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Interacting effects of climate and landscape physiography on piñon pine growth using an individual-based approach

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Abstract. Forest and woodland ecosystems play a crucial role in the global carbon cycle and may be strongly affected by changing climate. Here, we use an individual-based approach to model piñon pine (*Pinus edulis*) radial growth responses to climate across gradients of environmental stress. We sampled piñon pine trees at 24 sites across southwestern Colorado that varied in soil available water capacity (AWC), elevation, and latitude, obtaining a total of 552 piñon pine tree ring series. We used linear mixed-effect models to assess piñon pine growth responses to climate and site-level environmental stress (30-year mean cumulative climatic water deficit [CWD] and soil AWC). Using a similar modeling approach, we also determined long-term growth trends across our gradients of environmental stress. Piñon pine growth was strongly positively associated with winter precipitation. Summer vapor pressure deficit (VPD) was strongly negatively associated with piñon pine growth during years of low winter precipitation, whereas summer VPD had no effect on piñon pine growth during years of high winter precipitation. The strength of the relationship between the annual climatic variables (winter precipitation and summer VPD) and piñon pine growth was also influenced by site-level environmental stress, suggesting that the sensitivity of woodland ecosystems to changing climate will vary across the landscape due to differences in local physiographic conditions. Trees at sites with lower CWDs were more responsive to summer VPD, showing greater reductions in growth rates during warmer years. Trees at sites with greater soil AWC were more responsive to winter precipitation, showing higher growth rates during years of high precipitation. Piñon pine growth rates declined moderately over the past century across our study area, suggesting that recent increases in aridity have resulted in long-term growth declines.

Key words: climate change; climate–growth responses; climatic water deficit; dendrochronology; elevation; pinyon pine; plant population and community dynamics; semi-arid woodland; soil properties; tree growth.

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INTRODUCTION

Forest and woodland ecosystems play a crucial role in the global carbon cycle by removing billions of tons of CO_2 globally every year from the atmosphere and are thus an important carbon sink for anthropogenic CO_2 emissions (Bonan 2008, Canadell and Raupach 2008, Pan et al. 2011). Within the southwestern United States, climate models predict significant increases in aridity over the next century (Seager et al. 2013, Dai 2013, Williams et al. 2013), which may dramatically alter carbon uptake and storage in forest and woodland ecosystems through changes in tree recruitment, growth, and survival. These changes in vital rates may strongly affect not only carbon stocks (Kurz et al. 2008, Hicke et al. 2012) but also water and energy fluxes (Guardiola-Claramonte et al. 2011, Royer et al. 2011) and even affect climate globally (Bonan 2008, Jackson et al. 2008, Stark et al. 2016). Global climate models incorporate vegetation responses to climate (Bonan 1998, Cox et al. 2000), yet there is considerable uncertainty in the direction and magnitude of these ecosystem responses (Cox et al. 2000, Cramer et al. 2001). Understanding how forest and woodland ecosystems will respond to changing climate is an important step toward understanding potential feedback mechanisms between changing climate and forest and woodland structure.

Forests and woodlands of the southwestern United States are strongly affected by changing climate, particularly in semi-arid regions. Within the widely distributed semi-arid piñon (*Pinus edulis*)–juniper (*Juniperus osteosperma, J. monosperma*) woodlands of the southwestern United States, recent droughts accompanied by warmer temperatures have resulted in extensive piñon pine mortality (Breshears et al. 2005, Floyd et al. 2009, Clifford et al. 2013) and altered tree recruitment dynamics (Redmond and Barger 2013, Redmond et al. 2015). Furthermore, rates of tree growth are also strongly negatively associated with drought among piñon pine and other conifers of the southwestern United States (Adams and Kolb 2005, Williams et al. 2013, Barger and Woodhouse 2015), suggesting that there may also be long-term growth declines due to increasing temperatures and associated increases in water deficits (Barger and Woodhouse 2015).

However, the effects of changing climate on tree growth are unlikely to be uniform across a region. The direction and magnitude of tree growth responses to climate may vary due to local climatic and edaphic conditions (Fritts et al. 1965, LaMarche 1974, Wilmking et al. 2004, Carrer 2011, Galván et al. 2014, Barger and Woodhouse 2015), suggesting that tree growth responses to climate change may vary spatially across a region. Furthermore, these local climatic and edaphic environmental stress variables can also influence average tree growth rates across the landscape, in addition to tree growth responses to climate. Within semi-arid regions of the southwestern United States, areas with greater annual precipitation and lower temperatures have higher net primary production (Running et al. 2004), suggesting that trees in these areas have greater average growth rates.

Yet determining the effects of climate on tree growth is challenging due to the multiple potential drivers of tree growth responses across the landscape (Galván et al. 2014). Dendrochronology studies generally aggregate tree ring series from a region to determine how trees respond to climate and selectively sample trees located in stressful conditions that are more sensitive to climatic fluctuations (LaMarche 1982, Fritts and Swetnam 1989). Whereas this approach is necessary for reconstructing past climate, the approach limits our ability to forecast how trees may respond to future climate across broader spatial extents. Furthermore, most dendrochronological approaches standardize each tree ring series to produce a unitless ring width index (e.g., Cook 1985), which does not provide information regarding changes in actual biomass accumulation through time or other metrics necessary for modeling changes in carbon stocks across the landscape. To overcome these constraints, recent studies highlight the importance of using an individual-based approach to model tree growth responses to climate rather than focusing on the mean growth response within a species (Linares et al. 2010, Carrer 2011, Hereş et al. 2012, Galván et al. 2014, Macalady and Bugmann 2014).

