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The Impact of Climate and Elevation on the Growth and Mortality of Piñon Pine

Alice M. Fretz

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**THE IMPACT OF CLIMATE AND ELEVATION ON THE
GROWTH AND MORTALITY OF PINYON PINE**

by

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B.S. Biology & Environmental Science, Goshen College, 2013

THESIS

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Master of Science

Biology

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ABSTRACT

The Southwestern United States is currently experiencing severe drought, resulting in the mortality of many tree species. Piñon-juniper woodlands are an extensive biome in the Southwest, and are highly vulnerable to extended periods of drought that lead to tree mortality. Specifically, *Pinus edulis* populations are decreasing due to increasingly arid conditions. I used dendrochronology to investigate how tree growth rings of *Pinus edulis* reflect severe drought in living and dead trees. I also investigated how severe drought affects *Pinus edulis* along an altitudinal gradient. Tree core samples were taken from currently living and dead trees, as well as from trees at three elevations separated by 100 m in elevation. Growth rings were cross-dated and measured, and widths were statistically compared between all living and dead trees to find years where growth may have differed. Widths were also compared between the three elevation sites. I sought to differentiate between two mortality-related hypotheses: 1) trees that died had a

lifetime of underperforming compared to surviving trees and lacked the resources to deal with severe drought, or 2) trees that died consistently outperformed surviving trees and in doing so were closer to physiological limitations when stressed. I also hypothesized that, across elevations, trees at lower elevations would exhibit less growth and greater variability in growth compared to higher elevations. My results indicate that trees that died began to experience decreased growth compared to surviving trees following the drought of the 1950s, and that they had a higher variability in growth that was highly correlated with precipitation. I also found that trees at higher elevations had a higher variability in their growth, while trees at lower elevations may not be able to tolerate severe drought and may periodically die and then re-establish. Using tree rings offers the chance to compare growth patterns to known climate events and see the response of a tree. This knowledge is important for understanding how tree mortality will affect piñon-juniper woodlands in the future, and how to best predict ecosystem shifts.

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Introduction

Anthropogenic climate change is currently affecting ecosystems worldwide and is expected to cause a 2 - 4.5° C increase in global mean temperature by the year 2100 (IPCC 2014; Melillo et al. 2014). Although increased temperature alone will change the drought regime experienced by many ecosystems as warming increases evaporation and transpiration (Williams et al. 2013), a shift in precipitation patterns is also likely in many regions worldwide (Cox et al. 2013; Williams et al. 2013; Allen et al. 2010).

Of the most affected ecosystems, forests and woodlands are at a high risk of changing composition in the near-term and shifting species distributions in the longer-term (Hansen et al. 2013). In the semi-arid regions of western North America, trees are increasingly experiencing higher temperatures and less precipitation (Allen et al. 2010; Seager et al. 2007). This leads to a variety of physiological stressors and ultimately tree mortality (Van Mantgem et al. 2009; Saatchi et al. 2013; Peng et al. 2011; Allen et al. 2010; Williams et al. 2013). Consistent with these climate-driven changes, reports of tree mortality are also increasing globally (Allen et al. 2010). Yet, these patterns of mortality are poorly understood and difficult to predict for reasons that include variation in the longevity of tree species, uncertainty about the species-species limits that determine mortality thresholds, and regional variation in climatic variability (Adams et al. 2009). Developing our ability to predict future forest dynamics, mortality, and vegetation shifts requires improving our knowledge of the underlying mechanisms of environmental response and mortality.

One approach to understanding the limits of plant growth and the conditions leading to mortality is to evaluate variation in tree growth associated with climate fluctuation as well as disturbances such as fire, insect outbreaks, and severe drought. Drought is predicted to intensify in the Southwest within the next 100 years (Williams et al. 2013). Mortality can occur as environmental conditions exceed physiological tolerances (e.g. McDowell et al. 2008), when microbial infestation or outbreaks of insect pathogens inflict extensive damage, or as the result of interactions between such abiotic and biotic stresses. Moreover, the apparent proximate cause of tree death may conceal the effects of many stressors that can pre-condition trees for mortality over a period of years before mortality occurs (Edburg et al. 2012). Such disturbances can make mortality events erratic and episodic and challenge our ability to identify the controls on tree survival and growth (Michaels & Hayden 1987; Mast & Veblen 1994; Villalba & Veblen 1998).

In this study, we used dendrochronological methods (Cook & Leonardas 2013) to measure the inter-annual variation in growth for comparison with abiotic drivers, principally precipitation and temperature. These methods measure whole-tree growth and integrate a multitude of physiological factors such as whole-tree carbon limitations (Manion 1981; Waring 1987; McDowell et al. 2008) resulting from biotic stress, soil moisture deficit (Irvine et al. 1998) or xylem cavitation in response to drought or freezing stress (Mueller et al. 2005). Although growth rings may not capture the exact mechanism of mortality, they can be used to identify temporal variation among individuals in

differing environments and, following episodes of natural mortality, to compare performance between trees that die and those that survive.

We used the two approaches described above to address the effects of temperature and precipitation on growth and mortality of *Pinus edulis* in central New Mexico, USA. First, to understand the variation in growth with temperature and precipitation, we analyzed tree rings from three sites along an elevation gradient from the lower limit to middle elevation to test the hypothesis that at lower elevation sites trees would exhibit less growth and greater variability in growth compared to higher elevations. Second, we analyzed tree rings from trees that survived a 2013 episode of 60% piñon mortality near Mountainair NM. We also sampled from trees that died during this event, when both abiotic (drought) and biotic (bark beetles) stresses impacted the region. Severe drought began in the early 2000's and continued until 2013. In 2011, these severe conditions were exacerbated by a negative freeze, abnormally low annual precipitation, and extremely high warm-season temperatures. Our objective was to differentiate between two hypotheses: 1) Trees that died had a lifetime of underperforming compared to surviving trees and ultimately lacked the resources to deal with severe drought, or 2) Trees that died consistently outperformed surviving trees and in doing so were closer to physiological limitations when stressed.

Materials and Methods

Study sites

We studied two sites in New Mexico, USA, separated by approximately 30 km, to assess *Pinus edulis* growth patterns. Mean intra-annual precipitation values for the Sevilleta National Wildlife Refuge are shown in Figure 1. Note the highest annual precipitation is received during the summer monsoon months of July and August. The first site (see Anderson-Teixeira et al. 2011), near Mountainair (34.4357, -103.2636, elevation: 2,196 m) was used to assess evidence for performance differences preceding mortality. In 2013, piñon mortality was observed at this site, and currently over 60% of the piñon have died. During the mortality period, pine bark beetle (*Ips* species) was abundant, probably a result of the persistent drought from 2011-2013. The stand composition at the Mountainair (MA) site is primarily *Pinus edulis* (PIED) co-occurring

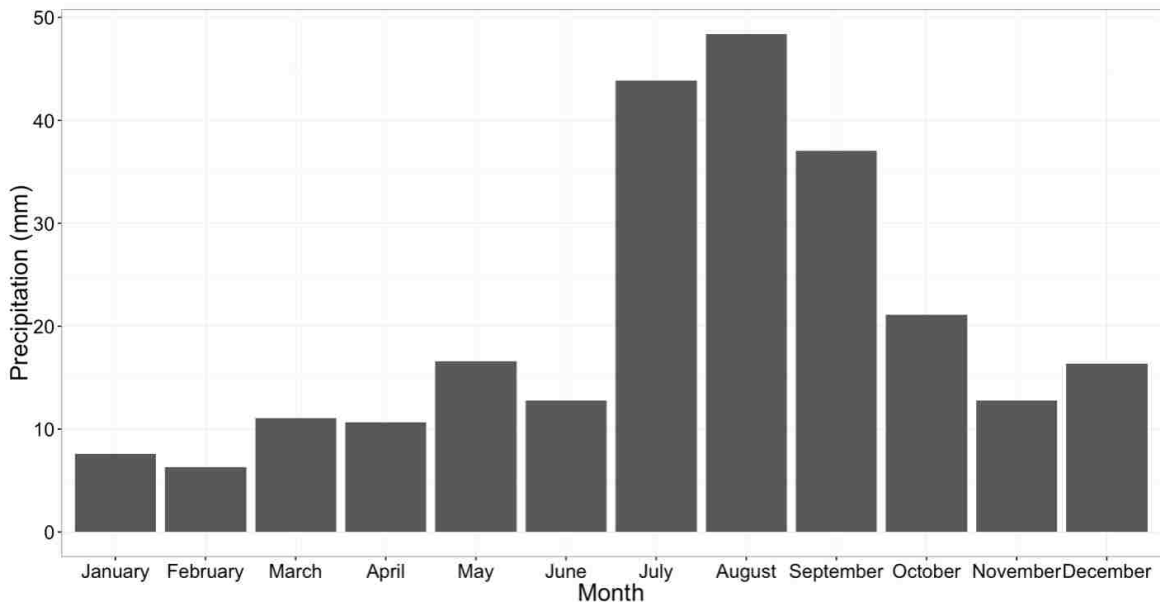


Figure 1. Mean monthly precipitation values in mm over time from Socorro County, NM. The values were obtained by averaging each month's mean precipitation from the past 40 years at one location in Socorro County.

with *Juniperus monosperma* (JUMO) and sparse *Quercus turbinella* (scrub oak). Mean annual precipitation and temperature of the MA site are shown in Figure 2.

