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Piñon pine (*Pinus edulis* Engelm.) growth responses to climate and substrate in southern Utah, U.S.A.

Nichole N. Barger · Connie Woodhouse

Abstract Piñon pines (*Pinus edulis* Engelm.) are a widely distributed species across the western United States (U.S.) providing habitat for wildlife species in addition to forest products for humans. Thus, understanding factors that promote the productivity of this species is important to predict future responses to environmental change. We examined piñon pine growth from tree-ring records and evaluated whether growth responses to climate may be explained by local site characteristics such as geologic substrate from the late 1900s through the early 2000s. Cluster analysis revealed two distinct clusters that differed in their growth response (i.e., tree-ring width) to July temperature of the current growing season (cluster 1, $r = -0.45$; cluster 2, $r = -0.31$). Clusters 1 and 2 displayed synchronous growth throughout the early to mid-twentieth century but growth patterns diverged in

the 1970s. Ring widths in cluster 1, which were most sensitive to average July temperature, showed a downward trend in the 1970s through the 2000s. By contrast, cluster 2 growth showed positive growth responses during the 1980s followed by growth declines during the multi-year drought of the 1990s. There was evidence that these growth patterns may be partially explained by geologic substrate (i.e., shale, sandstone, alluvial fan). Pearson's r values of tree growth over time were strongly negative on shales and sandstones ($r = -0.30$, $P = 0.009$; $r = -0.34$, $P = 0.003$), whereas those on alluvial fans were not significant ($r = 0.13$, $P = 0.23$). Reported values of soil available water capacity on the shale and sandstone substrates are low relative to the alluvial fans, which may partially explain the differential growth responses. Our findings suggest that consideration of increasing summer temperatures on low availability water capacity geologic substrates may be important in predicting future piñon pine growth declines.

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Introduction

Global trends in net primary productivity (NPP) have been positive since the middle of the twentieth century with the exception of 'dryland' forest types where water strongly limits growth (Boisvenue and Running

2006). As global average surface temperature has increased by approximately 0.76 °C over the past 50 years and is projected to increase over the next century (IPCC 2007), drought intensity and frequency, especially in the dryland regions of the Southwest United States (U.S.), are also expected to increase (Seager et al. 2007). Recent widespread drought-induced tree growth declines and mortality across the Southwest U.S. (Breshears et al. 2005; van Mantgem et al. 2009; Allen et al. 2010; Williams et al. 2010) suggest that there are limits in the ability of dryland tree species to adapt to increasing drought stress with changing climate.

Regional climate strongly regulates tree growth across low- and mid-elevation tree species across the Southwest U.S. More specifically cool season or winter precipitation and summer temperature and vapor pressure deficits explain much of the variability in tree drought stress and mortality in a range of tree species across this region (Williams et al. 2012). Regional climate effects on tree mortality and growth, however, may be mediated by site-level characteristics such as soil type and parent material. Soil factors such as depth, texture, and organic matter content have long been recognized as influencing soil water availability and subsequent tree growth in dryland environments (e.g., Fritts 1976; Adams and Kolb 2004). The soil environment so consistently influences tree growth that soil characteristics, such as soil depth, are important in selection of sites in dendroclimatic studies. Tree growth on shallow or skeletal soils with a low volume of mineral soil and available water capacity is consistently more sensitive to annual climate than trees that occur on deeper soils that retain moisture from previous years (Fritts 1976; Knutson and Pyke 2008).

One Southwest U.S. tree species in particular that experienced extensive regional mortality over the past decade is the piñon pine (*Pinus edulis* Engelm.). Piñon pines are a widely distributed tree species across much of the arid and semi-arid regions of the Southwest U.S. and provide a wide range of services to humans in addition to supporting wildlife species. Piñon pines are dominant or co-dominant with juniper species within piñon-juniper woodlands of the western U.S., covering 30 million ha across the U.S. and Mexico (West 1999). Similar to other lower and mid-elevation species across this region, piñon pine growth is reliant on high winter precipitation for soil water recharge and low summer temperatures for optimal growth (Fritts et al.

1965; Adams and Kolb 2005; Kempes et al. 2008; Barger et al. 2009). Evidence from previous studies also suggests that geologic substrate may influence the response of piñon pine to drought. In upland sites of northern Arizona, piñon pine canopy dieback during a drought was highest on drier, coarse-textured soils as compared to finer-textured soils (Koepke et al. 2010). Soil influences on piñon pine drought responses, however, are not always consistent. In a northern Arizona piñon pine/ponderosa pine forest ecotone in northern Arizona, drought sensitivity was similar across a range of geologic substrates (Adams and Kolb 2004). What is less clear is how longer-term changes in climate and local-scale factors may interact to influence future growth dynamics.

