

Topography alters tree growth–climate relationships in a semi-arid forested catchment

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Citation: Adams, H. R., H. R. Barnard, and A. K. Loomis. 2014. Topography alters tree growth–climate relationships in a semi-arid forested catchment. *Ecosphere* 5(11):148. <http://dx.doi.org/10.1890/ES14-00296.1>

Abstract. Topography and climate play an integral role in the spatial variability and annual dynamics of aboveground carbon sequestration. Despite knowledge of vegetation–climate–topography relationships on the landscape and hillslope scales, little is known about the influence of complex terrain coupled with hydrologic and topoclimatic variation on tree growth and physiology at the catchment scale. Climate change predictions for the semi-arid, western United States include increased temperatures, more frequent and extreme drought events, and decreases in snowpack, all of which put forests at risk of drought induced mortality and enhanced susceptibility to disturbance events. In this study, we determine how species-specific tree growth patterns and water use efficiency respond to interannual climate variability and how this response varies with topographic position. We found that *Pinus contorta* and *Pinus ponderosa* both show significant decreases in growth with water-limiting climate conditions, but complex terrain mediates this response by controlling moisture conditions in variable topoclimates. Foliar carbon isotope analyses show increased water use efficiency during drought for *Pinus contorta*, but indicate no significant difference in water use efficiency of *Pinus ponderosa* between a drought year and a non-drought year. The responses of the two pine species to climate indicate that semi-arid forests are especially susceptible to changes and risks posed by climate change and that topographic variability will likely play a significant role in determining the future vegetation patterns of semi-arid systems.

Key words: dendrochronology; ecohydrology; lodgepole pine; *Pinus contorta*; *Pinus ponderosa*; ponderosa pine; semi-arid; topoclimate; topographic wetness index; water use efficiency.

Received 5 September 2014; **accepted** 9 September 2014; **published** 26 November 2014. Corresponding Editor: D. P. C. Peters.

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INTRODUCTION

Topography and climate are critical in determining the spatial and temporal variation of forest carbon sequestration and growth. Topography drives the hydrologic dynamics of catchments and the response of forests to abiotic factors such as incoming solar radiation, soil moisture, and temperature. Despite knowledge of topographic influence on forest function at landscape scales, little is known about the

influence of complex terrain on tree growth and physiology within catchments—the building blocks of mountain landscapes. Topographic control of catchment hydrology and topoclimate will likely play an important role in shaping vegetation responses to future climate conditions (Dobrowski 2011, Liu et al. 2013, Williams et al. 2013). Climate projections for the western U.S. forecast increased temperatures and more frequent and extreme drought events (IPCC 2007). Therefore, filling this catchment-scale knowledge

gap is especially important for water-limited ecosystems.

Landscape scale studies of topography/tree-growth relationships find that growth responds to soil moisture conditions across broad gradients (i.e., elevation or aspect). Oberhuber et al. (1998) found that trees growing on similar hillslopes at the 1-km² scale responded similarly during drought conditions, indicating that topographic position influenced tree growth. In the Colorado Front Range, Fritts (1974) found at low elevations and on water-limited aspects, tree growth is responsive to precipitation, but temperature becomes increasingly important to growth with increasing elevation. In the subalpine zone of Colorado, Villalba et al. (1994) found that subalpine fir and Engelmann spruce responded differently to climate due to variable soil moisture at different topographic positions; however, lodgepole pine growth did not respond to topographic variability.

Within catchments, topography creates topoclimate which can vary significantly from regional climates in soil moisture availability and temperature. Topoclimate create habitats which may buffer against unfavorable regional climate conditions (microrefugia) or exacerbate climate stress despite favorable conditions (Ashcroft et al. 2009, Dobrowski 2011). Suggitt et al. (2011) recorded differences as high as 7°C between different slope aspects, and topographic control of soil moisture on hillslopes resulted in distinct species and basal area distributions (Tromp-van Meerveld and McDonnell 2006). Because semi-arid systems are sensitive to minor changes in water availability (Liu et al. 2013), topoclimate and microrefugia may prove to be especially important to the persistence of semi-arid species.

Current drought-induced mortality across the western U.S. indicates that semi-arid forests are especially vulnerable to prolonged drought (Breshears et al. 2009, van Mantgem et al. 2009, Williams et al. 2013). Species-specific responses to drought, such as differing water use strategies, can be linked to their ability to persist. Zweifel et al. (2009) observed that species which maintained higher stomatal conductance during drought were increasingly abundant over several decades relative to other species. Understanding how topographic position influences forest water relations

(i.e., stomatal conductance and carbon assimilation and allocation) will provide further insight into how forests respond to changing climate.

Determining the climatic, topographic, and hydrologic drivers of tree growth in complex terrain is central to understanding ecohydrologic dynamics of semi-arid forests. The goal of our study is to understand climate and topography effects on tree growth and physiology of two semi-arid pine species. To understand the potential response of tree growth to future climate, we ask (1) how does species-specific annual growth respond to interannual climate variability and how does this response vary with topographic position? To determine the physiological responses of the species to climate, we ask (2) how does species-specific water use efficiency respond to drought conditions and how does this response vary with topographic position? We address these questions through observations of *Pinus contorta* and *Pinus ponderosa* growing near their elevation range limits and temperature thresholds where they are expected to exhibit high sensitivity to climate (Fritts et al. 1965, Adams and Kolb 2004).

