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LIMITED EVIDENCE FOR CO2-RELATED GROWTH ENHANCEMENT IN NORTHERN ROCKY MOUNTAIN PINUS CONTORTA POPULATIONS: TRENDS IN GROWTH AND INTRINSIC WATER-USE EFFICIENCY ACROSS CLIMATE GRADIENTS

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LIMITED EVIDENCE FOR CO_2-RELATED GROWTH ENHANCEMENT IN NORTHERN ROCKY MOUNTAIN *PINUS CONTORTA* POPULATIONS: TRENDS IN GROWTH AND INTRINSIC WATER-USE EFFICIENCY ACROSS CLIMATE GRADIENTS

By

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ABSTRACT

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Limited evidence for CO_2-related growth enhancement in northern rocky mountain *Pinus contorta* populations: Trends in growth and intrinsic water-use efficiency across climate gradients

Chairperson: Dr. Ashley Ballantyne

Forests sequester large amounts of carbon annually; however, the degree to which enhanced forest productivity is due to more conducive climate or CO_2 fertilization remains uncertain. Increasing atmospheric CO_2 may enhance photosynthesis and/or decrease stomatal conductance thereby enhancing intrinsic water use efficiency (iWUE). While increasing iWUE has been observed in most trees globally, this increase does not necessarily translate into greater growth. This study aims to evaluate whether responses of radial growth and iWUE to increasing CO_2 vary across climatic gradients. To investigate interactions between climate and CO_2 and their impacts on tree physiology and growth, I used an environmental gradient approach as a natural global change experiment. I combined dendrochronology with carbon isotope analysis ($\delta^{13}C$) to assess the covariation of basal area increment (BAI) and iWUE for *Pinus contorta* over time. Stands were sampled at 18 sites spanning two climatically distinct 800 m elevation transects encompassing the majority of *P. contorta*'s regional elevational range. Trends in BAI and iWUE were analyzed for the past 65 years, and correlations with monthly temperature, precipitation and vapor pressure deficit (VPD) were assessed. Increases in iWUE were observed across all sites; however, concurrent BAI increases were only observed at the lowest elevation of the climatically warmer transect. All other sites experienced decreased or constant growth over the study period. The climatically warmer transect exhibited the strongest iWUE response, with the greatest increases (30-42%) observed at the low and mid elevations. In addition to being driven by rising CO_2, strong increases in iWUE appear to be driven by long-term increases in summer VPD. Correlations between climate variables and growth indicate that late summer climate of the previous year is important for growth across sites. These results indicate that because late summer climate is a strong driver of *P. contorta* growth, greater increases in iWUE observed at low elevations of the warmer transect may effectively extend the growing season by ameliorating some of the negative effects of summer drought on growth.

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INTRODUCTION

Forested ecosystems sequester large amounts of carbon annually and are integral in helping to mitigate increases in global atmospheric CO_2 concentrations (Bonan, 2008, Pan *et al.*, 2011). The degree to which rising atmospheric CO_2 concentrations are offset by forests is in part contingent on the stimulation of tree growth by this increase in CO_2. Increased atmospheric CO_2 can enhance photosynthesis (A) and/or decrease stomatal conductance (g_s), thereby increasing intrinsic water use efficiency (iWUE ≈ A/g_s) (Camarero *et al.*, 2015, Feng, 1999, McCarroll & Loader, 2004). Greater iWUE may indirectly increase growth by prolonging the growing season in moisture-limited environments, while elevated rates of photosynthesis may directly increase growth at the leaf and stand level (Ainsworth & Rogers, 2007, Keenan *et al.*, 2013, Morgan *et al.*, 2004, Soulé & Knapp, 2013).

Despite a nearly ubiquitous increase in iWUE over time (Feng, 1999), tree radial growth (henceforth, growth) responses to concomitant increases in CO_2 are not unequivocally positive (Andreu-Hayles *et al.*, 2011, Gómez-Guerrero *et al.*, 2013, Nock *et al.*, 2011, Tognetti *et al.*, 2000, Wu *et al.*, 2015). The extent of growth response to rising CO_2 is likely site-specific (Camarero *et al.*, 2015, Lévesque *et al.*, 2014, Peñuelas *et al.*, 2008). Experimental evidence from free-air CO_2 enrichment (FACE) sites suggests that the positive effect of CO_2 on growth may depend in part on plant age, and nutrient and water status (Ellsworth *et al.*, 2012, Norby *et al.*, 2010). Therefore, if variables other than CO_2 are more limiting to plant growth, an increase in CO_2 would likely have no direct fertilization effect on growth (Körner, 2000, Körner, 2003). Further investigation of site-specific growth trends in response to recent increases in CO_2 is therefore necessary in order to better understand and accurately model regional variability in forest-growth dynamics in response to changes in CO_2.

While plants typically show a positive growth response to increasing atmospheric CO_2 concentrations in experimental settings, concomitant changes in regional temperature and precipitation may modify the fertilization effect of CO_2. Where cold temperatures limit tree growth, rising CO_2 and corresponding temperature increases are expected to stimulate growth (Giammarchi *et al.*, 2017, Huang *et al.*, 2017, Salzer *et al.*, 2009, Silva *et al.*, 2016). In these situations, higher iWUE is likely a result of a strong increase in assimilation, rather than a decrease in stomatal conductance. Alternatively, at sites where moisture availability limits growth, increasing temperatures and evaporative demand may limit the potential for a fertilization effect of CO_2 on growth (McLane *et al.*, 2011). However, increases in iWUE driven by a decline in stomatal conductance in response to enhanced atmospheric CO_2, may help ameliorate moisture limiting effects, having an indirect influence on growth (Fatichi *et al.*, 2016, Norby *et al.*, 1999, Wall *et al.*, 2001, Wayne *et al.*, 1998). Temperature tends to vary with elevation (Körner, 2007), and consequently, in regions where seasonal snowfall occurs, higher elevations tend to retain soil moisture longer into the growing season. Elevation gradients therefore provide a natural laboratory in which to investigate the effects of climate and plant water status on growth and to better understand site-specific growth trends for species with broad ranges (McDowell *et al.*, 2010). Relatively few studies, however, employ elevation as a tool to investigate long-term variability in the influence of climate and water availability on growth and iWUE responses to atmospheric CO_2 concentration.

Measurements of stable carbon isotope ratios ($\delta^{13}C$) and basal area increment (BAI) from tree rings have been used extensively to understand changes in iWUE and tree growth, respectively, in response to increasing CO_2 (Lévesque *et al.*, 2014, Linares *et al.*, 2009, Soulé & Knapp, 2015, Tognetti *et al.*, 2014). With baseline knowledge of changes in atmospheric CO_2 and its carbon isotopic composition ($\delta^{13}C_{atm}$), iWUE can be approximated by measuring carbon isotopes in tree rings (Farquhar *et al.*, 1982, Francy & Farquhar, 1982). Investigation of elevational variability in past trends of radial growth and iWUE may provide insight into how climate and water stress enhance or limit the effects of rising CO_2 on future growth.

The northern Rocky Mountains of the United States provide a useful region in which to examine the extent that growth response to CO_2 is affected by concurrent climate changes. In this region growing season length and vapor pressure deficit (VPD) have significantly increased, and snowpack decreased in the past century (Pederson *et al.*, 2010), having likely consequences for both tree growth (Lendzion & Leuschner, 2008, Restaino *et al.*, 2016) and water use efficiency (Andreu-Hayles *et al.*, 2011). Previous studies of regional variability of tree growth and iWUE response to rising CO_2 in the northern Rocky Mountains have been mainly limited to low-elevation treeline species (e.g. *Pinus ponderosa*, *Pseudotsuga menziesii*), and have shown substantial interspecific variability in trends and conflicting results in terms of iWUE response to increasing CO_2 (Knapp & Soulé, 2011, Marshall & Monserud, 1996, Soulé & Knapp, 2015). Subalpine conifers with large elevational ranges such as lodgepole pine (*Pinus contorta* var. *latifolia*) have been largely absent from these studies, despite future climate change being expected to substantially impact lodgepole pine's range in this region (Coops & Waring, 2011, Hansen & Phillips, 2015).

In Montana, lodgepole pine spans an elevational range from approximately 800-2800 m a.s.l. and occurs on both the western (windward) and eastern (leeward) sides of the continental divide (USDA Forest Service 2012). Climate differs markedly across this range with the windward side generally experiencing less extreme seasonal temperature variability, wetter conditions and lower adiabatic lapse rates. In contrast, the leeward side is characterized by more extreme temperatures, drier conditions and higher lapse rates (Sweet et al. 2015, Z. Holden, pers. comm.). These climatic dynamics drive regional patterns of water balance that have important consequences for ecosystem assemblage and function. A comparison of BAI and iWUE trends across lodgepole pine's elevational and east-west range within Montana provides useful data for investigating the impacts of climate and plant water status on growth response to rising atmospheric CO_2, and for improving our understanding of future growth and carbon uptake potential for this economically and ecologically important species.

In this study, a dendrochronological approach is used to assess how lodgepole pine growth has varied temporally across climatic gradients, and I aim to understand whether changes in climate and atmospheric CO_2 have affected tree growth differently across sites. This study explores whether certain climatic conditions are more conducive to a positive relationship between iWUE and BAI. Based on known climatic variability across sites and previous studies that also employ climatic gradient approaches (Peñuelas *et al.*, 2008, Silva & Anand, 2013, Wu *et al.*, 2015), I hypothesize that (i) iWUE increases will be greatest at climatically drier sites, responding to both rising temperatures and changes in atmospheric CO_2, and (ii) increases in iWUE will correspond to long-term growth increases only at the highest elevation sites where increasing atmospheric CO_2 and temperature are more likely to act in concert to enhance tree growth over time.

