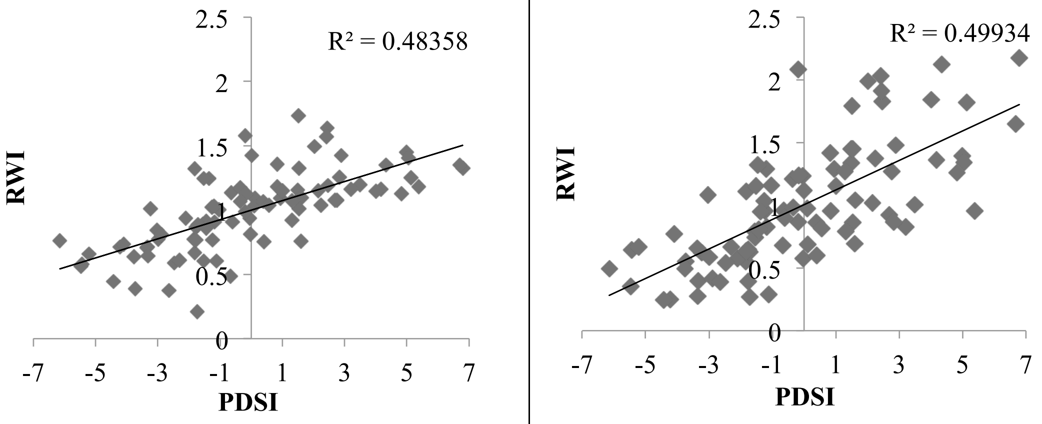
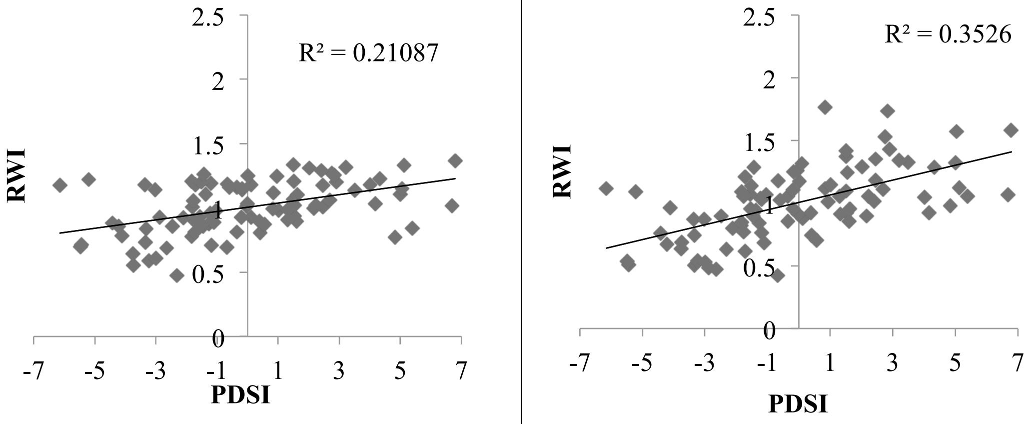


Figure 41. Correlation coefficients for the relationship between RWI and PDSI by month. Lowercase "p" indicates a month previous to growing season. Shaded bars indicate statistically significant correlations at the $P<0.05$ level. Hatched bars indicate correlations that are not significant.



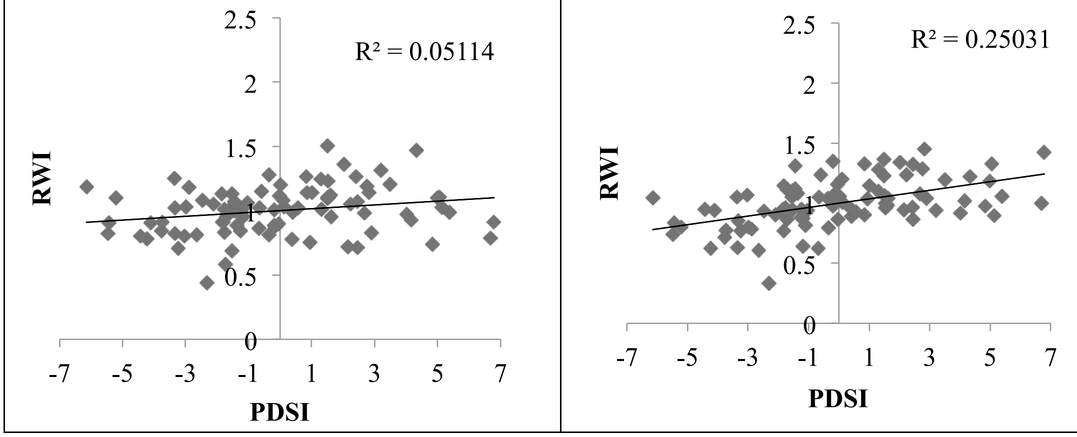
a) Xeric Site: Ponderosa Pine *

b) Xeric Site: Douglas fir *



c) Intermediate Site: Ponderosa Pine *

d) Intermediate Site: Douglas fir *



e) Mesic Site: Ponderosa Pine *

f) Mesic Site: Douglas fir *

Figure 42. Scatterplots showing the relationship between average summer (May through August) PDSI and RWI. A * indicates significance at $P<0.05$.

Correlation between growth and precipitation was generally positive, but did not show a relationship that was as strong as with PDSI, nor for as many months. The significant positive correlations with precipitation tend to occur in the previous year's autumn and the spring and summer of the growing year (Figure 43). This follows a typical hydrologic cycle for the Southwest region. It should be noted that there is a slightly stronger relationship with precipitation at the xeric site than at the mesic site for both species. For ponderosa pine, there is a decline across the gradient, from xeric to mesic, in the number of months that show a statistically significant relationship with precipitation index. Douglas fir does not exhibit the same pattern. Correlation analysis for the single station precipitation data revealed similar patterns to the divisional data, but showed weaker relationships (Figure 44).

