

# Limited evidence for CO<sub>2</sub>-related growth enhancement in northern Rocky Mountain lodgepole pine populations across climate gradients

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## Abstract

Forests sequester large amounts of carbon annually and are integral in buffering against effects of global change. Increasing atmospheric CO<sub>2</sub> may enhance photosynthesis and/or decrease stomatal conductance ( $g_s$ ) thereby enhancing intrinsic water-use efficiency (iWUE), having potential indirect and direct benefits to tree growth. While increasing iWUE has been observed in most trees globally, enhanced growth is not ubiquitous, possibly due to concurrent climatic constraints on growth. To investigate our incomplete understanding of interactions between climate and CO<sub>2</sub> and their impacts on tree physiology and growth, we used an environmental gradient approach. We combined dendrochronology with carbon isotope analysis ( $\delta^{13}\text{C}$ ) to assess the covariation of basal area increment (BAI) and iWUE over time in lodgepole pine. Trees were sampled at 18 sites spanning two climatically distinct elevation transects on the lee and windward sides of the Continental Divide, encompassing the majority of lodgepole pine's northern Rocky Mountain elevational range. We analyzed BAI and iWUE from 1950 to 2015, and explored correlations with monthly climate variables. As expected, iWUE increased at all sites. However, concurrent growth trends depended on site climatic water deficit (CWD). Significant growth increases occurred only at the driest sites, where increases in iWUE were strongest, while growth decreases were greatest at sites where CWD has been historically lowest. Late summer drought of the previous year negatively affected growth across sites. These results suggest that increasing iWUE, if strong enough, may indirectly benefit growth at drier sites by effectively extending the growing season via reductions in  $g_s$ . Strong growth decreases at high elevation windward sites may reflect increasing water stress as a result of decreasing snowpack, which was not offset by greater iWUE. Our results imply that increasing iWUE driven by decreasing  $g_s$  may benefit tree growth in limited scenarios, having implications for future carbon uptake potential of semiarid ecosystems.

## KEYWORDS

basal area increment, carbon isotopes, climate change, elevation gradients, intrinsic water-use efficiency, *Pinus contorta*, rise of atmospheric CO<sub>2</sub> concentrations, tree rings

## 1 | INTRODUCTION

Forested ecosystems sequester large amounts of carbon annually and are thus integral in helping to buffer against increases in global atmospheric CO<sub>2</sub> concentrations (Bonan, 2008; Pan et al., 2011). The degree to which rising atmospheric CO<sub>2</sub> concentrations are offset by forests is in part contingent on the stimulation of tree growth by this increase in CO<sub>2</sub> (McMahon, Parker, & Miller, 2010). Greater atmospheric CO<sub>2</sub> concentrations and the resulting increase in global temperatures have both direct and indirect consequences for tree growth. However, great uncertainty still remains as to how changes in climate and CO<sub>2</sub> may interact to influence the carbon uptake potential of forests in the future (Fernández-de-Uña, McDowell, Cañellas, & Gea-Izquierdo, 2016; Silva, Anand, & Leithhead, 2010; Tei et al., 2017).

Increased atmospheric CO<sub>2</sub> can alter tree growth via both direct and indirect effects on plant phenology and physiology. Higher CO<sub>2</sub> can enhance photosynthesis ( $A$ ) and/or decrease stomatal conductance ( $g_s$ ), thereby increasing intrinsic water-use efficiency ( $iWUE \approx A/g_s$ ) (Camarero, Gazol, Galvan, Sanguesa-Barreda, & Gutierrez, 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 are not unequivocally positive (Andreu-Hayles et al., 2011; Gómez-Guerrero et al., 2013; Martínez-Sancho et al., 2017; Nock et al., 2011; Tognetti, Cherubini, & Innes, 2000; Wu et al., 2015). The extent of growth response to rising CO<sub>2</sub> is seemingly climate and species-specific (Camarero et al., 2015; Lévesque, Siegwolf, Saurer, Eilmann, & Rigling, 2014; Martínez-Sancho et al., 2017; Peñuelas, Hunt, Ogaya, & Jump, 2008). Experimental evidence from free-air CO<sub>2</sub> enrichment (FACE) sites suggests that the positive effect of CO<sub>2</sub> on growth may depend in part on plant age, nutrient, and water status (Ellsworth et al., 2012; Norby, Warren, Iversen, Medlyn, & McMurtrie, 2010). Therefore, if variables other than CO<sub>2</sub> are more limiting to plant growth, an increase in CO<sub>2</sub> would likely have no direct fertilization effect on growth (Körner, 2000, 2003). Further investigation of climate-specific growth trends in response to recent increases in CO<sub>2</sub> is therefore necessary in order to better understand and accurately model regional variability in forest growth dynamics in response to changes in CO<sub>2</sub>.

While plants typically show a positive growth response to increasing atmospheric CO<sub>2</sub> concentrations in experimental settings, concomitant changes in regional temperature and precipitation may modify the fertilization effect of CO<sub>2</sub>. Where cold temperatures limit tree growth, rising CO<sub>2</sub> and corresponding temperature increases are expected to stimulate growth (Giammarchi, Cherubini, Pretzsch, & Tonon, 2017; Huang et al., 2017; Salzer, Hughes, Bunn, &

Kipfmüller, 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. In contrast, at sites where moisture availability limits growth, increasing temperatures and evaporative demand may limit the potential for a fertilization effect of CO<sub>2</sub> on growth (McLane, Daniels, & Aitken, 2011). However, increases in  $iWUE$  driven by a decline in stomatal conductance in response to enhanced atmospheric CO<sub>2</sub> may help ameliorate moisture-limiting effects, having an indirect influence on growth (Fatichi et al., 2016; Norby, Wullschlegel, Gunderson, Johnson, & Ceulemans, 1999; Wall et al., 2001; Wayne, Reekie, & Bazzaz, 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 climate-specific growth trends for species with broad ranges (McDowell, Allen, & Marshall, 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 increasing atmospheric CO<sub>2</sub> concentrations (but see Peñuelas et al., 2008; Wu et al., 2015).