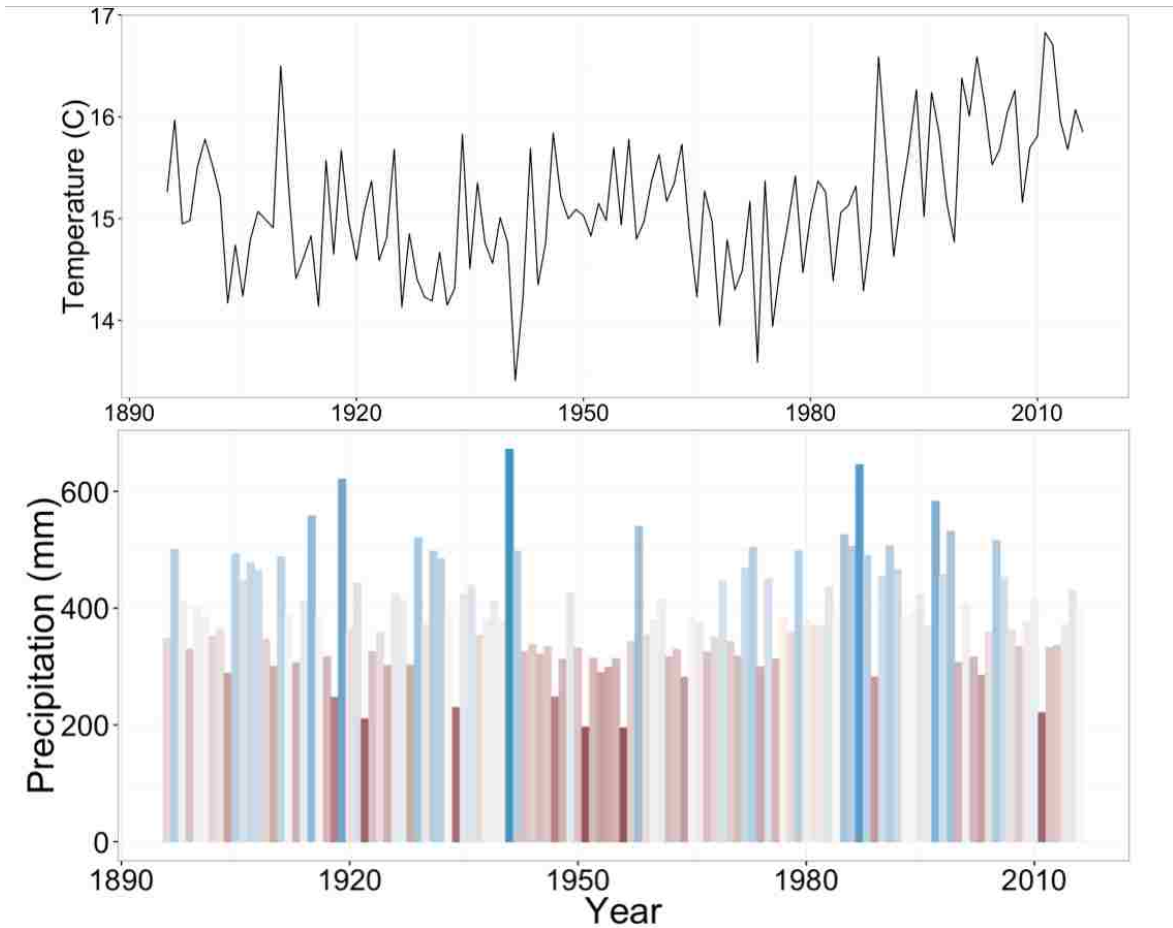


Figure 2. The top panel shows mean annual temperature in °C against time taken from Mountainair, NM. The bottom panel shows mean annual precipitation in mm against time taken from the same location. The red bars depict precipitation values that are below the mean, and the blue bars depict values that are above the mean. Opacity of the bars corresponds with how far above or below the mean each value falls.

The second site is utilized as an elevation gradient in the Los Piños mountains on the east side of the Sevilleta (SEV) National Wildlife Refuge (34.3861, -106.5266). We sampled from three separate elevations. The lowest elevation is at 1,796 m and near the lower limit of piñon growth. The mid-level site is at 1,911 m, and the highest site is at

1,971 m. This site will be referred to as the high elevation site, but in actuality is near the middle limit of piñon growth. The sites are similar in topography, aspect, and climate.

The stand composition at the lowest site consists of small PIED with primarily JUMO.

Stand compositions at the middle and high sites are a mix of PIED and JUMO. Figure 3 shows mean annual precipitation and temperature of the SEV site.

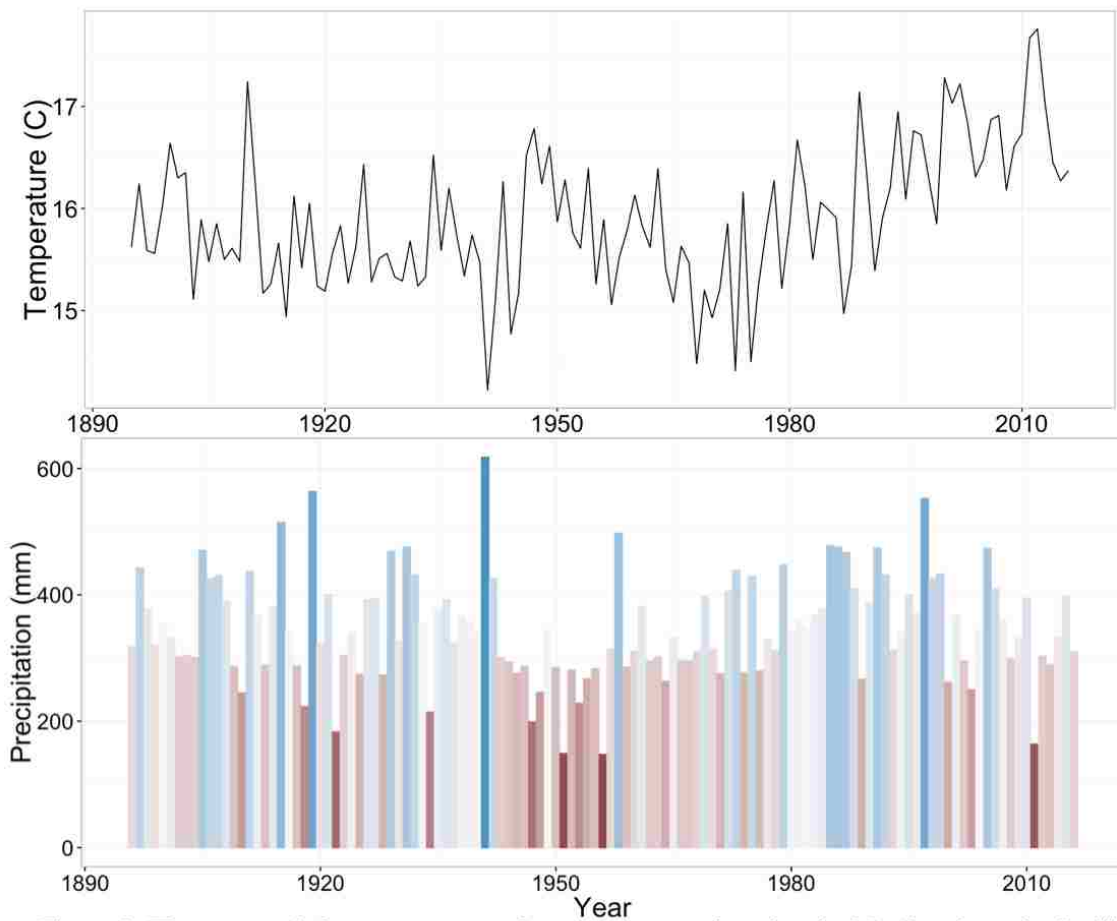


Figure 3. The top panel shows mean annual temperature against time in °C taken from the Sevilleta National Wildlife Refuge, NM. The bottom panel shows mean annual precipitation in mm against time taken from the same location. The red bars depict precipitation values that are below the mean, and the blue bars depict values that are above the mean. Opacity of the bars corresponds with how far above or below the mean each value falls.

Field sampling and laboratory procedures

In June 2016, two overlapping 50 m x 50 m plots were selected at the Mountainair site, one with primarily dead trees and the other with primarily live trees. Dead trees were classified as such if they had zero visible current growth. Live trees were assessed to ensure there were no signs of mortality, i.e. dried leaves or dead branches without growth. Within each plot, trees were randomly selected using the above classifications. Sampling was limited to trees with DBH (diameter at breast height) > 12 cm. A total of 25 live trees and 20 dead trees were selected. Two opposing increment cores were collected from each live tree with the aim of taking each core near the 1 m level on the trunk. After extracting the core(s), DBH of the tree, coring height, direction the growth slope was facing, and degree of the core was recorded. Degree of the core is based on the slope of the ground the tree was growing on. Uphill corresponds with 0° and the core degree is estimated clockwise around the trunk.

Similar tree core collection protocols were followed at the SEV and Mountainair sites. A 50 m x 50 m plot was selected at each elevation, and ten trees were selected within the middle and high elevation sites. At the low elevation, only four trees larger than 12 cm were located. The majority of PIED growing at this low elevation exists on the slopes of small arroyos that are frequented by running water. Two cores were taken from each tree and the same measurements as above were taken.

In the laboratory, cores from both the SEV and Mountainair sites were prepared, cross-dated, and the ring widths were measured using the methods of Swetnam et al. (1988) and Stokes & Smiley (1968), after the cores were dried and mounted onto grooved

wooden mounts for stability. The cores were then sanded with successively finer gritted sandpaper, ending with 15 micron finishing paper and cross-dated using a microscope. Ring-widths were measured using a Velmex (Velmex, Inc.) measuring system and recorded with Tellervo software (Laboratory of Tree-Ring Research, University of Arizona). Three cores from dead trees and two from live trees were not included in the study because we were unable to be cross-date them.