Here, we use an individual-based approach to model piñon pine (*Pinus edulis*) radial growth responses to climate across an edaphic (soil available water capacity [AWC]) and climatic (climatic water deficit [CWD]) gradient of environmental stress. Our specific objectives were to (1) evaluate how piñon pine mean growth rates and growth responses to climate vary across gradients of environmental stress and (2) determine long-term piñon pine growth trends across gradients of environmental stress. We hypothesized that piñon pine growth rates would be lower in areas with greater environmental stress (i.e., high CWDs and low soil AWC). We also hypothesized that piñon pine growth would be more sensitive to interannual climatic fluctuations and would show growth declines over the last century in these areas of greater environmental stress.

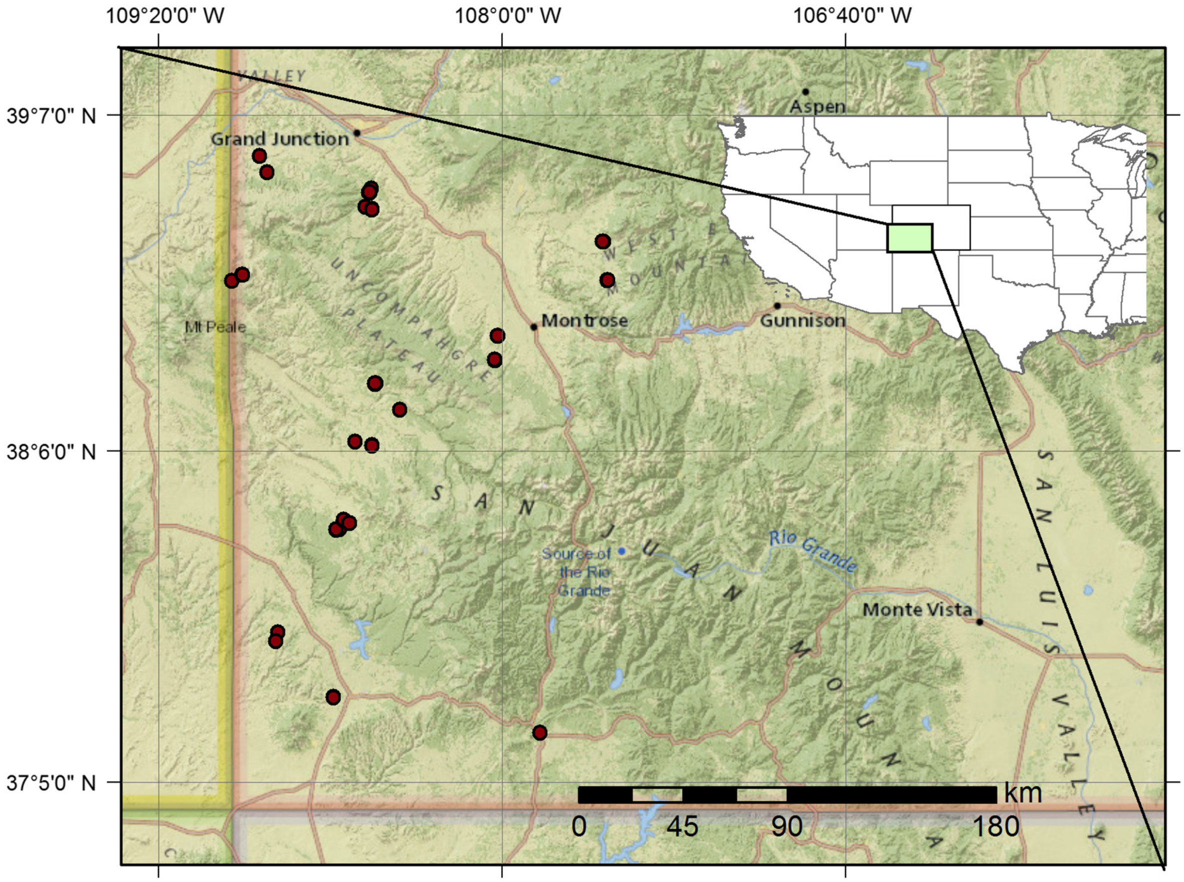

Fig. 1. Map showing the 24 study sites in southwestern Colorado. Map was created using ESRI software (ArcMap version 10.1), and the basemap used is the National Geographic World Map, which includes data from National Geographic, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, and increment P Corp.

METHODS

Study sites

In 2013, we sampled 24 sites across southwestern Colorado that spanned gradients of elevation (1827–2317 m), soil AWC (1.45–28.0 cm), and latitude (Fig. 1; Appendix S1: Table S1). Potential sites were selected using Geographic Information Systems (ArcMap 10.1, Redlands, California, USA), Digital Elevation Models (USGS 2013), and NRCS soil maps (NRCS 2004) to ensure that sites encompassed a broad elevational and soil AWC range. In the field, we selected study sites from the potential sites as those that had mature live piñon trees and did not have any signs of fuel-reduction treatments or fire.