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<sub>2</sub> (Lévesque et al., 2014; Linares, Delgado-Huertas, Julio Camarero, Merino, & Carreira, 2009; Soulé & Knapp, 2015; Tognetti, Lombardi, Lasserre, Cherubini, & Marchetti, 2014). With baseline knowledge of changes in atmospheric CO<sub>2</sub> and its carbon isotopic composition ( $\delta^{13}C_{atm}$ ),  $iWUE$  can be approximated by measuring carbon isotopes in tree rings (Farquhar, O'Leary, & Berry, 1982; Francey & 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<sub>2</sub> on future growth.

The northern Rocky Mountains of the United States are a useful region in which to examine the extent to which growth response to CO<sub>2</sub> is affected by concurrent climate changes. In this region growing season length and vapor pressure deficit (VPD) have significantly increased, and snowpack has decreased in the past century (Pederson, Betancourt, & McCabe, 2013; Pederson, Graumlich, Fagre, Kipfer, & Muhlfeld, 2010), having likely consequences for both tree growth (Lendzion & Leuschner, 2008; Restaino, Peterson, & Littell, 2016) and water-use efficiency (Andreu-Hayles et al., 2011). Previous studies of regional variability of tree growth and  $iWUE$  response to rising CO<sub>2</sub> in the northern Rocky Mountains have been mainly limited to low-elevation montane species, and have shown substantial interspecific variability in trends and conflicting results in terms of  $iWUE$  response to increasing CO<sub>2</sub> (Knapp & Soulé, 2011; Marshall & Monserud, 1996; Soulé & Knapp, 2015). Subalpine conifers with large elevational ranges such as lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) 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 to 2,800 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 higher elevations being cooler and wetter, and lower elevations being warmer and drier. Additionally, the windward side of the Continental Divide generally experiences 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, Oyler, Jencso, Running, & Ballantyne, 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<sub>2</sub>, and for improving our understanding of future growth and carbon uptake potential for this economically and ecologically important species.

In this study, we use a dendrochronological approach to assess lodgepole pine's iWUE and growth dynamics across climatically contrasting sites representative of lodgepole pine's broad climatic distribution. Our aim was to understand whether and how climate alters the relationship between iWUE and growth over time as CO<sub>2</sub> increases, and explore which climatic conditions are more conducive to radial growth enhancement (BAI increases) as iWUE increases due to rising CO<sub>2</sub>. 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), we hypothesize that (i) iWUE increases will be greatest at climatically drier sites, responding to both rising temperatures and changes in atmospheric CO<sub>2</sub>, and (ii) increases in iWUE will correspond to long-term growth increases only at the highest elevation sites where increasing atmospheric CO<sub>2</sub> and temperature are more likely to act in concert to enhance tree growth over time.

## 2 | MATERIALS AND METHODS

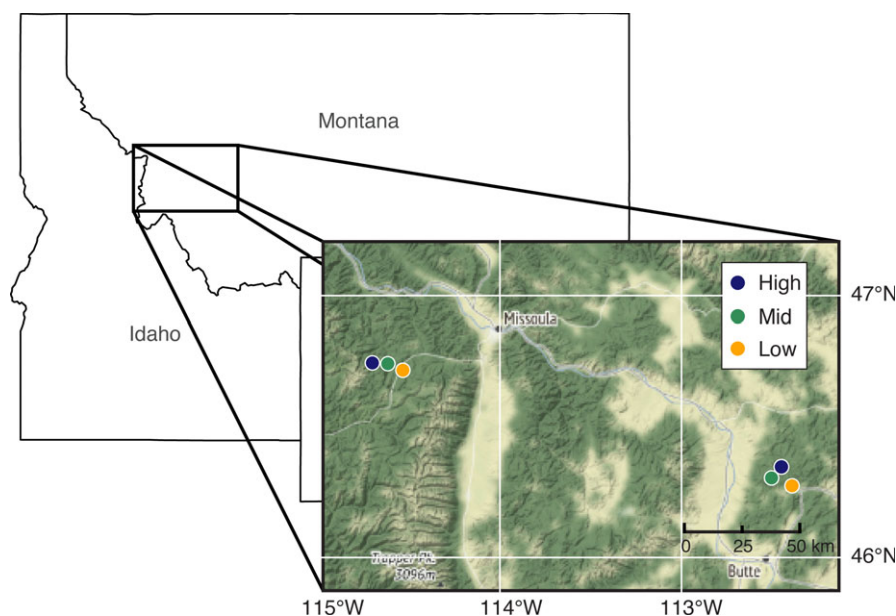
### 2.1 | Study species and sites

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 addition 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 encompassing the majority of lodgepole pine's elevational range on both sides of the Continental Divide in the northern Rocky Mountains of the

United States (Figure 1). Each elevational transect is comprised of nine 10 m circular 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, <https://websoilsurvey.sc.egov.usda.gov>). Stands across the west transect range from 1,290 to 2,130 m, whereas stands across the east transect range from 1,830 to 2,510 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 engelmannii* 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 codominance, similar edaphic conditions, slope, aspect, stand density, age, level of disturbance, and similar canopy cover in order to ensure constant ambient CO<sub>2</sub> across sites (Hultine & Marshall, 2000). Past mortality within stands, as evidenced by standing dead or downed decaying wood, did not appear to be above typical background levels for lodgepole in this region, with the exception of a 2007–2009 mountain pine beetle (*Dendroctonus ponderosae*) related mortality event across the eastern transect, which was accounted for in the analyses. 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).