Tree growth patterns

The basic growth characteristics of all the trees sampled that we measured included mean ring width (RW) in micrometers and standard deviation of the live trees and dead trees in the Mountainair site, and in the live trees at each elevation site at the SEV. We also measured the mean RW for the past 20 years and mean RW for the most recent five years for both live and dead trees. We calculated mean RW pre-1940s and post-1940s to assess if the severe drought that began in the late 1940s impacted growth rate. To compare differences in lifetime RW between live and dead trees, the differences between the two group means was also calculated.

In order to remove the inherent effect of biological growth over time and to calculate average growth chronologies, ring-width indices (RWI) were calculated for all trees using a negative exponential curve of the mean of each site. RW alone is not always a reliable metric to use because one tree's growth may overly influence the mean RW of a site. Young trees appear to have a high growth rate because their trunk circumference is so small. Old trees also exert an unfair influence on mean growth rate because they

appear to have smaller growth rings due to a larger trunk circumference. These effects may cause one year of a tree's growth to appear larger or smaller than what most of the trees at a site actually experienced. However, including RW along with RWI in this analysis retains the physical differences in growth rates between live and dead trees (Macalady & Bugmann 2014) while also removing the effects of age. We used RWI to calculate chronologies without those effects and to highlight the trajectory of growth in the dead against the surviving trees. In addition, we removed the youngest three living trees from analysis in order to make the stands more similarly aged. The live and dead trees are from the same stand and gross differences in growth combined with RWI may give key insights into determining mortality patterns of a specific tree. We use RWI to create chronologies of the elevation sites to show the growth trajectory over time, and RW was also included but not as heavily examined as the stands were of vastly different ages.

Climate comparisons

To assess climate responses among the trees sampled, we compared RW and RWI to precipitation data acquired from PRISM (PRISM Climate Group, Oregon State University). We examined the linear relationship between mean hydrological year precipitation against RW and RWI of live trees, dead trees, and all three elevation sites. We also examined the linear relationship between RW and RWI to winter precipitation (October of previous year through March of current year) and to monsoon precipitation (July through October), separately. We calculated running correlations using a 30-year

window between precipitation, RW, and RWI. Each of these analyses was further broken down by comparing the RW/RWI and precipitation data by decade to see variation over longer-term weather cycles such as those driven by ENSO and PDO. We used ANCOVA to test the null hypothesis that RW and RWI respond to precipitation in the same way by decade. In these models, RW and RWI were dependent variables, precipitation was the independent variable, site was a factor, and decade was a covariate. A significant site \times covariate interaction would indicate that the slope of the RW/RWI-precipitation relationship differs in the same decade between sites.

The same analyses as above, excluding the ANCOVA model and running correlations, were also completed using mean temperature data acquired from PRISM for each site and PDSI acquired from the National Drought Mitigation Center (University of Nebraska-Lincoln). Precipitation, temperature, and PDSI were used as the potential climate metrics driving the patterns we observed in RW and RWI.

Results

General growth trends

Piñon growth varied over time and between the four sites. Along the elevation gradient, orientation of the sampled slope did not vary between the three sites (see Table 1). Mean DBH for each site varied, with the mid-elevation site (PJM) having the largest mean DBH at 29.14 cm. The highest elevation site (CMH) had the subsequent largest DBH, followed by the trees at the lowest elevation (GDL) with the smallest. Within the

live (Live₂₀₁₃) and dead (Dead₂₀₁₃) trees at the Mountainair site (MA), Dead₂₀₁₃ had a slightly larger DBH than Live₂₀₁₃.

Table 1. The site characteristics of all the sites where core samples were taken. APJ = live trees and DPJ = dead trees taken near Mountainair, NM. CMH = highest elevation, PJM = mid-elevation and GDL = lowest elevation taken near Sevilleta NWR, NM. Slope aspect correlates with the orientation the growing slope was facing. The range for DBH of all trees was 11.6 - 50.6 cm, and the range for age of all trees was 34 - 176 years.

Site	Slope Aspect	Mean DBH \pm 1 se (cm)	Mean RW (\pm se)	Mean RWI (\pm se)	Mean Age \pm 1 se
APJ	W	15.96 \pm 0.39	0.907 \pm 0.031	0.916 \pm 0.032	112 \pm 5.03
DPJ	E	19.27 \pm 0.78	0.927 \pm 0.034	0.955 \pm 0.036	135 \pm 6.85
CMH	SW	21.79 \pm 1.09	1.283 \pm 0.058	0.926 \pm 0.047	111 \pm 5.32
PJM	S	29.14 \pm 1.57	1.202 \pm 0.059	0.971 \pm 0.033	112 \pm 8.87
GDL	N	15.75 \pm 0.62	2.733 \pm 0.182	0.933 \pm 0.056	45 \pm 1.66

Elevation gradient growth rates over time

Along the elevation gradient at SEV, growth varied significantly between the three elevations. The trees at the lowest site (GDL) had the highest growth rates across the elevation gradient, but the age of these trees was also significantly (up to 100 years) younger than trees at either of the other two sites (average establishment date of 1970). The low elevation site trees were also small (mean DBH = 15.75 cm) compared to the other two sites although they were among the largest piñon within the site. Lifetime growth rate was the lowest at the mid-elevation site (PJM) and not significantly different from lifetime growth rates at the highest site (CMH; see Table 1). Despite this, the mid-elevation site had a significantly higher growth rate than the highest site during the 1900s ($p = 0.03$) and 1950s ($p = 0.009$).

We observed different patterns when analyzing RWI. The mid-elevation site had the greatest lifetime RWI, the low elevation site followed, and the highest site had the lowest lifetime RWI (Figure 4). Although the high elevation site had the lowest lifetime RWI, this population had a significantly higher variance in RWI (Table 2) than the other two. Variance within the mid-elevation site followed, and finally the population at low elevation site had the lowest variance.

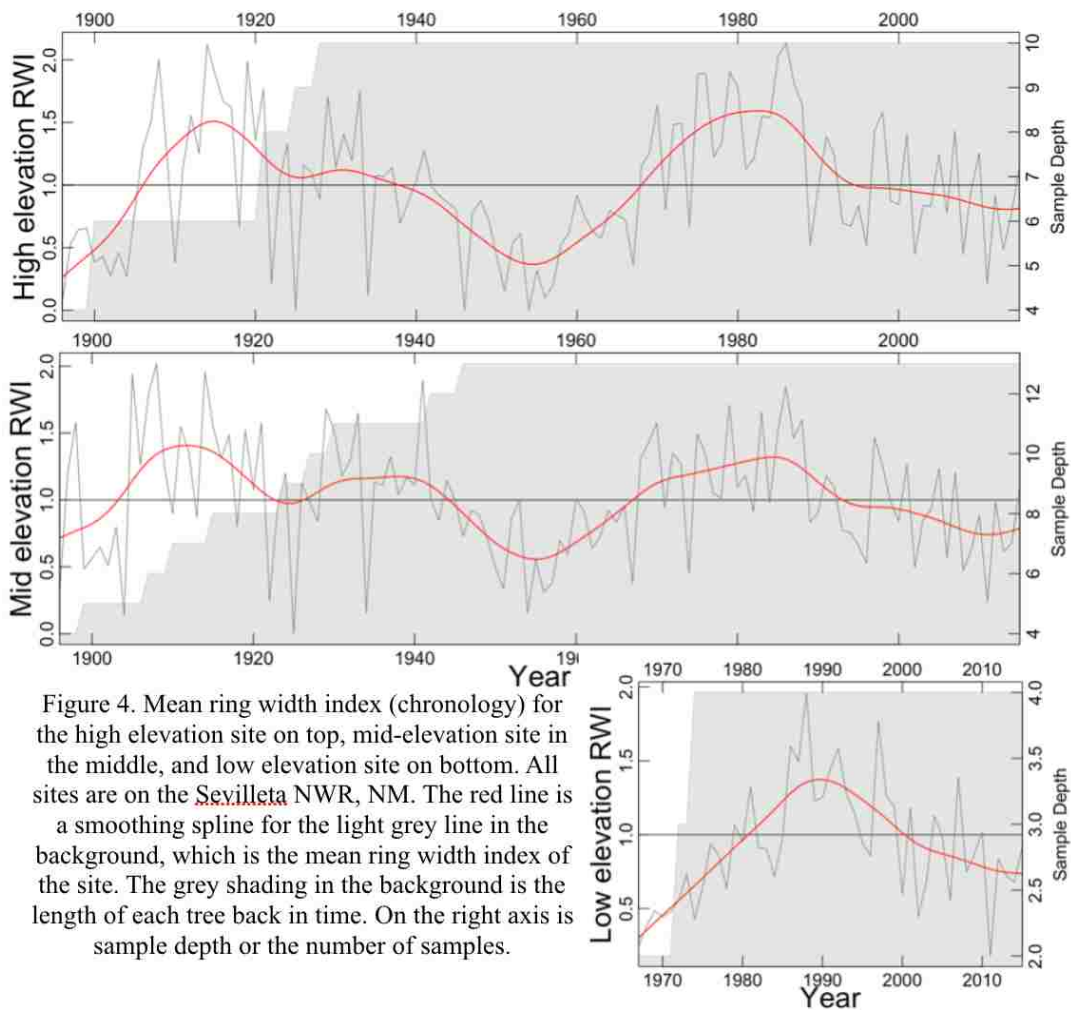


Figure 4. Mean ring width index (chronology) for the high elevation site on top, mid-elevation site in the middle, and low elevation site on bottom. All sites are on the Sevilleta NWR, NM. The red line is a smoothing spline for the light grey line in the background, which is the mean ring width index of the site. The grey shading in the background is the length of each tree back in time. On the right axis is sample depth or the number of samples.

Table 2. The variance within RWI of all the sites where core samples were taken. APJ = live trees and DPJ = dead trees taken near Mountainair, NM. CMH = highest elevation, PJM = mid-elevation and GDL = lowest elevation taken near Sevilleta NWR, NM.