Mean annual precipitation was 368 mm across our study area from 1900 to 2012, with 25% of annual precipitation occurring during the summer months (Fig. 2; PRISM Climate Group 2014). Mean monthly temperatures averaged 8.8°C, with July having the warmest temperatures (21.5°C) and January having the coolest temperatures (−3.1°C) on average (PRISM Climate Group 2014). Average summer (May through July) vapor pressure deficit (VPD), an important driver of growth in the southwestern United States, was 14.2 hPa and was highest in July (17.9 hPa; PRISM Climate Group 2014).

Dendrochronological methods

At each site, we established three 50 m long transects, spaced 25 m apart, and sampled 25–30

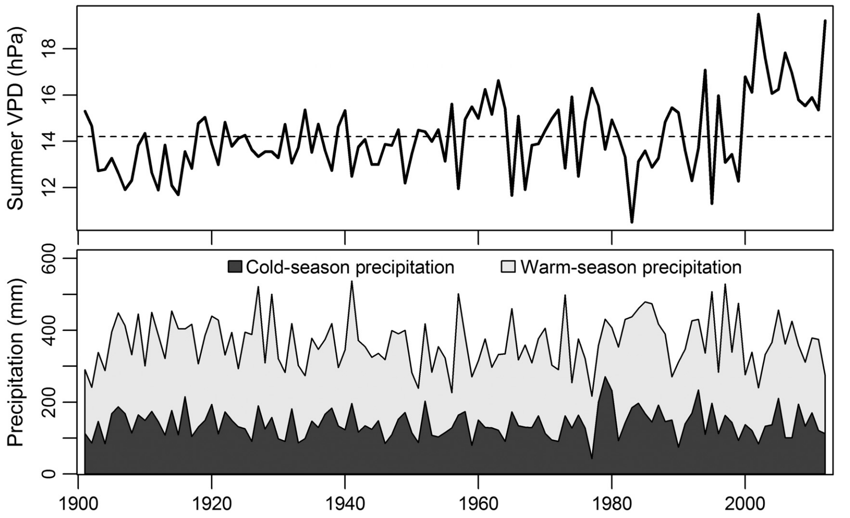

Fig. 2. Changes in summer (May, June, July) vapor pressure deficit (VPD; top) and seasonal precipitation (bottom) across our study area from 1901 to 2012. Horizontal dashed line shows the 1900 to 2012 mean summer VPD. Cold-season precipitation was calculated as total precipitation from November through March, and warm-season precipitation was calculated as total precipitation from April through October. Climate data are from the PRISM Climate Group (2014) and were averaged across the study sites.

mature piñon trees with a basal trunk diameter (BTD) greater than 20 cm that were closest to the transects. One intact core was taken from each tree at 20–30 cm height using a 5.15-mm increment borer, and the diameter at core height was recorded. Tree cores were then air-dried, mounted, and progressively sanded using standard dendrochronological techniques (Fritts 1976, Stokes and Smiley 1996). Cores were then visually cross-dated using previously developed piñon chronologies from southwestern Colorado (Woodhouse et al. 2013*a*, *b*, *c*). All tree rings between 1901 and 2012 were measured to the nearest 0.001 mm using a sliding stage micrometer (Velmex Inc., Bloomfield, New York, USA). We confirmed visual cross-dating statistically using the program COFECHA (Holmes 1983) and omitted any tree cores that were weakly correlated ($r \leq 0.10$) with the remainder of the samples from subsequent analyses. This resulted in a total of 552 tree cores across the 24 sites that were used for the analyses.

Annual climatic variables

We examined the effect of two climatic variables on piñon pine growth that we hypothesized a priori would most strongly influence tree growth: winter (October through March) precipitation (PPT) and summer (May–July) VPD, calculated annually from 1901 to 2012. Previous research has found these two climatic variables to be the strongest predictors of piñon pine growth (Adams and Kolb 2005, Williams et al. 2013, Macalady and Bugmann 2014, Barger and Woodhouse 2015). To ensure that these two climatic variables were strongly related to piñon growth in our study area, we also examined boxplots of the correlation coefficients between individual tree growth (standardized by applying a 20-year moving spline to emphasize high frequency, interannual variability in growth) and monthly precipitation, mean monthly maximum and minimum temperature, and mean monthly VPD. These boxplots revealed that summer VPD and winter precipitation were indeed most strongly correlated with piñon growth (Appendix S1: Fig. S1; Fig. 3). Similar to VPD, summer minimum and maximum temperatures, particularly in June, were also strongly correlated with piñon growth (Appendix S1: Fig. S1), but because summer temperature and summer VPD were highly correlated (Pearson's $r > 0.65$), we only included summer VPD in our model. All climate data were obtained from the PRISM Climate Group (2014). PRISM climate data are based on observational data from weather stations, which are used as inputs for algorithms interpolating

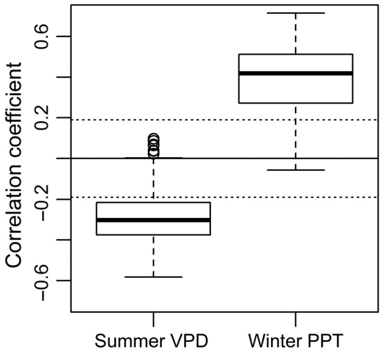

Fig. 3. Pearson's product–moment correlation coefficient of ring width index and climatic variables, summer vapor pressure deficit (VPD) and winter precipitation (PPT), for all piñon trees ($n = 552$). Bolded middle lines represent median values, boxes represent interquartile ranges, and whiskers equal 1.5 times the interquartile range. Horizontal dashed lines show the threshold needed to obtain a significant correlation coefficient given the sample size ($n = 112$), with $\alpha = 0.05$.

climate across complex terrain (Daly et al. 2004). While PRISM data are not effective for assessing multi-decadal climate trends due to changes in station equipment and station locations that can result in trends unrelated to climate, these data are appropriate and useful for our purpose of assessing annual variability in climate across our study area (PRISM Climate Group 2014, Oyler et al. 2015).