MATERIALS AND METHODS

Study sites

Lodgepole pine is a widespread subalpine conifer that occurs throughout western Canada and extends south through the northern and central Rocky Mountains of the United States across a wide elevational range (Lotan & Critchfield, 1990). In additional to a broad elevational range, lodgepole pine experiences a range of climatic conditions driven by physical dynamics associated with the Continental Divide. Stands for this study occur across two elevational transects each spanning approximately 800 m, and encompass the majority of lodgepole pine's elevational range in the northern Rocky Mountains of the United States. Each elevational transect is comprised of nine plots occurring over three distinct elevational bands. The west transect occurs in Lolo National Forest in the Lolo Creek drainage of the Bitterroot mountains on the west side of the Continental Divide, while the east transect is located in the Beaverhead-Deerlodge National Forest in the Bolder River drainage of the Boulder mountains on the east side of the Continental Divide. Soils across all sites originate from granitic batholith parent materials (NRCS, 2007). Stands in the west transect range from 1290 to 2130 m, whereas stands in the east transect range from 1830 to 2510 m (Table 1). Lodgepole pine typically co-occurs with *Pinus ponderosa* and *Pseudotsuga menziesii* at low elevations, *P. ponderosa, P. menziesii*, and *Larix occidentalis* at mid elevations, and *Pinus albicaulis*, *Abies lasiocarpa*, and *Picea engelmanii* at high elevations in this region. Understory is generally limited, with sparse grasses at low elevations and primarily *Vaccinium scoparium* at mid and high elevations. Initial transect and site selection was opportunistic and based on a combination of lodgepole pine presence and dominance or co-dominance, similar edaphic conditions, slope, aspect, stand density, age, level of disturbance, and similar canopy cover in order to ensure constant ambient CO_2 across sites (Hultine & Marshall, 2000). There was a minimum of 100 m between plots within the same elevational band so as to limit spatial autocorrelation. The majority of lodgepole pine-dominant stands within the region are even-aged, fire-regenerated stands, and are thus similar in structure (Anderson, 2003).

Climate data

While the study region as a whole experiences a semi-arid climate, forests on the west side of the Continental Divide generally experience a warmer, wetter climatic regime than sites on the east side of the Divide (Sweet *et al.*, 2015). Lapse rates additionally drive variability in temperature across elevations, with higher elevations having cooler temperatures that result in higher snowfall and later seasonal snowmelt (Minder *et al.*, 2010). In order to quantify lapse rates and their variability from west to east across the Continental Divide, temperature loggers (LogTag Recorders, Auckland, New Zealand) were installed in each plot for the 2016 growing season (June-September). Data loggers also recorded relative humidity, and these data were used in conjunction with temperature data to calculate vapor pressure deficit (VPD) as part of an assessment in variability in potential for water stress across sites (Buck, 1981). Long-term climate data corresponding to each transect were obtained from the regional meteorological station closest to each transect with records dating back to 1950 (NCDC-CDO, https://www.ncdc.noaa.gov/cdo-web/). Monthly data for the west transect were obtained from the Missoula International Airport, MT station at an elevation of 973 m, while data for the east transect were gathered from the Boulder, MT station at an elevation of 1495 m. Climate stations were within 20-45 km of study sites. Vapor pressure deficit was calculated using temperature and relative humidity (RH) data from climate stations. Relative humidity data were not available from the Boulder, MT station, so values from the Helena, MT station (approx. 40 km north) were instead used. Climatic water deficit (CWD), a measure of available water for plants, is a biologically relevant climate variable that incorporates both precipitation and temperature (Dobrowski *et al.*, 2013). Gridded, 800 m resolution, data were additionally obtained for further analysis of how this climate variable influences elevational variability in relationships between BAI and iWUE, and more generally, how this climate variable differs across both transects and elevations.

Tree-ring sampling and radial growth

Within each 10 m circular plot, increment cores were obtained from the 15 most dominant trees. Dominance was established by assessing stem diameter, height, and visual health. Two cores per tree were sampled using a 5 mm increment borer at approximately 1.4 m height. Cores were sanded, master chronologies were developed for each elevational band, and cores were crossdated and measured using standard dendrochronological techniques (Stokes & Smiley, 1968). Ring width measurements were obtained using the program CooRecorder (Larsson, 2014). Crossdating accuracy was quantitatively checked with COFECHA (Holmes, 1983) for each elevation-specific chronology of the two transects. Individual cores that correlated poorly with master chronologies were eliminated from further analyses, with no more than 5 cores eliminated from each site.

Radial growth was determined by calculating basal area increment (BAI). By converting ring widths to BAI the decrease in ring width that occurs with increasing tree size can be overcome (Biondi & Qeadan, 2008). BAI was calculated via the following formula:

$BAI = \pi(r^2_t - r^2_{t-1})$ *(Eq. 1)*

where r_t is the tree radius at the year (t) of tree ring formation, and r_{t-1} is the tree radius at year t-1. BAI was calculated for each core using the 'dplR' package in R (Bunn, 2008), and then averaged by tree (n=429 cores, 240 trees). In order to calculate BAI, tree radius at each annual growth ring must be determined. When increment cores did not include pith, distance from the inner-most dated ring to the pith was determined based on growth in the earliest observed years and curvature of the earliest observable rings (Larsson, 2014). Basal area increment chronologies for the west transect spanned from 1950-2015, while the east transect encompassed 1950-2010. The east transect was cut off at 2010 due to a widespread regional mountain pine beetle (*Dendroctonus ponderosae*) outbreak that began in 2009 and resulted in a strong growth release the following year (Gannon & Sontag, 2009). Complete BAI chronologies averaged 89.5 (± 9.9) years for the west transect and 113.0 (± 36.1) years for the east transect (Supplemental Figure 1). It is worth noting that trees from the high elevation plots of the east transect were generally approximately 50 years older than at the mid and low elevation plots.

Carbon isotope data and determination of iWUE

Intrinsic water use efficiency (iWUE) is representative of the ratio between photosynthetic assimilation (A) and stomatal conductance (g_s) and can be assessed through the carbon isotope ratio ($\delta^{13}C$) of tree rings. At each plot, two trees were selected for stable carbon isotope analysis that were the most site-dominant. Two increment cores (henceforth, isotope cores) per tree were taken 5-10 cm below the location of the radial growth cores from the same tree. The isotope cores were crossdated based on radial growth chronologies, then planed, and separated into 5-year segments using a scalpel. Five-year, plot-aggregated changes in isotopic composition were analyzed by pooling the 5-year segments for the four cores from each plot. The first 25 years of tree growth were excluded from analysis to remove a possible "juvenile effect" on carbon isotope signatures from respired CO_2 within the canopy during initial tree growth (McCarroll & Loader, 2004). Pooled samples were homogenized and coarsely milled with a 40 mesh Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) before processing to remove extractives. Samples were batch processed to lignin, cellulose and hemicellulose in commercial digestion pouches (ANKOM Technology, Boston, MA, USA) in order to remove the possible contribution of extractives such as resins, waxes and oils to $\delta^{13}C$ variability between the heartwood and the sapwood (Steven Leavitt, personal communication; Leavitt & Danzer, 1993). Processed samples were then ground to a fine powder and weighed prior to $\delta^{13}C$ analysis at Washington State University's Stable Isotope Core Laboratory (Pullman, WA, USA).

Results of isotopic analysis were combined with atmospheric $\delta^{13}C$ records to determine ^{13}C discrimination between atmospheric CO_2 and plant carbon ($\Delta^{13}C$), which accounts for the atmospheric decline in $\delta^{13}C$ due to fossil fuel emissions (Francey & Farquhar, 1982, McCarroll & Loader, 2004). Discrimination was determined from (Farquhar & Richards, 1984, Farquhar *et al.*, 1982):

$\Delta^{13}C = \frac{(\delta^{13}C_a - \delta^{13}C)}{\left(1+\frac{\delta^{13}C}{1000}\right)}$ *(Eq. 2)*

where $\delta^{13}C_a$ is the atmospheric carbon isotope signature and $\delta^{13}C$ is the signature of the wood. $\Delta^{13}C$ can also be related to the ratio of intercellular (c_i) to atmospheric (c_a) CO$_2$ by:

$\Delta^{13}C \approx a + (b - a)\frac{C_i}{Ca}$ *(Eq. 3)*

where a is the constant fractionation during diffusion through stomata (4.4‰) (O'Leary, 1981), and b is the fractionation during carboxylation by Rubisco and PEP carboxylase (approximately 27‰) (Farquhar & Richards, 1984). Values obtained from Equation 2 can be used in Equation 3 to solve for c_i. Atmospheric CO_2 values and its isotopic composition were obtained from published data (McCarroll & Loader, 2004, NOAA-ESRL, https://www.esrl.noaa.gov/gmd/dv/data/).

According to Fick's law [A = $g_c(c_a - c_i)$, where g_c = stomatal conductance for CO_2 and A = net assimilation], the ratio of c_i/c_a reflects the ratio of assimilation and stomatal conductance for CO_2. Because iWUE is the ratio of assimilation (A) to stomatal conductance for water vapor (g_w) and g_w = $1.6g_c$, the relationship between c_i/c_a (or p_i/p_a) and $\Delta^{13}C$ can be used to calculate iWUE:

iWUE $\approx (c_a - c_i)(\frac{1}{1.6})$ *(Eq. 4)*

In order to account for elevational differences in CO_2 partial pressures, c_a and c_i were converted to p_a and p_i in accordance with Hultine and Marshall (2000). p_a-p_i was used as a proxy of iWUE in this study as it constitutes the numerator in the elevation-corrected iWUE equation. The west transect isotope chronologies spanned from 1951-2015, while the east transect ranged from 1951-2010. The east transect isotope chronology was also cut off at 2010 to eliminate any possible isotopic effects resulting from the strong growth release corresponding to the regional mountain pine beetle outbreak.