Site	Variance (σ^2)
APJ	0.18
DPJ	0.26
CMH	0.28
PJM	0.19
GDL	0.16

Effects of climate on growth across elevations

Along the elevation gradient, trees at the two highest elevations differed in response to precipitation during the 1950s, which was when they had the largest difference in growth. At these sites, precipitation was much lower during the 1950s than

Table 3. Climate summary of the site on the Sevilleta NWR, NM broken down by decade.

Decade	Mean precip \pm 1 se (mm)	Mean growing season temp \pm 1 se ($^{\circ}$ C)
1897 - 1910	353.35 \pm 17.1	15.82 \pm 0.11
1911 - 1920	372.47 \pm 33.5	15.73 \pm 0.22
1921 - 1930	335.41 \pm 25.9	15.56 \pm 0.12
1931 - 1940	362.86 \pm 21.8	15.67 \pm 0.13
1941 - 1950	327.38 \pm 37.4	15.71 \pm 0.28
1951 - 1960	276.3 \pm 31.1	15.74 \pm 0.13
1961 - 1970	318.64 \pm 13.1	15.52 \pm 0.17
1971 - 1980	353.57 \pm 22.2	15.36 \pm 0.21
1981 - 1990	392.16 \pm 20.9	15.97 \pm 0.20
1991 - 2000	400.15 \pm 26.4	16.25 \pm 0.15
2000 - 2015	334.02 \pm 19.1	16.89 \pm 0.12

any other decade in the past 130 years (Table 3). The mid-elevation site had much higher growth rates than the high elevation site, but when standardized to RWI, had similar growth patterns (Figure 4). Across all three elevation sites, there is a higher correlation between growth rates and hydrologic year precipitation than with winter precipitation. Figure 5

shows the relationship between hydrologic year precipitation and RWI for each elevation.

If we look solely at slope values, the highest elevation site has a significantly higher slope ($m = 0.0038$) than the other two ($m = 0.0032$ for middle and low elevations). Looking at the R^2 values for the same plots, the middle elevation site has a higher value ($R^2 = 0.4$) than the high ($R^2 = 0.36$) and low ($R^2 = 0.34$) elevations.

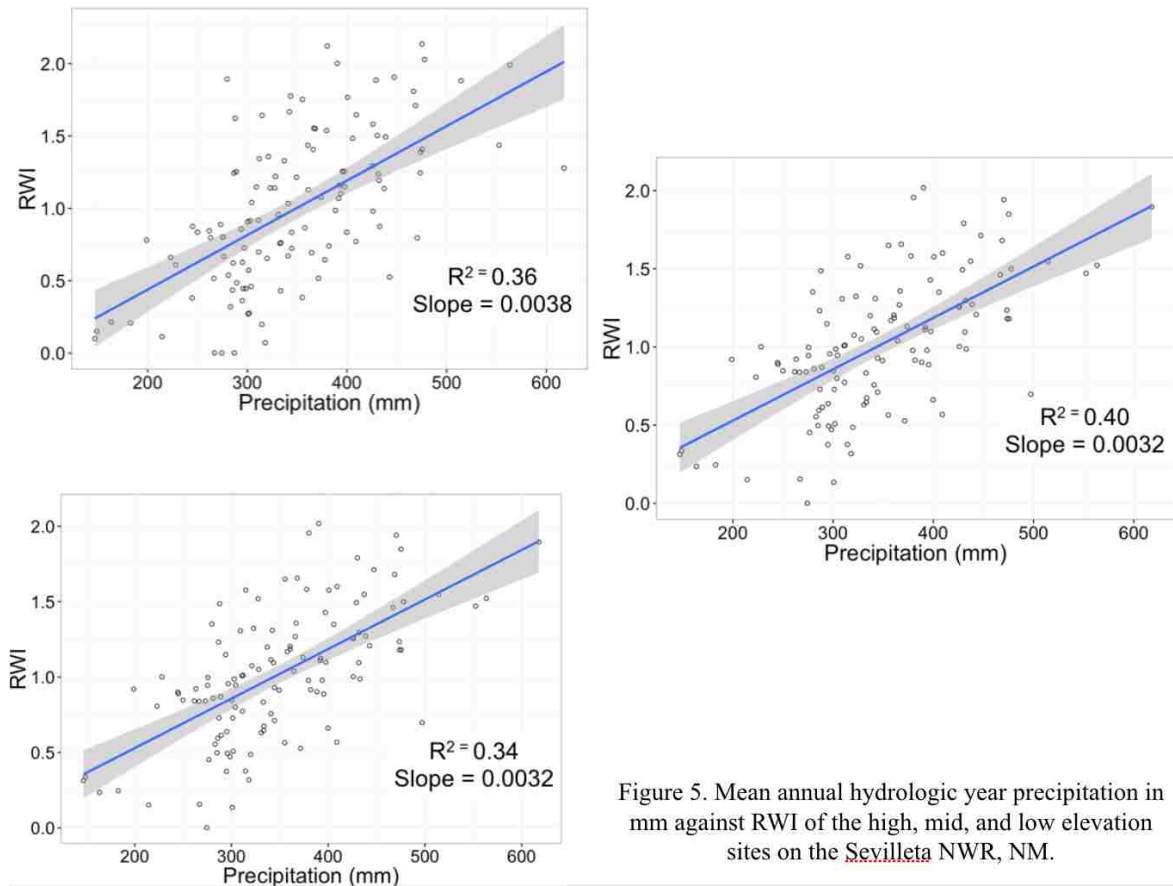


Figure 5. Mean annual hydrologic year precipitation in mm against RWI of the high, mid, and low elevation sites on the Sevilleta NWR, NM.

Live and dead tree growth rates over time

At the MA site, $Dead_{2013}$ trees did not significantly differ in their mean lifetime growth rate from $Live_{2013}$. Lifetime was defined as 1870 - 2012, when the last $Dead_{2013}$ trees died. The earliest that a $Dead_{2013}$ tree stopped producing rings was in 2004, but the majority of trees stopped producing rings in the years from 2008 to 2012. Visible full-tree

mortality was first observed in 2012, but more drastically in 2013. Dead₂₀₁₃ had a higher variance (Table 2) within lifetime RW than Live₂₀₁₃, and growth rates of Dead₂₀₁₃ were significantly lower during the late 1940s, 1950s, and 1990s (Table 4; Figures 6 & 7). During the most recent growth period (2000 - 2012), Dead₂₀₁₃ also had a lower, although non-significant, growth rate than Live₂₀₁₃. While there are significant growth differences throughout the 1940s ($p = 0.049$), growth of surviving trees more significantly exceeded growth of Dead₂₀₁₃ during the last five years of that decade ($p = 0.028$) and into the drought of the 1950s ($p = 0.026$).

Table 4. The climate and growth summary of the site near Mountainair, NM broken down by decade.

Decade	Mean precip ± 1 se (mm)	Mean growing season temp ± 1 se (°C)	Mean RW ±1 se (live)	Mean RW ± 1 se (dead)	Mean RWI ± 1 se (live)	Mean RWI ± 1 se (dead)
1897 - 1910	393.75 ± 17.9	15.16 ± 0.16	0.825 ± 0.093	0.852 ± 0.089	0.834 ± 0.103	0.966 ± 0.112
1911 - 1920	408.86 ± 36.7	14.88 ± 0.16	1.069 ± 0.093	1.217 ± 0.117	1.042 ± 0.082	1.189 ± 0.096
1921 - 1930	366.93 ± 27.8	14.73 ± 0.17	0.887 ± 0.121	0.942 ± 0.140	0.809 ± 0.129	0.834 ± 0.151
1931 - 1940	398.22 ± 23.8	14.79 ± 0.16	0.927 ± 0.101	0.901 ± 0.119	0.846 ± 0.106	0.944 ± 0.141
1941 - 1950	380.18 ± 39.9	14.86 ± 0.23	1.109 ± 0.080	0.813 ± 0.093	0.995 ± 0.078	0.907 ± 0.113
1951 - 1960	321.99 ± 33.8	15.22 ± 0.12	0.901 ± 0.112	0.502 ± 0.106	0.778 ± 0.118	0.633 ± 0.140
1961 - 1970	355.9 ± 15.5	14.86 ± 0.18	1.121 ± 0.087	0.968 ± 0.092	1.055 ± 0.091	1.179 ± 0.120
1971 - 1980	396.82 ± 24.6	14.69 ± 0.19	1.016 ± 0.118	0.925 ± 0.116	1.083 ± 0.141	1.178 ± 0.149
1981 - 1990	446.88 ± 32.2	15.19 ± 0.21	1.353 ± 0.121	1.272 ± 0.105	1.579 ± 0.154	1.548 ± 0.155
1991 - 2000	442.21 ± 26.3	15.52 ± 0.21	1.032 ± 0.081	0.739 ± 0.065	1.121 ± 0.106	0.864 ± 0.086
2000 - 2012	367.23 ± 22.4	16.01 ± 0.12	0.528 ± 0.076	0.423 ± 0.072	0.582 ± 0.109	0.437 ± 0.085