### 2.2 | Climate data

While the study region as a whole experiences a semiarid 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 snow melt (Minder, Mote, & Lundquist, 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 at each plot for the 2016 growing season (June–September; Holden, Klene, Keefe, & Moisen, 2013). 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 of 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



**FIGURE 1** Location of the two elevational transects and three corresponding elevational bands (low, mid, high) encompassing the 18 study sites. Maps modified from *ggmap* package (Kahle & Wickham, 2013) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**TABLE 1** Transect and elevational climatic characteristics associated with study sites

	Elevation (m)	$T_{\min}$ (°C)	$T_{\max}$ (°C)	$T_{\text{avg}}$ (°C)	VPD (kPa)	CWD (mm)	AWC (mm)
West							
Low	1,290 (3.2)	3.7 (0.1)	24.9 (0.2)	14.3 (0.1)	0.63 (0.06)	419.0 (0.9)	106.3 (1.5)
Mid	1,630 (29.4)	8.4 (1.4)	23.1 (1.4)	14.4 (0.9)	0.48 (0.00)	276.1 (13.2)	96.7 (7.7)
High	2,130 (28.3)	7.8 (1.4)	17.9 (0.3)	12.2 (0.2)	0.55 (0.01)	118.7 (11.5)	87.0 (3.5)
East							
Low	1,830 (19.9)	4.6 (0.6)	22.5 (0.3)	13.3 (0.1)	0.75 (0.02)	324.9 (7.6)	106.5 (1.5)
Mid	2,170 (17.8)	3.5 (0.5)	19.3 (0.2)	10.9 (0.1)	0.54 (0.00)	183.6 (0.0)	118.0 (5.1)
High	2,510 (23.7)	4.6 (0.2)	17.6 (0.5)	10.1 (0.1)	0.59 (0.01)	137.8 (2.2)	117.3 (2.2)

Data 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 and AWD are from 240 m resolution gridded data corresponding to individual study plots.

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. Gridded, 240 m resolution soil available water holding capacity (AWC) data corresponding to study sites were obtained in order to additionally provide some insight into variability of soil properties across the study areas, as differences in soil depth and texture, particularly across elevations, may influence tree growth (Landguth, Holden, Mahalovich, & Cushman, 2017). 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 assessment of how this climate variable differs across both transects and elevations.

### 2.3 | 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 dried, sanded, and visually crossdated using standard dendrochronological techniques (Stokes & Smiley, 1968). Master chronologies were developed for each elevational band, and cores were scanned at 2400 dpi. 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 plot.

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). Additionally, BAI is a good proxy of annual above-ground biomass, and positive BAI can be maintained even after trees reach maturity (Gómez-Guerrero et al., 2013; Silva & Anand, 2013; Weiner & Thomas, 2001). BAI was calculated via the following formula:

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

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 to 2015, while the east transect encompassed 1950–2010. The east transect was cut off at 2010 due to a widespread regional mountain pine beetle outbreak that began around 2007–2009 and resulted in a strong growth release the following years (Gannon & Sontag, 2009). Complete BAI chronologies averaged 89.5 ( $\pm 9.9$ ) years for the west transect and 113.0 ( $\pm 36.1$ ) years for the east transect (Figure S1). 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.

## 2.4 | 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 ( $\delta^{13}\text{C}$ ) of tree rings. At each plot, two trees were selected for stable carbon isotope analysis that were visually 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, 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  $\text{CO}_2$  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  $\delta^{13}\text{C}$  variability between the heartwood and the sapwood (Steven Leavitt, pers. comm.; Leavitt & Danzer, 1993). Processed samples were then ground to a fine powder and weighed prior to  $\delta^{13}\text{C}$  analysis at Washington State University's Stable Isotope Core Laboratory (Pullman, WA, USA).

Results of isotopic analysis were combined with atmospheric  $\delta^{13}\text{C}$  records to determine  $^{13}\text{C}$  discrimination between atmospheric  $\text{CO}_2$  and plant carbon ( $\Delta^{13}\text{C}$ ), which accounts for the atmospheric decline in  $\delta^{13}\text{C}$  due to fossil fuel emissions (Francey & Farquhar, 1982; McCarroll & Loader, 2004). Discrimination was determined from (Farquhar & Richards, 1984; Farquhar et al., 1982):

$$\Delta^{13}\text{C} = \frac{(\delta^{13}\text{C}_a - \delta^{13}\text{C})}{\left(1 + \frac{\delta^{13}\text{C}}{1,000}\right)} \quad (2)$$

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

$$\Delta^{13}\text{C} \approx a + (b - a) \frac{c_i}{c_a} \quad (3)$$

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  $\text{CO}_2$  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 [ $A = g_s(c_a - c_i)$ , where  $g_s$  = stomatal conductance for  $\text{CO}_2$  and  $A$  = net assimilation], the ratio of  $c_i/c_a$  reflects the ratio of assimilation and stomatal conductance for  $\text{CO}_2$ . Because iWUE is the ratio of assimilation ( $A$ ) to stomatal conductance for water vapor ( $g_w$ ) and  $g_w = 1.6g_s$ , the relationship between  $c_i/c_a$  (or  $p_i/p_a$ ) and  $\Delta^{13}\text{C}$  can be used to calculate iWUE:

$$\text{iWUE} \approx (c_a - c_i) \left( \frac{1}{1.6} \right) \quad (4)$$

In order to account for elevational differences in  $\text{CO}_2$  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 to 2015, while the east transect ranged from 1951 to 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.



## 2.5 | 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 seasonal climate drivers of BAI variability over time (Bunn, 2008; Millar et al., 2012). For all other analyses, trends in BAI were not removed as long-term trends were of interest in this study. Correlations between BAI and maximum, rather than minimum, temperatures were reported 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, Hogg, Lieffers, & Huang, 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 climate variables deemed most biologically relevant from previous growth-climate analyses, and additionally, 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 climate. One-way ANOVA was used to assess differences across elevations and transects in percent change of BAI between the 1950s and 2000s. Post hoc Tukey's HSD tests were used to further assess differences between elevations. Percent change of  $p_a-p_i$  was not assessed with ANOVA due to small sample sizes. 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  $p < .05$  level of significance.