Correlation between growth and temperature was generally negative for both previous year's and current year's growing season (Figure 45). The strongest negative correlations tended to occur in the spring and summer months of the current year which corresponds with the strong relationship found with PDSI. The strongest negative relationships were found at the xeric site, although Douglas fir at the intermediate site also showed strong relationships for the summer months of June and July (r= -0.46 & -0.34 respectively).

The 89 year study period from 1925-2014 was chosen because it is the longest period of time that is able to incorporate the most tree ring data for each species across the moisture gradient and climate data are available for that time.

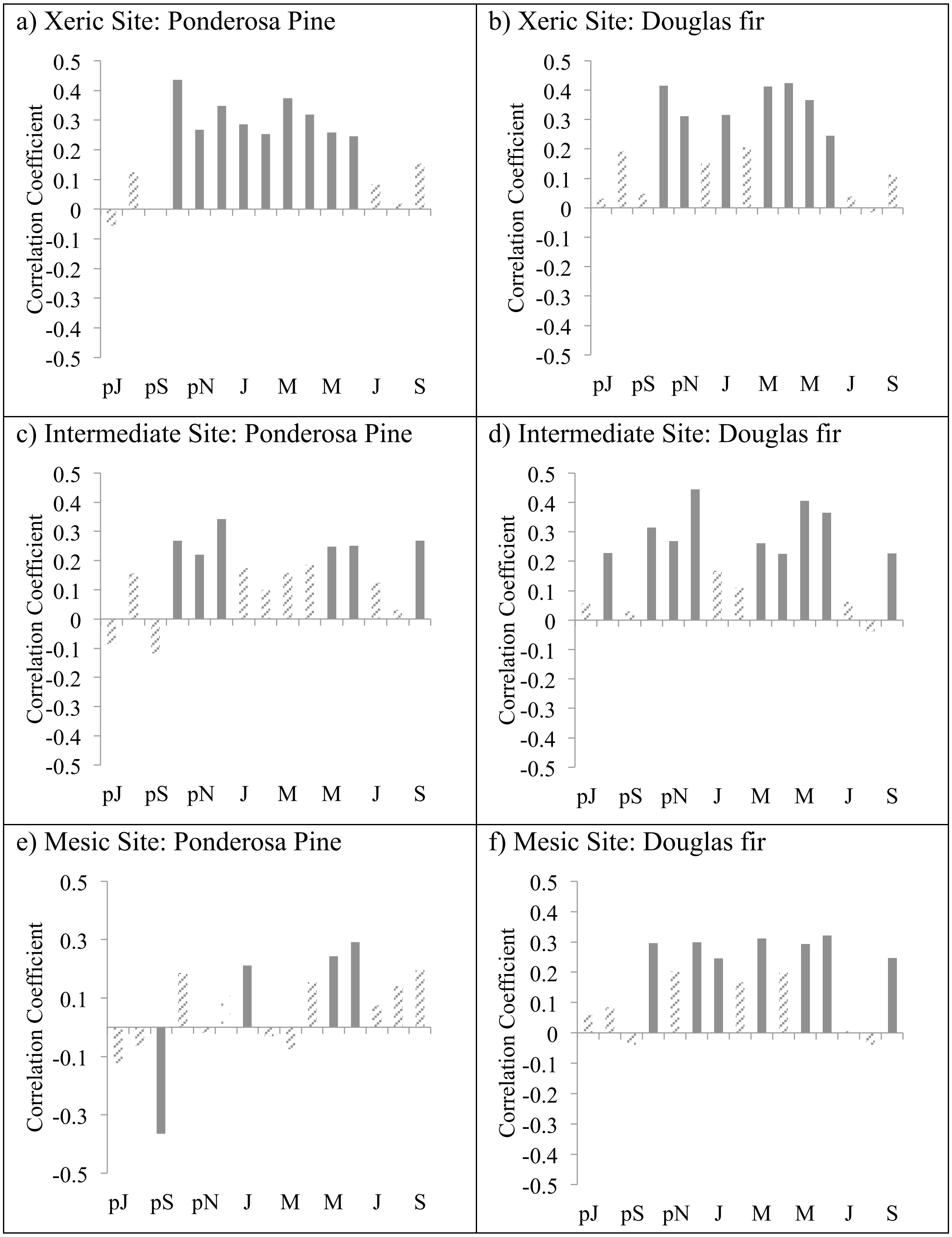
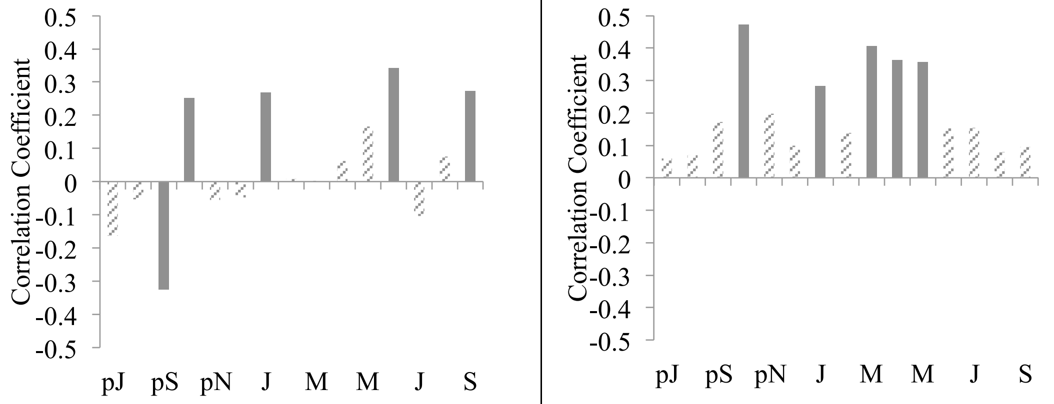
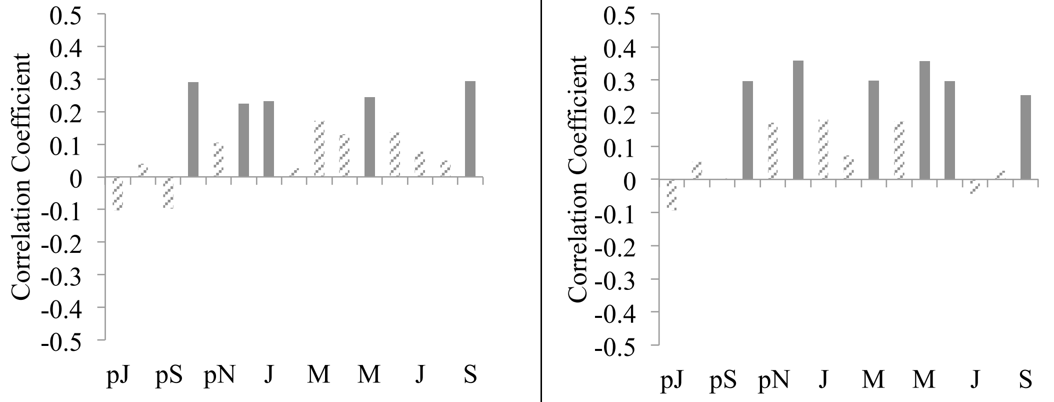