Site-level environmental stress variables

We examined the effect of two site-level abiotic predictor variables on piñon pine growth that we hypothesized a priori would influence environmental stress: mean 30-year cumulative CWD and soil AWC. Soil AWC data were obtained from the NRCS soil survey (NRCS 2004), which were validated in the field as part of this study. Field validation of NRCS soil map data was done by taking soil depth measurements using a 1.5 m long soil probe at each transect end (six per site). In instances where there was a mismatch of at least 50 cm in the NRCS soil map data and our soil depth measurements (four instances in total), we examined soil map data from nearby areas (within 1 km) to identify the correct soil map unit. Mean 30-year cumulative CWD is the amount of water by which potential evapotranspiration exceeds actual evapotranspiration on average over the past 30 years and is a biologically meaningful measure of water balance that is strongly correlated with vegetation distribution (Stephenson 1990, 1998). CWD was estimated using a Thornthwaite-type water balance model (Thornthwaite 1948, Dingman 2002) following the equations provided in Lutz et al. (2010). CWD incorporates 30-year averages of monthly precipitation and temperature (800-km resolution, obtained from PRISM Climate Group 2014), heat load (calculated based on slope, aspect, and latitude), soil AWC (held constant at 200 mm for all sites), and day length (see Appendix S2 for more details on CWD calculations), and was negatively correlated with elevation (Pearson's $r = -0.86$).

Modeling growth–climate relationships

We used a linear mixed-effect modeling approach to identify the effects of annual variability in climate and site-level environmental stress on tree growth. For all models, the intercepts for site and for tree (nested within site) were included as random effects and we included a first-order autoregressive correlation structure ("corAR1" in function *lme* in the R package "nlme"; Pinheiro et al. 2015) to account for violation of independence of the residuals from repeated annual growth measurements on a given tree. The two annual climatic variables (winter PPT and summer VPD), the two site-level environmental variables (CWD and soil AWC), and the interactions between the annual climatic variables and the site-level environmental variables were included as fixed effects. We also included an interaction term between the two annual climatic variables in our model because we hypothesized that the effects of summer VPD would be greatest during years of low winter precipitation. Raw ring width was the response variable, which we log-transformed to meet model assumptions. To account for changes in tree growth with age/size, several detrending procedures are commonly performed to remove age-related trends from the raw ring widths, such as fitting a negative exponential curve (Cook 1985). Whereas these detrending procedures enhance the climate–growth signal, the downside is that they produce a unitless ring width index that has a mean of one for every tree and thus, remove the ability to assess how site-level physiographic variables affect tree growth.

To overcome this constraint, we used the raw ring width measurements as our response variable in our analysis but also included tree basal area of the previous year (both linear and quadratic terms) as fixed-effect predictor variables in our model, thereby removing geometric bias in radial increment. We used raw ring width measurements rather than basal area increment because raw ring widths were not as strongly influenced by tree age compared to basal area increment (Appendix S1: Fig. S2). Predictor variables were not strongly correlated with one another (Pearson's $r \leq 0.47$), and the variance inflation factor for each predictor variable was ≤ 1.5.

We performed model averaging using Bayesian Information Criteria (BIC) to account for model uncertainty and reduce parameter estimation bias (Lukacs et al. 2009, Hegyi and Garamszegi 2010). To do this, we compared alternative models predicting tree growth using combinations of our fixed-effect variables (climate and environmental variables) with BIC using the *dredge* function in the R package "MuMin" and then performed model averaging with shrinkage based on model weights using the *model.avg* function (R package "MuMin"). We based our model selection on BIC because our sample size greatly exceeds the parameter space of the model (Aho et al. 2014). We also report the marginal and conditional R^2 of the full model (function *r.squaredGLMM* in the R package "MuMin" using the method proposed by Nakagawa and Schielzeth (2013)), which was within 0.01 units of all top models (ΔBIC < 10). Analyses were done in R using the *lme* function in the package "nlme" (Pinheiro et al. 2015). We also used the package *data.table* (Dowle et al. 2014) in R to organize tree ring data.

Modeling long-term growth trends

To assess long-term growth trends in piñon and whether these trends vary depending on site-level physiographic variables, we used a similar linear mixed-effect modeling approach as above with random intercepts for tree nested within site and with tree ring width as our response variable. We included year (both linear and quadratic components), site-level environmental variables (CWD and soil AWC), and the interactions between year and the site-level variables as fixed effects in the model. To avoid early stages of growth when age/size strongly influences growth (Appendix S1: Fig. S3), we only used trees that were at least 100 years old in 1901 (i.e., trees that dated back to at least 1801), which resulted in a total of 187 trees across 21 sites used for this analysis. Among these older trees, there was no relationship between ring width and basal area ($R^2 = 0.006$; Appendix S1: Fig. S3), suggesting that any long-term growth trends would be due to changes in climate or stand structure rather than size-related trends.