Linear mixed-effects modeling (LMM) was used to assess the relative importance of  $\text{CO}_2$  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  $\text{CO}_2$ , precipitation, temperature and VPD. Growing season (June–September) 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 we were 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  $>2$ , 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  $>10$  are indicative of high collinearity among response variables (Dormann et al., 2013). However,

collinearity was not observed in any of the best-fit models. Predictive power of the best-fit model for each transect–elevation combination was assessed by plotting observed vs. predicted values (Figure S2). 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, Bates, DebRoy, & Sarkar, 2014).

## 3 | RESULTS

### 3.1 | Site characteristics

As anticipated, temperature, VPD, and CWD tended to decrease with elevation (Table 1). We 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 are warmer across the west transect, any greater precipitation received by 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. Soil AWC was also variable across sites. We expected AWC to be lowest at high elevations due to relatively rockier and shallower soils; however, this pattern was only observed at the west transect (Table 1).

Average growing season minimum temperatures recorded from temperature loggers were generally highest at low elevations, particularly at the west transect, reflecting a tendency for cool air pooling in valley bottoms to occur over night in these areas during summer months (Table 1). Average growing season maximum temperatures were generally highest at low elevations and decreased with elevation, reflecting a lapse rate of approximately  $8.3^\circ\text{C}/1,000\text{ m}$  across the west transect, and  $7.2^\circ\text{C}/1,000\text{ m}$  across the east transect (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).

### 3.2 | Regional climatic changes

Long-term regional changes in climate varied between the two transects (Figures 2 and S3). Overall, winter warming occurred across both transects, particularly for January and March. Changes in precipitation were not consistent across transects, but minor increases in VPD were observed. Warming was generally stronger for the west transect, where significant increases in summer temperature were observed, as opposed to the east transect where minimal changes occurred over the period of study. No changes in precipitation were observed for the west transect, but winter decreases and May

increases of precipitation occurred for the east transect (Figures 2 and S3).

### 3.3 | BAI and intrinsic water-use efficiency

Over the study period, BAI only increased significantly at the low elevation of the west transect ( $\tau = 0.37$ ,  $p < .001$ ; Figure 3e). Significantly negative BAI trends were observed at all other elevations, with the exception of the high elevation of the east transect, which experienced negative, but nonsignificant changes in BAI over the period of study (Figure 3f). Contrary to expectations, the strongest decrease in BAI was observed at the highest elevation of the west transect ( $\tau = -0.63$ ,  $p < .001$ ; Figure 3e). The degree to which BAI changed over the study period depended on elevation ( $F = 10.20$ ,  $p < .001$ ), but not transect (Figure 4b). While differences between all elevations were observed at the west transect, differences were nonsignificant across the east (Figure 4b).

Temporal changes in isotopic discrimination and  $p_a-p_i$  varied across elevations and transects (Figure 3). Discrimination remained constant at all elevations except the low and mid elevations of the east transect, where it increased (Figure 3b). As anticipated,  $p_a-p_i$  increased at all elevations of both transects (Figure 3c,d). The low and mid elevations of the west transect experienced the greatest change in  $p_a-p_i$  with increases of  $28.7 (\pm 4.5) \%$  and  $25.0 (\pm 0.8) \%$ , respectively. Increases across all other sites ranged from  $10.6 (\pm 2.0) \%$  to  $14.9 (\pm 3.1) \%$ . 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 (Figures 3c and 4a).

Correlations between  $p_a-p_i$  and BAI were strongest across the west transect where they varied from strongly negative to positive from high to low elevations, respectively (Figure 5a,c,e). The low-elevation sites of the west transect were the singular example of a positive correlation between BAI and  $p_a-p_i$  ( $r = .5$ ,  $p < .01$ ). Across the

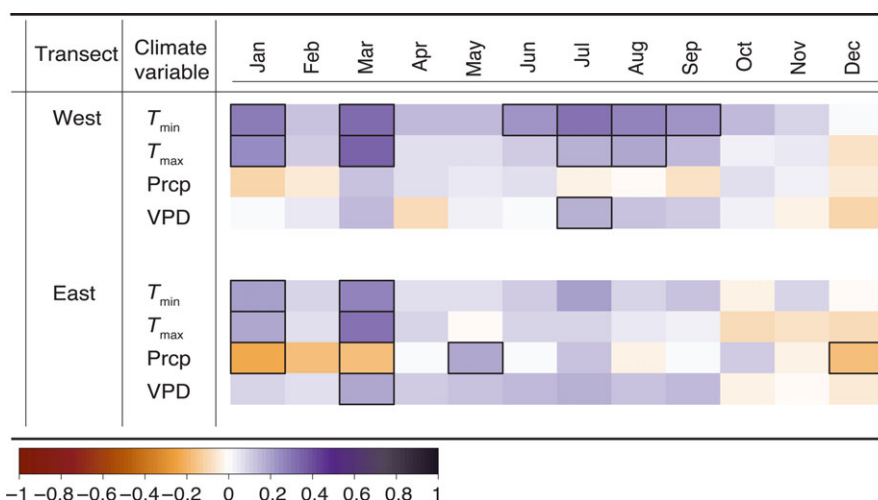
east transect, all correlations between the two variables were negative, and were weakly, or nonsignificantly correlated (Figure 5b,d,f). Further analysis of the slope of the resulting regression lines with climatic variables revealed that variability in the relationships between the correlation of BAI and  $p_a-p_i$  across all sites may in part be driven by environmental variability in climatic water deficit (Figure 6). No other climate variables assessed showed a clear relationship with the slope (data not shown).