Figure 43. Correlation coefficients for the relationship between RWI and precipitation index by month. Lowercase "p" indicates a month previous to growing season. Shaded bars indicate statistically significant correlations at the P<0.05 level. Hatched bars indicate correlations that are not statistically significant.



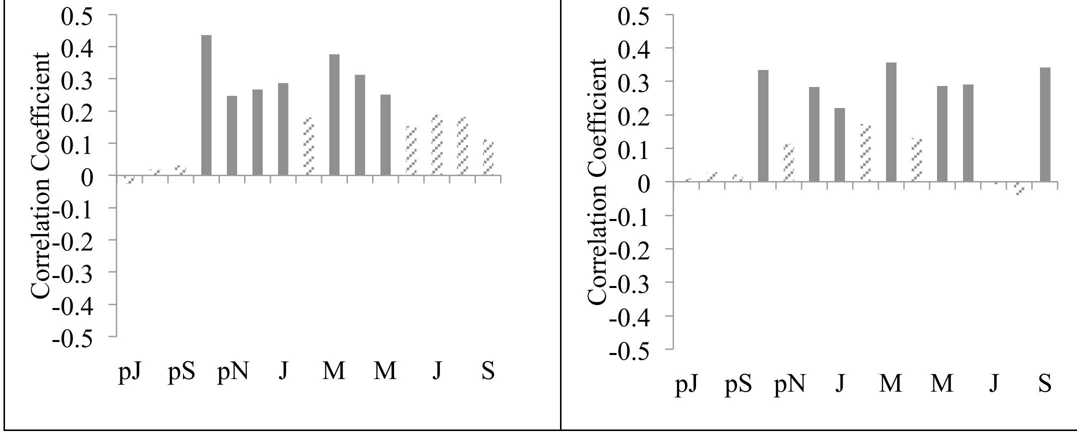
a) Xeric Site: Ponderosa Pine

b) Xeric Site: Douglas fir



c) Intermediate Site: Ponderosa Pine

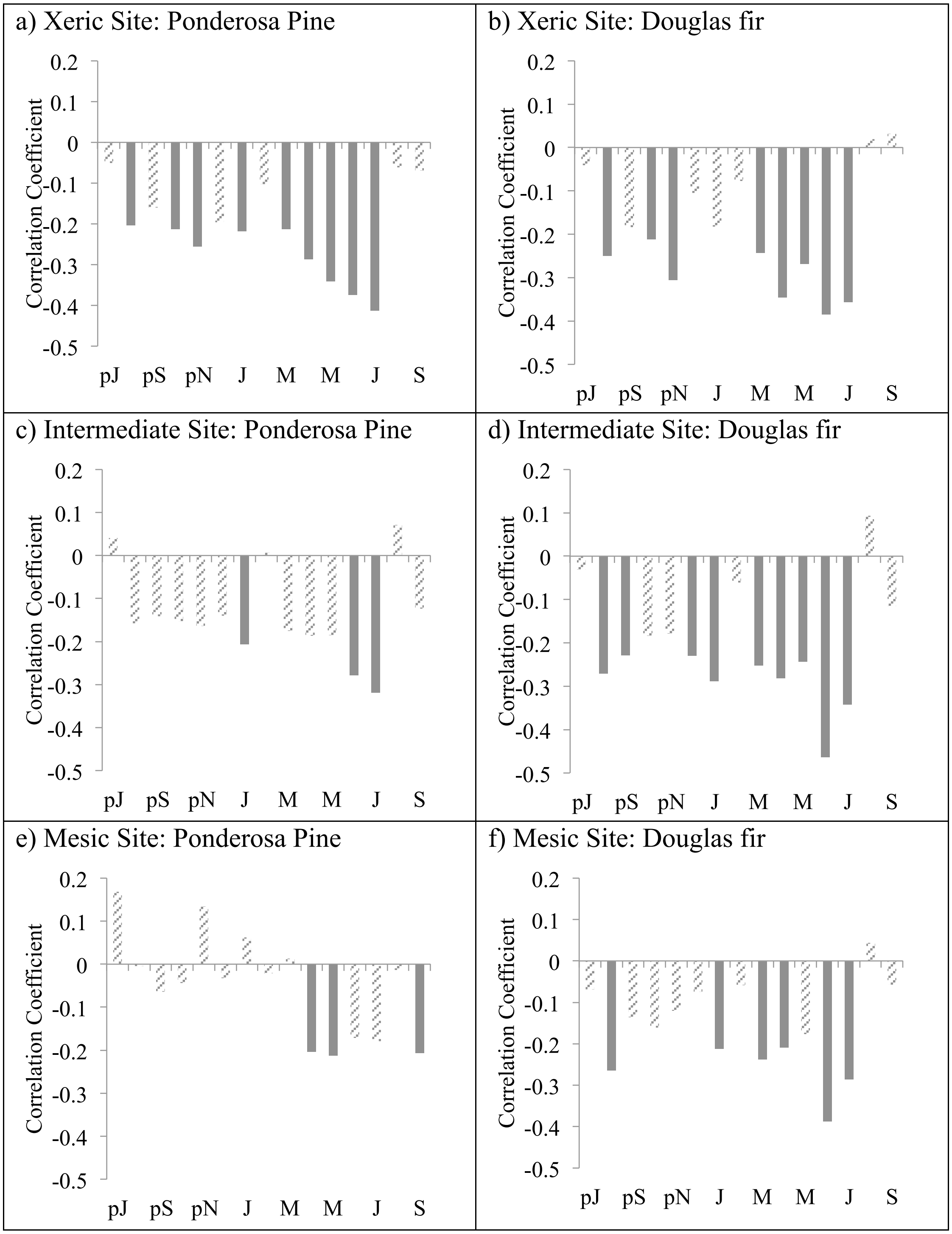
d) Intermediate Site: Douglas fir



e) Mesic Site: Ponderosa Pine

f) Mesic Site: Douglas fir

Figure 44. Correlation coefficients for the relationship between RWI and precipitation at the Pecos climate station by month. Lowercase "p" indicates a month previous to growing season. Shaded bars indicate statistically significant correlations at the P<0.05 level. Hatched bars are not statistically significant.



a) Xeric Site: Ponderosa Pine

b) Xeric Site: Douglas fir

c) Intermediate Site: Ponderosa Pine

d) Intermediate Site: Douglas fir

e) Mesic Site: Ponderosa Pine

f) Mesic Site: Douglas fir

Figure 45. Correlation coefficients for the relationship between RWI and temperature by month. Lowercase "p" indicates a month previous to growing season. Shaded bars indicate statistically significant correlations at the P<0.05 level. Hatched bars indicate correlations that are not statistically significant.

How do trees at their distributional limit respond to a severe multi-year drought?

Drought case study 1950-1956

In order to understand how tree growth responds to extreme climatic events across a moisture gradient, I analyzed the drought period of 1950-1956. The Friedman's test revealed that growth (average BAI) differed among the time periods pre-drought, drought, and post-drought for both species across the moisture gradient (Table 8). At the xeric site both species showed a significant decrease in growth during the