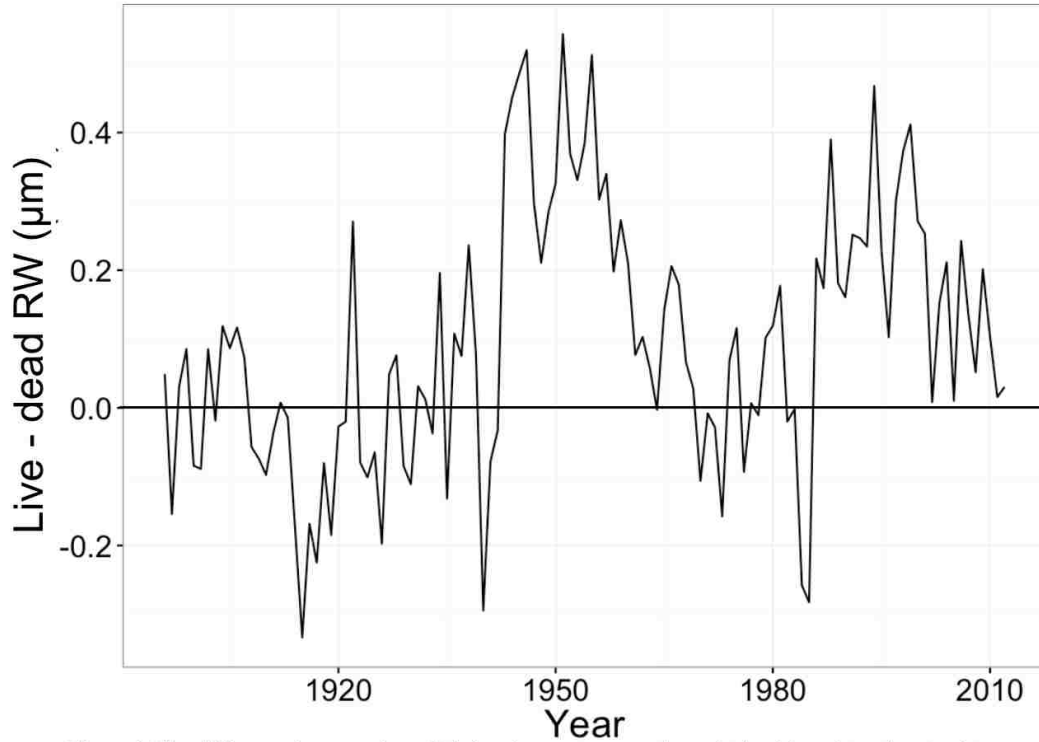


Figure 6. The difference in mean ring width in micrometers over time obtained by subtracting dead tree mean ring width from live tree mean ring width. Above 0.0 indicated that live trees grew more than dead, and below 0.0 indicates that dead trees grew more than live. Ring widths obtained from tree cores taken near Mountainair, NM.

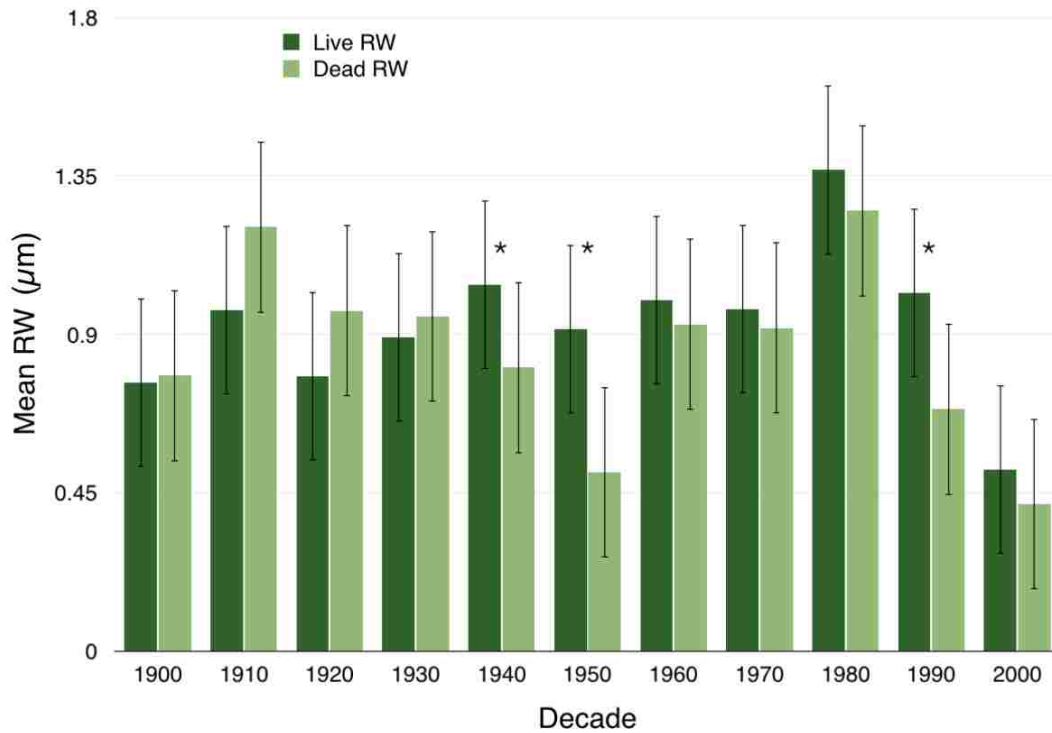


Figure 7. Ring widths from trees at the site near Mountainair, NM. Living tree mean ring width in micrometers (dark green) and dead tree mean ring width in micrometers (light green) by decade with standard deviation bars for each mean.

The growth rates between Live₂₀₁₃ and Dead₂₀₁₃ did not significantly differ prior to the 1940s, but significantly differed following the 1940s (Figure 8). During the 1990s there was a difference in growth between Live₂₀₁₃ and Dead₂₀₁₃ trees ($p = 0.0158$), although that difference did not increase during the last five years ($p = 0.045$). The mean age of the two groups of trees was not significantly different after removing the three youngest tree from Live₂₀₁₃, therefore these growth differences are unlikely to result from age. As seen in Figure 9, RWI followed the same trend of Dead₂₀₁₃ trees exhibiting a larger variance in lifetime RWI ($\sigma^2 = 0.26$) than live trees ($\sigma^2 = 0.18$). The decades that differed for RW did not significantly differ for RWI, although they do show visual differences in Figure 9. Figure 9 also makes evident when Dead₂₀₁₃ trees began dying. The Dead₂₀₁₃ chronology ends in 2012, while the Live₂₀₁₃ chronology continues until 2015. Figure 10 illustrates the differences in RWI between Live₂₀₁₃ and Dead₂₀₁₃ and

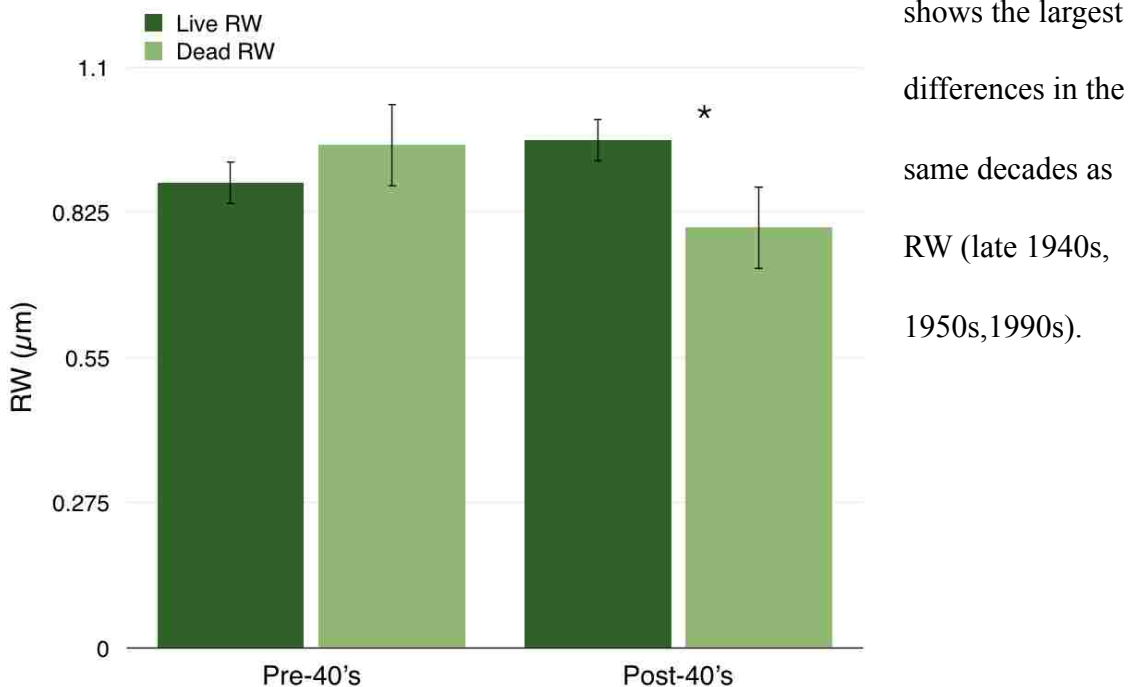


Figure 8. The mean ring width in micrometers pre-1940s and post-1940s for living and dead trees sampled near Mountainair, NM. The dark green bars represent living trees and the light green bars represent dead trees.