Data analysis

Basal area increment, p_a-p_i, and monthly climate variable trends over time and their significance were assessed using Mann-Kendall trend analysis. Pearson's correlations were used to test the influence of monthly temperature (t_{min}, t_{max}), precipitation (prcp) and leaf-to-air vapor pressure deficit (VPD) on BAI. For growth-climate analyses both climate and BAI were detrended using a spline method in order to remove long-term changes and isolate interannual drivers of BAI variability (Bunn, 2008, Millar *et al.*, 2012). Maximum temperatures were used with BAI due to overall stronger correlations of the specific temperature variable. Lodgepole growth has previously been shown to respond particularly to climatic conditions of the previous growing season (Case & Peterson, 2007, Chhin *et al.*, 2008). Therefore, correlations were assessed from July of the previous growing season to September of the current growing season.

Pentadal values of BAI were additionally regressed with p_a-p_i to determine whether changes in p_a-p_i are associated with elevation-specific radial growth responses. Slopes of BAI~p_a-p_i regressions were further regressed with 30-year (1981-2010) normals of CWD in order to assess whether observed variability in BAI-p_a-p_i relationships may be a function of this biologically relevant climate variable. One-way ANOVA was used to assess differences across elevations and transects in percent change of BAI and p_a-p_i between the 1950s and 2000s. Post-hoc Tukey's HSD tests were used to further assess differences between elevations. To account for differences in site specific growth rates log-transformation of BAI was necessary to ensure normality of residuals across all sites. All analyses were assessed using a $p < 0.05$ level of significance.

Linear mixed effects modeling (LMM) was used to assess the relative importance of CO_2 and climate on elevational differences in p_a-p_i (Fernández-de-Uña *et al.*, 2016). LMMs with a random intercept associated with plot and a first-order autocorrelation structure were fit to model p_a-p_i as a function of atmospheric CO_2, precipitation, temperature and VPD. Growing season (June-Sept) averages were used for each variable as prior correlation analysis had shown the strongest influence of climate on p_a-p_i during growing season months. Long term trends were not removed from these data as I was interested in how long term environmental variability influences long term trends in p_a-p_i. The Akaike information criterion (AIC) was used to assess the strength of each fitted model. Lower AIC values indicate a better model fit, and when the difference in AIC between two models was equal to or greater than 2, the model with the lower AIC was considered superior (Burnham & Anderson, 2003). Variance inflation factors (VIFs) were also calculated for each model to assess collinearity. VIF values greater than 10 are indicative of high collinearity among response variables (Dormann *et al.*, 2013). Predictive power of the best-fit model for each transect-elevation combination was assessed by plotting observed versus predicted values. All analyses were conducted in R version 3.1.2 (R Core Team 2014). Mann-Kendall analyses were carried out in the package ‘Kendall’ (McLeod, 2005), and LMMs were fit using the package ‘nlme’ (Pinheiro *et al.*, 2014).

RESULTS

Site characteristics

As anticipated, temperatures, VPD, and CWD tended to decrease with elevation (Table 1). I expected that climate would be warmer and wetter across the west transect due to regional orographic effects of the Continental Divide. However, results from the 2016 growing season and 30-year CWD normals across our sites indicate that although temperatures may be warmer across the west transect, any greater precipitation received by the this transect does not translate into lower water deficits. On the contrary, the low elevation of the west transect had by far the greatest CWD of all sites, likely driven by the site’s lower elevation and subsequently higher temperatures (Table 1).

Average growing season t_{min} recorded from temperature loggers ranged from 3.7 (± 0.1) °C at the low elevations to 7.8 (± 1.4) °C at the high elevations for the west transect, reflecting a tendency for cool air pooling in valley bottoms to occur over night in this area during summer months. Average growing season t_{min} across the east transect was similar at low and high elevations. Average growing season t_{max} across the west transect ranged from 24.9 (± 0.2) °C at the low elevations to 17.9 (± 0.3) °C at the high elevations, reflecting a lapse rate of approximately 8.3 °C/1000 m. Average growing season t_{max} across the east transect ranged from 22.5 (± 0.3) °C at the low elevations to 17.6 (± 0.5) °C at the high elevations, reflecting a lapse rate of approximately 7.2 °C/1000 m (Table 1). Calculations of VPD based on RH and temperature data from plot data loggers indicated lower VPD at high elevations across both transects, as anticipated, indicating lower atmospheric demand for water than at the lower elevations. Average growing season VPD of the lowest elevation was slightly higher for the east transect than the west. Thirty-year CWD normals indicated decreasing water deficit with elevation, and variability of CWD across elevations was higher for the west transect (Table 1).

BAI and intrinsic water-use efficiency

Over the study period, BAI only increased significantly at the low elevation of the west transect ($\tau=0.37$, $p<0.001$; Figure 1). Significantly negative BAI trends were observed at all other elevations, with the exception of the low and high elevation of the east transect, which experienced negative, but non-significant changes in BAI over the period of study. Contrary to expectations, the strongest decrease in BAI was observed at the highest elevation ($\tau=-0.63$, $p<0.001$; Figure 1). Percent change of BAI over the study period varied across elevations for the west transect and the east transects ($F=46.12$, $p<0.001$; $F=4.36$, $p<0.05$, respectively). However, while differences between all elevations were observed at the west transect, differences were non-significant at the east (Figure 2b).

Temporal changes in isotopic discrimination and p_a-p_i varied across elevations and transects (Figure 1). Discrimination remained constant at all elevations except the low and mid elevations of the east transect, where it increased. As anticipated, p_a-p_i increased at all elevations of both transects (Figure 1). The low and mid elevations of the west transect experienced the greatest change in p_a-p_i with increases of 28.7 (±4.5) % and 25.0 (±0.8) %, respectively. Increases across all other sites ranged from 10.6 (±2.0) % to 14.9 (±3.1) %. Variability among elevational bands in p_a-p_i was greatest across the east transect. However, differences in percent change of p_a-p_i over the study period were far greater across elevations for the west transect (Figure 1; Figure 2a).

Correlations between p_a-p_i and BAI were strongest across the wester transect where they varied from strongly negative to positive from high to low elevations, respectively (Figure 3). The low elevations of the west transect were the singular example of a positive correlation between BAI and p_a-p_i ($r = 0.5$, $p < 0.01$). Across the east transect, all correlations between the two variables were negative, and were weakly, or non-significantly correlated (Figure 3). Further exploration revealed that variability in the relationships between the correlation of BAI and p_a-p_i and may in part be driven by environmental variability in climatic water deficit (Figure 4).

Effect of environmental variables on p_a-p_i

The response of p_a-p_i to environmental variables (i.e. climate, CO_2) differed across elevations and transects (Table 2). Linear mixed-effects models indicated that temporal changes in p_a-p_i were generally most responsive to changes in atmospheric CO_2 alone across elevations and transects, with a few exceptions. Models that considered growing season VPD as a fixed effect in addition to CO_2 were superior for modeling p_a-p_i response at the low and mid elevations of the west transect where temporal changes in p_a-p_i were greatest. Additionally, the best-fit model at the mid elevation of the east transect included growing season precipitation in addition to CO_2 (Table 2; Supplemental Figure 2).

Interannual climatic influences on BAI

Radial growth responds to different climate variables at different elevations. Interannual responses of BAI to monthly climate variables differed across both elevations and transects (Figure 5). In general, BAI across the west transect was more responsive to all climate variables than at the east transect. For the west transect, BAI was weakly negatively, but significantly, associated with higher summer t_{max} and lower precipitation of the current growing season at the mid elevation. Basal area increment for all elevations was strongly negatively associated with late summer (August, September) drought (i.e. higher t_{max}, lower precipitation, and higher VPD) of the previous growing season. Additionally, BAI at the highest elevation was negatively associated with November precipitation of the previous year and positively associated with April t_{max} of the current year. Across the east transect, BAI was strongly negatively associated with August t_{max} of the previous year at all elevations, and positively associated with December t_{max} of the previous year at the high elevation. Precipitation was generally positively associated with BAI across elevations, but particularly at the low and mid sites. Vapor pressure deficit for August of the previous year was weakly negatively associated with BAI (Figure 5).

Regional climatic changes

Long-term regional changes in climate varied between the two transects (Figure 6). The west transect has experienced regional increases in January, March, July and August t_{max}, increasing January, March, and June through September t_{min}, as well as increasing July VPD. However, the west transect has not experienced any significant changes in monthly precipitation. The east transect has also experienced increases in January and March t_{min} and t_{max}, as well as increasing July t_{min}, and increasing March VPD. In addition, December, January and March precipitation declined, and May precipitation increased over the study period for the east transect (Figure 6).

DISCUSSION

Consistent with other studies (Feng, 1999, Peñuelas *et al.*, 2011, Silva & Anand, 2013, Soulé & Knapp, 2015), I found that p_a-p_i (i.e. iWUE) increased over time at all sites (Figure 1). Increases were strongest at the warmest site with the highest CWD, in agreement with our first hypothesis. However, strong increases were also observed at the mid elevation of the same transect where CWD was substantially lower. I show that strong increases in p_a-p_i are likely a response of trees to concurrent increases in CO_2 and summer VPD. Despite increasing p_a-p_i over time across all sites, growth increases were only related to greater p_a-p_i at the lowest elevation of the west transect where temperature and CWD were greatest and increase of p_a-p_i most substantial (Table 1; Figure 3). Variability in the relationship between BAI and p_a-p_i is likely in part driven by environmental variability in water deficit, where a positive relationship between BAI and p_a-p_i is more likely where CWD is greater (Figure 4). I therefore posit that strong increases in p_a-p_i may be driven in part by a strong decrease in stomatal conductance, which may have indirect benefits for tree growth via an effective amelioration of late summer drought conditions and an extension of the growing season, particularly in seasonally water-limited systems and where water deficits are relatively high.