drought and sustained growth suppression in the five year period after the drought. Growth during the drought period showed a significant decline from pre-drought conditions for both species at the intermediate site, however, growth in the post-drought period showed a recovery. Nemenyi test did not detect differences between growth pre- and post-drought at the intermediate site (Table 9). Growth at the mesic distributional limit showed a very different pattern in response to drought and was different for each species (Figure 46). Ponderosa pine experienced an increase in mean BAI during and after the drought period. Furthermore, the post-drought growth was significantly greater than pre-drought growth. Douglas fir growth, on the other hand, declined slightly in response to the drought period, but showed a significant recovery in the post-drought period.

The ponderosa pine at the xeric site was the only case where the post-drought growth was still significantly lower than the pre-drought growth. At the mesic site, however, post-drought was able to exceed the growth pre-drought growth and exceed the average BAI for the total study period.

Table 8. Friedman's test results. D.f.= 2 for all comparisons.

Site & Species	$\chi 2$	*P*-value
Xeric		
Ponderosa pine	10.571	0.005
Douglas fir	12.000	0.002
Intermediate		
Ponderosa pine	9.556	0.008
Douglas fir	12.250	0.002
Mesic		
Ponderosa pine	18.200	0.000
Douglas fir	10.333	0.006

Table 9. Nemenyi post-hoc results. Bolded Q values indicate pairwise comparisons that are significantly different (P<0.05). The critical value of Q=3.314 at P<0.05.

Xeric	Ponderosa Pine	Douglas Fir
Pair	Q	Q
Pre vs Post	**3.503**	2.449
Pre vs Drought	**3.846**	**4.899**
Drought vs Post	-0.343	-2.449
Intermediate		
Pre vs Post	2.180	2.156
Pre vs Drought	**3.552**	**4.287**
Drought vs Post	-1.372	-2.131
Mesic		
Pre vs Post	**-4.654**	-1.617
Pre vs Drought	-2.694	2.866
Drought vs Post	-1.960	**-4.483**