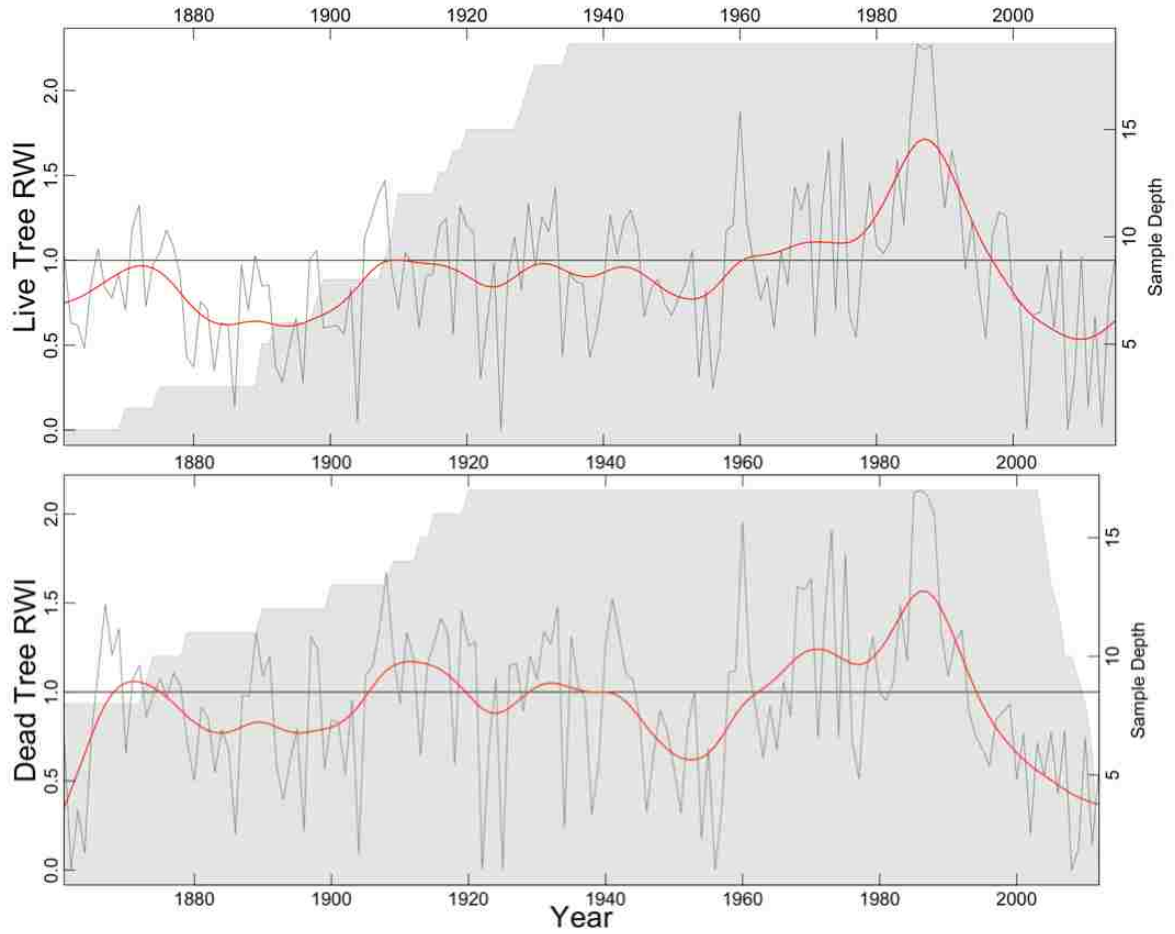


Figure 9. The mean ring width index, or chronologies, for dead and live trees from our site near Mountainair, NM. The red line is a smoothing spline overtop of the light grey line, which is the mean RWI. The grey shading in the background is the length of each tree in time. On the left axis is the standardized index value. On the right axis is sample depth or the number of trees included in the chronology.

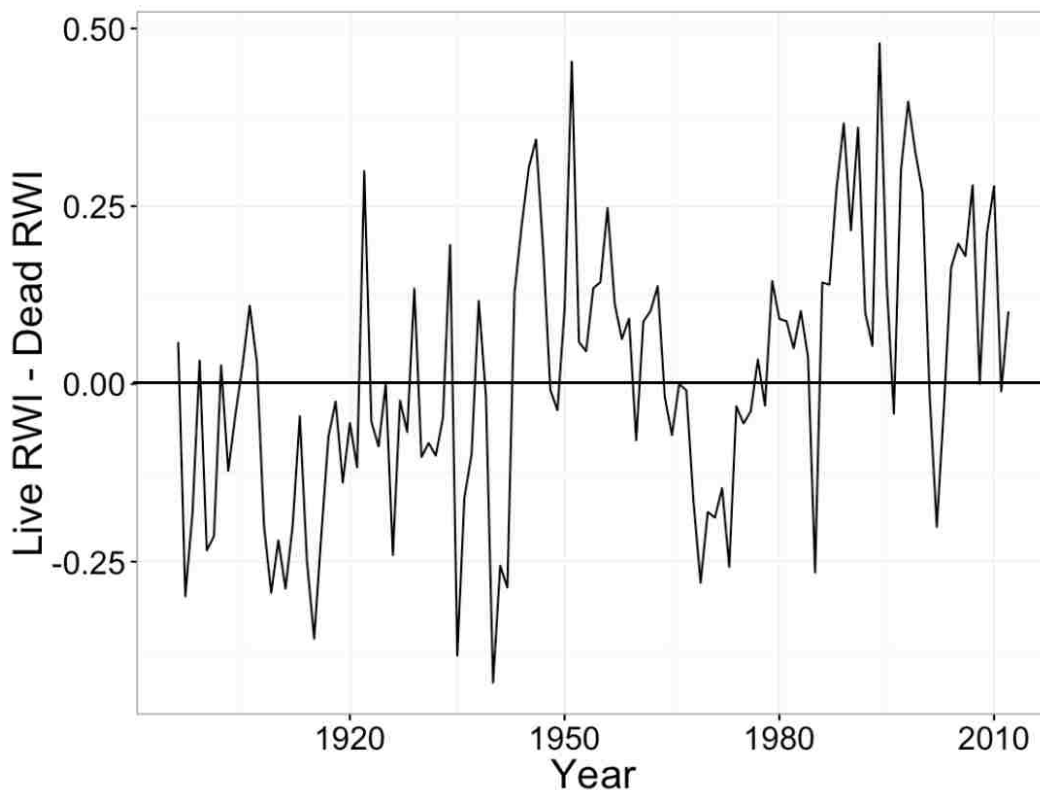


Figure 10. The difference in mean ring width index over time obtained by subtracting dead tree mean RWI from live tree mean RWI. Above 0.0 indicated that live trees grew more than dead, and below 0.0 indicates that dead trees grew more than live. RWI obtained from ring widths of tree cores taken near Mountainair, NM.

Effects of climate and stress on growth

Incorporating climate data into the analysis shows that the growth of live and dead trees varied the most significantly during dry and warm conditions. During the most recent growth period (2000 - 2012), both live and dead trees at the MA site had decreased growth compared to their lifetime mean (Table 4; Figure 7). Mean precipitation was lower than at any time since the drought of the 1950s (Table 4) and mean temperature was the highest recorded within the past 130 years (Table 4). PDSI values were also at their most negative values in recent recorded history (Figure 11). The majority of Dead₂₀₁₃ sampled also showed evidence of bark beetle infestation.

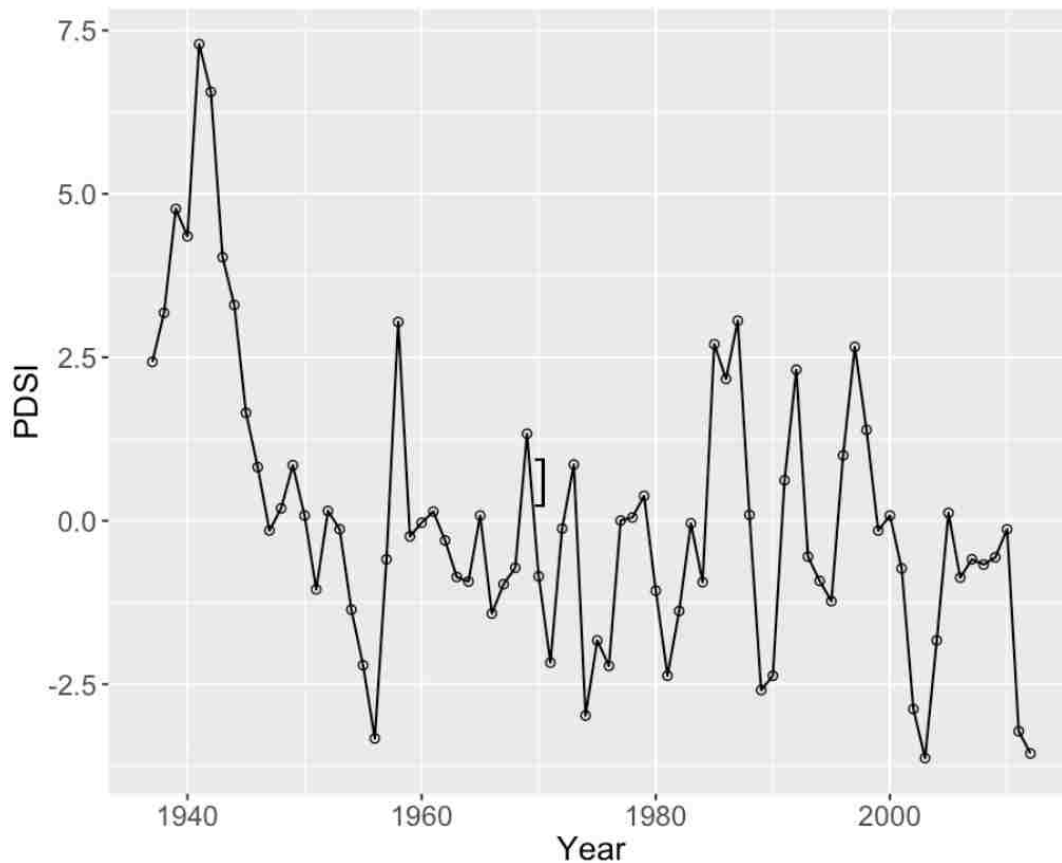


Figure 11. The mean PDSI (Palmer Drought Severity Index) over time from Estancia, NM, approximately 45 km north of both our our research sites.