### 3.4 | Effect of environmental variables on $p_a-p_i$

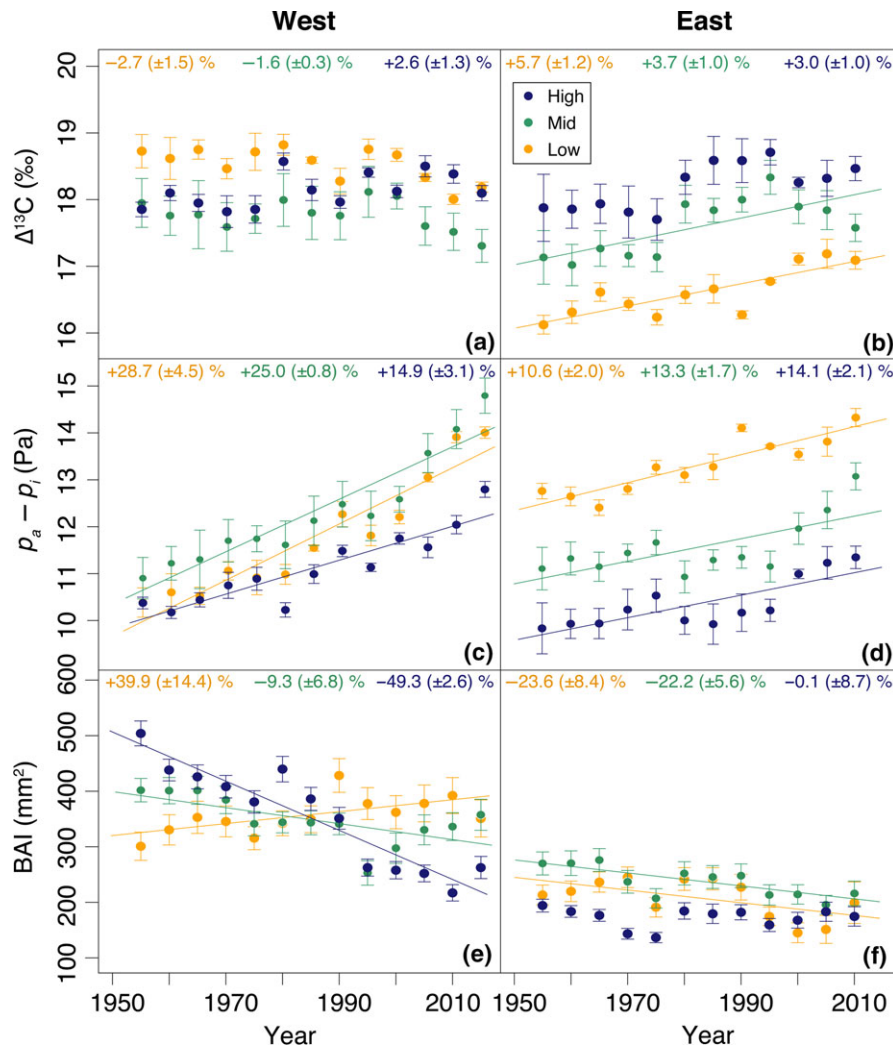
The response of  $p_a-p_i$  to environmental variables (i.e., climate,  $\text{CO}_2$ ) differed across elevations and transects (Table 2). Linear mixed-effects models indicated that temporal changes in  $p_a-p_i$  were generally most responsive to changes in atmospheric  $\text{CO}_2$  alone across elevations and transects, with a few exceptions. Models that considered growing season VPD as a fixed effect in addition to  $\text{CO}_2$  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  $\text{CO}_2$  (Table 2).

### 3.5 | Interannual climatic influences on BAI

Interannual responses of BAI to monthly climate variables differed across both elevations and transects (Figure 7). In general, BAI across the west transect was more responsive to all climate variables than across the east transect. For the west transect, BAI for all elevations was strongly negatively associated with late summer (August, September) drought (i.e., higher  $t_{\text{max}}$ , lower precipitation, and higher VPD) of the previous growing season. At mid elevation sites, BAI was also weakly negatively, but significantly, associated with summer drought of the current growing season. Across the east transect, BAI



**FIGURE 2** 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 ( $p < .05$ )



**FIGURE 3** Trends in discrimination ( $\Delta^{13}\text{C}$ ; a,b),  $p_a - p_i$  (c,d), and BAI (e,f) across elevations from 1951 to 2015 (west) and 1951 to 2010 (east). Data points are 5-year means (BAI) and 5-year pooled values ( $\Delta^{13}\text{C}$ ,  $p_a - p_i$ ). Trend lines indicate significant ( $p < .05$ ) changes over time and % indicates percent increase over the study period ( $\pm 1$  SE). Error bars are  $\pm 1$  SE

was strongly negatively associated with August  $t_{\text{max}}$  of the previous year at all elevations, and weakly negatively associated with previous year August VPD. Summer precipitation was positively associated with BAI predominately at low and mid elevation sites (Figure 7).