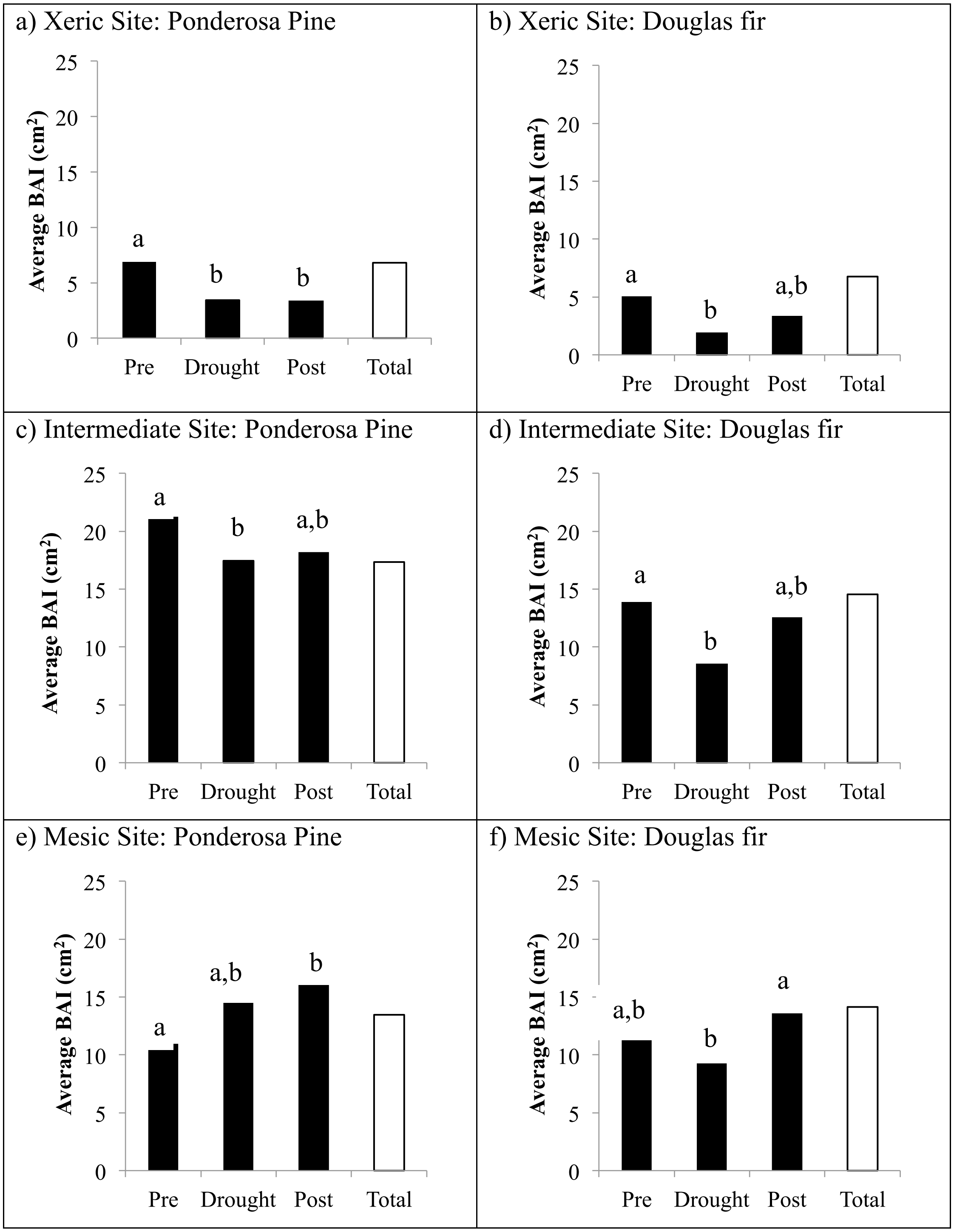


Figure 46. Growth response to1950s drought. The white bar indicates the average annual BAI for the entire study period. Letters indicate differences among periods. Periods labeled with different letters had significantly different mean BAI.

CHAPTER V

DISCUSSION AND CONCLUSION

Do trees grow more slowly at their distributional limits than elsewhere within their spatial distribution?

Patterns of growth across the three sites show that tree growth for both species is significantly slower at the xeric site than at either the intermediate or mesic sites suggesting that the low moisture distributional limit is controlled by a physiological intolerance to low moisture. The average raw ring widths are narrowest and the basal area increments are smallest at the drier distributional limits of the moisture gradient. Basal area increment and raw ring width analyses show slightly different patterns of growth at the mesic site. According to raw ring width analyses, there is slight reduction in growth suggesting that trees are growing slower at both the high *and* low moisture distributional limits than in the center of the range. However, raw ring width does not represent the most valuable dataset for comparing long-term growth trends due to the fact that ring width declines with age. According to basal area increment data, which removes age-related trends, there is not a similar pattern of slower growth at the mesic site as the species tolerance limit (physiological) model may suggest. This is likely because the mesic site is not actually the maximum physiological moisture tolerance limit for these species. Despite the expectation of greater moisture availability at the mesic site resulting in better growth, we see a pattern where tree growth increases across the gradient from xeric to intermediate and then plateaus.

This “plateau” pattern suggests that different environmental factors control the xeric and mesic distributional limits. In other words, the xeric distributional limit may be driven by abiotic factors (i.e. moisture available for growth), whereas the mesic distributional limit may be driven by biotic factors (Wiens 2011). Competition from other tree and shrub species is likely the driving factor for the pattern of growth at the mesic site. In the field I noted that while Douglas fir was found throughout the mesic site even down in the lowest points of the valley, ponderosa pine was restricted to positions slightly higher on the slopes. Although the fundamental niche of the ponderosa pine may suggest that it is able to thrive in a wetter location, the realized niche (i.e. where and how ponderosa pine is actually interacting with this landscape) suggests that they might be competitively excluded from the moister areas at this site by other species. The mesic distributional limit is therefore closer to the ecological limit than the physiological one. The pattern of growth found here corresponds to Smith and Huston’s (1989) asymmetrical model of growth where distributions are skewed toward the low resource end of the gradient where they are cut off by physiological limitations. A long “tail” of the distribution curve exists towards the high resource end of the gradient where conditions could potentially allow many plants to persist, however, competition acts as a driving force to eliminate certain individuals thereby creating distributional limits. If biotic interaction is driving the distributional limit here, it is important to note that relative competitive ability can change over time as site conditions change (Smith & Huston 1989).