While there was not a significant difference between Live₂₀₁₃ and Dead₂₀₁₃ in RW and RWI (living RWI $R^2 = 0.34$, $p = 3.22 \times 10^{-12}$; dead RWI $R^2 = 0.39$, $p = 5.89 \times 10^{-14}$) lifetime response to precipitation (Figure 12), significant differences in RW and RWI did occur during the 1950s drought (living 1950s RWI $R^2 = 0.21$, $p = 0.118$; dead 1950s RWI $R^2 = 0.46$, $p = 0.04$). This decade had the lowest decadal precipitation mean at this site within the past 130 years. While mean temperature in the 1950s was not the hottest, PDSI during this time period was among the lowest (-0.56) in recent history (Figure 11). Dead₂₀₁₃ and Live₂₀₁₃ trees responded differently to precipitation during the 1940s, 1950s, and 1990s in terms of growth rates (Figure 6). During all three of these decades, Live₂₀₁₃

trees maintained a higher RW and RWI than trees that later died (Figure 7). Even though Live₂₀₁₃ trees maintained a higher growth rate during this time, Dead₂₀₁₃ physically grew more per mm of precipitation received (Figure 13) during the 1950s ($m = 0.01$, $R^2 = 0.47$). Figure 14 depicts the correlation between Dead₂₀₁₃ and Live₂₀₁₃ RWI and mean winter precipitation, and shows that from ~1950 to ~1980, Dead₂₀₁₃ was more highly

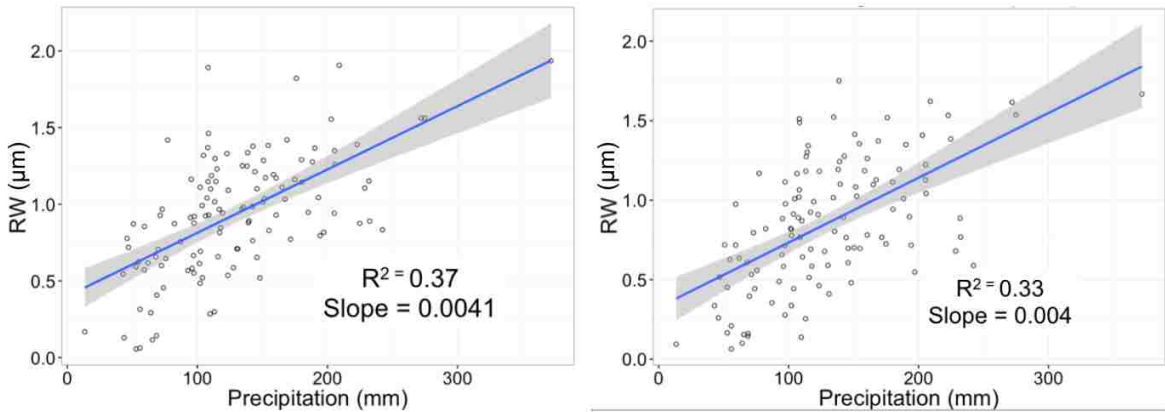


Figure 12. Mean ring width in micrometers of tree core samples taken near Mountainair, NM against precipitation in millimeters. The panel on the left is mean living tree RW and the panel on the right is mean dead tree RW. The blue line is a linear best fit, and the grey shading is a 95% confidence interval.

correlated with winter precipitation than Live₂₀₁₃.

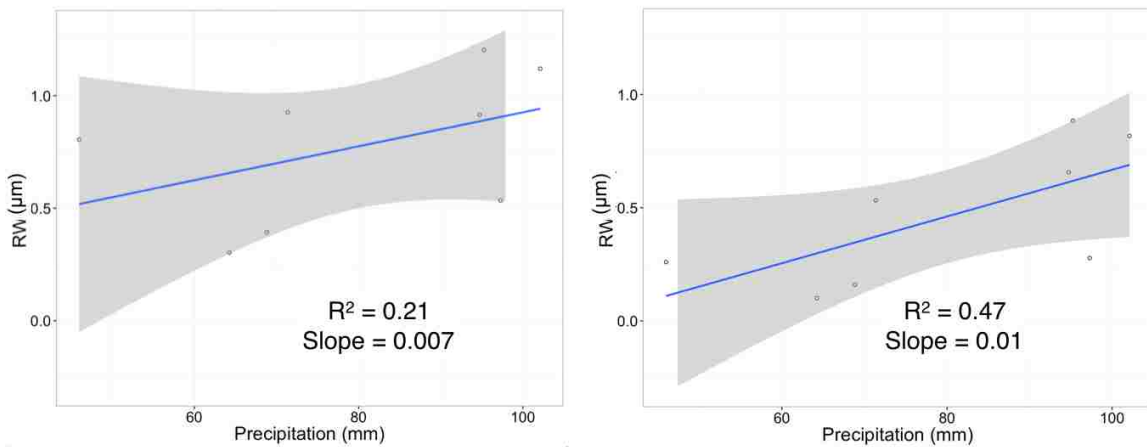


Figure 13. Mean ring width during the 1950s in micrometers of tree core samples taken near Mountainair, NM against precipitation in millimeters. The panel on the left is mean living tree RW and the panel on the right is mean dead tree RW. The blue line is a linear best fit, and the grey shading is a 95% confidence interval.



Figure 14. The correlation (r) of mean RW in micrometers and winter precipitation in millimeters against time for living (yellow) and dead (grey) trees sampled near Mountainair, NM.

Discussion

Our analysis of piñon pine populations in New Mexico suggest that deviations from the lifetime mean within radial tree growth are almost exclusively driven by periods of drought (Table 2; Figures 7 and 8). Prior to the major drought of the early 2000s, the 1950s drought was the most extreme within the past two centuries (Betancourt et al. 1993), bringing about the most widespread tree die off event of the century. Our study shows that during the drought of the 1950s, piñon tree growth from all of our sites was affected and many did not recover to their pre-drought growth rates and succumbed to mortality (Table 2; Figure 4; Figure 7; Figure 9).

Growth-related differences in piñon across elevations

Although mortality was not observed in 2000 and 2013 at the Sevilleta site, elevation is a significant factor that has an effect on the success of piñon (Meddens et al. 2015; Greenwood & Weinberg 2008). Each site along the altitudinal gradient that was sampled was approximately 100 m removed from the other sites and each exhibited unique growth patterns. As seen in Figure 4 and Table 4, the trees at the highest site had a higher lifetime variance ($\sigma^2 = 0.28$) in their rings and were outgrown by the mid-elevation trees during the drought of the 1950s. The high inter-annual growth variability at the high elevation site may indicate that these trees are more responsive to changing conditions and precipitation they receive (Andreu et al. 2007). Trees at this elevation may be more

sensitive to climate, which is the main factor driving these growth changes (King et al. 2013; Briffa et al. 1998).

From our data, Figure 5 shows that the mid-elevation population has the strongest relationship with precipitation received ($R^2 = 0.40$). When the trees along the elevation gradient receive precipitation, the response is to increase their growth more at the lowest two elevations. While the lowest and highest two elevations both have weaker relationships with precipitation received, they are still tightly correlated with precipitation (high elevation $R^2 = 0.36$, slope = 0.0038; low elevation $R^2 = 0.34$, slope = 0.0032). As mentioned above, RWI at the mid-elevation site in particular is strongly associated with precipitation received ($R^2 = 0.40$). This shows that mid-elevation trees respond strongly to climate, and although it does not result in as much increased growth as the high elevation, the response is more tightly correlated (Figure 5). A higher correlation with growth and increased precipitation is also a factor exhibited by Dead₂₀₁₃. A higher variance within ring widths (Table 4; Figure 13) is another factor. This indicates that the trees at the highest elevation may be behaving more similarly to the Dead₂₀₁₃ trees in regards to variance. Also, there may be some factor at the highest site, i.e. caliche spatial heterogeneity (Machette 1985), that differ from the lower two elevations. It also indicates that trees at the mid-elevation are most perceptive to precipitation changes.

In contrast to the long lifetimes of trees at the highest two elevations, the trees at the lowest elevation are much younger (Figure 4). These trees did not experience the drought of the 1950s, and up until the drought of the 2000s, their growth had not suffered at the same level as the other two elevations. These trees were established in the early

1970s when conditions were favorable (Table 3) and the severe drought had been over for 10 years (Figure 11). It is possible that the piñon at elevations this low and close to the lower limit of piñon growth periodically die and then reestablish once conditions are favorable (Suarez & Kitzberger 2008). These trees were also all growing in an arroyo microsite, where water is concentrated by the landscape and trees are more likely to receive more precipitation. For this reason, mortality regimes at this site may be different from the higher two elevations. Trees may succumb to death rather than struggle to survive when conditions are unfavorable. Temperatures at low elevations are predicted to continue increasing (Williams et al. 2010; Cayan et al. 2010), and the piñon growing at this site may begin to be encroached upon by lower elevation species, as well as the piñon themselves beginning to move up in elevation (Gray et al. 2006; Allen & Breshears 1998).

Climate and growth patterns leading to mortality

One of the characteristic factors of the Dead₂₀₁₃ population is the higher lifetime variability within the growth rings (Table 4). Growth during the decades of the 1910s, 1950s, and 1990s are significantly different between Dead₂₀₁₃ and Live₂₀₁₃, and make evident the differences within the range of growth these two groups of trees experienced (Figures 6, 7, 9, 10). Dead₂₀₁₃ had a wide range of RW values, and seemed to vary growth the most during periods of large climatic deviations (Table 2; Figure 2). It is noteworthy that the growth of Dead₂₀₁₃ did not significantly diverge until the drought of the 1950s (Figure 8). Prior to the 1940s, Dead₂₀₁₃ consistently kept up with the growth of Live₂₀₁₃,

and in some cases had years where growth was higher than that of Live₂₀₁₃ (Figure 7). The first major drought experienced by these trees was enough to drive one group in the directions of declining growth while another group continued to outperform those trees. This may be a sign of the decline-disease theory that suggests that an individual's response to long-term processes like drought is often the underlying cause of mortality (Macalady & Bugmann 2014; Franklin 1987).