In this study, we examined piñon pine growth responses to climate over the past century across sites in southern Utah (Fig. 1). Previous research on piñon pine at these sites suggested that a downward trend in ring width occurred over the past several decades (Barger et al. 2009) with additional evidence that variable growth responses may be related to geologic substrate (Grow 2003). As summer temperature has increased over the past several decades with little to no change in precipitation across this region, we hypothesized that overall drought stress has increased, resulting in piñon pine growth declines. In addition, we hypothesized that these growth declines may be further exacerbated on geologic substrates that exhibit low available water capacity.

Methods

Study sites

Study sites were located on three geologic substrates within Grand Staircase-Escalante National Monument (GSENM) in southern Utah (Table 1). Tree-ring width was used as an index of piñon pine growth over the last century. Tree cores (one per tree) were collected from No Man's Mesa (NM) and Deer Springs Mesa (DS) located within GSENM in 2003. Increment cores were mounted, sanded, and visually cross-dated using standard dendrochronological methods (Stokes and Smiley 1968). Following cross-dating, tree-ring widths were measured on a Velmex ring width measuring system. Raw ring widths were reported to 0.001 mm. Raw ring width for six additional sites
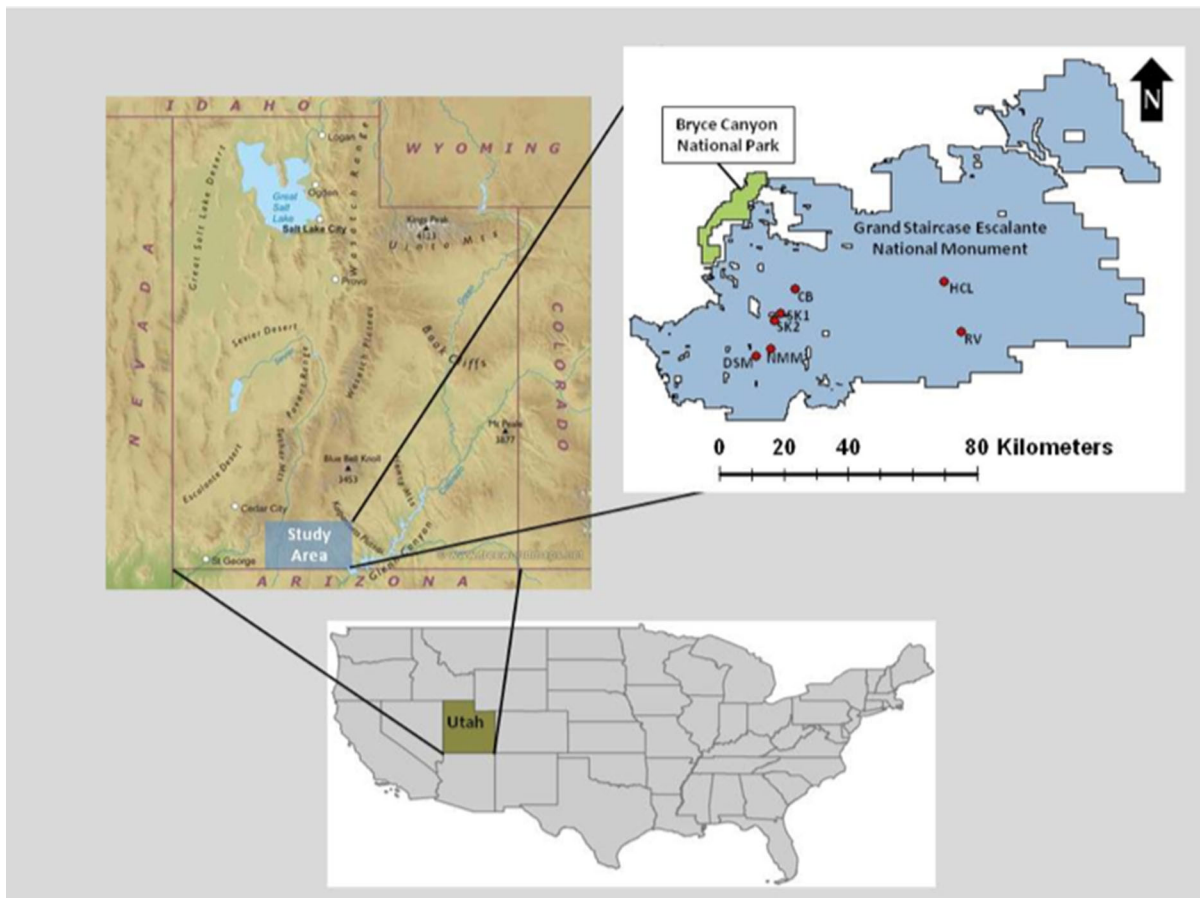
Fig. 1 Location of study sites within Grand Staircase—Escalante National Monument in southern Utah, United States. Study sites were located on a range of soil types and geologic substrates. The map located in the *upper left* corner was accessed electronically from an open access map database at http://mapserv.utah.gov/arcgis/service