Ultimately, ponderosa pine and Douglas fir growth is slower at the low moisture distributional limit compared to elsewhere within their spatial distribution. The similarity of growth at the intermediate and mesic sites suggests that the high moisture distributional limit is controlled by different factors than those that control the low moisture one.

Are trees at their species' distributional limits more sensitive to climate variability (i.e. stronger correlation to climate variables) than trees near the center of their distribution?

The general model of tree growth along an environmental gradient proposes that growth is limited and more sensitive to climate at the distributional limits (Fritts & Swetnam 1989, Hart et al. 2010). Again we find a result similar to the pattern of growth rate, where the growth at the low moisture distributional limit shows a greater sensitivity to climate than elsewhere within the spatial distribution. This pattern of highly sensitive dry sites is important because prior work has found greater tree ring variation to be associated with a strong correlation with drought-induced mortality (Ogle, Whitham, & Cobb 2000) particularly at drier, low elevation sites in the Southwest (Allen & Breshears 2008). Mean sensitivity indicates a response to an aggregate of all climate variables; however, analysis of specific climate variables provided a more detailed account of which factors are the most influential for growth in this region.

PDSI exerts the strongest influence on radial growth across all sites among the climate variables for two main reasons: 1) moisture stress is the most important limiting factor for growth in this region, and 2) the index incorporates multiple variables including precipitation, temperature, soil moisture and geographic region (Hart et al. 2010, Dolnac et al. 2013). Growth at the mesic site was not strongly impacted by regional drought most likely because water availability remains higher here even during drought periods.

The stronger relationship with climate divisional precipitation data compared to the single station precipitation data is most likely because divisional data are a combination of many climate stations which reduces the local climate effects to which the trees may not respond (Grissino-Mayer 1997). The strong, positive relationship with previous year's autumn and current year's spring and summer months supports previous work that suggests tree growth in the Southwest responds to a hydrologic water year that spans from previous August to current year July (Rose et al. 1981, Grissino-Mayer 2001).

The overall negative relationship between RWI and monthly temperatures for species across all sites suggests that higher temperatures limit growth in this region. Negative growth-temperature relationships could be due to greater carbon allocation for respiration during periods of high temperatures (Adams & Kolb 2005). The strongest negative response occurs in June and July, which are typically the warmest months for this region and are also when droughts are most intense. Differences in the tree growth-climate relationship for ponderosa pine and Douglas fir could be due to different life history strategies. Douglas fir growth, for example, has a stronger, negative relationship to temperature at the mesic and intermediate sites than ponderosa pine, possibly suggesting different adaptations to drought.

While the differences in the strength of the tree growth-climate relationship across the sites were not large, they show that climate does impact growth differently under different microsite conditions within the same region. In general, the decline in tree growth-climate relationships across the moisture gradient from xeric to mesic is likely because water availability is one of the most important factors for growth in this region. The lower moisture distributional limit was most severely impacted by climate suggesting that this limit is driven by a physiological intolerance to low moisture. Growth at these locations are important because they can serve as sensitive indicators of climate change and have the potential to be more severely affected by change which could lead to growth reduction, mortality and even broad ecotone shifts (Allen & Breshears 2008). The weaker growth-climate relationships and lower climate sensitivity associated with growth at the mesic sites suggest that the high moisture distributional limit is not climatically driven. Site moisture characteristics will likely continue to play a large role in how tree growth-climate relationships will develop under changing climate conditions (Dolanc et al. 2013).

How do trees at their distributional limits respond to a severe multi-year drought?

The severe regional drought from 1950-1956 reduced growth during the drought years for both species across the gradient, but the post-drought response varied between sites. The results of the case study drought analysis indicate that growth at the xeric end of the moisture gradient is more impacted by drought than elsewhere in the range. Since moisture is an important limiting factor for forest growth, it seems plausible that trees growing on drier soils and more open canopy, south-facing slopes would experience a greater reduction in growth during a drought. We have already shown that growth is slower at the xeric site overall. During a drought, trees at a drier location will put more resources into their roots than to their shoots (including radial increment) in an effort to reduce water loss (Ogle, Whitham & Cobb 2000). Furthermore, they are also likely at the edge of their fundamental niche and physiological moisture limit.

Trees at the intermediate and mesic site show little differences between growth before and after a major drought. Presumably, this is because trees are less limited by moisture. Since they already grow in more productive sites, a regional drought may not be as impactful at these local sites. Interestingly, ponderosa pine growth at the mesic site showed that post-drought growth was significantly higher than pre-drought growth suggesting that trees at this site were able to quickly recover and the drought did not show long-term negative effects. These findings support of the work of Adams and Kolb (2005) who found the radial growth for both ponderosa pine and Douglas fir in Arizona to be more sensitive to drought at drier, low-elevation stands than in wetter stands. The inability of ponderosa pine at the xeric site to recover to at least pre-drought growth, in comparison to the mesic site, suggests that trees at the low moisture distributional limit are at their minimum physiological tolerance limit.

In conclusion, patterns suggest that for ponderosa pine and Douglas fir in the Southern Rocky mountains, the xeric distributional limits are of critical importance when assessing tree growth response to drought along a moisture gradient. Regional droughts are predicted to be longer and more severe than the 1950s drought as the climate continues to warm. As a result these locations could be more likely to experience a shift in distribution as a result of severe drought than elsewhere in the species' range.