METHODS

Study area.—This study was conducted at Gordon Gulch, a 2.6-km² headwater catchment located within the montane zone of the Boulder Creek watershed and Arapahoe National Forest in the Colorado Front Range, Colorado, USA (40.02° N, 105.48° W) (Fig. 1). It has a semi-arid climate, receiving a mean of 51 cm of precipitation per water year with the majority in April, May, and July (1986–2012 data from National Atmospheric Deposition Program (NADP) station CO94 and 1986–2012 Parameter-elevation Regressions on Independent Slopes Model (PRISM) data) (NADP, <http://nadp.sws.uiuc.edu/sites/siteinfo.asp?id=CO94&net=NTN>; PRISM, <http://prism.oregonstate.edu>). Mean annual temperature is 7°C (2003–2013 data from National Climatic Data Center (NCDC) station 053629) (<http://www.ncdc.noaa.gov/cdo-web/>). The vegetation is typical of Front Range montane zones (Peet 1981). North-facing slopes have dense *P. contorta* stands while south-facing slope composition varies by position in the catchment. In the lower basin, south aspects consist of

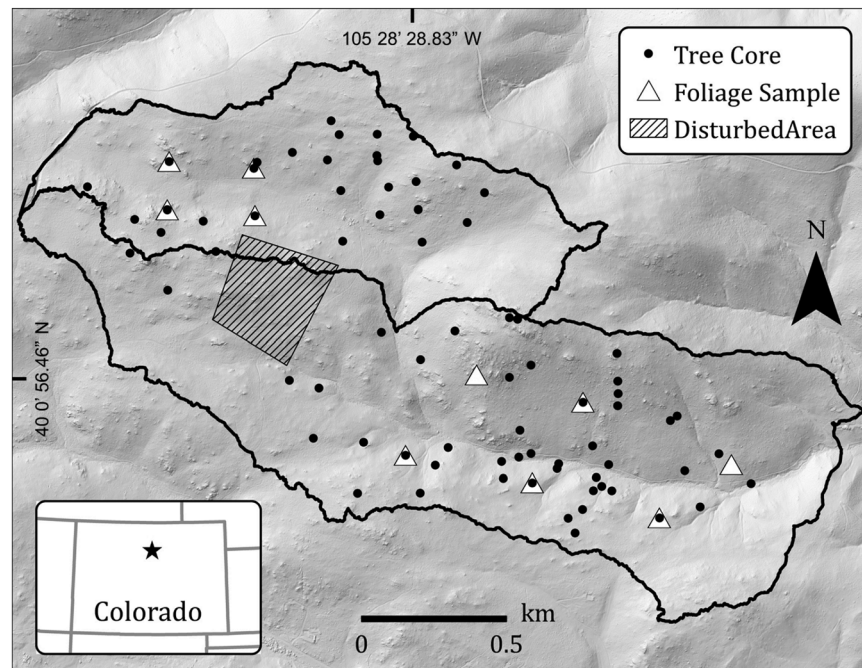


Fig. 1. Terrain map of Gordon Gulch and sampling locations within the catchment. Upper and lower sub-basins of study area are outlined. Disturbed area shown by hatched polygon demonstrates a recently logged area not included in this study.

widely spaced *P. ponderosa* with grasses and shrubs, while upper basin south aspects consist of mixed *P. ponderosa*–*P. contorta* stands. At 2446–2737 m elevation, Gordon Gulch sits at the upper elevation range limit of *P. ponderosa* and the lower elevation range limit of *P. contorta* for the Colorado Front Range (Peet 1981). Records of forest disturbance indicate that Gordon Gulch was subject to a stand replacing fire in 1859 (Goldblum and Veblen 1992). Stumps in the study area indicate sparse logging in the 1930s and 1970s; sample plots avoided logged areas.

Tree-ring data.—To examine the response of tree growth to climate and topography, we sampled increment cores from two to three dominant *P. contorta* and *P. ponderosa* trees in each of 75 plots in the catchment (208 sampled trees: 123 *P. contorta*, 85 *P. ponderosa*). Most cores were collected in 2011 and 2012 with additional cores collected in 2013. Plot locations were selected to include a wide range of variability in forest composition and topographic positions within the study area (Appendix: Table A1). Increment cores were mounted, sanded, and measured according to standard dendrochronological pro-

cedures (Stokes and Smiley 1968). Annual ring widths were measured to the nearest 0.01 mm using WinDENDRO software (Regent Instruments, Quebec, Canada). All cores were visually cross-dated using a master chronology developed from *P. ponderosa* of the central Front Range. We assessed cross-dating quality using the computer program COFECHA (Holmes 1983) in which 50-year segments (overlapped by 25 years) were compared to the COFECHA master chronology. Cores having poor cross-dating quality (correlation with master chronology <0.3) or inadequate quality for visual measurement and cross-dating were removed from the analyses (37 *P. contorta* removed, 15 *P. ponderosa* removed). To account for the age-growth relationship within trees, tree-ring series were detrended with a negative exponential curve in R using the package dplR (Bunn 2008). Ring-width index (RWI) was calculated for each tree-ring series by dividing the observed raw ring width values by the negative exponential curve predicted values and standard chronologies were developed for each species in various topographic positions by averaging RWI records. Residual

chronologies were created (an autoregressive model was fit and residuals calculated) to remove within-chronology autocorrelation (Bunn 2008); as required for statistical analyses. To examine growth relationships with regard to topography and annual climate parameters, we calculated annual basal area increment (BAI):

$$\text{BAI} = \pi r_t^2 - \pi r_{t-1}^2 \quad (1)$$

where r_t is the radius of the tree at the end of an annual ring and r_{t-1} is the radius of the tree at the start of annual ring formation.

Foliar $\delta^{13}\text{C}$ data.—We measured foliar $\delta^{13}\text{C}$ in 30 trees across the study site for two years with contrasting climate to examine how tree intrinsic water use efficiency (iWUE) varies by species and topographic position. Foliar $\delta^{13}\text{C}$ provides an estimate of tree iWUE, the ratio of carbon assimilated to stomatal conductance (A/g_s) (Farquhar et al. 1989). In C_3 plants, during times of water stress, stomatal conductance and the ratio of intercellular to ambient atmospheric C are decreased, thereby decreasing photosynthetic ^{13}C discrimination and increasing ^{13}C fixation and iWUE (Farquhar et al. 1989). Foliage formed during the 2011 (moderately wet; PDSI = 2.4; precipitation = 38.2 cm) and 2012 (severe drought; PDSI = -3.3; precipitation = 31 cm) growing seasons was collected from both *P. contorta* and *P. ponderosa* between October and December 2012. We sampled foliage from three dominant trees in ten plots distributed across the catchment (17 *P. contorta*, 13 *P. ponderosa*; Fig. 1). Foliage samples were collected from branches exposed to full sun in the upper third of the canopy. Samples were dried at 35°C for 50 hours, ground with mortar and pestle, and extracted to holocellulose (Leavitt and Danzer 1993). Holocellulose samples were combusted in an elemental analyzer (Carlo Erba EA 1110 Series, Thermo Scientific, Waltham, Massachusetts, USA), and analyzed by continuous flow mass spectrometry (VG/Fisons SIRA Series II mass spectrometer, Thermo Scientific) to determine the ^{13}C isotope composition at the University of Colorado. Stable isotope abundance of $\delta^{13}\text{C}$ is expressed relative to the Pee Dee Belemnite standard (Farquhar et al. 1989):

$$\delta^{13}\text{C}(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (2)$$

where R is the ratio of ^{13}C to ^{12}C of the sample or standard. Precision of analysis was 0.12‰ and accuracy was 0.04‰. We also measured nitrogen (N) content of ground bulk foliage to determine if photosynthetic capacity differed between individual trees or between the two sample years of foliage. Foliar N was measured using a Thermo Finnigan FLASH EA 1112 Series CHN Analyzer at the University of Colorado.