(Table 1; Round Valley (RV); lower Henderson Canyon (HCL); Coal Bench (CB); Deer Springs (DS), Skutumpah (SK1 and SK2) were downloaded from the International Tree-Ring Data Bank (ITRDB, NOAA 2013a). All tree-ring data from the ITRDB were collected between 1998 and 2000 (Grow 2002). Although the ITRDB has tree-ring data available for piñon pines across the Colorado Plateau ecoregion, we chose these study sites due to the fact that geologic substrate could be confirmed from our past work (Barger et al. 2009) and had been reported in a previous publication (Grow 2003).

Tree core selection

To examine the influence of climate on piñon pine growth over the last century, we focused on tree-ring response to climate from 1896 (the period instrumental climate records are available) through the early 2000s. Collection dates from each study site ranged from 1998 through 2004. Piñon pine growth and subsequent tree-ring width in early life stages may be influenced by a number of factors, which makes applying common detrending strategies (e.g., negative exponential curve) a challenge. In many of the cores, we observed low growth rates in the first several decades after establishment with growth increases thereafter. Piñon pine recruitment in these ecosystems often occurs beneath tree or shrub canopies. This recruitment strategy may partially explain low growth rates in the first several decades when light is strongly limiting growth beneath the plant canopy. Once the sapling emerges from the plant canopy, light is no longer limiting to growth resulting in increased growth

Table 1 Description of the study sites in southeastern Utah. Piñon pine chronologies were developed from sites that ranged in substrate but occurred at similar elevations. Collection years varied from 1998 to 2003

Substrate	Site (collector/years)	Sample size	Location	Elevation (m)
Shale residuum	Skutumpah 1 (D. Grow/2000)	7	37°30′N, 112°04′W	1800
	Skutumpah 2 (D. Grow/2000)	7	37°28′N, 112°06′W	
Sandstone residuum and alluvium	No Mans Mesa (C. Woodhouse/2003)	24	37°20′N, 112°07′W	2200
	Deer Spring Mesa (D. Grow/1998; Adams/Barger, 2004)	20	37°18′N, 112°11′W	2200
	Round Valley (D. Grow/1999)	10	37°25′N, 111°53′W	2100
Alluvium from sandstone and limestone (alluvial fan)	Lower Henderson Canyon (D. Grow/1999)	7	37°39′N, 111°58′W	2100
	Coal Bench (D. Grow/2000)		37°37′N, 112°00′W	2100

rates. Following this early period, piñon pine growth often follows a pattern similar to an open-canopy forest, which is often detrended with a negative exponential curve (Cook 1985). This decline in tree-ring width over the life of the tree may be largely attributed to changes in geometry (as diameter increases ring width decreases) and biological age. To avoid the early growth periods when a number of non-climatic factors such as competition for resources from canopy nurse plants, geometric changes, and biological age strongly influence tree-ring widths, we selected trees that were at least 100 years of age in 1896 or dated back to at least 1796. Once all cores younger than 1796 were removed (only one core each in the shale and alluvial fan sites), sample size ranged from 6 to 24 trees within a site for a total of 81 trees across all study sites. Since it was unknown whether pith dates were obtained in tree-ring data reported on the ITRDB, tree age ranged from at least 207 to 624 years across all sites.