## 4 | DISCUSSION

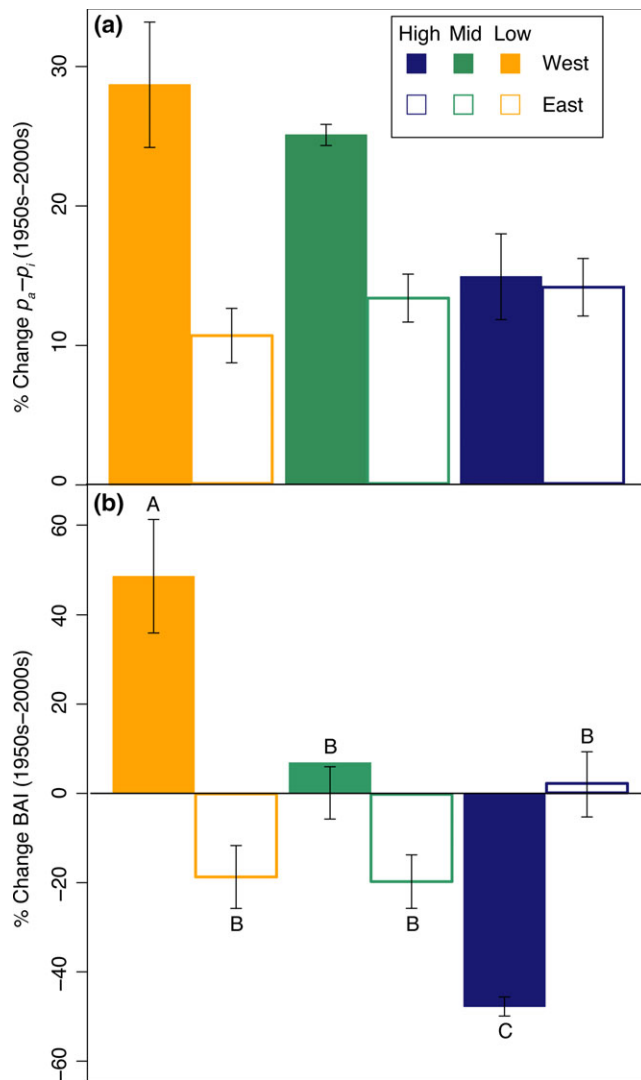
Consistent with other studies (Feng, 1999; Peñuelas, Canadell, & Ogaya, 2011; Silva & Anand, 2013; Soulé & Knapp, 2015), we found that  $p_a - p_i$  (henceforth, iWUE) increased over time at all sites (Figure 3c,d). Increases were strongest at the warmest site with the highest CWD, in agreement with our first hypothesis. However, strong increases also were observed at the mid elevation of the same transect where CWD was substantially less. We show that strong increases in iWUE are likely a response of trees to concurrent increases in  $\text{CO}_2$  and summer VPD. However, concurrent effects on growth over time depended on CWD, with significant growth

increases only at the driest sites where increases in iWUE were greatest (Figure 6). Strong growth declines at the high-elevation sites on the west side of the Continental Divide where CWD is historically lowest may be a product of increased drought impacts over the study period due to declining snowpack (Pederson et al., 2013; Figure 3e). We therefore posit that strong increases in iWUE may be driven in part by a relatively strong decline in stomatal conductance, which may ameliorate late summer drought and extend the growing season with positive effects on growth at the historically driest sites only. Our results show that increasing iWUE benefits tree growth in limited scenarios, with implications for future carbon uptake potential of semiarid ecosystems.

### 4.1 | Widespread increases of iWUE do not translate to greater growth

Our results are consistent with previous studies demonstrating that changes in isotopic discrimination and increases in iWUE are highly





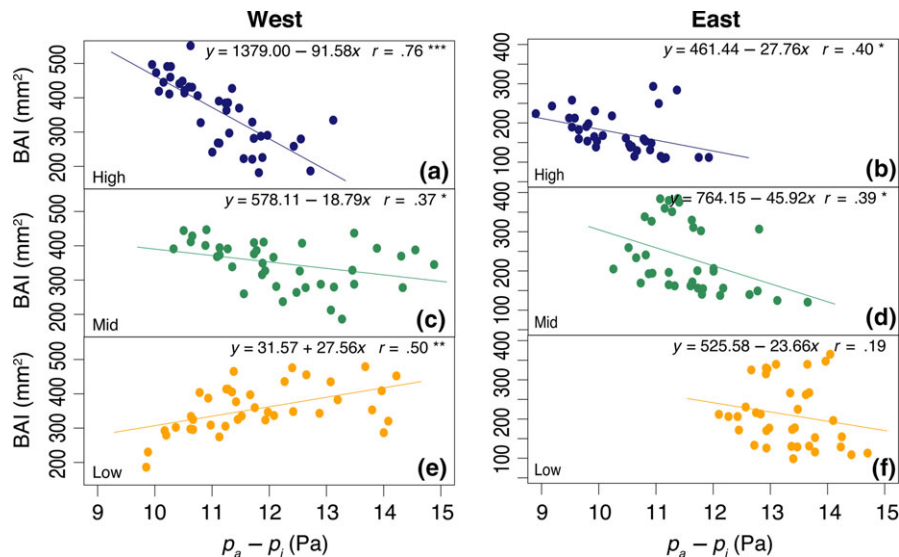
**FIGURE 4** Percent change for  $p_a - p_i$  (a) and BAI (b) between the 1950s and the 2000s. Error bars are  $\pm 1$  SE; letters in panel b indicate significant differences between elevations ( $p < .05$ )

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 & Soule, 2011; Lévesque et al., 2014; Linares et al., 2009; Martínez-Sancho et al., 2017; Peñuelas et al., 2011; Wu et al., 2015). Growth declines despite increasing iWUE have also been observed for the arid and semiarid 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 semiarid systems such as our study system, concurrent increases in water limitation over the study period may override any benefit of greater iWUE for growth, which might explain the general trend we observe of a negative relationship between growth and iWUE (Andreu-Hayles et al., 2011; Gómez-Guerrero et al., 2013).