Climate data.—We examined climate data to determine the tree growth response to annual and monthly climate conditions. Monthly precipitation and temperature PRISM data were obtained for the time period 1895–2013 at approximately 4 km² grid cell resolution (PRISM 2014). We acquired Palmer Drought Severity Index (PDSI) data for the time period 1895–2013 for Colorado region 4 (South Platte) from the National Climate Data Center (<http://www.ncdc.noaa.gov/cdo-web/>). The Palmer Drought Severity Index is a measure of meteorological drought based on a water balance model including local precipitation and temperature indices (Palmer 1965, Heddinhaus and Sabol 1991). Five classes of PDSI were used to classify water availability and moisture conditions of different years (Fig. 2).

Topographic data.—We calculated topographic indices across the study site to examine the influence of topographic position on tree growth and iWUE. Topographic data were modeled from an aerial light detection and ranging (LiDAR)-derived 1m resolution digital elevation model (DEM) of the study area (Anderson et al. 2012). Raster surfaces of upslope accumulated area (UAA), slope, aspect, and growing season (April–September) incoming solar radiation (ISR) were generated using the ArcMap spatial analyst toolbox (ESRI 2012). Raster surfaces were aggregated to 9-m resolution to avoid the effects of 1-m scale microtopography anomalies. A topographic wetness index (TWI) raster grid was generated from the slope and UAA raster surfaces using the formula:

$$\text{TWI} = \ln(a/\tan\beta) \quad (3)$$

where a is the UAA per unit contour length and β is the local slope (Beven and Kirkby 1979). Topographic wetness index accounts for the topographic control of water movement in sloped landscapes and the associated control on soil

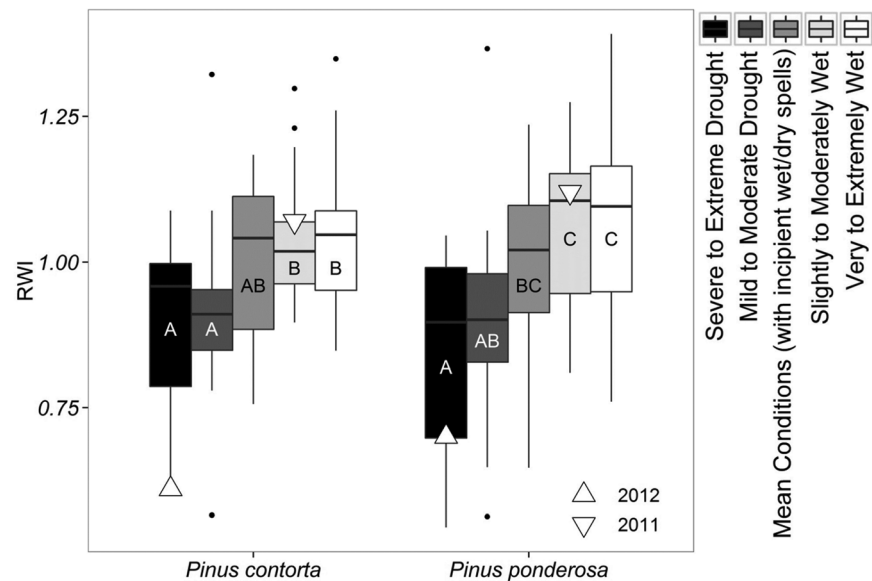


Fig. 2. Ring-width index (RWI) in years with variable moisture and temperature conditions determined by growing season (Apr–Sept) PDSI (1895–2013). Boxes without a common letter are significantly different from one another ($p < 0.01$). Letter codes only refer to significant differences within a species. Categories of PDSI: (1) severe to extreme drought ($n = 24$, PDSI values below -3), (2) mild to moderate drought ($n = 38$, PDSI values -1 to -2.99), (3) mean conditions ($n = 46$, PDSI values -0.99 to 0.99), (4) slightly to moderately wet ($n = 44$, PDSI values 1 to 2.99), and (5) very to extremely wet ($n = 86$, PDSI values 3 and above). Box center line indicates the median with the first and third quartiles indicated by the lower and upper extremes of the box, respectively. Whiskers indicate points within 1.5 times the interquartile range above or below the median.

moisture. High TWI values represent potentially wetter areas of converging terrain and low TWI values represent potentially drier areas of diverging topography. The range of TWI values in Gordon Gulch is 0.6–10.3 with the greatest frequency (95%) occurring over 2.5–6. Increment core plots capture a range of TWI values from 2.3 to 5.1 (representing 90% of the study area) while foliage sample plots capture a range of TWI values from 1.9 to 4.2 (representing 70% of the study area). Values from each topographic raster surface were extracted at all plot locations and used in statistical analyses.

Statistical analyses.—All statistical analyses were completed using R. To determine the species-specific annual growth response to drought, we compared ring-width index (RWI) in variable PDSI conditions using a one-way ANOVA. Linear regression models were constructed to assess species-specific annual growth response to climate and topographic positions; BAI was used as the dependent variable with

precipitation, temperature, and PDSI (water year and growing season) as climate predictor variables and elevation, UAA, slope, growing season ISR, and TWI as topographic predictor variables. We fit linear mixed-effects models (LMEM) for each species to determine the combined effect of climate and topography variables on BAI and to identify the most important climatic and topographic predictors of annual growth of each species (Bates et al. 2013). The individual tree was used as the random-effects term included in all models. Models were fit by maximum likelihood and the model for each species was chosen based on minimizing the Akaike information criterion (AIC), a goodness-of-fit statistic commonly used in model selection. Bayesian information criterion (BIC) was also measured to determine model goodness of fit.