Cluster analysis

To evaluate common patterns in tree-ring response to climate across our study sites, each tree-ring series was correlated with monthly total precipitation and average temperature variables. Multiple sources of climate data that varied from regional climate data to more local climate station data were evaluated for the strength of the tree growth/climate relationship. At the more regional level, we included climate division data (Utah Division 7, NOAA 2013b) encompassing a 55,775 km^2 area of southeast Utah. Divisional data were reported as monthly means, which were calculated from climate stations within that division. At the more local level, we obtained individual climate

station data from the Western Regional Climate Center (2013). Research sites ranged from 7 to 42 km from the nearest station. A third source of climate data was obtained from the PRISM (Parameter Regression on Independent Slopes Model) climate group at Oregon State University (Daly et al. 2008). PRISM climate data are a spatial dataset that derives climate observations from a range of climate monitoring networks into a model that incorporates more local topographic features. These gridded climate data are reported at 4 km resolution. The large spatial extent of the NOAA divisional data encompassed all of our research sites. At the more local and regional scale, we used study site coordinates to obtain nearest station data from WRCC and the nearest PRISM grid point climate data for the study sites. Upon examination of the three sources of climate data as predictors of tree growth, the strongest relationships were obtained from the PRISM data. PRISM climate data were likely a better predictor of tree growth due to the influence of various orographic features in this region. Following this, we conducted all analyses using this data source. SK1 and SK2 shared a similar PRISM climate dataset due to the proximity of the sites to each other.

Since PRISM monthly climate variables for the site grid points were highly correlated across our sites ($r > 0.90$) and the sites were within 42 km or closer to one another, we averaged the monthly climate variables into a single climate dataset. Analysis of autocorrelation in tree rings (i.e., previous years tree growth influences growth in later years) revealed that climate in the previous 2 years influenced tree growth in the current year. Thus, monthly average temperature and monthly total precipitation of the previous 2 years through September of the current growing season (68 climate variables) were correlated with the

ring width of the current growing season for each series. The resulting correlation matrix included 5508 correlation values. This matrix of correlation coefficients was used as the input for a K-means cluster analysis (clustered by cores) to 1) identify the important climate variables that influence piñon pine growth and 2) evaluate divergent patterns in tree growth response to climate across the study sites (Wilmking et al. 2004). The K-means cluster procedure uses an algorithm to classify correlation coefficients into relatively homogeneous groups. In this procedure, we sought to identify clusters that displayed clearly divergent patterns in their response to climate. Beginning with two clusters, we increased the number of clusters until no new patterns were revealed in the climate response correlation and no significant changes occurred in the cluster mean. Differences in cluster means were evaluated with a Student's *t* test with two clusters and a one-way analysis of variance (ANOVA) with 3 or more clusters. Once clusters were identified, cores in each cluster were averaged to create a cluster chronology.

Geologic substrate analysis

To evaluate piñon pine growth response on different geologic substrates, tree-ring data were pooled by three geologic substrate types that differed in their reported available water capacity (AWC) (Beaudette and O'Green 2009). AWC in the soil survey is expressed as the difference in the amount of water held between field capacity and wilting point. Since wilting point is set at the value at which sunflower seedlings will permanently wilt, differences in AWC are influenced by substrate chemical and physical properties such as organic matter content, bulk density, texture, and rooting depth. In this study, we use AWC as an index of the relative difference of substrates to store and make water available to plants. SK1 and SK2 sites were shale residuum (shale) characterized by low AWC (1 cm). Similarly sites NM, DS, and RV occurred on sandstone residuum and alluvium (sandstone) with an estimated AWC of 3 cm. Trees from HCL and CB occurred on alluvium from sandstone and limestone (alluvial fan) with higher estimates of AWC ranging from 13 to 15 cm, respectively. For each tree, raw tree-ring widths were converted to dimensionless tree-ring indices by dividing raw ring width at each year by the mean of all ring widths within a tree. Series were grouped by geologic substrate and averaged by year to create chronologies for each substrate type.

Statistical analysis

To evaluate tree growth trends over time, we calculated Pearson's correlation coefficients by cluster and geologic substrate (Shale, Sandstone, Alluvial Fan) across the time period of 1898 through 2004 for each of these chronologies. From the cluster analysis, we identified climate variables that were significantly correlated with tree-ring width within each cluster during the current growing season. These climate variables were then used as independent variables in a stepwise linear regression model evaluating tree-ring width as a function of climate over the last century. A 5-year smoothing term was applied to both tree growth and climate variables to dampen the short-term annual variability while enhancing medium-term (i.e., decadal) trends in the data (Wilmking et al. 2004). To evaluate the stability in the climate predictors of tree growth over the last half century, we divided the century into an early (1898–1949) and late period (1950–2004).