RESULTS

Growth responses to climate and environmental stress

Piñon pine growth was strongly positively associated with winter precipitation and strongly negatively associated with summer VPD (Table 1, Fig. 3). However, the strength of the relationship between summer VPD and piñon pine growth varied strongly depending on the amount of winter precipitation (Table 1, Fig. 4). Piñon pine growth was strongly negatively affected by summer VPD during years of low winter precipitation, whereas summer VPD had no effect on piñon pine growth during years of high winter precipitation (Fig. 4).

The strength of the relationship between the annual climatic variables (summer VPD and winter precipitation) and piñon growth was mediated by site-level attributes. Trees at sites with low mean 30-year cumulative CWD (i.e., cooler, wetter sites) were more responsive to summer VPD (i.e., steeper slope in Fig. 5A). Trees at these sites tended to have greater growth during years of low summer VPDs compared to trees at high CWD sites.

Trees at sites with greater soil AWC were more sensitive to winter precipitation than those at sites with lower soil AWC (Fig. 5B). These high soil AWC sites had deeper soils (mean depth = 1.24 m) compared to low soil AWC sites (mean depth = 0.42) and were thus likely able to store more water during years of high precipitation and thereby increase the amount of available water for the trees. Indeed, trees at high soil AWC sites tended to have greater growth during high precipitation years compared to trees at low soil AWC sites (Fig. 5B).

Long-term growth trends

Our model results suggest that piñon growth rates are declining at an accelerating rate over time

Table 1. Model averaged coefficients predicting the effects of tree size, site-level environmental stress (soil available water capacity [AWC] and mean annual climatic water deficit [CWD]), and climate (winter precipitation [PPT_{winter}] and summer vapor pressure deficit [VPD_{mjj}]) on tree growth (ring width, log-transformed).

Variables	β_{std} (95% CI)	SE	*z* value
Intercept	6.14 (6.014 to 6.265)	0.064	96.03
Basal area	−0.271 (−0.294 to −0.248)	0.012	22.99
(Basal area)^2	0.025 (0.017 to 0.033)	0.004	5.94
AWC	0.093 (−0.04 to 0.227)	0.068	1.37
CWD	−0.069 (−0.203 to 0.065)	0.068	1.01
PPT_{winter}	0.265 (0.258 to 0.273)	0.004	68.53
VPD_{summer}	−0.185 (−0.194 to −0.176)	0.005	40.97
PPT_{winter} × VPD_{summer}	0.193 (0.186 to 0.200)	0.004	53.38
AWC × PPT_{winter}	0.036 (0.030 to 0.043)	0.003	11.06
AWC × VPD_{summer}	0.001 (−0.006 to 0.009)	0.004	0.33
CWD × PPT_{winter}	0.000 (−0.003 to 0.002)	0.001	0.13
CWD × VPD_{summer}	0.034 (0.026 to 0.042)	0.004	8.22

Notes: Variables are in boldface if the 95% confidence interval (95% CI) of the standardized model average coefficient (β_{std}) does not overlap zero. The marginal and conditional R^2 of the full model is 0.23 and 0.46, respectively.

over the past century (Table 2, Fig. 6), yet there is a high level of uncertainty (see confidence intervals in Fig. 6). There was no significant interaction between year and our site-level environmental stress variables (soil AWC and CWD) in our models of piñon growth over time (Table 2), suggesting that piñon growth trends over time did not vary across our environmental stress gradients.

Discussion

Predicted increases in aridity over the next century in the southwestern United States may dramatically affect terrestrial carbon stocks through changes in tree growth, recruitment, and survival (Seager et al. 2013, Kurz et al. 2008, Hicke et al. 2012, Williams et al. 2013). Our