We used correlation function analyses to determine the influence of monthly climate on RWI of each species as well as topographic positions within each species (Zang and Biondi

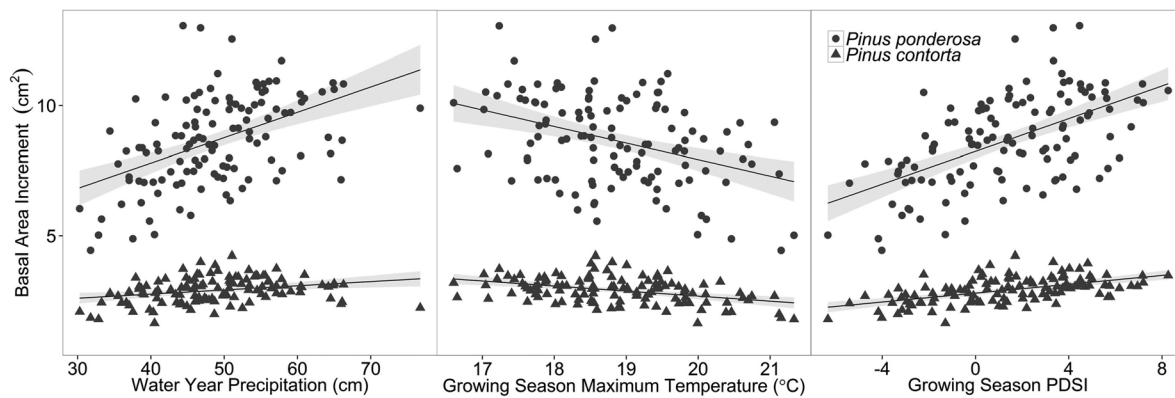


Fig. 3. Significant linear relationships between BAI and climate variables ($p < 0.01$). Adjusted R^2 values for water year precipitation, growing season maximum temperature, and growing season PDSI are 0.07, 0.16, and 0.29, respectively, for *Pinus contorta* and 0.23, 0.14, and 0.32, respectively, for *P. ponderosa*. Slope values for water year precipitation, growing season maximum temperature, and growing season PDSI are 0.02, -0.19 , and 0.08 , respectively, for *P. contorta* and 0.10 , -0.63 , and 0.31 , respectively, for *P. ponderosa*. In all relationships, the slopes of each species are significantly different from one another ($p < 0.01$).

2013). Correlation function analysis calculates bootstrapped correlation coefficients (1000 simulations) to determine significant correlations between annual growth and monthly climate and is recommended over response function analysis due to its ease of interpretation, replicability, and conservative nature (Blasing et al. 1984). To determine the species-specific iWUE response to drought, we conducted repeated measures ANOVA analysis. Individual tree was used as the repeated factor to determine the within tree variability of $\delta^{13}\text{C}$ between 2011 (non-drought year) and 2012 (drought year); interactions between year and topographic position were included. Year was used as the repeated factor to determine the species-specific within-year effect of topography on $\delta^{13}\text{C}$. Foliar N was included as a predictor variable to determine if photosynthetic capacity influenced annual variability in tree iWUE.

RESULTS

Growth response to climate.—Detailed chronology data can be found in (Appendix: Table A2, Fig. A1). *P. contorta* and *P. ponderosa* growth responded significantly to interannual variability in climate conditions. Ring-width index of both species was significantly reduced in drought years compared to non-drought years

($p < 0.01$) (Fig. 2). *P. contorta* and *P. ponderosa* growth were 39% and 30% below the mean, respectively, in 2012 and 7% and 12% above the mean in 2011, respectively. Linear regression and correlation function analyses found that both coarse (annual, seasonal) and fine (monthly) temporal scale climate has significant species-specific impacts on temporal variability of annual tree growth in the catchment (Fig. 3, Tables 1 and 2). Linear regression analyses found water year precipitation ($p < 0.01$), growing season maximum temperature ($p < 0.01$), and growing season PDSI ($p < 0.01$) as the best climate predictors of annual growth (BAI) for both *P. contorta* and *P. ponderosa* (Fig. 3). Annual growth of both species increased with higher water year precipitation, lower growing season maximum temperature, and higher growing season PDSI. More of the variability in *P. ponderosa* growth was explained by water year precipitation in comparison to *P. contorta* (adjusted $R^2 = 0.23$ and 0.07 , respectively, and slope = 0.10 and 0.02 , $p < 0.01$, respectively), suggesting higher sensitivity to precipitation for *P. ponderosa*. Although significant, adjusted R^2 values of climate–growth relationships were not high (Fig. 3). Highest adjusted R^2 values for both species appeared in the relationship with growing season PDSI (0.29 and 0.32 for *P. contorta* and *P. ponderosa*, respectively).

Table 1. Correlation function analyses of *Pinus contorta* and *P. ponderosa* tree-ring chronologies with monthly precipitation. Positive values indicate significant positive correlations; negative values indicate significant negative correlations ($p < 0.05$). Months analyzed include previous year June through December and current year January through October. Only months with significant correlations are shown.

Chronology	<i>n</i>	Previous year		Current year		
		Jun	Apr	May	Jun	
<i>P. contorta</i>	86					0.38
Elevation < 2600 m	38	0.16				0.33
Elevation > 2600 m	48					0.38
TWI: low	29					0.37
TWI: high	21					0.28
Aspect: north	23	0.17				0.32
Aspect: south	19					0.47
<i>P. ponderosa</i>	70		0.24	0.25		0.38
Elevation < 2600 m	29		0.31	0.30		0.42
Elevation > 2600 m	41		0.21	0.22		0.37
TWI: low	25		0.21	0.21		0.33
TWI: high	20		0.24			0.41
Aspect: south	61		0.24	0.25		0.36

Correlation function analyses found significant relationships between *P. contorta* and *P. ponderosa* growth (RWI) and monthly climate conditions (Tables 1 and 2). Both species responded positively to high precipitation in current June and responded negatively to high maximum temperatures in current June and July and previous year July and October, indicating that the climate conditions of these months are important to annual tree growth across the catchment. *P. contorta* growth decreased with high maximum temperatures in current September and previous September and November, indicating sensitivity

to fall climate conditions. *P. ponderosa* growth increased with high precipitation in current April and May and decreased with high maximum temperatures in current May, indicating sensitivity to spring climate conditions.