Results

Cluster analysis revealed two distinct clusters that differed in their response to July temperature of the current growing season (Fig. 2a cluster 1, $r = -0.45$; cluster 2, $r = -0.31$). Precipitation responses across the two clusters were similar with a positive association of ring width to January precipitation (Fig. 2b; cluster 1 and 2, $r = 0.32$). Although January precipitation and July temperature were highly correlated with tree-ring width across the century (Fig. 2b), we observed no response to January precipitation in both clusters later in the century (Fig. 3a, b, 1950–2004). Early in the century (1898–1949), January precipitation and July temperature explained 65–71 % of the variability in ring width index across both clusters. Across the time period of 1950–2004, January precipitation was no longer a significant predictor of ring width index across both clusters (Fig. 3a, b). Clusters 1 and 2 responses to average July temperature were similar early in the twentieth century and began to diverge in the late 1960s. Although cluster 1
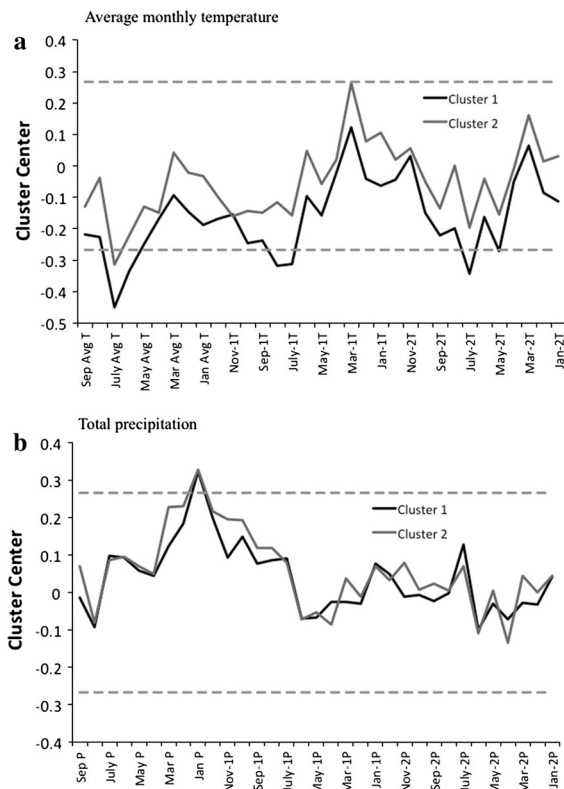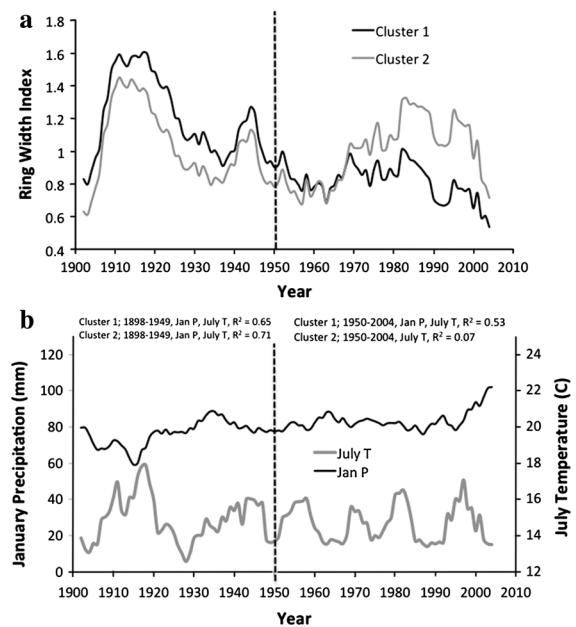
Fig. 2 K-means cluster analysis of ring width and climate correlation coefficients. Values are mean correlation coefficients or 'cluster center' for each climatic variable. *X*-axis values are reported from the current growing on the *far left of the axis* through 2 years previous to the current growing season on the *far right of the axis*. The *dashed gray line* indicates Pearson's product moment critical values at $P < 0.01$

Fig. 3 a Tree-ring width changes over time. Tree-ring width index values are graphed as a 5-year moving average to smooth the high-frequency variability in the data. b Average July temperature and total January precipitation during the time period from 1898 through 2004. The relationship between ring width in each of the clusters and July average temperature and January average precipitation was evaluated with a multiple linear regression in two time periods. The early century time period included the years 1898 through 1949. The late century time period included the years 1950 through 2004. R^2 values for tree-ring width as a function of July average temperature and January average precipitation are reported for each time period at the top of the figure

remained sensitive to July temperature later in the century ($R^2 = 0.53$), cluster 2 showed a reduced sensitivity to July temperature ($R^2 = 0.07$) (Fig. 3b).