The differences in growth of piñon that we observed implicate climate patterns in the long-term control of growth and in the determination of survival (Table 2; Figures 12 & 13). It is important to note that the mortality event that began in 2012 was the third extreme drought event within 60 years. Trees that survived the drought of the 1950s recovered their defenses during the wet decades of the 1960s, 1970s, and 1980s, but were hit again with another severe drought during the early 2000s. Once this drought began, the trees may have not had time to recover their defenses, may have had possible tissue loss from the early 2000s drought (Mueller et al. 2005; Plaut et al. 2013), and may have been in a vulnerable state when PDSI was extremely low in 2011 (Figure 11).

Previous studies have found that tree response to precipitation (Bigler et al. 2006; Mueller et al. 2005; Allen et al. 2010) and temperature (Adams et al. 2009; Allen et al. 2010) are inciting factors leading to mortality. Figures 13 and 14 show that Dead₂₀₁₃ trees were more highly correlated with and more dependent on precipitation throughout their lifetime. Their growth was ultimately more impacted when precipitation was decreased and temperature was high (Table 2; Figures 2 & 14). Adams et al. (2009) suggests that warmer temperatures shorten the time to drought-induced mortality by nearly a third, and

that temperature-dependent differences in cumulative respiration costs imply carbon starvation as the primary mortality mechanism. In contrast, Live₂₀₁₃ trees were not as highly correlated with precipitation, and their growth remained more steady during fluctuating levels of precipitation (Figures 13 & 14). This may indicate that tree mortality is a product of increased sensitivity to climate. McDowell et al. (2010) found a similar result in *Pinus ponderosa* where trees that died during a drought grew less but responded more strongly to precipitation in extremely dry years.

Causes of piñon mortality

Drastic changes in precipitation and temperature are factors that contribute to chronic water stress and are suggested to lead directly to low leaf-level gas exchange and carbon starvation (McDowell et al. 2010; Adams et al. 2009). Following the drought of the 1950s, remaining carbon reserves within Dead₂₀₁₃ may have not been enough to spur full recovery (Anderegg et al. 2011; Breshears et al. 2008). Once the drought of the early 2000s began, conditions contributed to decreased mean growth and may have exacerbated the precipitation dependence that caused a higher variability in growth Dead₂₀₁₃ trees were experiencing (Ogle et al. 2008; Suarez et al. 2004; Millar et al. 2007). Carbon uptake and reserve storage could have been some of the limiting factors in tree growth following the 2000s drought. It is possible these things led to decreased defenses by the trees and ultimately death (McDowell et al. 2008; McDowell et al. 2010; McDowell et al. 2011). Macalady & Bugmann (2014) suggest that trees that survived such extreme drought events like the 1950s and 2000s may have been storing excess

carbon from increased photosynthesis during wet periods more efficiently than trees that subsequently died. Those that died may have possibly depleted their carbon reserves during drought conditions and the remaining carbon was not enough to spur recovery, particularly following the 2000s (Gaylord et al. 2016). Trees that ultimately survived were then able to utilize their stored carbon when water potential was very negative and growth suffered in other trees.

Another reason that Dead₂₀₁₃ may have not shown visible signs of death until 2013 was because of the less aggressive bark beetle population in the area from 2000 - 2002 (Meddens et al. 2012). PDSI was extremely low during these years (Figure 11), but until 2004 and 2005, there was not the added stress of having to defend as much against a biotic agent like bark beetle. They had been suffering from decreasing growth for the past 20 years of their lives though (Figure 4), and may have not been functioning at full capacity. If the population of bark beetle began to increase in the late 2000s, trees that already may have been carbon starved had a reduced ability to defend themselves in the event of an attack (Raffa et al. 2008; Allen et al. 2010). Once the trees were infected with bark beetle, their transpiration rates likely decreased and the focus was on defense and not growth (Edburg et al. 2012). The culmination of effects from increased bark beetle after 2010 and the decreased precipitation during 2011 on physiological functions may have ultimately been the overarching cause of death for these trees. As Breshears et al. (2008) found, piñon mortality is often times driven by water stress which leads to carbon starvation and is exacerbated by disturbances such as bark beetle.

There may also be other factors that contributed to mortality of Dead₂₀₁₃. While we can reason why the trees died physiologically, there are some causes not measured that may have played a part. There may be unknown genetic variance between Dead₂₀₁₃ and Live₂₀₁₃ that pre-selects which trees are more likely to die in severe drought and which ones will better allocate resources to survive. There is evidence that drought tolerance within piñon is related to certain loci (Cobb et al. 1994; Ogle et al. 2000). There also may be site-specific differences such as caliche spatial heterogeneity, which would allow some trees access to deeper ground water while others physically cannot reach (Cunningham & Burk 1973). There may also be competition from juniper or other shrubs that limits the growth of piñon and prevents them from fully developing (Padien & Lajtha 1992; Greenwood & Weisberg 2008). Finally, Dead₂₀₁₃ and Live₂₀₁₃ may have allocated carbon differently, i.e. Live₂₀₁₃ using more carbon for consistent growth and building reserves, while Dead₂₀₁₃ using carbon for excess branch or root growth.

From our hypotheses, we can determine that Dead₂₀₁₃ trees have not suffered their whole lives, and did not underperform compared to Live₂₀₁₃ until after the drought of the 1950s. Following the 1950s, Dead₂₀₁₃ trees relied more heavily on precipitation, and their growth reflected this much more than prior to the 1950s. After the 1950s, they may have been placed closer to their physiological limitations which may have contributed to their death. A combination of our two original hypothesis seems to describe how these trees behaved. Along the elevation gradient, trees at lower elevations exhibited more growth and less variability than trees at the middle and highest elevations. Trees at the lowest

elevation showed the least resilience to drought, as evidenced by the young age of the group of trees.

Future directions

In order to fully understand the reasons behind piñon mortality, there are additional steps to take. The exact mechanism driving mortality is still unknown. Current evidence supports an interaction of carbon limitations and hydraulic failure, with the role of bark beetle appearing to accelerate mortality. Additional studies combining tree ring sampling with physiological measurements would offer data to support or reject our hypotheses of reasons for mortality. This would include measuring leaf-level carbon intake, sap flow, and tree ring growth together to be able to accurately predict how likely a tree is to die.

There is also preliminary unpublished isotopic data measured by Diana Macias and Marina Martinez that suggests Dead₂₀₁₃ used carbon differently than Live₂₀₁₃ during the wet 1980s. The carbon isotope ratio of photosynthetic products provides an integrated measure of the stomatal regulation of tree gas exchange. The enzyme RUBISCO discriminates against CO₂ containing the heavy carbon isotope (¹³C) as opposed to the more common carbon isotope ¹²C. This discrimination is more strongly expressed when stomata are open. A more negative carbon isotope ratio is indicative of less stomatal limitation. Macias and Martinez analyzed one Dead₂₀₁₃ core and one Live₂₀₁₃ core and found that during the 1980s, Dead₂₀₁₃ exhibited greater discrimination against ¹³C. This suggests that when conditions were favorable, Dead₂₀₁₃ outperformed Live₂₀₁₃. Our data shows reduced growth in these trees during this time, and this suggests Dead₂₀₁₃ may

have been allocating carbon differently. They may have been spending it on roots or reproduction, or may have been in a microsite that influenced water availability. This is promising data and would offer insight into the elemental way both groups of trees were using carbon prior to and during mortality (Leavitt & Long 1989).

Conclusions

Our results show that piñon trees that died in early 2013 may have been experiencing decreased growth not for their whole lifetime, but since the drought of the 1950s. These trees had higher variance within their ring widths and were more responsive to climate, and this may indicate that they were outperforming for more of their life and were pushed closer to their limits. Trees along different elevations are also highly receptive to precipitation changes, particularly those at the highest elevation we sampled and those among the lower limit of piñon growth. Those among the highest elevations may already be showing signs of decreasing growth. Trees at the lower limit may not be able to tolerate severe drought, and may periodically die and then re-establish.

This research has added to and solidified existing ideas regarding the enigmatic process of tree mortality. A combination of deductive reasoning and published studies have led to the understanding that vascular stress and lowered defense mechanisms are some of the primary physiological mechanisms behind tree mortality. These are the inciting factors that lead to infections by insects and increased herbivory that ultimately bring on death, although mortality is also possible in the absence of these factors (e.g.

Sevanto et al. 2014). Observing mean growth rate through tree rings indicates that response to climate is a determining factor affecting the length of a tree's lifetime. Differences between groupings of trees that have died from extreme drought and the variability within their rings gives an idea of what factors regulate growth rates in these trees. Older trees experience one extreme drought event and from that may experience lasting impacts on their vascular system and carbon reserves. A second drought like the one in the early 2000s appears to push the tree farther away from recovery. Looking at the growth patterns in trees that died is useful for predicting which trees may die in the future. It is also important to observe how trees along different elevations are handling extreme drought events, and if they continue to behave similarly to trees that died. It would be beneficial to revisit these same sites in 20 years to see which trees have suffered the most or succumbed to mortality.

Piñon trees are very evidently dying and making way for new vegetation. This is predicted to be the start of range shifts within the Southwest (Gray et al. 2006; Allen & Breshears 1998), perhaps enabling juniper to expand in what was once a mixed piñon-juniper woodland. Eventually this could mean shrubs like creosote shifting up in elevation and latitude, which will change our understanding of current biomes. Tree mortality is becoming more ubiquitous and is predicted to increase within the next 100 years (Williams et al. 2013). The challenges of managing and studying these shifting ecotones is a continual process and one that will continue to need investigation. Understanding the mechanisms behind this mortality will help us be prepared to study and manage our changing ecosystems.

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