Growth response to climate with regard to topography.—Although only a small portion of *P. ponderosa* annual growth variability can be explained by TWI (adjusted $R^2 = 0.06$); linear regression indicated higher *P. ponderosa* growth (BAI) in areas of higher TWI ($p = 0.03$) (Appendix: Fig. A2). Correlation function analyses showed that topographic position influences

Table 2. Correlation function analyses of *Pinus contorta* and *P. ponderosa* tree-ring chronologies with monthly maximum temperature. Positive values indicate significant positive correlations; negative values indicate significant negative correlations ($p < 0.05$). Months analyzed include previous year June through December and current year January through October. Only months with significant correlations are shown.

Chronology	<i>n</i>	Previous year				Current year					
		Jul	Sep	Oct	Nov	Mar	May	Jun	Jul	Aug	Sep
<i>Pinus contorta</i>	86	−0.34	−0.22	−0.31	−0.24			−0.35	−0.36		−0.21
Elevation < 2600 m	38	−0.35	−0.22	−0.30	−0.24			−0.34	−0.34		
Elevation > 2600 m	48	−0.29	−0.20	−0.30	−0.21			−0.33	−0.34		−0.21
TWI: low	29	−0.30	−0.22	−0.32	−0.24			−0.35	−0.36		−0.20
TWI: high	21	−0.31	−0.25	−0.29		0.18		−0.23	−0.36		−0.23
Aspect: north	23	−0.34	−0.23	−0.28	−0.21			−0.32	−0.33		
Aspect: south	19	−0.33		−0.33	−0.23			−0.32	−0.41		
<i>Pinus ponderosa</i>	70	−0.33		−0.31			−0.22	−0.38	−0.40		
Elevation < 2600 m	29			−0.30				−0.28	−0.26	0.22	
Elevation > 2600 m	41	−0.33		−0.30				−0.38	−0.39		
TWI: low	25	−0.36		−0.29			−0.23	−0.35	−0.41		
TWI: high	20	−0.20		−0.26				−0.28	−0.30		
Aspect: south	61	−0.36		−0.32	−0.17		−0.22	−0.39	−0.41		

how species-specific growth (RWI) patterns respond to monthly climate conditions (Tables 1 and 2). While magnitude of correlation coefficients presented in this study may seem low, values demonstrated in this study (Tables 1 and 2) are comparable to those found in identical analyses of other studies at similar and closely located sites (Villalba et al. 1994, Fekedulegn et al. 2003, Adams and Kolb 2005). In comparison to *P. contorta* distributed across all topographic positions in the catchment, *P. contorta* growth in high TWI areas did not decrease with high maximum temperatures in previous November, but, instead, increased with high March maximum temperatures. Similarly, *P. ponderosa* growing in high TWI areas did not show increased growth with high May precipitation or decreased growth with high May maximum temperatures. In topographically wetter areas, both species had fewer negative correlations with warm temperatures and *P. ponderosa* was less responsive to precipitation. The slight temporal differences in the effect of TWI on tree growth for each species was not caused by variable TWI ranges of each species as the TWI ranges occupied by *P. contorta* and *P. ponderosa* were 2.34–5.03 (mean: 3.77) and 2.34–5.09 (mean: 3.84), respectively.

Annual growth modeled by climate and topography.—Linear mixed-effects model analyses found that climate and topographic indices are significant predictors of annual growth (BAI) for both species. While some predictor variables included in the three best fit LMEMs for each species were not significant, they were included in the models to minimize the AIC and improve model fit. The best fit LMEM of *P. contorta* growth included growing season PDSI and TWI as fixed effects predictors of annual growth with UAA and elevation also included as predictors in the second and third best fit LMEMs (Appendix: Table A3). These three best fit *P. contorta* LMEMs predicted increased *P. contorta* growth in years of higher PDSI ($p < 0.01$) and in catchment positions with high TWI values ($p = 0.08$), low UAA values ($p = 0.09$), and at higher elevations ($p = 0.22$). The best fit LMEM of *P. ponderosa* growth included growing season PDSI, growing season ISR, and slope as significant fixed effect predictor variables ($p \leq 0.02$) with UAA and elevation also included as predictors in the second and third best fit LMEMs (Appendix:

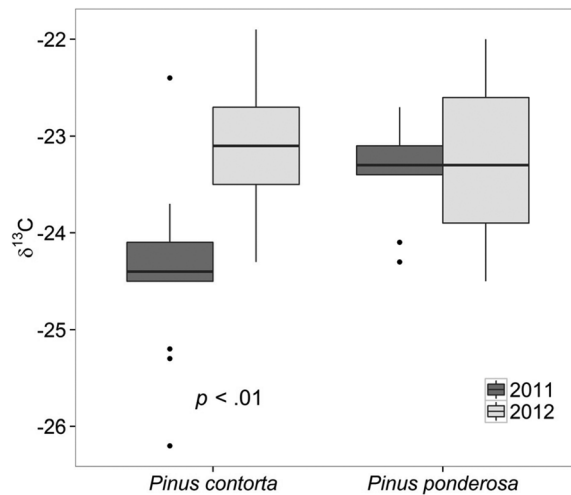


Fig. 4. Foliar $\delta^{13}\text{C}$ in non-drought (2011) and drought (2012) years for *Pinus contorta* and *P. ponderosa*.

Table A2). The top three best-fit *P. ponderosa* LMEMs predicted increased *P. ponderosa* growth in years with higher growing season PDSI ($p < 0.01$) and in catchment positions with high growing season ISR values ($p < 0.01$), high slope angles ($p = 0.02$), high UAA values ($p = 0.72$), and at lower elevations ($p = 0.20$). Conditional R^2 values for *P. contorta* and *P. ponderosa* were 0.64 and 0.71, respectively, indicating that climate and topography can explain much of the variability in annual tree growth.