Ring widths in the two clusters displayed synchronous growth throughout the early to mid-twentieth century (Fig. 3a). However, growth patterns diverged across these clusters in the 1970s. Ring widths in cluster 1, which were most sensitive to average July temperature, showed a significant downward trend in the 1970s through the 2000s ($r = -0.73$, $P < 0.0001$). By contrast, cluster 2 showed positive growth responses during the 1980s followed by growth declines during the multi-year drought of the mid-1990s.

When we examined cluster membership by substrate, we observed that sites occurring on shale and sandstone had 70 and 78 % of members within cluster 1 (Fig. 4). Trees from alluvial fan sites, however, were

more evenly split between the two clusters with 54 % of trees as members of cluster 2 and 46 % of tree as members of cluster 1 (Fig. 4). Trees on the shale and sandstone substrates also showed evidence of growth declines since the late 1800s. Piñon pine ring widths were significantly and negative correlated with time at the shale ($r = -0.30$, $P = 0.009$) and sandstone (-0.34, $P = 0.005$) sites (Fig. 5). In contrast, there was no relationship between ring width and time at the alluvial fan site ($R = 0.13$, $P = 0.23$).

Discussion

Understanding the effects of changing climate on piñon pine growth and how this may be regulated by environmental variables such as substrate type is not only important for overall piñon-juniper woodland
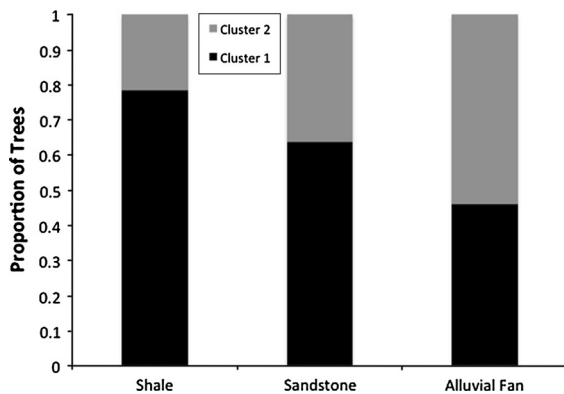
Fig. 4 Cluster membership by substrate type. *Values* show the proportion of trees within each substrate that were members of each cluster

health, but also for reduced tree growth which is a strong predictor of future mortality (Ogle et al. 2000). Furthermore, declines in growth may also contribute to the longer-term capacity for these ecosystems to take up atmospheric CO_2 with potential feedbacks to the terrestrial carbon [C] cycle in this region (Breshears and Allen 2002).

Summer temperatures have been increasing across this region of the Colorado Plateau over the last century. On average July temperature increased by ca. 0.7 °C late in the twentieth century (1950–2000) as compared to the early twentieth century (1898–1949) (Fig. 3b). Results of our study on growth trends in piñon pine suggest that two clusters that differ in their response to summer temperature also differ in their growth trends (Fig. 2). Cluster 1 tree growth was strongly related to early summer temperature and declines from the 1970s through the 2000s. In contrast, cluster 2, which showed a weakened correlation to early summer temperature since the 1950s, showed growth increases during the 1980s followed by growth declines in the 1990s with the onset of a multi-year drought.