One of the greatest biogeographic questions concerns the factors that control distributional limits of species. In order to gain a better understanding on how range limits control broad biogeographic patterns, we must also understand how ecological niche theory plays a role in creating limits on species. Despite discussion in the literature, few studies have analyzed radial growth patterns along environmental gradients in the context of niche theory. In this study, I showed that distributional limits for tree species could be explained by both abiotic and biotic factors at different places along a moisture gradient. In the Southwest, growth at the xeric site shows slower growth, higher sensitivity to climatic variability, and a greater response to severe drought. Growth at the mesic site appeared to be less impacted by climate and severe drought. This suggests that as climate is projected to continue changing, growth at the dry end of the distributional limits for both ponderosa pine and Douglas fir may change in response. Changes in vegetation dynamics at the wetter end of the distributional limits will likely be more dependent on how competing species will respond to climate change.

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APPENDIX

Table 10. Residual chronologies. PP= ponderosa pine. DF= Douglas fir.

Year	Mesic PP	Intermediate PP	Xeric PP	Mesic DF	Intermediate DF	Xeric DF
1925	0.822	0.731	0.711	0.631	0.506	0.273
1926	1.095	1.065	1.082	1.366	1.371	1.447
1927	1.031	0.926	1.092	1.009	0.874	0.686
1928	1.06	0.979	1.003	0.941	1.063	1.158
1929	1.503	1.334	1.154	1.225	1.415	1.337
1930	0.753	1.243	1.093	1.037	1.008	1.292
1931	0.953	1.099	1.098	1.039	0.953	1.039
1932	1.073	1.177	1.192	1.322	1.353	1.825
1933	0.991	0.958	0.769	0.949	1.04	0.951
1934	0.784	0.859	0.715	0.623	0.674	0.25
1935	1.232	0.935	1.013	0.959	0.921	0.863
1936	1.027	0.931	0.892	1.052	1.069	0.789
1937	0.897	1.013	0.939	1.156	1.257	1.232
1938	1.133	0.78	0.773	0.951	0.821	0.548
1939	0.843	0.876	1.02	0.881	0.841	1.033
1940	0.888	1.104	1.246	1.083	0.941	0.946
1941	0.911	1.367	1.323	1.427	1.583	2.174
1942	0.788	1.018	1.348	0.998	1.066	1.648
1943	0.911	1.207	1.321	1.147	1.092	1.112
1944	1.139	1.118	1.179	0.901	1.118	0.952
1945	1.023	1.186	1.135	1.049	1.176	0.957
1946	0.71	0.587	1.01	0.769	0.541	0.619
1947	0.833	0.906	0.867	0.959	1.057	0.647
1948	0.825	1.199	1.423	1.038	1.43	1.479
1949	1.358	1.308	1.492	1.341	1.291	1.988
1950	1.033	0.606	0.774	0.8	0.53	0.585
1951	0.913	0.553	0.388	0.775	0.686	0.551
1952	0.961	1.193	1.032	0.875	1.032	1.291
1953	1.05	0.922	0.935	0.9	0.799	0.576
1954	1.248	1.179	0.706	1.053	0.87	0.657
1955	1.079	0.856	0.589	0.933	0.898	0.542
1956	0.905	0.713	0.58	0.838	0.51	0.642
1957	1.12	0.898	0.76	0.983	0.858	0.691
1958	1.052	1.022	1.037	1.236	1.056	1.374
1959	0.998	0.859	0.913	1.12	0.898	1.322
1960	1.282	1.163	1.175	1.04	1.053	1.208
1961	1.117	1.033	0.811	0.863	0.911	0.574
1962	0.95	1.18	0.886	1.117	1.207	0.629
1963	0.804	1.143	0.84	1.065	0.873	1.083
1964	0.841	0.644	0.637	0.714	0.635	0.494
1965	1.191	1.269	1.077	1.288	1.529	1.268
1966	1.08	1.18	1.029	1.198	1.314	0.971
1967	0.953	0.709	0.908	0.639	0.762	0.826
1968	0.878	1.141	1.124	1.067	1.25	1.241

Table 10 Continued.