Widespread increases of p_a-p_i do not translate to greater growth

This study finds that increases in p_a-p_i (i.e. iWUE), driven in part by increasing atmospheric CO_2, are spatially variable and may only have the potential to benefit growth in limited situations. These results are consistent with previous studies demonstrating that increases in iWUE are highly site-specific and do not necessarily result in increased productivity (i.e. BAI) at the tree level (Andreu-Hayles *et al.*, 2011, Gómez-Guerrero *et al.*, 2013, Knapp & Soulé, 2011, Lévesque *et al.*, 2014, Linares *et al.*, 2009, Peñuelas *et al.*, 2011, Wu *et al.*, 2015). Growth declines despite increasing iWUE have also been observed for the arid and semi-arid systems of the Mediterranean (Andreu-Hayles *et al.*, 2011, Lévesque *et al.*, 2014), central Mexico (Gómez-Guerrero *et al.*, 2013) lower elevation forests in northwestern China (Wu *et al.*, 2015), as well as in the more mesic Tropics (Nock *et al.*, 2011, van der Sleen *et al.*, 2015). Particularly in semi-arid systems, such as our study system, concurrent increases in water limitation over the study period may override any benefit of greater iWUE for growth (Andreu-Hayles *et al.*, 2011, Gómez-Guerrero *et al.*, 2013).

In contrast to our second hypothesis and the assumption that the combination of elevated CO_2 and temperature will increase the productivity of higher elevation forests (Salzer *et al.*, 2009, Silva *et al.*, 2016, Silva & Anand, 2013), I found a particularly strong decrease of growth over time at the higher elevation of the west transect, while growth remained consistently low at the east transect (Figure 1). These results are not consistent with those of previous studies showing that increasing iWUE is more likely to lead to growth increases at higher elevations (Giammarchi *et al.*, 2017, Huang *et al.*, 2017, Peñuelas *et al.*, 2008, Wu *et al.*, 2015).

Growth trends may partly reflect ageing processes. Lodgepole pine generally experience a natural decline in stem growth around 30 years, with fairly consistent, but lower growth maintained from a stand age of about 50 until reaching ages greater than 200 years when growth again declines substantially (Ryan *et al.*, 1997, Smith & Resh, 1999). Stands in this study were generally between 95-130 years old, with the exception of the trees at the high elevation of the east transect that were often over 200 years. While some degree of the observed growth trend may therefore be a result of a natural growth decline, the variability of that decline across sites, and the clear increase in growth at the low elevation of the west transect despite a stand age of approximately 100 years, indicate that the stands in our study are likely responding to additional factors other than age. Further, if lodgepole pine growth generally declines substantially after roughly 200 years, the absence of a growth decline at the high elevation sites of the east transect may actually be indicative of some realized benefit to growth (e.g. warmer temperatures) as has been found previously (Peñuelas *et al.*, 2008, Salzer *et al.*, 2009, Wu *et al.*, 2015).

Strong p_a-p_i increases driven by CO_2 and temperature

The increases in p_a-p_i observed were generally weaker than has been reported in previous studies. Increases in iWUE of around 10 to 60% over the past 50 years have been observed globally, with the majority of observations being greater than 20% (Silva & Anand, 2013). However, our results are fairly consistent with the approximately 14 and 20% increases found for *Pseudotsuga menziesii* and *Pinus ponderosa*, respectively in the same region over a similar time period (Soulé & Knapp, 2015). Relatively weak increases in iWUE have additionally been reported for alpine sites in China (Liu *et al.*, 2007), boreal sites in Finland and Russia (Gagen *et al.*, 2008, Sidorova *et al.*, 2008), and tropical sites in Thailand (Nock *et al.*, 2011). Two exceptions to the relatively weak increase in p_a-p_i were the low and mid elevation sites of the west transect, where increases were nearly double those of other sites (Figures 1, 2). The increases at these sites were far more in line with observations of temporal changes in iWUE globally (Keller *et al.*, 2017, Peñuelas *et al.*, 2011, Silva & Anand, 2013).

Differences in iWUE are driven by the balance of stomatal conductance to photosynthetic rate, which is driven, in part, by environmental conditions like CO_2 concentration and climate (Fernández-de-Uña *et al.*, 2016). Although other factors, like age, height and/or competition may contribute to temporal variability in iWUE, these factors have been found to be less important than environmental variables like CO_2 and climate in other conifers (Copenhaver-Parry & Cannon, 2016, Fernández-de-Uña *et al.*, 2016, Giammarchi *et al.*, 2017, McDowell *et al.*, 2006). Elevated CO_2 has been shown to result in decreasing stomatal conductance as well as increasing photosynthetic assimilation, two conditions that result in greater iWUE (Battipaglia *et al.*, 2013). Warming temperatures, when associated with higher VPD, may also result in lower stomatal conductance, additionally contributing to long term trends in iWUE (Lewis *et al.*, 2002, Saurer *et al.*, 2014). Conversely, smaller increases in iWUE over time may be a result of relatively less stimulation of photosynthesis by higher CO_2 due in part to some other environmental factor constraining photosynthesis more than CO_2 (Körner, 2003), or a less pronounced decrease in stomatal conductance due to relatively minor increases in water limitation over time.

Results from LMMs indicate that changes in summer climate, particularly VPD, combined with temporal changes in CO_2 over the study period may contribute to the relatively strong increases in p_a-p_i observed at the low and mid elevations of the west transect, while p_a-p_i at other sites is primarily being driven by changes in CO_2 alone (Figure 2a; Table 2). These results are consistent with those found for *Quercus* and *Pinus* species in the Mediterranean (Fernández-de-Uña *et al.*, 2016), *Picea* in northern Europe (Giammarchi *et al.*, 2017), and temperate forests across central Europe (Saurer *et al.*, 2014). Correlations of p_a-p_i with monthly climate variables also indicate a particularly strong importance of summer temperature and VPD on p_a-p_i across the west site, and specifically at the low elevation (Supplemental Figure 3).

Site-specific growth enhancement may be in part driven by amelioration of late summer drought conditions

Growth is limited by different climate variables across elevations (Case & Peterson, 2007, Lo *et al.*, 2010). Understanding how specific growth-climate relationships vary across elevations and transects may provide a link for interpreting why increases in p_a-p_i at some sites are or are not related to a growth enhancement. I analyzed the relationship of monthly climate variables to annual radial growth across our sites. Radial growth is most strongly correlated with late summer climate of the previous growing season, supporting the notion that late summer soil moisture is particularly important for radial growth (Dougherty *et al.*, 1994) (Figure 5). This result is consistent with findings for lodgepole pine across a range of elevations in the North Cascades (Case & Peterson, 2007), Alberta (Chhin *et al.*, 2008), and British Columbia (Cortini *et al.*, 2010, Lo *et al.*, 2010). Annual ring width for conifers is primarily driven by earlywood formation (Dougherty *et al.*, 1994, Ziaco *et al.*, 2014). Earlywood formation occurs during the start of the growing season when water is less limiting, and is in part a result of the utilization of carbohydrates stored from the previous growing season (Kagawa *et al.*, 2006, Litton *et al.*, 2007, Lo *et al.*, 2010). A warmer and drier late summer climate therefore has implications for carbon storage, in that earlier cessation of growth due to late summer drought allows for less carbon to be stored for the following growing season.

In general, I found stronger growth-climate correlations and a greater importance of late summer climate of the previous growing season across the west transect (Figure 5). Contrary to expectations, there was not much variability in the growth-climate relationships across elevations at either transect, with the exception, to some degree, of precipitation. Summer precipitation in particular appears to become less influential for growth as elevation increases, as has been found in lodgepole pine systems in interior British Columbia (Lo *et al.*, 2010). Physiological variability (i.e. p_a-p_i, $\Delta^{13}C$) across elevations is more apparent at the east transect, although this does not appear to translate to variability in growth (Figure 1). This may suggest that a historically cooler and drier climate on the east side of the Continental Divide results in those lodgepole pine populations being generally more adapted to climatic conditions unfavorable to growth.

One of the benefits, in terms of increasing carbon gain, of higher iWUE may be an extension of the growing season longer into the late summer drought period (Fatichi *et al.*, 2016, Soulé & Knapp, 2013, Wullschleger *et al.*, 2002). In systems that are typically limited by seasonal drought, like those of lodgepole pine in the northern Rocky Mountains of the United States, an increase in iWUE that is driven by lower stomatal conductance may decrease water loss and allow trees to accumulate carbon later in the growing season (Fatichi *et al.*, 2016). The strong increases of p_a-p_i observed at the low elevation of the west transect may therefore effectively extend the growing season and enhance growth by ameliorating some effects of late summer drought. The observed relationship between CWD and the slope of the BAI~p_a-p_i regressions further supports this hypothesis, as a positive relationship between BAI and p_a-p_i appears increasingly likely where CWD is greater (Figure 4). However, further testing of this hypothesis is necessary, and the isolation of earlywood and latewood growth-climate relationships may be helpful to explore this to a greater degree.

There are additionally some inherent uncertainties with a study of this nature. Some of the elevational variability observed in temporal BAI and p_a-p_i trends is probably moderated to some degree by site-specific factors like soil nutrient availability or species interactions. Although I chose sites with similar parent material, changes in nutrient availability and species interactions that are not a response to climate cannot be determined in retrospect from a study of this type. The absence of a growth increase at most sites could additionally be a result of greater partitioning of carbon to belowground or reproductive processes with age, although, partitioning of above ground net primary productivity to wood generally increases with stand age (Litton *et al.*, 2007). Decreasing water availability driven by higher temperatures and greater evaporative demand, however, may increase carbon partitioning to belowground pools, and decrease partitioning to wood (Litton *et al.*, 2007).