Intrinsic water use efficiency response to climate and topography.—Foliar $\delta^{13}\text{C}$ response to drought differed between the two species. *P. contorta* foliage was more enriched in $\delta^{13}\text{C}$ in 2012 in comparison to 2011, indicating an increase in iWUE during drought ($p < 0.01$; Fig. 4). *P. ponderosa* foliar $\delta^{13}\text{C}$ did not change between 2011 and 2012, indicating no change in iWUE in response to drought (Fig. 4). Foliar N composition did not change from 2011 to 2012 in either *P. contorta* (2011 = $1.06\% \pm 0.10\%$, 2012 = $1.07\% \pm 0.12\%$; $p = 0.75$) or *P. ponderosa* (2011 = $1.17\% \pm 0.19\%$, 2012 = $1.09\% \pm 0.11\%$; $p = 0.09$). Foliar N composition also did not vary between species ($p = 0.15$). Repeated measures ANOVA analyses indicated no topographic effects on iWUE or in the response of iWUE to drought conditions.

DISCUSSION

How does P. contorta and P. ponderosa growth respond to climate?

P. contorta and *P. ponderosa* exhibit clear radial growth responses to climate conditions. Similar to previous research, growth of both species decreased in response to low precipitation, high temperatures, and drought conditions on annual to monthly scales (Villalba et al. 1994, Adams and Kolb 2004). We hypothesize that measured negative growth relationships with high spring (*P. ponderosa*) and fall (*P. contorta*) temperatures may be related to an extended growing season. These high temperature patterns may lengthen the growing season and increase water stress (in the absence of significant summer rainfall) ultimately decreasing total carbon assimilated and/or increasing use of stored carbon (Oberhuber et al. 2011, Brzostek et al. 2014). Hu et al. (2010) found that longer growing seasons decreased forest productivity in Colorado Front Range subalpine forests due to increased water stress. Similar to Hu et al. (2010), we find that high temperatures at the start or end of the growing season decrease total annual growth accumulated. While growth responses to climate are similar between species for several months of the year, *P. contorta* and *P. ponderosa* show variable sensitivity to precipitation and temperature in different seasons.

P. contorta is sensitive to fall climate conditions (both in the current year and in the previous year) with decreased growth in years having high fall maximum temperatures. This may be due to reduction of stored carbon during warm falls, making stored carbon less available for growth at the start of the following year. Remobilization of stored carbon toward early spring radial growth is common in deciduous species (e.g., Skomarkova et al. 2006, Zweifel et al. 2006), and has also been observed, albeit less often, in conifers (Hansen and Beck 1990, Kagawa et al. 2006, Oberhuber et al. 2011). Kagawa et al. (2006) and Hansen and Beck (1990) found that a portion of early wood formation relied on carbon stores in larch stems and Scots pine branches. Increased temperatures, increased vapor pressure deficit, and drought stress, however, can reduce total carbon assimilation (Ruehr et al. 2009) and increase carbon

allocation to maintenance respiration (Ryan 1991) and belowground biomass (Meier and Leuschner 2008), thereby decreasing carbon available for radial growth or storage. With decreased total carbon assimilation, decreased allocation to carbon reserves, or depletion of reserves in response to high temperatures, less carbon may be available for growth at the start of the following growing season.

In contrast to *P. contorta*, *P. ponderosa* is sensitive to spring climate conditions, responding to precipitation and temperature conditions in April and May. In our study catchment, *P. ponderosa* is more abundant on south aspects, where high incoming solar radiation and warmer temperatures make snowpack transient throughout the winter. Intermittent snowpack at the start of the growing season causes south aspect soils to be dry throughout spring except during short periods directly following precipitation events (Hinckley et al. 2012). In contrast, north aspects with a consistent snowpack have higher soil moisture content than south aspects and have more efficient soil moisture storage with elevated moisture conditions enduring through late spring (Hinckley et al. 2012). Decreased spring water availability makes south aspect *P. ponderosa* growth more sensitive to spring precipitation events and temperature conditions. In areas of high TWI where water is more available, however, *P. ponderosa* is less sensitive to May precipitation or high maximum temperatures.

We find that fine scale topographic variability within the catchment affects spatial patterns of tree growth and tree growth response to climate. Topography drives water and energy differences across complex terrain, creating variable topoclimatic conditions along topographic gradients which encompass varying levels of air temperature, evapotranspiration, soil moisture, and vegetation patterns on the landscape (Bennie et al. 2008). Topoclimatic departures from local climate conditions in temperature and soil moisture may provide microrefugia habitats for vegetation or may stress species beyond their limits (Ashcroft et al. 2009, Dobrowski 2011). Topoclimate explained a significant portion of the variability in tree growth across our study catchment for both *P. contorta* and *P. ponderosa*. Our species-specific statistical models create a conceptual framework regarding topographic

areas that may be more suitable for tree growth under drought stress conditions. The models predict increased *P. contorta* growth in potentially wetter areas with higher TWI and increased *P. ponderosa* growth in areas receiving higher ISR, suggesting that these are topographic positions where *P. contorta* and *P. ponderosa* may persist longer under predicted climate change. At its lower elevation range limit, *P. contorta* is near its water limitation and upper temperature threshold (Peet 1981, Stohlgren and Bachand 1997). Therefore, wetter areas which converge on or near the stream and are subject to cold air drainage (Pypker et al. 2007) may provide microrefugia habitat for *P. contorta*. At its upper elevation range limit, *P. ponderosa* is near its low temperature threshold and may respond positively to higher temperatures associated with increases in light availability.

How does intrinsic iWUE respond to drought?

Intrinsic water use efficiency did not vary by topographic position in the catchment; however, we found strong species-specific iWUE differences in response to drought conditions. More enriched foliar $\delta^{13}\text{C}$ in the drought year (2012) compared with the non-drought year (2011) indicated increased *P. contorta* iWUE in response to drought. Smit and van den Driessche (1992) recorded similar findings for *P. contorta* with increased iWUE in lower soil moisture settings. *P. ponderosa*, however, did not show any change in $\delta^{13}\text{C}$ in response to drought conditions. This was unexpected as *P. ponderosa* is known to exhibit stomatal closure and increased iWUE to minimize water loss during water stress (Adams and Kolb 2004). However, in a northern Arizona study, Adams and Kolb (2004) also found that *P. ponderosa* iWUE decreased with elevation, and suggested this was due to increased moisture availability at higher elevations. Considering our study site is higher in elevation and higher in latitude than the Arizona site (2000–2600 m elevation), we might expect greater soil moisture at our catchment resulting in less drought-induced increases in iWUE in *P. ponderosa*. Other mechanisms may also explain the lack of $\delta^{13}\text{C}$ response. While not significantly different, foliar N composition was slightly higher in 2011 than in 2012 ($p = 0.09$); increases in foliar N may increase photosynthetic capacity and foliar