Year	Mesic PP	Intermediate PP	Xeric PP	Mesic DF	Intermediate DF	Xeric DF
1969	1.107	1.019	1.323	0.997	1.243	1.446
1970	1.143	0.984	1.153	1.148	1.146	1.153
1971	1.043	0.887	0.604	0.815	0.681	0.289
1972	1.131	1.199	1.246	1.102	1.139	1.154
1973	0.713	1.007	1.638	0.865	1.182	1.91
1974	1.022	0.837	0.645	0.853	0.743	0.395
1975	1.105	1.207	1.733	1.063	1.098	1.792
1976	0.911	1.007	0.667	0.771	0.848	0.639
1977	0.688	0.869	0.603	0.943	0.952	0.744
1978	0.889	0.925	0.988	0.976	0.953	0.868
1979	1.099	1.108	1.447	1.187	1.321	1.391
1980	0.985	0.806	0.751	0.894	0.744	0.6
1981	1.181	0.927	0.806	0.786	0.483	0.416
1982	1.151	1.159	0.908	1.236	1.026	0.898
1983	0.983	1.059	1.078	1.078	1.109	0.924
1984	1.011	0.986	0.921	1.099	0.914	0.792
1985	1.107	1.152	1.406	1.329	1.568	1.34
1986	1.206	1.135	1.194	1.196	1.324	1.002
1987	0.988	0.842	1.18	1.058	1.057	0.952
1988	1.313	1.315	1.16	0.941	1.341	0.827
1989	0.585	0.814	0.209	0.863	0.616	0.267
1990	0.778	0.898	1.064	0.953	0.92	0.861
1991	1.142	1.256	1.254	1.452	1.733	0.864
1992	0.736	0.771	1.126	0.977	0.979	1.259
1993	0.925	1.029	1.16	1.018	0.923	1.36
1994	0.972	1.182	1.144	0.919	1.043	1.843
1995	1.027	1.329	1.25	0.899	1.119	1.82
1996	0.861	0.691	0.486	0.625	0.421	0.676
1997	1.265	1.291	1.567	0.967	1.015	2.029
1998	0.719	0.998	1.149	0.945	0.896	1.019
1999	1.469	1.223	1.352	1.22	1.286	2.119
2000	0.812	0.687	0.375	0.609	0.473	0.386
2001	0.811	0.81	1.066	0.793	0.854	0.984
2002	0.821	0.697	0.562	0.744	0.536	0.349
2003	0.908	0.781	0.731	0.939	0.962	0.771
2004	1.022	0.872	1.036	0.928	0.701	0.817
2005	1.244	0.905	1.07	1.28	1.056	1.271
2006	1.013	1.054	0.766	0.889	0.771	0.394
2007	1.264	0.994	1.354	1.33	1.762	1.415
2008	1.201	1.252	1.422	1.055	1.17	1.117
2009	1.073	1.262	0.858	1.314	1.284	0.803
2010	1.007	1.149	1.579	1.351	1.104	2.083
2011	0.804	0.884	0.446	0.95	0.758	0.242
2012	1.103	1.219	0.656	0.803	1.091	0.665
2013	1.185	1.176	0.764	1.046	1.115	0.495
2014	0.437	0.472	0.608	0.331	0.631	0.667

Table 11. Diameter measurements for all series and subsequent bark thickness values needed to calculate BAI. DBH, diameter at breast height. DBT, double bark thickness. DIB, diameter inside bark.

Site Type	Species	Tree No.	DBH (cm)	DBT (cm)	DIB (cm)	Basal area (cm^2)
Mesic	PP	001	53.2	5.853	47.347	1760.626
Mesic	PP	002	67	7.233	59.767	2805.476
Mesic	PP	003	62.5	6.783	55.717	2438.140
Mesic	PP	004	36.8	4.213	32.587	834.003
Mesic	PP	005	70.5	7.583	62.917	3108.995
Mesic	PP	006	41.2	4.653	36.547	1049.019
Mesic	PP	007	68	7.333	60.667	2890.605
Mesic	PP	008	42.8	4.813	37.987	1133.314
Mesic	PP	009	69.8	7.513	62.287	3047.044
Mesic	PP	010	75	8.033	66.967	3522.135
Mesic	DF	022	52.6	9.958	42.642	1428.120
Mesic	DF	023	53.4	10.094	43.306	1472.942
Mesic	DF	024	46.6	8.938	37.662	1114.028
Mesic	DF	025	44.6	8.598	36.002	1017.988
Mesic	DF	026	41.5	8.071	33.429	877.680
Mesic	DF	028	57.4	10.774	46.626	1707.441
Mesic	DF	030	81.1	14.803	66.297	3452.051
Mesic	DF	031	37.3	7.357	29.943	704.174
Mesic	DF	036	33.8	6.762	27.038	574.167
Mesic	DF	039	61.2	11.420	49.780	1946.253
Intermediate	PP	001	57	6.233	50.767	2024.164
Intermediate	PP	002	57.1	6.243	50.857	2031.347
Intermediate	PP	006	53	5.833	47.167	1747.264
Intermediate	PP	011	74.5	7.983	66.517	3474.958
Intermediate	PP	012	52.6	5.793	46.807	1720.694
Intermediate	PP	014	55	6.033	48.967	1883.169
Intermediate	PP	018	48	5.333	42.667	1429.768
Intermediate	PP	019	51.1	5.643	45.457	1622.869
Intermediate	PP	020	66.5	7.183	59.317	2763.389
Intermediate	DF	003	42	8.156	33.844	899.607
Intermediate	DF	004	40.4	7.884	32.516	830.393
Intermediate	DF	005	49.5	9.431	40.069	1260.975
Intermediate	DF	007	50.4	9.584	40.816	1308.430
Intermediate	DF	008	52.4	9.924	42.476	1417.022
Intermediate	DF	009	55.7	10.485	45.215	1605.664
Intermediate	DF	010	57.1	10.723	46.377	1689.253

Table 11. Continued.

Site Type	Species	Tree No.	DBH (cm)	DBT (cm)	DIB (cm)	Basal area (cm^2)
Intermediate	DF	016	46.3	8.887	37.413	1099.346
Intermediate	DF	017	51.9	9.839	42.061	1389.468
Xeric	PP	011	34	3.933	30.067	710.000
Xeric	PP	012	36	4.133	31.867	797.556
Xeric	PP	013	40	4.533	35.467	987.936
Xeric	PP	015	35	4.033	30.967	753.141
Xeric	PP	016	30.8	3.613	27.187	580.496
Xeric	PP	017	30.2	3.553	26.647	557.665
Xeric	PP	018	34.5	3.983	30.517	731.411
Xeric	PP	020	35	4.033	30.967	753.141
Xeric	DF	004	30.5	6.201	24.299	463.731
Xeric	DF	005	30	6.116	23.884	448.026
Xeric	DF	006	30.5	6.201	24.299	463.731
Xeric	DF	007	35.2	7.000	28.200	624.579
Xeric	DF	008	35.5	7.051	28.449	635.658
Xeric	DF	009	40.1	7.833	32.267	817.724
Xeric	DF	010	34.9	6.949	27.951	613.598