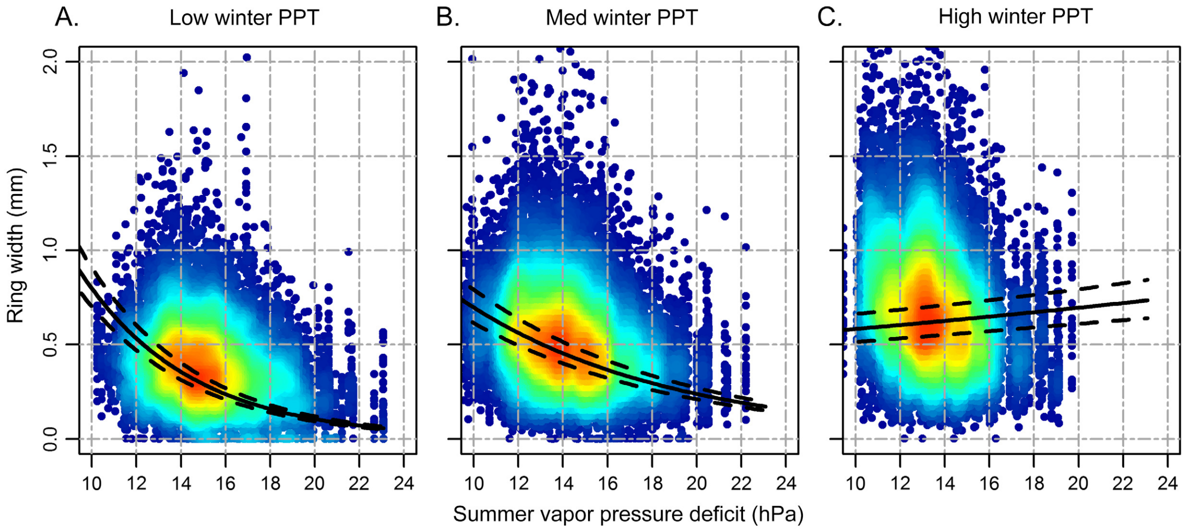

Fig. 4. Partial residual plots of tree growth response to summer vapor pressure deficit during years of low (10% quartile; Left), medium (50% quartile, Middle), and high (90% quartile, Right) winter precipitation (PPT). Partial residual plots were made using the "visreg" package in R. We used the "densCols" function in R to create smooth density plots that color points based on the density of points in that area of the plot, ranging from dark red (high density) to dark blue (low density).

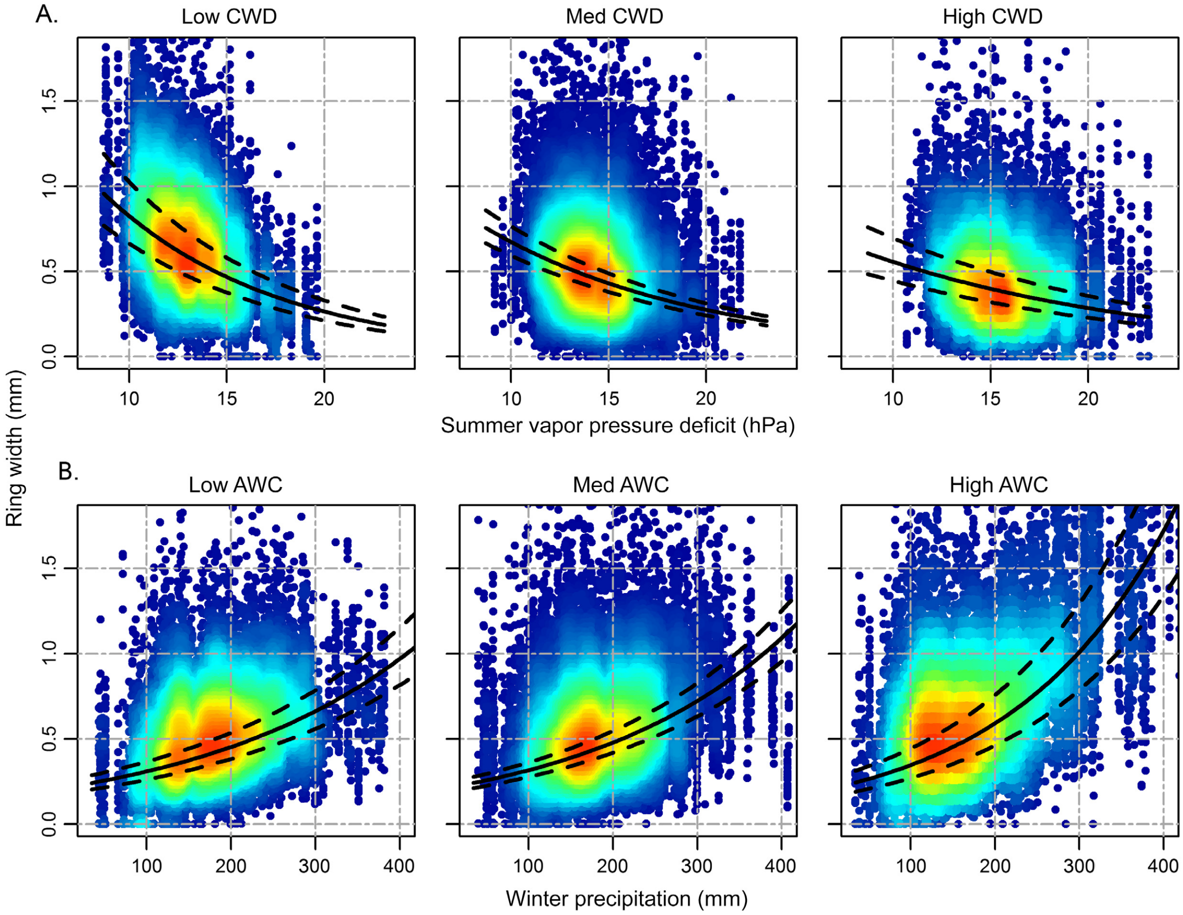

Fig. 5. (A) Partial residual plots of tree growth response to summer vapor pressure deficit (A) and winter precipitation (B) at sites with low (10% quartile; Left), medium (50% quartile, Middle), and high (90% quartile, Right) historic (1970–2010) mean annual climatic water deficit (CWD; A) and soil available water capacity (AWC; B). Partial residual plots were made using the "visreg" package in R. We used the "densCols" function in R to create smooth density plots that color points based on the density of points in that area of the plot, ranging from dark red (high density) to dark blue (low density).

findings suggest that the sensitivity of woodland ecosystems to changing climate will vary across the landscape due to differences in local physiographic conditions. Furthermore, this study highlights the utility of individual-based modeling to investigate how tree mean growth rates and tree growth responses to climate are affected by local physiography.