iWUE (Green and Mitchell 1992, Jassal et al. 2010). However, in a *P. ponderosa* nitrogen fertilization and herbicide treatment study where foliar N composition values ranged from 0.9% to 1.3% across treatments, there was no difference in actual WUE between treatments (Powers and Reynolds 1999); as the foliar N composition values in our study fall within the same range for the same species, it is unlikely that higher 2011 foliar N greatly increased iWUE. *P. ponderosa* can also use deeper water sources than lodgepole pine and redistribute water in the soil profile to avoid water stress during water-limited conditions (Brooks et al. 2002). Access to deep soil water would decrease water stress and allow this species to maintain higher rates of stomatal conductance and low iWUE during short-term drought. Alternatively, the lack of change in *P. ponderosa* foliar $\delta^{13}\text{C}$ could also be due to 2012 foliage being formed from carbon stores from previous years. Both Kagawa et al. (2006) and Offermann et al. (2011) found that stored carbohydrates assimilated in previous years are used in current year foliage formation. This process may be more pronounced during drought and pine species may rely heavily on carbon reserves during drought seasons for radial growth (Oberhuber et al. 2011). Our study lacks the fine temporal patterns of $\delta^{13}\text{C}$ during needle formation or stomatal conductance to determine the exact processes that may be at play at our site.

Implications for semi-arid forest response to future climate

Examining tree–climate relationships in complex terrain of semi-arid systems increases our understanding of the complex relationships between ecology, topography, and hydrology and allows us to better understand how these systems may respond to future climate. The negative growth response of both *P. contorta* and *P. ponderosa* in warm and dry conditions suggests decreased growth of these species in a warmer, drier future. Future increases in temperature will not only have a first-order impact on growth, but will also affect timing and magnitude of snow melt (Barnett et al. 2005), further limiting water availability to vegetation. Earlier snowmelt of shallower snowpacks will decrease water availability (Barnett et al. 2005) in spring and summer

months: months that climate has significant impacts on growth. In addition to impacts on growth, increased water limitation will also impact tree physiological processes such as stomatal aperture and iWUE especially in semi-arid ecosystems where enhanced climate sensitivity may exacerbate forest response to climate (Liu et al. 2013). The stomatal closure in *P. contorta* during drought conditions indicates that future increases in frequency and extremity of drought events will increase tree stress, possibly leading to very low carbon assimilation and ultimately mortality. While this response was only observed for *P. contorta*, we expect that *P. ponderosa* may have a similar response under more prolonged drought conditions. Reduction in *P. ponderosa* stomatal conductance in response to intense drought has been measured (Koepke and Kolb 2013). Although topoclimate may provide pockets of favorable conditions for mature trees, seedlings show increased sensitivity to climate conditions in comparison to mature stands (Hogg and Schwarz 1997). After a disturbance/mortality event, regeneration patterns may not match the vegetation distribution and species composition that existed pre-disturbance in a warmer, drier future. Therefore, regeneration dynamics must be considered in predictions of forest response to future climate conditions.

CONCLUSION

We measured tree growth and iWUE responses to climate, as well as the influence of topography on growth–climate relationships. We found that tree growth is decreased and iWUE is increased (*P. contorta* only) in drought conditions, and that fine scale spatial variability in topoclimate has significant species-specific effects on tree growth patterns. Our results suggest that semi-arid forests may experience decreases in tree growth and increases in tree iWUE in a warmer, drier climate and topoclimate can weaken climate effects on tree function. In semi-arid ecosystems, species-specific responses to drought and topographic position will play a key role in determining future forest composition and distribution.

ACKNOWLEDGMENTS

We thank Tom Veblen and Dan Doak and two anonymous reviewers for comments on an earlier version of this manuscript. Support was provided by the U.S. Department of Energy's Terrestrial Ecosystem Science Program (DOE Award #DE-SC0006968). The Boulder Creek CZO is supported by the National Science Foundation (NSF EAR-0724960). Any opinions, findings, and conclusions or recommendations expressed do not necessarily reflect the views of the DOE or NSF.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Study site forest characteristics as measured from forest plots. Measures of percent (%) density of species, DBH, stand density, and basal area are means across the respective region of the study area.

Basin and aspect	<i>Pinus contorta</i> density (%)	<i>Pinus ponderosa</i> density (%)	DBH (cm)	Stand density (trees/100 m ²)	Basal area (m ² /100 m ²)	Forest plots	Tree cores
Lower Basin	84	10	20.1	19.4	0.43	60	95
Aspect: N	94	1	13.6	31.7	0.50	30	36
Aspect: S	34	62	28.0	6.1	0.32	25	44
Upper Basin	82	16	17.7	17.5	0.46	15	61
Aspect: N	85	14	14.1	23.7	0.54	6	19
Aspect: S	76	19	20.2	13.0	0.41	8	42

Table A2. Descriptive statistics of tree-ring chronologies.

Chronology	Record†	No. trees	SI‡	MRW§	Standard chronology			Residual chronology		
					σ¶	φ#	EPS	σ¶	φ#	EPS
<i>Pinus contorta</i>	1880–2012	86	0.57	0.67	0.38	0.82	0.96	0.41	−0.026	0.97
Elevation < 2600 m	1892–2012	38	0.58	0.61	0.32	0.80	0.92	0.40	−0.026	0.93
Elevation > 2600 m	1882–2012	48	0.58	0.72	0.43	0.84	0.95	0.41	−0.027	0.96
TWI: Low	1892–2012	29	0.56	0.63	0.38	0.82	0.88	0.39	−0.036	0.91
TWI: High	1903–2012	21	0.52	0.67	0.37	0.80	0.90	0.44	−0.014	0.89
Aspect: North	1897–2011	23	0.55	0.63	0.38	0.82	0.91	0.39	−0.030	0.91
Aspect: South	1928–2011	19	0.65	0.76	0.42	0.82	0.90	0.40	−0.030	0.91
<i>Pinus ponderosa</i>	1873–2013	70	0.62	1.14	0.60	0.74	0.95	0.42	0.003	0.96
Elevation < 2600 m	1925–2011	29	0.62	1.19	0.60	0.69	0.90	0.42	0.003	0.91
Elevation > 2600 m	1875–2013	41	0.62	1.11	0.60	0.77	0.92	0.42	0.003	0.94
TWI: Low	1899–2011	25	0.58	1.06	0.57	0.74	0.86	0.43	0.012	0.90
TWI: High	1908–2011	20	0.57	1.08	0.57	0.76	0.84	0.41	−0.010	0.87
Aspect: South	1878–2013	61	0.63	1.19	0.62	0.72	0.95	0.43	0.003	0.96

† Record is the record period of the chronology which contains ≥ 15 tree-ring series.