Growth declines since the 1970s (as observed in cluster 1) in piñon pine would be logically predicted with increases in early summer temperature. Increasing temperature may reduce not only net photosynthesis by increasing respiratory costs (Adams et al. 2009) but also decrease opportunities for photosynthesis and net C gain by increasing soil water evaporation inducing drought conditions. In this region of the Colorado Plateau, the first xylem cells
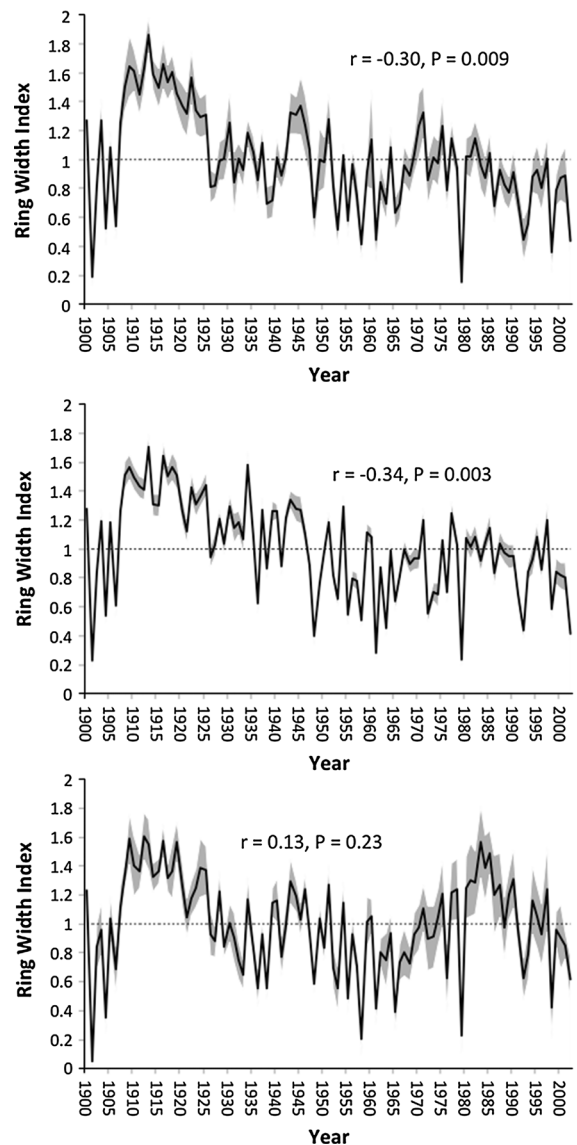
Fig. 5 Correlation of tree-ring width and time (1898–2004) within each substrate type. Pearson's correlation coefficients and associated *P* values are reported on each panel. *Black lines* are mean tree-ring width index values. *Gray bands* are 95 % confidence intervals

in piñon pines are just being formed approximately during the last week of May (Fritts 1976). Relatively wet conditions in the late spring are followed by hot and dry conditions in June and July before the onset of monsoonal precipitation in mid to late July. Thus, the important months for piñon pine growth may often occur under drought-like conditions.

During the summer months, piñon pines have been shown to maintain high photosynthetic capacity to take advantage of precipitation events even during this drought period in early summer (West et al. 2007). Maintenance of photosynthetic capacity in piñon pines, however, may come at a cost of higher vulnerability to xylem cavitation during drought periods (Linton et al. 1998; Williams and Ehleringer 2000; West et al. 2007; McDowell et al. 2008; Breshears et al. 2009). As drought conditions intensify with increasing temperature across this region, investment in maintaining photosynthesis and direct temperature effects on increasing respiratory costs during this summer dry period may result in declines in carbon gains and subsequent growth declines.

In contrast to growth declines within cluster 1, cluster 2 showed a weakened relationship to July temperature and January precipitation in the time period from the 1950s through 2000s relative to the early century time period. These results suggest that factors other than climate may be increasing in importance within this cluster. Although there was no trend in increasing growth over time in cluster 2, the time period from the 1980s through 2000 showed above average growth relative to cluster 1. Atmospheric CO_2, which increased by 16 % from 1960 through 2000, is a potential mechanism by which growth in cluster 2 may be decoupled from climate later in the century. Carbon dioxide fertilization may enhance tree growth in environments that undergo drought stress (reviewed in Huang et al. 2007), which is often linked to increases in water use efficiency. Increases in piñon pine water use efficiency over the last century, as estimated in piñon pines from tree-ring stable isotopes, track the atmospheric CO_2 record across a broad range of Southwest U.S. study sites (Feng 1999). Enhanced growth has also been observed in other semi-arid conifers in the western U.S. Western juniper (*Juniperus occidentalis*), a widely distributed semi-arid conifer in the western U.S., showed positive growth responses since the mid-century with indication that changes in atmospheric CO_2 may be driving these trends (Knapp and Soule 2001). In contrast to our study, enhanced growth responses in Western juniper occurred in sites where environmental stress was greatest.

This period of enhanced growth in cluster 2 trees in the 1980s, however, was followed by growth declines across both clusters with the onset of a multi-year drought in the 1990s and centered on a severe drought in 1996. Based on these growth patterns, is there a prediction of what cluster may be more vulnerable to drought-induced mortality? In comparisons of piñon pines that survived past drought events to those that died, trees with reduced growth and higher annual ring width variability were more likely to die (Macalady and Bugmann 2014, Ogle et al. 2000). Physiological factors such as carbon starvation or 'depletion of nonstructural carbohydrates' and hydraulic failure (McDowell et al. 2013, Adams et al. 2009) may lead to growth reductions and subsequent tree death. The reduced growth in cluster 1 relative to cluster 2, given that mean sensitivity was similar (see Tables 2, 3 in Appendix), suggests that cluster 1 trees may be more vulnerable to future drought-induced mortality.