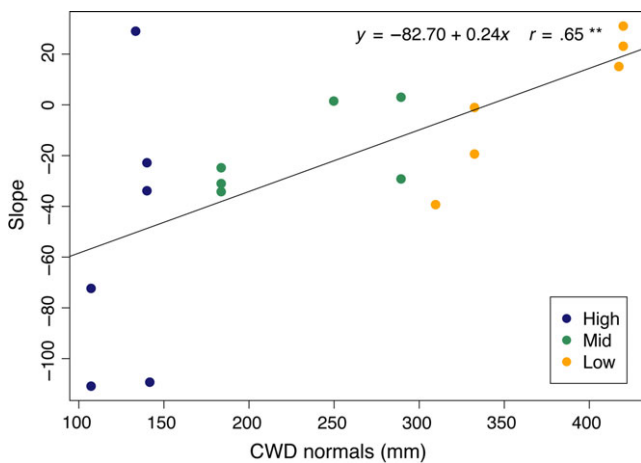
In contrast to our second hypothesis and the assumption that the combination of elevated  $\text{CO}_2$  and temperature will increase the

productivity of higher elevation forests (Salzer et al., 2009; Silva et al., 2016; Silva & Anand, 2013), we 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 3e,f). 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). The substantial increase of growing season temperatures across the region corresponding to the west transect may be contributing to increasing water stress at these high elevation sites, which without a strong increase in iWUE, may be overriding any benefit of higher temperatures and  $\text{CO}_2$  on growth. Similarly, historical baseline conditions may affect how trees respond to environmental changes, with decreases in regional snowpack more negatively affecting trees at sites with historically wetter conditions, lower water stress, and lower AWC (Pederson et al., 2013, 2011; Table 1). These results are also interesting in the context of the 'divergence problem' (D'Arrigo, Wilson, Liepert, & Cherubini, 2008), which refers to the unexpected anomalous reduction in forest growth indices and temperature sensitivity detected in tree ring width records from many temperature-limited circumpolar northern latitude sites since around the middle 20th century concurrent with temperature increases. Indeed, we do see some evidence of a weakening growth–climate relationship at these seasonally temperature-limited high-elevation sites where growth has declined (Figure S4). However, this weakening of growth–climate relationships also occurs at nontemperature-limited low elevations where growth has increased over the same period, and it is not consistent across transects. In general, the reasons for divergence effects are not clear but likely indicate complex tree growth responses to the integrated effects of abiotic and biotic factors.

Growth trends may partly reflect aging 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  $>200$  years when growth again declines substantially (Ryan, Binkley, & Fownes, 1997; Smith & Resh, 1999). Stands in this study were generally between 95 and 130 years old, with the exception of the trees at the high elevation of the east transect that were often over 200 years. Trees at these older sites did not experience any significant change in growth over the study period (Figures S1 and 3f). While some degree of the observed growth trend may therefore be a result of a natural growth decline, the variability of the growth 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. Furthermore, 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 could actually reflect 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).



**FIGURE 5** Relationships between BAI and  $p_a - p_i$  across elevations and transects. Pearson's correlation coefficients are indicated by  $r$ -values, and equations for the regression lines are included. Significance levels: \* $p < .05$ , \*\* $p < .01$ , \*\*\* $p < .001$



**FIGURE 6** 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: \*\* $p < .01$

#### 4.2 | Strong iWUE<sub>i</sub> increases driven by CO<sub>2</sub> and VPD

The increases in iWUE observed were generally weaker than have been reported in previous studies. Increases in iWUE of around 10%–60% over the past 50 years have been observed globally, with the majority of observations being >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,

McCarroll, Robertson, Loader, & Jalkanen, 2008; Sidorova, Siegwolf, Saurer, Naurzbaev, & Vaganov, 2008), and tropical sites in Thailand (Nock et al., 2011). Two exceptions to the relatively weak increase in iWUE were the low and mid elevation sites of the west transect, where increases were nearly double those of other sites (Figures 3c and 4a). 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).

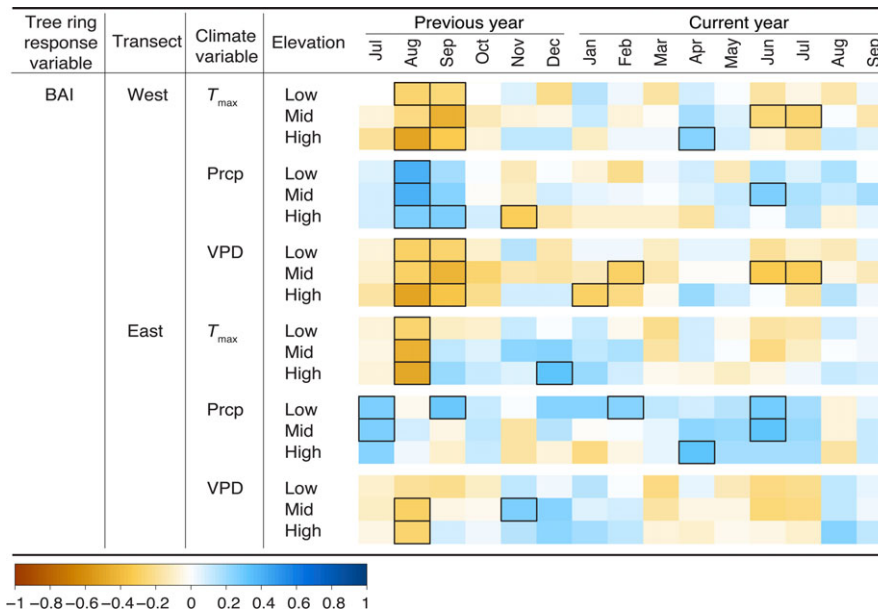
Differences in iWUE are driven by the balance of stomatal conductance to photosynthetic rate, which is driven, in part, by environmental conditions like CO<sub>2</sub> concentration and climate (Fernández-de-Uña et al., 2016). Although other factors, like age, height, and/or competition may contribute to temporal variability in iWUE, these factors have been found to be less important than environmental variables like CO<sub>2</sub> and climate in other conifers (Copenhaver-Parry & Cannon, 2016; Fernández-de-Uña et al., 2016; Giammarchi et al., 2017; McDowell, Adams, Bailey, Hess, & Kolb, 2006). Elevated CO<sub>2</sub> 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 resulting in higher VPD also may result in lower stomatal conductance, additionally contributing to long-term trends in iWUE (Lewis, Lucash, Olszyk, & Tingey, 2002; Saurer et al., 2014). Conversely, smaller increases in iWUE over time, like those observed at the majority of our sites, may be a result of relatively less stimulation of photosynthesis by higher CO<sub>2</sub> due in part to some other environmental factor constraining photosynthesis more than CO<sub>2</sub> (Körner, 2003), or a less pronounced decrease in stomatal conductance due to relatively minor increases in water limitation over time.