‡ Series intercorrelation: a measure of the strength of the common signal present among all series in the chronology.

§ Mean ring width (mm).

¶ Standard deviation (σ): σ is a more reliable and robust descriptive statistic of tree-ring chronologies than mean sensitivity (ζ) (Bunn et al. 2013).

First-order autocorrelation (φ): the autocorrelation coefficient (ranging from −1 to 1) of the chronology at a lag of 1 year. φ is a more reliable and robust descriptive statistic of tree-ring chronologies than ζ (Bunn et al. 2013).

|| Expressed population signal: the correlation between the mean of sampled chronologies and the population as defined by Wigley et al. (1984).

Table A3. Summary of the linear mixed-effects models fit to explain the variability in annual BAI (transformed to a power of 0.33) for *Pinus contorta* and *P. ponderosa*.

Species	ΔAIC	ΔBIC	Conditional R^2	Marginal R^2	Fixed effect	Coefficients	p
<i>P. contorta</i>	0	0	0.63	0.06	PDSI	0.015	<0.01
					TWI	0.085	0.08
	0.21	0.21	0.63	0.06	PDSI	0.015	<0.01
					UAA	−0.001	0.09
<i>P. ponderosa</i>	0.45	7.41	0.63	0.07	PDSI	0.015	<0.01
					Elevation	4.6e−4	0.22
					TWI	0.076	0.12
<i>P. ponderosa</i>	0	0	0.68	0.16	PDSI	0.028	<0.01
					ISR	5.4e−6	<0.01
					Slope	0.019	0.02
	0.24	7	0.68	0.18	PDSI	0.028	<0.01
					Elevation	−9.8e−4	0.20
					ISR	6.1e−6	<0.01
					Slope	0.016	0.06
	1.86	8.62	0.68	0.17	PDSI	0.028	<0.01
					ISR	5.3e−6	<0.01
					Slope	0.018	0.03
					UAA	9.7e−5	0.72

Notes: Fixed effects used in models include growing season PDSI (PDSI), water year precipitation (cm), growing season maximum temperature (°C), topographic wetness index (TWI), growing season incoming solar radiation (ISR) (W/m²), elevation (m), slope (°), and upslope contributing area (UAA) (m²). Models shown here were the best three models for each species as determined by minimizing the Akaike information criterion (AIC). Marginal R^2 is based on only fixed effects. Conditional R^2 is based on fixed plus random effects.

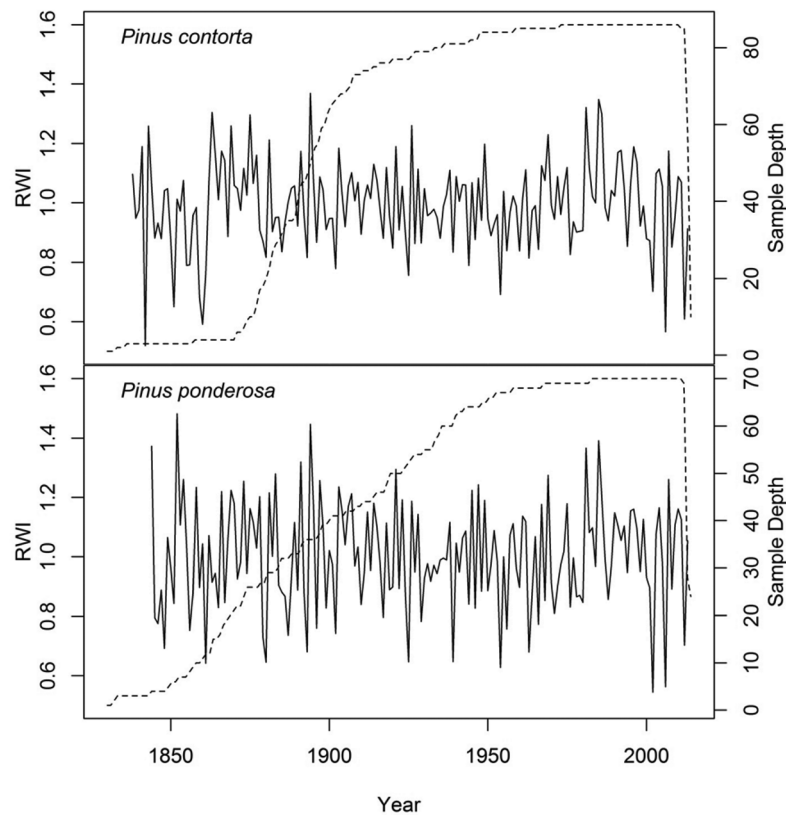


Fig. A1. Tree-ring chronologies of *Pinus contorta* and *P. ponderosa* with sample depth (number of cores). Solid line is RWI; dashed line indicates sample depth. Time period of *P. contorta* chronology is 1833–2013. Time period of *P. ponderosa* chronology is 1842–2013.

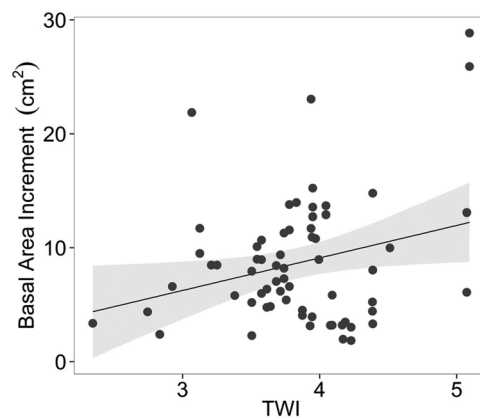


Fig. A2. *Pinus ponderosa* mean basal area increment as a function of TWI (adjusted $R^2 = 0.06$; $p = 0.03$) ($n = 65$). Basal area increment values were averaged for all measured tree rings; earliest and latest years included were 1842 and 2013, respectively.