Implications and conclusions

Despite ubiquitous increases in photosynthetic assimilation with elevated CO_2 in experimental settings, the realized effects of rising atmospheric CO_2 on forests are less certain and spatially variable (Babst *et al.*, 2014, Peñuelas *et al.*, 2011, Saurer *et al.*, 2014, Silva & Anand, 2013). I also find limited evidence for a fertilizing effect of CO_2 on individual tree growth, although our results do suggest that elevated CO_2 may provide some benefit to tree growth via increased iWUE in sites where water deficits are greater and growth is especially limited by late summer drought. This indirect benefit of greater iWUE to growth has not been explicitly explored in the majority of studies with similar objectives and is an exciting avenue for further research. This study adds to a growing body of literature showing that there are limited instances in which increasing atmospheric CO_2 precipitates any benefit to tree growth. If growth increases are indeed less common than growth decreases and modulated by climate, the assumption that forests will continue to sequester greater amounts of carbon as atmospheric CO_2 increases may not be realized. However, elevated CO_2 may alternatively be beneficial to carbon dynamics in forest systems by increasing regeneration or forest density (Kauppi *et al.*, 2010, Pan *et al.*, 2011), effects that cannot be quantified by a study of this nature. The realization of increasing productivity of forest systems on a regional scale, however, may ultimately be spatially heterogeneous even within a species, and depend on the interacting effects of increasing atmospheric CO_2 on phenology, climate and physiology.

TABLES AND FIGURES

Table 1. Transect and elevational climatic characteristics. Values are means of three sites at each elevation; values in parentheses are one SE. Temperature and RH values were measured for the 2016 growing season, and VPD was calculated from these values. CWD are 30-year normals from 800 m resolution gridded data corresponding to individual study plots.

		Elevation (m a.s.l)	**T_{min} (^oC)**	**T_{max} (^oC)**	**T_{avg} (^oC)**	**VPD (kPa)**	**CWD (mm)**
West	**Low**	1290 (3.2)	3.7 (0.1)	24.9 (0.2)	14.3 (0.1)	0.63 (0.06)	419.03 (0.9)
	Mid	1630 (29.4)	8.4 (1.4)	23.1 (1.4)	14.4 (0.9)	0.48 (n/a)	276.11 (13.2)
	High	2130 (28.3)	7.8 (1.4)	17.9 (0.3)	12.2 (0.2)	0.55 (0.01)	118.66 (11.5)
East	**Low**	1830 (19.9)	4.6 (0.6)	22.5 (0.3)	13.3 (0.1)	0.75 (0.02)	324.87 (7.6)
	Mid	2170 (17.8)	3.5 (0.5)	19.3 (0.2)	10.9 (0.1)	0.54 (n/a)	183.61 (n/a)
	High	2510 (23.7)	4.6 (0.2)	17.6 (0.5)	10.1 (0.1)	0.59 (0.01)	137.78 (2.2)

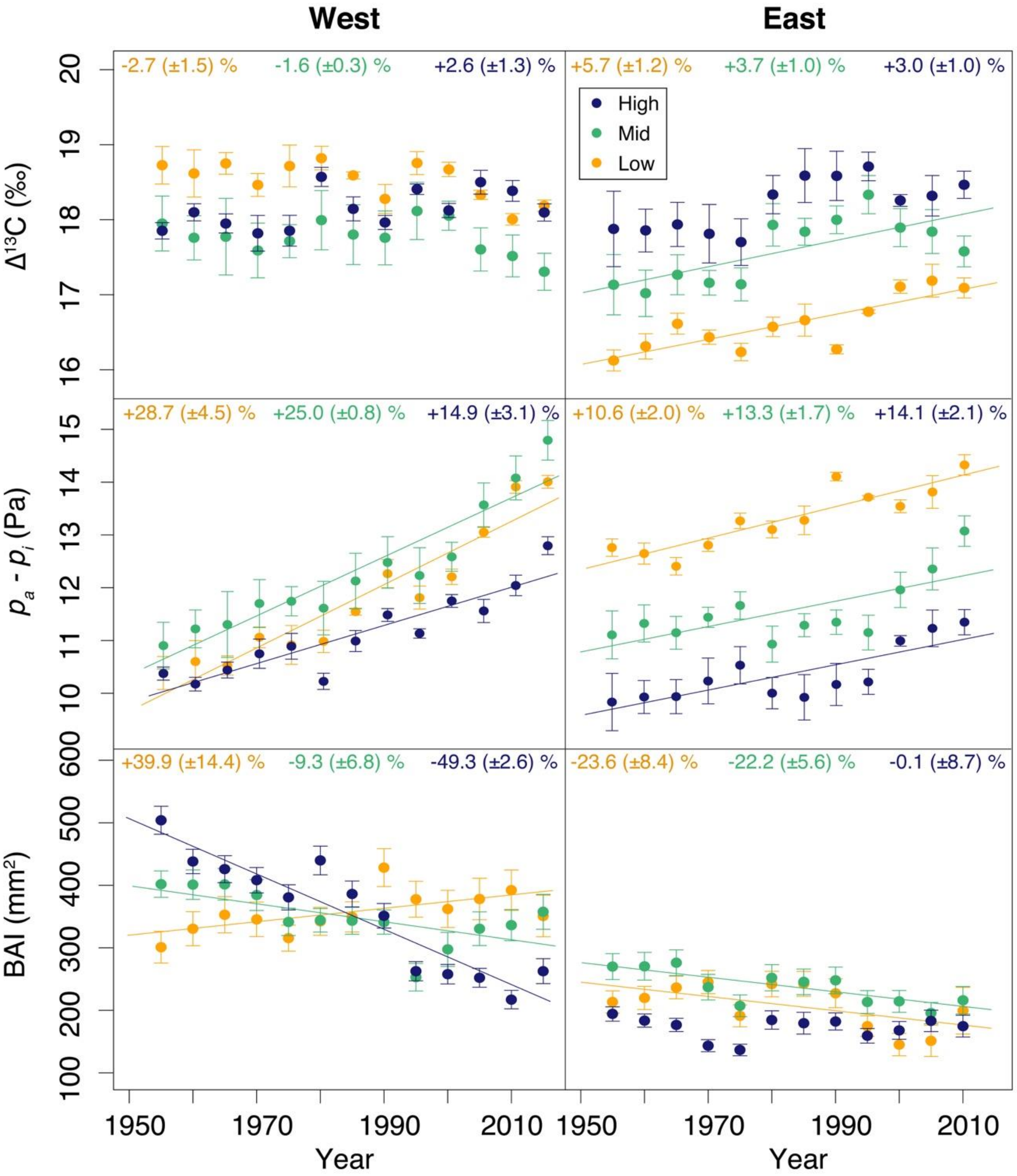


Figure 1. Trends in discrimination (Δ^{13}C), p_a-p_i, and BAI across elevations from 1951-2015 (west) and 1951-2010 (east). Data points are 5-yr means (BAI) and 5-yr pooled values (Δ^{13}C, p_a-p_i). Trend lines indicate significant (p < 0 .05) changes over time and % indicates percent increase over the study period (± 1 S.E).

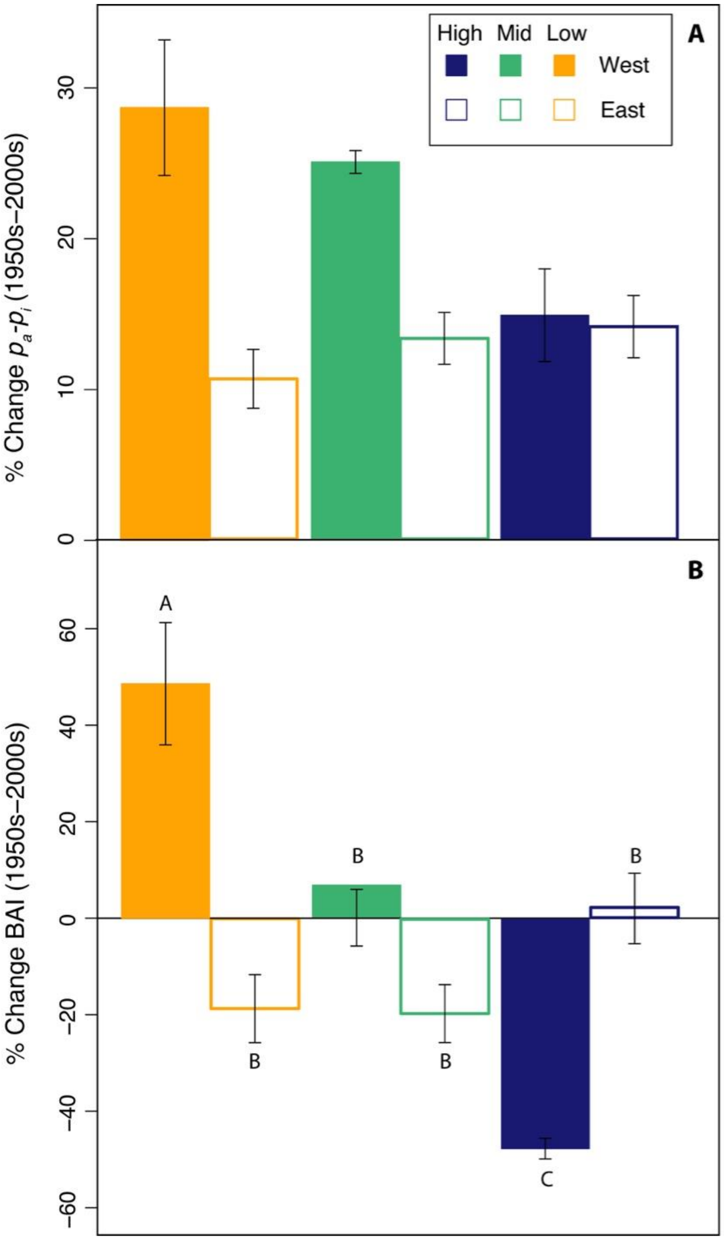


Figure 2. Percent change for p_a-p_i (A) and BAI (B) between the 1950s and the 2000s. Error bars are ± SE; letters in panel B indicate significant differences between elevations ($p<0.05$).