Results from linear mixed-effects models indicate that changes in summer climate, particularly VPD, combined with temporal increases

Model fixed effects	Low		Mid		High	
	West	East	West	East	West	East
CO <sub>2</sub>	6.15	<b>0</b>	11.38	15.11	<b>0.73</b>	<b>0.01</b>
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 <sub>2</sub> + Temp	3.70	3.83	8.42	15.65	5.08	1.91
CO <sub>2</sub> + Prcp	15.78	10.24	18.93	<b>0.10</b>	10.30	1.23
CO <sub>2</sub> + VPD	<b>0</b>	1.95	<b>0</b>	0.97	0.71	0
CO <sub>2</sub> + Temp + Prcp	15.45	14.85	20.20	0.71	17.2	4.31
CO <sub>2</sub> + Temp + VPD	3.02	5.86	4.25	5.29	0	3.12
CO <sub>2</sub> + Prcp + VPD	7.81	10.44	12.66	3.31	12.87	7.42
CO <sub>2</sub> + Temp + Prcp + VPD	11.57	16.76	16.88	0	11.61	4.57

Models with differences <2 and fewer parameters are considered superior (bold). Climate variables are growing season (Jun–September) means.

**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



**FIGURE 7** Interannual relationships between monthly climate variables and radial growth (BAI). 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 ( $p < .05$ )

in CO<sub>2</sub> over the study period may contribute to the relatively strong increases in iWUE observed at the low and mid elevations of the west transect, while iWUE at other sites is primarily being driven by changes in CO<sub>2</sub> alone (Figure 4a; 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). Relationships of iWUE with monthly climate variables also indicate a particularly strong importance of summer temperature and VPD on iWUE across the west site, and specifically at the low elevation (Figure S5).

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

Growth may be limited by different climate variables across sites that span climatic ranges (Case & Peterson, 2007; Lo, Blanco, Seely, Welham, & Kimmins, 2010). Understanding how specific growth–climate relationships vary across elevations and transects may provide a link for interpreting why increases in iWUE at some sites are or are not related to a growth enhancement. Radial growth is most strongly correlated with late summer climate of the previous

growing season across all sites, but particularly across the west transect, supporting the notion that late summer soil moisture is particularly important for radial growth (Dougherty, Whitehead, & Vose, 1994; Figure 7). 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, Biondi, Rossi, & Deslauriers, 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, Sugimoto, & Maximov, 2006; Litton, Raich, & Ryan, 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, we found stronger growth–climate correlations and a greater importance of late summer climate of the previous growing season across the west transect (Figure 7). Contrary to the expectation that growth–climate relationships should vary across environmental gradients, there was not much variability in the growth–climate relationships across elevations at either transect, with the exception perhaps of precipitation. Summer precipitation in particular appears to become slightly 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., iWUE,  $\Delta^{13}\text{C}$ ) across elevations is more apparent at the east transect (Figure 3b,d), although this does not appear to translate to variability in growth (Figure 3f). 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 into late summer (Fatichi et al., 2016; Soulé & Knapp, 2013; Wullschleger, Tschaplinski, & Norby, 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), with consequences for radial growth. The strong increases of iWUE 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. There appears to be some support for this explanation in the weakening of the relationship between late summer drought of the previous growing season and growth over the study period at low-elevation sites where growth has increased (Figure S4). The observed relationship between CWD and the slope of the BAI–iWUE regressions further supports this explanation, as a positive relationship between BAI and iWUE occurs only where CWD is greatest (Figure 6). Although it was beyond the scope of this study, further isolating earlywood and

latewood growth–climate relationships may be helpful to explore this explanation 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 iWUE trends is probably moderated to some degree by site-specific factors like soil nutrient availability or species interactions. Although we 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. Additionally, variability in soil texture and depth across sites may contribute to growth differences, particularly if soils closer to valley bottoms (i.e., lower elevations) are deeper and capable of retaining water longer into the summer drought period. However, this still does not explain elevational variability in changes to growth over the study period, as soil depth and texture have not likely changed over this period. 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 aboveground 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).

## 5 | IMPLICATIONS AND CONCLUSIONS

Despite ubiquitous increases in photosynthetic assimilation with elevated  $\text{CO}_2$  in experimental settings, the realized effects of rising atmospheric  $\text{CO}_2$  on forests are less certain and spatially variable (Babst et al., 2014; Martínez-Sancho et al., 2017; Peñuelas et al., 2011; Saurer et al., 2014; Silva & Anand, 2013). We also find limited evidence for a fertilizing effect of  $\text{CO}_2$  on individual tree growth, although our results do suggest that elevated  $\text{CO}_2$  may ameliorate tree drought stress via increased iWUE at sites where water deficits are greater and growth is especially limited by late summer drought. Similar studies in this region of conifers that co-occur with lodgepole pine at the lower elevational margins of its range also find some evidence of a positive relationship between iWUE and radial growth (Knapp & Soulé, 2011; Soulé & Knapp, 2013, 2015). 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  $\text{CO}_2$  has precipitated any benefit to tree growth over the latter half of the past century and contradicts the assumption that rising temperatures and atmospheric  $\text{CO}_2$  concentrations should act in concert to enhance tree growth at theoretically cold-limited high elevation sites. 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  $\text{CO}_2$  increases may not be realized. However, elevated  $\text{CO}_2$  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<sub>2</sub> on phenology, climate, and tree physiology.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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