Piñon pine growth

Consistent with previous studies (Adams and Kolb 2005, Barger et al. 2009, Williams et al. 2013, Barger and Woodhouse 2015), piñon pine growth was strongly affected by winter precipitation and summer VPD. Piñon pine growth was strongly negatively affected by summer VPD during years of low winter precipitation, whereas summer VPD had no effect on piñon pine growth during years of high winter precipitation (Fig. 4). VPD is the highest during the summer months in this region of the southwestern United States (Williams et al. 2013). High VPDs increase evapotranspiration, resulting in reduced soil moisture and increased tree water demand and potentially leading to prolonged stomatal closure during periods of low soil moisture (Gollan et al. 1985, Ball et al. 1987, Leuning 1995), thereby decreasing photosynthesis and growth rates (McDowell et al. 2010,

Table 2. Model averaged coefficients of our long-term growth model to determine the effects of year, our site-level environmental stress variables (soil available water capacity [AWC] and mean annual climatic water deficit [CWD]), and their interactions on tree growth.

Variables	β_{std} (95% CI)	SE	*z* value
Intercept	5.74 (5.66 to 5.83)	0.04	130.92
AWC	0.00 (−0.02 to 0.02)	0.01	0.01
CWD	0.00 (−0.05 to 0.04)	0.02	0.19
Year	−17.72 (−19.82 to −15.62)	1.07	16.58
Year^2	−4.29 (−6.38 to −2.21)	1.06	4.03
AWC × year	0.00 (−0.33 to 0.32)	0.17	0.01
AWC × year^2	−0.12 (−1.68 to 1.43)	0.79	0.16
CWD × year	0.00 (−0.01 to 0.01)	0.00	0.00
CWD × year^2	0.00 (−0.02 to 0.02)	0.01	0.00

Notes: Variables are in boldface if the 95% confidence interval (95% CI) of the standardized model average coefficient (β_{std}) does not overlap zero. The marginal and conditional R^2 of the full model is 0.02 and 0.14, respectively.

Breshears et al. 2013). Winter precipitation is important for soil water recharge and is positively correlated with tree growth of southwestern U.S. conifer species (Fritts et al. 1965, Williams et al. 2013). Our results suggest that increases in summer VPD due to increasing temperatures associated with global climate change will have a strong adverse effect on forest growth during years of low precipitation. These results further confirm recent research that highlights how the combination of drought and summer VPD, which is primarily driven by warm temperatures, strongly adversely affects forest health in semi-arid ecosystems (Allen et al. 2015).

Our findings suggest that the sensitivity of woodland ecosystems to changing climate varies across edaphic and climatic gradients of environmental stress. Counter to our initial hypothesis, we found that trees growing in areas with lower mean CWDs (i.e., cooler, wetter areas) were more sensitive (steeper slope) to summer VPD than trees growing in warmer, drier areas (Fig. 5A). Trees growing in these cooler, wetter areas tended to have higher growth rates during years of low summer VPDs (Fig. 5A), leading to increased sensitivity (steeper slope) to summer VPD. Previous research has highlighted the trade-off between drought adaptation and forest productivity (Ryan and Yoder 1997, Nardini et al. 2012). We hypothesize that trees growing in the more stressful (hotter, drier) areas have functional traits that allow them to better tolerate drought but also reduce their ability to grow as much during wet years.

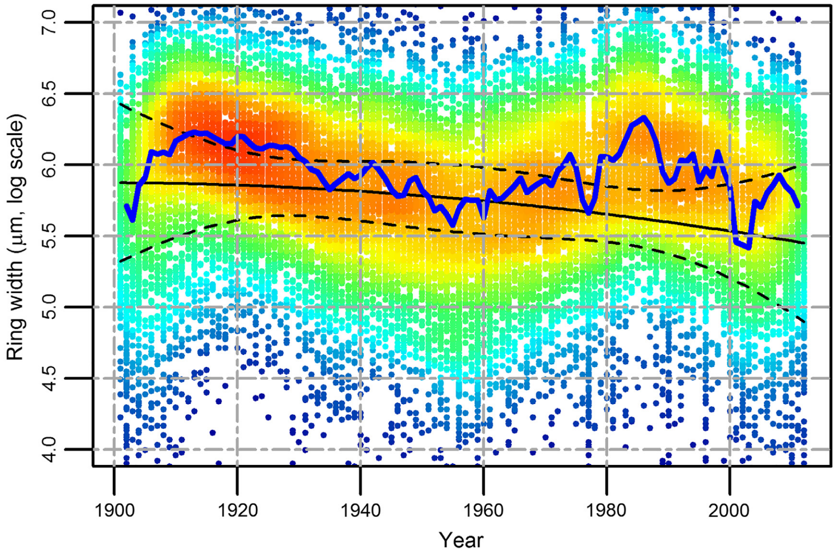

Fig. 6. Plots of tree growth (log-transformed) over time (from 1901 to 2012) across all study sites. Due to the high number of points (20,832), we used the "densCols" function in R to create smooth density plots that color points based on the density of points in that area of the plot, ranging from dark red (high density) to dark blue (low density). The solid blue line is the three-year moving averages of mean growth rates.