It is clear that these two clusters exhibited different growth trends and responses to winter precipitation and summer temperature since the 1960s. The question remains as to whether these responses may be related to site-level environmental variables. Our sites are located at similar elevations and experienced relatively similar climate due to their close proximity but differed in geologic substrate. Geologic substrates and the soil types that occur across these different substrates may differ in a wide range of chemical and physical characteristics such as depth, organic matter, texture, permeability, and rooting depth. We predicted that soils occurring on geologic substrates with reduced capacity for water storage and plant water availability (low AWC) would be more vulnerable to drought stress related to increasing temperatures. This prediction was generally consistent whereby 70–78 % of trees within the low AWC geologic substrates (i.e., shale and sandstone residuum) were members of cluster 1 (Fig. 4). In comparison 46 % of the trees that occurred on alluvial fans were members of cluster 1.

Trees from low AWC substrates (shales and sandstones) showed significant growth declines since the late 1800s, whereas those on the higher AWC substrate (alluvial fan) showed little change (Fig. 5). At our sites, the differences in AWC are likely due to differences in soil depth. Reported soil depth from the digital soil survey on the shale and sandstone substrates ranged in depth from 13 to 46 cm, whereas soil depth on the alluvial fan substrates were greater than 150 cm. A study of soil properties associated with regional piñon pine mortality in the early 2000s shows a similar relationship to soil AWC observed in our

study, whereby 70 % of mapped piñon pine mortality across a large region of the Colorado Plateau occurred on soils with an AWC less than 10 cm (Peterman et al. 2012). In a study of parent material influences on piñon pine growth and mortality, parent material had no influence on mortality but piñon pine canopy dieback was higher on the drier, volcanic cinder soils (Koepke et al. 2010). The inconsistent effects of soils and parent material across these studies may be partially explained by the multiple variables that interact to influence the plant water availability.

Data considerations

Since we obtained tree-ring data from previous studies, we had a limited sample size from the substrates that were on the very low (shale, $n = 13$) and high (alluvial fan, $n = 14$) ends of soil AWC. Our study, however, highlights the potential usefulness of reporting additional site-level data, in this case geologic substrate, for understanding drivers of tree growth responses to future climatic change. Tree-ring data are collected extensively across the globe to address a broad range of questions, ranging from climate reconstruction to more historical ecological studies. Thus, additional reporting of site-level characteristics such as soil type and geologic substrate, data that are rarely reported in tree-ring publications or in the ITRDB but do not require a large investment of time or money, could enhance the applicability of tree-ring data to a broader range of questions related to forest and woodland response to global environmental change. Recent efforts to standardize tree-ring data reporting (e.g., Tree-Ring Data Standard or TriDaS, tridas.org, Jansma et al. 2010) may provide a platform to report additional site and tree-level data (e.g., tree diameter and height, soil depth, and type).

Conclusions

Piñon pines have experienced significant regional mortality over the last two decades and predictions of increasing drought intensity and frequency over the next century may further increase the vulnerability of this species to population declines. In our study, piñon pine growth declines were observed in trees that were highly sensitive to summer temperature. In contrast, trees less sensitive to summer temperature showed no change in growth. These patterns in growth declines may be partially explained by substrate differences—trees showing strong growth declines occurred on soils with low available water capacity. Taken together, our findings suggest that future piñon pine growth may be more vulnerable to growth declines with increasing summer temperature on soils with low available water capacity.

Appendix

See Tables 2, 3.

Table 2 Individual tree data for the K-means cluster analysis. Minimum diameter at breast height (DBH) was calculated as the sum of all raw ring widths. Minimum tree age and minimum DBH values are reported as means ± 1 SE

	Cluster 1	Cluster 2
Number of trees	55	26
RBAR	0.64	0.56
Expressed population signal (EPS)	0.99	0.97
Mean sensitivity (MS)	0.35	0.38
Minimum age (years)	325 (13)	340 (19)
Minimum DBH (cm)	33 (1)	31 (2)

Table 3 Individual tree data across different substrates. Minimum diameter at breast height (DBH) was calculated as the sum of all raw ring widths. Minimum tree age and minimum DBH values are reported as means ± 1 SE

	Shale	Sandstone	Alluvial
Number of trees	13	54	14
RBAR	0.61	0.58	0.59
Expressed population signal (EPS)	0.96	0.99	0.95
Minimum age (years)	314 (29)	331 (13)	343 (21)
Minimum DBH (cm)	34 (2)	32 (1)	33 (2)

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