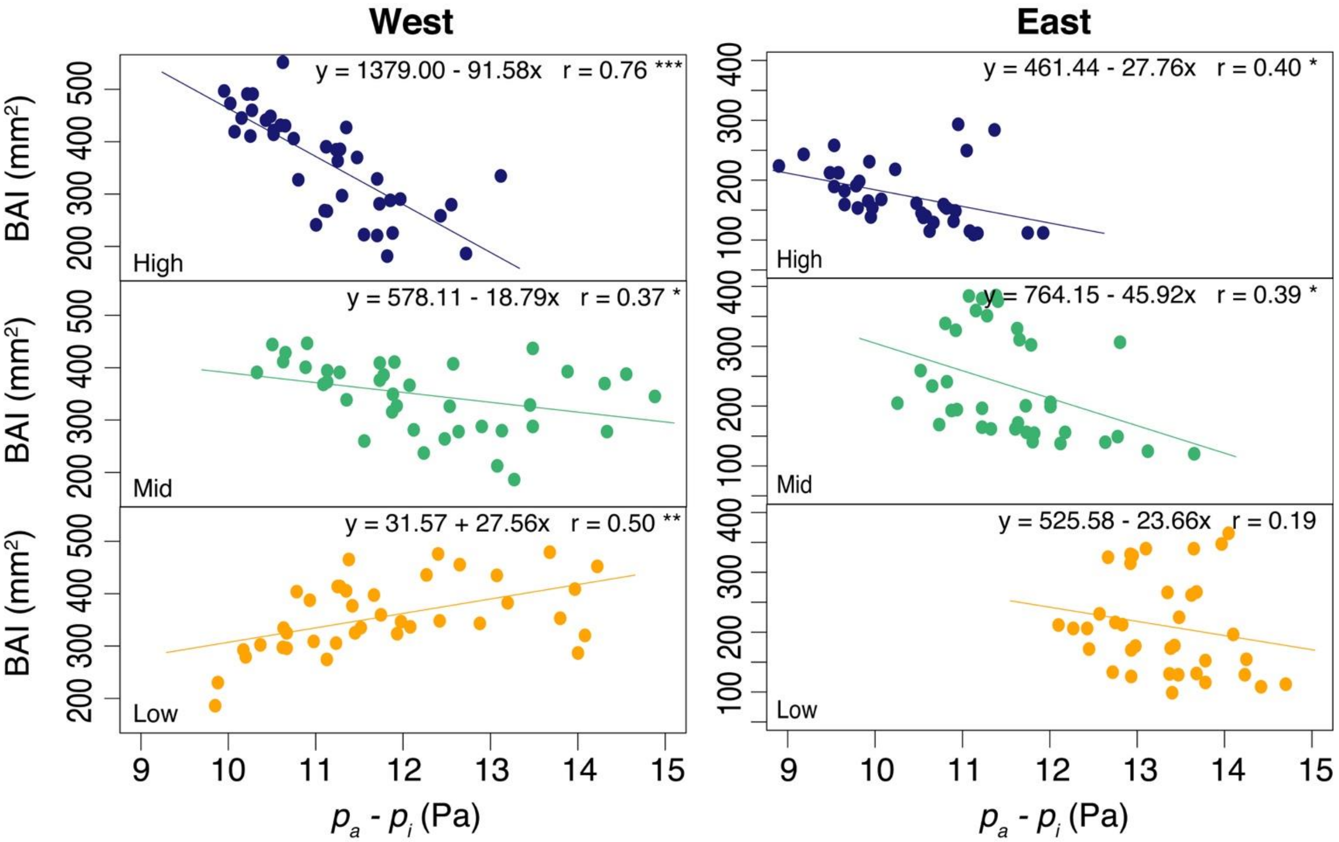


Figure 3. Relationships between BAI and p_a-p_i across elevations. Pearson's correlation coefficients are indicated by r-values, and equations for the regression lines are included. Significance levels: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

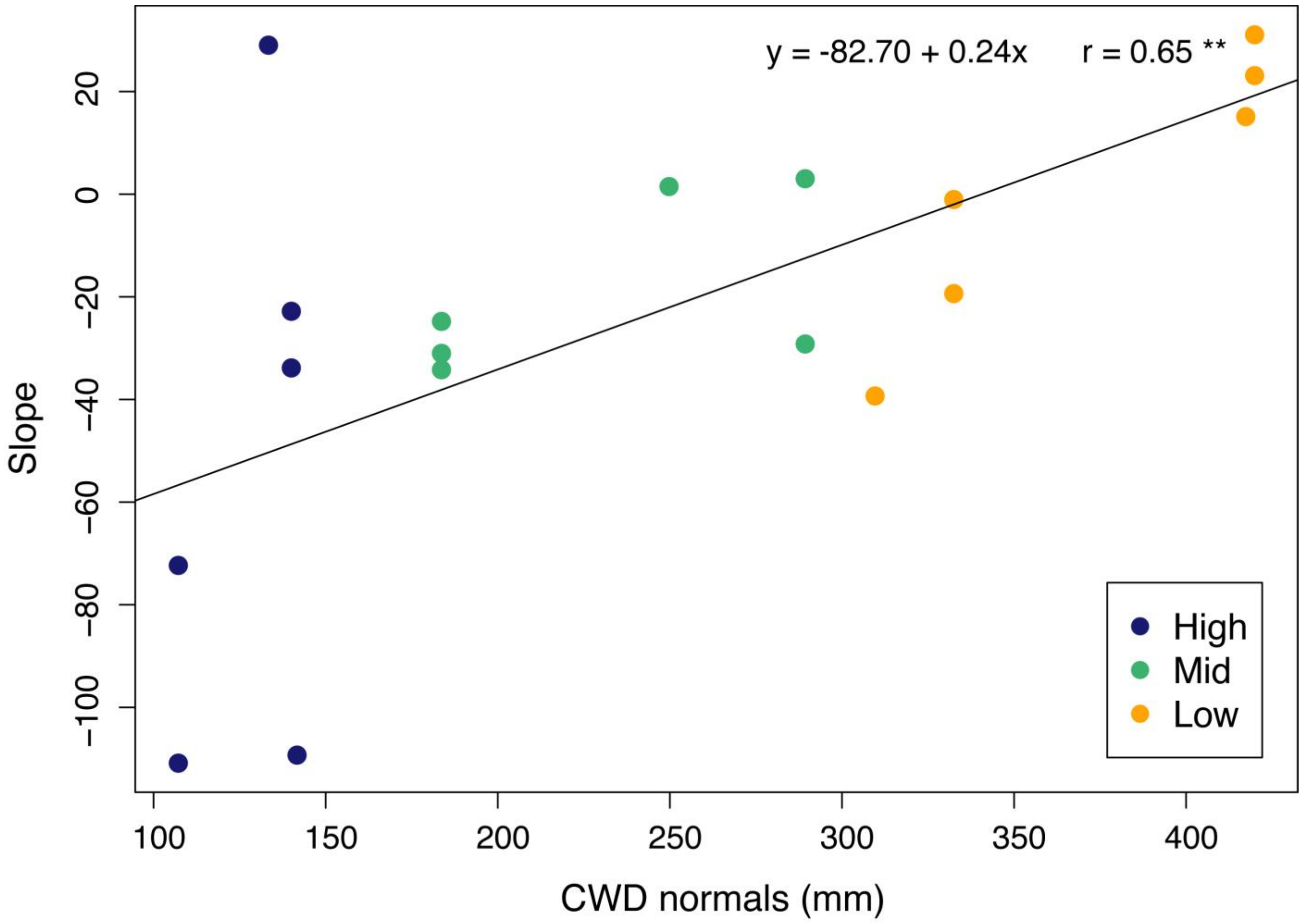


Figure 4. Relationships between the slope of the BAI~p_a-p_i regressions and CWD normals (1981-2010) corresponding to individual plots (n=18). East and west transects are combined. Pearson's correlation coefficient is indicated by r-value, and regression equation is included. Significance levels: $^{**}p < 0.01$.

Table 2. Differences in AIC for the p_a-p_i LMMs; calculated as the difference between AIC of the model and that with the lowest AIC. Models with differences <2 and fewer parameters are considered superior (bold). Climate variables are growing season (Jun-Sep) means.