These findings suggest that predicted increases in temperatures associated with global climate change will result in greater growth declines of trees growing in cooler, wetter areas, which are often considered less sensitive to climate change (Allen and Breshears 1998, Ogle et al. 2000, Koepke et al. 2010, but see Redmond et al. 2012).

Piñon trees at sites with high soil AWC were more sensitive (steeper slope) to winter precipitation than trees at sites with low soil AWC (Fig. 5B). This finding is counter to our initial hypothesis that trees in regions of greater environmental stress (i.e., low soil AWC) would be more sensitive to climate and differs from previous findings in another semi-arid ecosystem (Knutson and Pyke 2008). Furthermore, this result is inconsistent with common site selection practices in dendroclimatic research (Fritts 1976), which often target trees in shallow, coarse-textured soils as they are considered to be more sensitive to climate. We hypothesize that at sites with greater potential for water storage, growth is highly correlated with precipitation because trees are able to overcome water resource limitation through long-term soil water storage, thereby increasing growth later into the growing season. Conversely, in locations where total winter precipitation exceeds available soil water storage capacity, the effect of precipitation on growth saturates because more precipitation is lost as runoff and does not contribute to tree growth. Indeed, trees at high soil AWC sites had greater growth rates during years of high precipitation than trees at low soil AWC sites (Fig. 5B). Recent research has found that trees with lower growth rates during years of high precipitation are more likely to die during drought (Macalady and Bugmann 2014), suggesting that trees located in areas with low soil water storage are more likely to die during drought. Our results also suggest that the timing of precipitation may be more important for trees in areas with low soil water storage because those trees cannot benefit from a lot of precipitation during a short time period, especially if that precipitation occurs outside of the growing season. Climate models project that precipitation events will likely become more extreme over the next century (IPCC 2014), and these results suggest that predicted increases in precipitation variability would have particularly negative impacts on trees growing in areas with low soil water storage. Furthermore, these results indicate that even if climate change results in more winter precipitation, the increased winter precipitation would not be able to counteract the negative effects of predicted increases in summer VPD on tree growth in areas of low soil AWC.

We found evidence of long-term declines in piñon pine growth rates over the past century within our study area (Fig. 6), likely due to the hotter and drier climate conditions over the past several decades (Fig. 2). Consistent with previous studies (Williams et al. 2013, Barger and Woodhouse 2015), these results suggest that increases in aridity associated with global climate change have already and will continue to result in long-term growth declines among piñon pine. Although our model results suggest that tree growth rates are declining over time at an accelerating rate, there is a high level of uncertainty. Detecting growth declines is challenging because of the high decadal variability in growth rates due to climate, particularly given the relatively short time span of our tree ring series.

We found no evidence that growth trends over time varied across the two gradients of environmental stress (CWD and soil AWC). This may be due to the difficulty in detecting growth declines given the relatively short time span of our tree ring series. Alternatively, growth trends over time may be driven by other unmeasured factors, such as competition among neighboring trees, prevalence of insect infestations, or genetic differences.

Individual-based modeling approach

Recent dendroecology studies emphasize the need to use a more individual-based approach to enhance understanding of tree growth responses to climate (i.e., Carrer 2011, Galván et al. 2014). Here, we show how mixed-effect modeling can be used to understand how tree growth is influenced by environmental factors at different scales and how tree growth–climate relationships may vary across the landscape. By incorporating tree size into the model, the approach used here removes growth patterns related to tree size, without requiring tree ring standardization. As such, this approach allowed us to explicitly model growth, rather than a standardized growth index, which is particularly useful for ecosystem modelers interested in gross rates of carbon uptake by the terrestrial biosphere.

The individual-based approach used here was effective at modeling the effects of climate and site-level environmental stress on piñon pine growth. However, there are several limitations to this modeling approach and situations where this approach may not be appropriate. In our case, we had extensive a priori knowledge of the dominant climatic variables that affect piñon pine growth (i.e., Williams et al. 2013, Barger and Woodhouse 2015) and thus had an appropriate number of climatic variables to include in our model given our sample size. For species or areas where there is limited a priori information, researchers would need to first perform analyses to identify the dominant climatic variables before using a mixed-effect modeling approach. Tree ring standardization may also be necessary if there are strong growth responses to localized disturbance events. Furthermore, this approach would not be appropriate if the primary goal is to reconstruct past climate.

Conclusions and Climate Change Implications

Increasing temperatures and altered precipitation regimes associated with global climate change are predicted to dramatically affect forest and woodland ecosystems due to changes in tree recruitment, growth, and survival. Our results suggest that the effects of climate change on forest growth may vary across gradients of local physiographic conditions. We found that tree growth responses to annual climatic fluctuations varied across the landscape due to differences in soil properties and local climate. This result has important implications for woodland carbon dynamics, particularly because previous research has found strong associations between tree growth sensitivity to climate and tree mortality during drought (Ogle et al. 2000, McDowell et al. 2010, Macalady and Bugmann 2014). Furthermore, our results suggest that the effects of changing climate may vary across the region: Areas with low soil AWC will likely be negatively affected by increasing temperatures regardless of changes in precipitation, whereas areas with high soil AWC will likely be more strongly affected by drought, particularly when accompanied by warmer temperatures. Piñon pine growth rates declined moderately over the past century across our study area in southwestern Colorado, suggesting that recent increases in aridity have resulted in long-term growth declines.

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