	Low		**Mid**		**High**	
Model fixed effects	*west*	*east*	*west*	*east*	*west*	*east*
CO_2	6.15	**0**	11.38	15.11	**0.73**	**0.01**
Temperature	37.25	25.08	45.59	19.9	28.41	9.40
Precipitation	91.57	45.57	99.87	36.08	59.46	29.15
VPD	64.06	25.15	71.25	2.13	36.49	8.4
CO_2 + Temp	3.70	3.83	8.42	15.65	5.08	1.91
CO_2 + Prcp	15.78	10.24	18.93	**0.10**	10.30	1.23
CO_2 + VPD	**0**	1.95	**0**	0.97	0.71	0
CO_2 + Temp + Prcp	15.45	14.85	20.20	0.71	17.2	4.31
CO_2 + Temp + VPD	3.02	5.86	4.25	5.29	0	3.12
CO_2 + Prcp + VPD	7.81	10.44	12.66	3.31	12.87	7.42
CO2 + Temp + Prcp + VPD	11.57	16.76	16.88	0	11.61	4.57

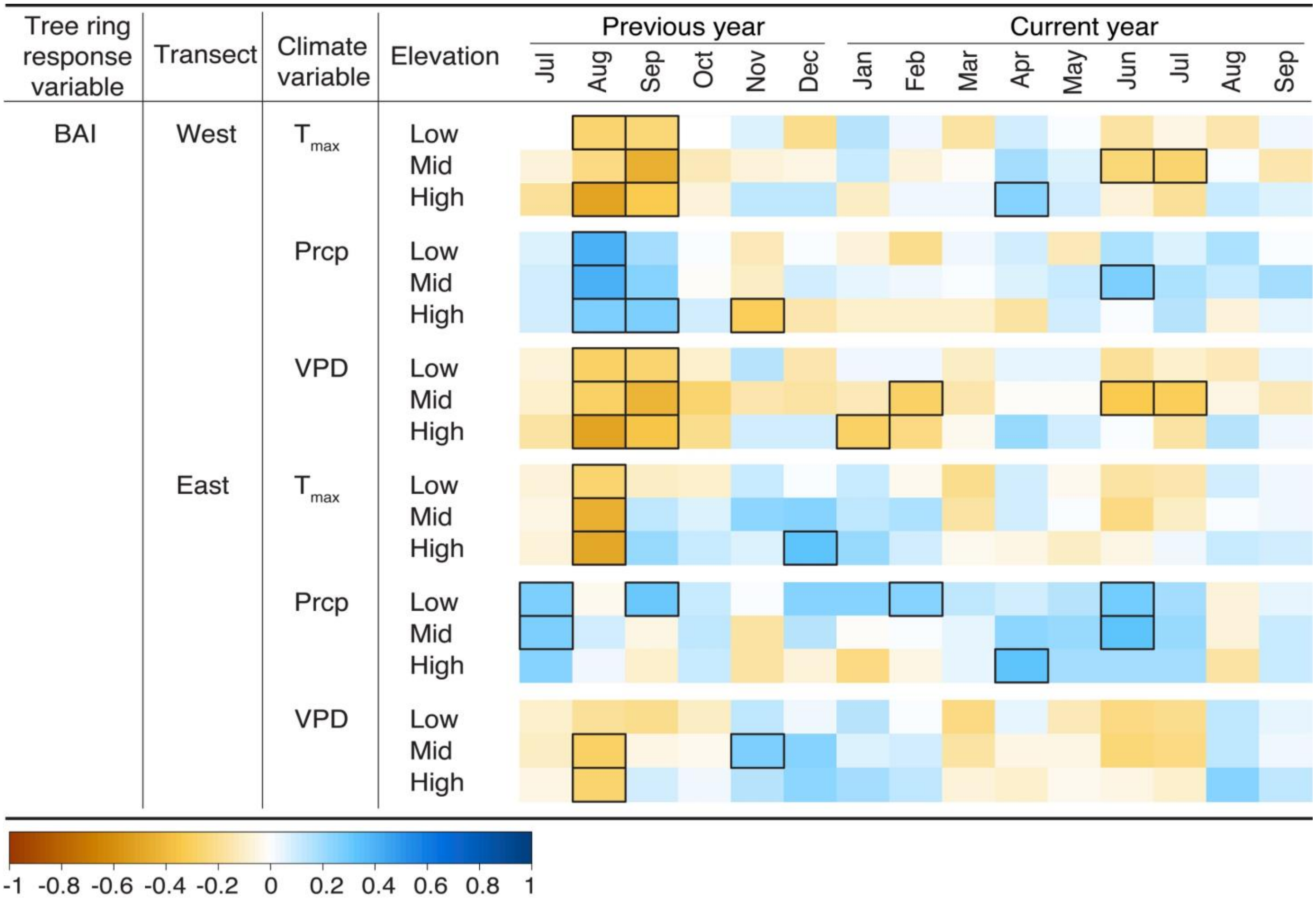


Figure 5. Relationships between interannual climatic variability and radial growth. Colors correspond to Pearson's correlation coefficients between detrended BAI and monthly climate variables (T_{max}, prcp, VPD) across transects and elevations. Black boxes indicate significance ($p < 0.05$).

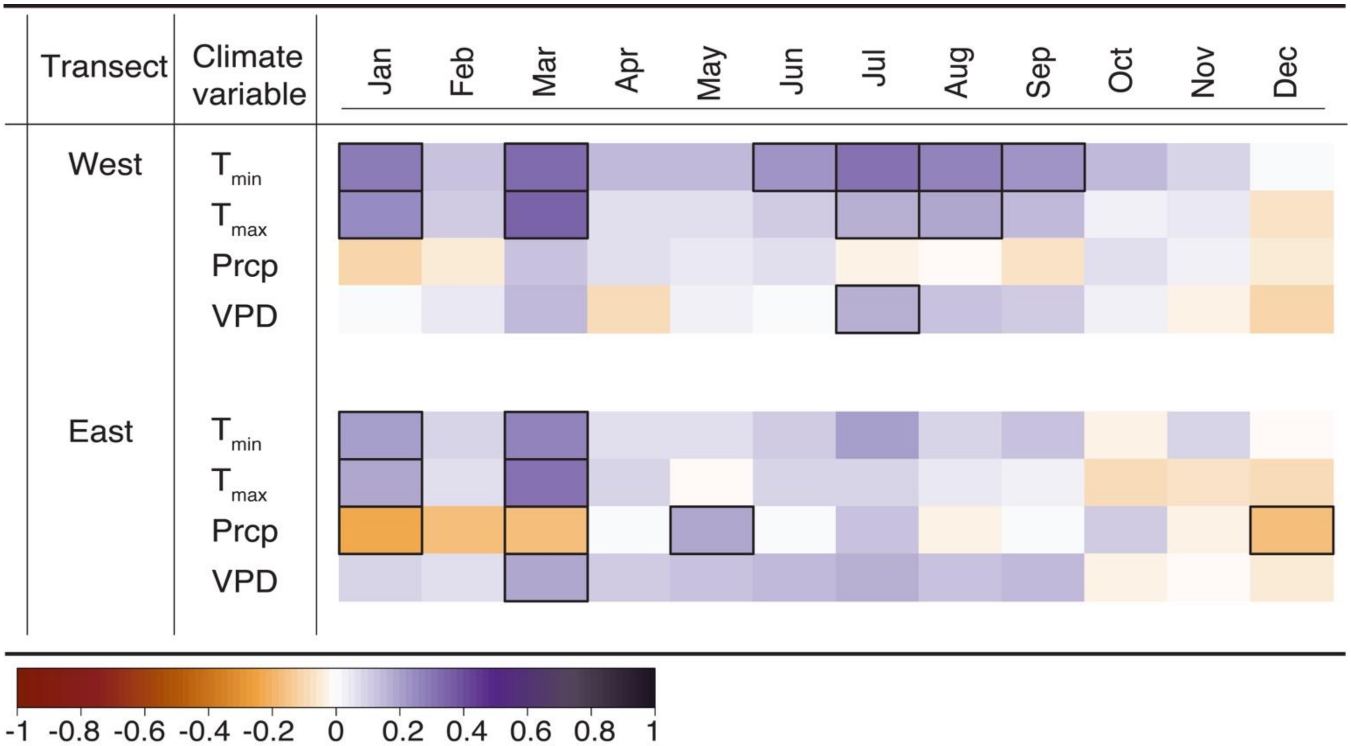
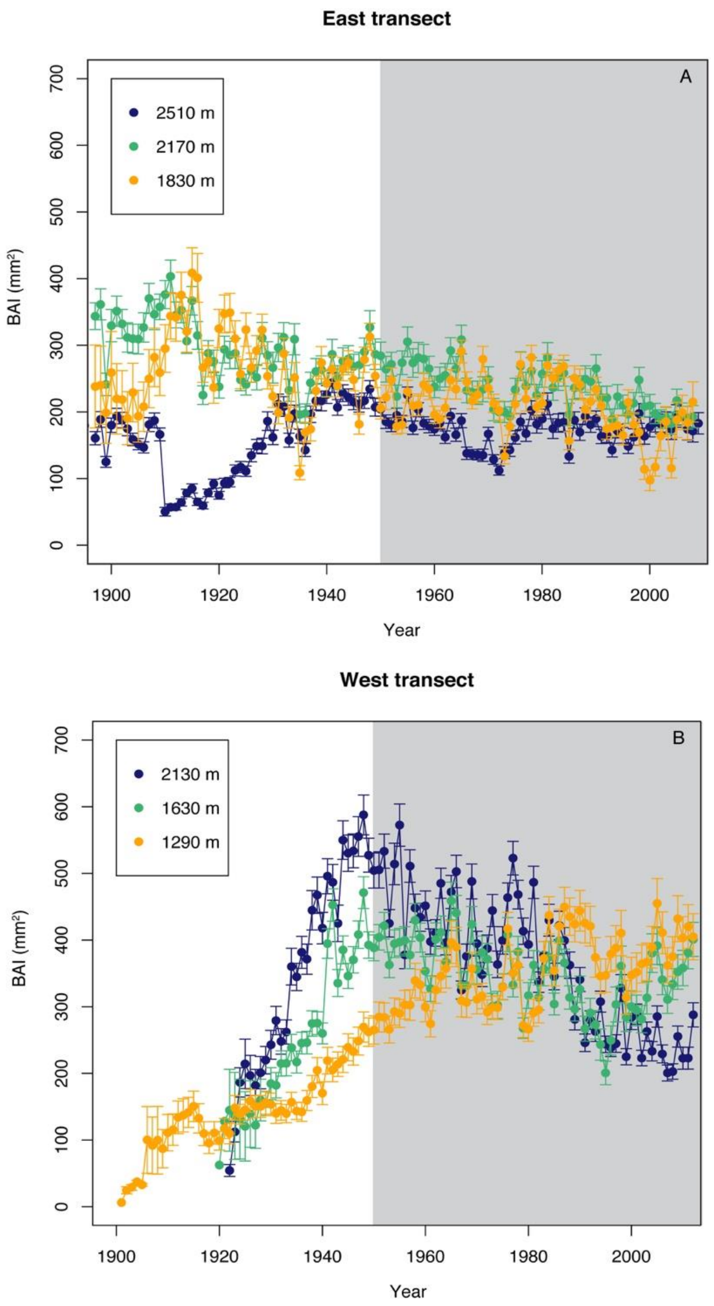
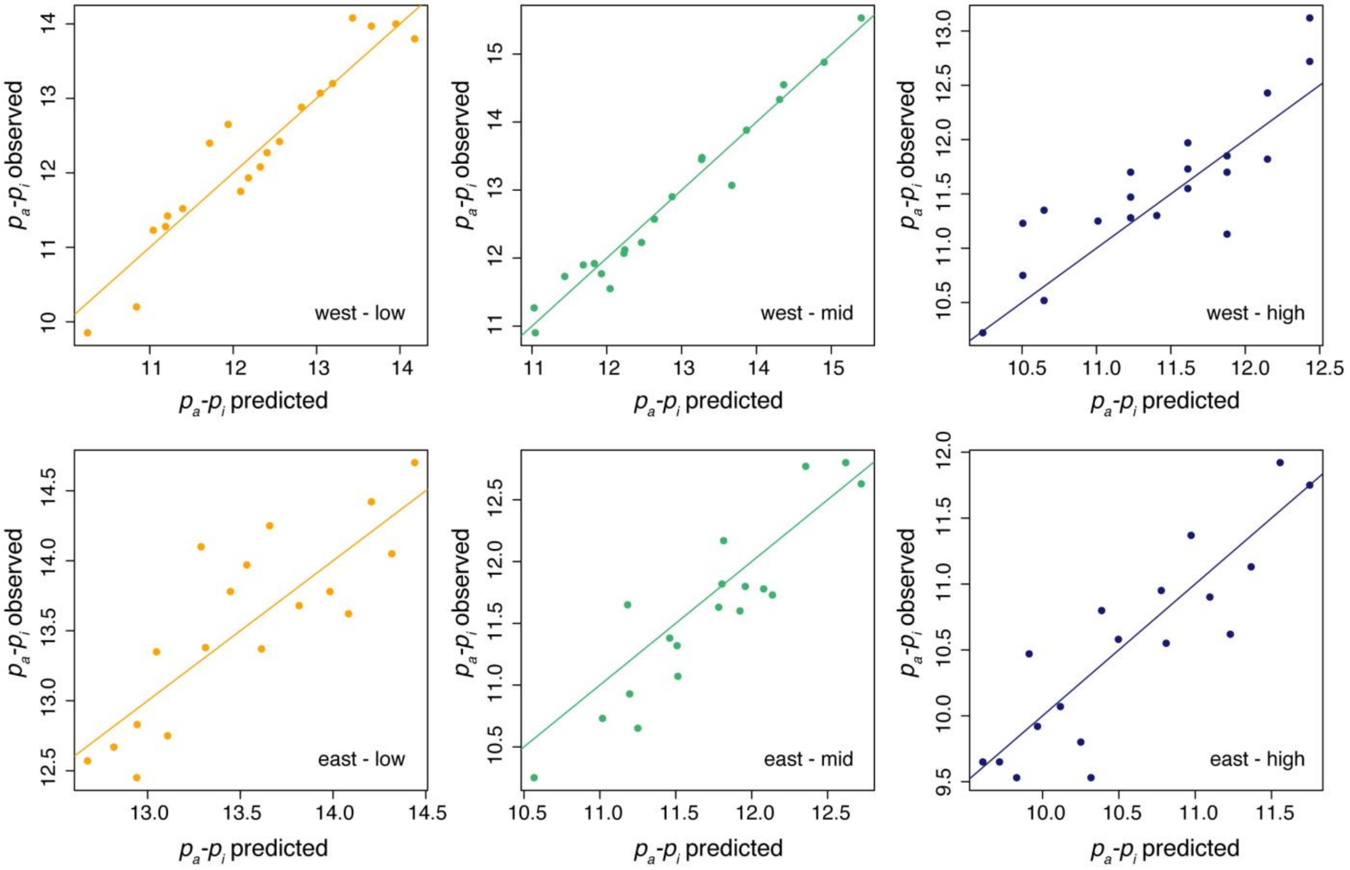


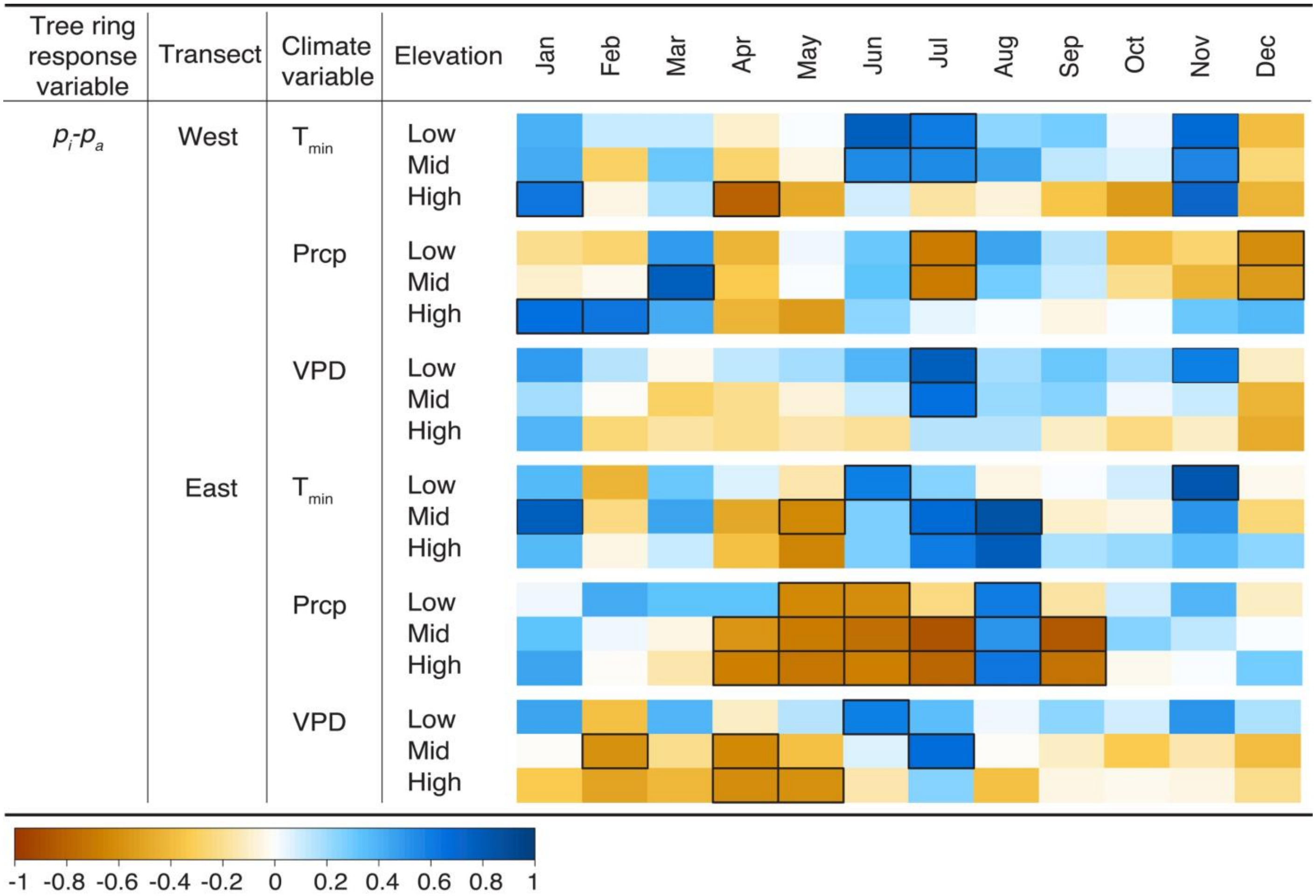
Figure 6. Trends in monthly climate variables from climate stations corresponding to the west and east transects. Colors correspond to Mann-Kendall tau statistics for trends in climate variables over time. Positive values indicate increases in the variable over time, while negative values indicate decreases. Black boxes indicate significant trends ($p < 0.05$).



Supplemental Figure 1. Mean basal area increment (mm^2) for *Pinus contorta* across the east and west transects from 1900 to 2010. Shading indicates years post-1950. East transect sites (A) consist of nine sites across three elevations: 1830 m (n=67 cores, 38 trees), 2170 m (n=76 cores, 39 trees), 2510 m (n=67 cores, 40 trees). West transect sites (B) consist of nine sites across three elevations: 1290 m (n=65 cores, 39 trees), 1630 m (n=80 cores, 44 trees), 2130 m (n=74 cores, 40 trees). Error bars are +/- SE.



Supplemental Figure 2. Predictive power of p_a-p_i linear mixed models (LMMs). Observed versus predicted values using the LMM that was selected as superior (Table 2) for each transect-elevation combination.



Supplemental Figure 3. Pearson's correlation coefficients between detrended iWUE and monthly climate variables across transects and elevations. Black boxes indicate significance ($p < 0.05$).

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