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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B.A. Environmental Studies, University of California, Santa Cruz, CA, 2015

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ABSTRACT

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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

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 CO₂ fertilization remains uncertain. Increasing atmospheric CO₂ 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 CO₂ vary across climatic gradients. To investigate interactions between climate and CO₂ 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 (δ¹³C) 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 CO₂, 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\textsubscript{2} concentrations (Bonan, 2008, Pan et al., 2011). The degree to which rising atmospheric CO\textsubscript{2} concentrations are offset by forests is in part contingent on the stimulation of tree growth by this increase in CO\textsubscript{2}. Increased atmospheric CO\textsubscript{2} can enhance photosynthesis (A) and/or decrease stomatal conductance (g\textsubscript{s}), thereby increasing intrinsic water use efficiency (iWUE ≈ A/g\textsubscript{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\textsubscript{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\textsubscript{2} is likely site-specific (Camarero et al., 2015, Lévesque et al., 2014, Peñuelas et al., 2008). Experimental evidence from free-air CO\textsubscript{2} enrichment (FACE) sites suggests that the positive effect of CO\textsubscript{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\textsubscript{2} are more limiting to plant growth, an increase in CO\textsubscript{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\textsubscript{2} is therefore necessary in order to better understand and accurately model regional variability in forest-growth dynamics in response to changes in CO\textsubscript{2}.

While plants typically show a positive growth response to increasing atmospheric CO\textsubscript{2} concentrations in experimental settings, concomitant changes in regional temperature and...
precipitation may modify the fertilization effect of CO\textsubscript{2}. Where cold temperatures limit tree growth, rising CO\textsubscript{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\textsubscript{2} on growth (McLane et al., 2011). However, increases in iWUE driven by a decline in stomatal conductance in response to enhanced atmospheric CO\textsubscript{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\textsubscript{2} concentration.

Measurements of stable carbon isotope ratios (δ\textsuperscript{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\textsubscript{2} (Lévesque et al., 2014, Linares et al., 2009, Soulé & Knapp, 2015, Tognetti et al., 2014). With baseline knowledge of changes in atmospheric CO\textsubscript{2} and its carbon isotopic composition (δ\textsuperscript{13}C\textsubscript{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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ (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 CO₂, 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 CO₂ 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 CO₂, and (ii) increases in iWUE will correspond to long-term growth increases only at the highest elevation sites where increasing atmospheric CO₂ 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 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 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 Boulder 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 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 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:

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

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 (δ^{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 δ^{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 δ^{13}C analysis at Washington State University’s Stable Isotope Core Laboratory (Pullman, WA, USA).

Results of isotopic analysis were combined with atmospheric δ^{13}C records to determine δ^{13}C discrimination between atmospheric CO_2 and plant carbon (Δ^{13}C), which accounts for the atmospheric decline in δ^{13}C due to fossil fuel emissions (Francey & Farquhar, 1982, McCarroll & Loader, 2004). Discrimination was determined from (Farquhar & Richards, 1984, Farquhar et al., 1982):
\[
\Delta^{13}C = \frac{(\delta^{13}C_a - \delta^{13}C)}{(1 + \frac{\delta^{13}C}{1000})} \quad (Eq. 2)
\]

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:

\[
\Delta^{13}C \approx a + (b - a) \frac{c_i}{c_a} \quad (Eq. 3)
\]

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 \((\text{approximately } 27\%)\) (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 \((\text{McCarroll & Loader, 2004, NOAA-ESRL, https://www.esrl.noaa.gov/gmd/dv/data/})\).

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 \(c_i/c_a\) \((\text{or } p_i/p_a)\) and \(\Delta^{13}C\) can be used to calculate iWUE:

\[
iWUE \approx (c_a - c_i)(\frac{1}{1.6}) \quad (Eq. 4)
\]

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 \((t_{\text{min}}, t_{\text{max}})\), precipitation \((\text{prcp})\) and leaf-to-air vapor pressure deficit \((\text{VPD})\) 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 $p_{o}-p_{i}$ 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 $p_{o}-p_{i}$. 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 $t_{\text{min}}$ recorded from temperature loggers ranged from 3.7 ($\pm$ 0.1) °C at the low elevations to 7.8 ($\pm$ 1.4) °C at the high elevations for the west transect, reflecting a tendency for cool air pooling in valley bottoms to occur overnight in this area during summer months. Average growing season $t_{\text{min}}$ across the east transect was similar at low and high elevations. Average growing season $t_{\text{max}}$ across the west transect ranged from 24.9 ($\pm$ 0.2) °C at the low elevations to 17.9 ($\pm$ 0.3) °C at the high elevations, reflecting a lapse rate of approximately 8.3 °C/1000 m. Average growing season $t_{\text{max}}$ across the east transect ranged from 22.5 ($\pm$ 0.3) °C at the low elevations to 17.6 ($\pm$ 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 $\Delta^{3}{\text{C}}$ 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, $\Delta^{3}{\text{C}}$ increased at all elevations of both transects (Figure 1). The low and mid elevations of the west transect experienced the greatest change in $\Delta^{3}{\text{C}}$ 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 $\Delta^{3}{\text{C}}$ was greatest across the east transect. However, differences in percent change of $\Delta^{3}{\text{C}}$ over the study period were far greater across elevations for the west transect (Figure 1; Figure 2a).

Correlations between $\Delta^{3}{\text{C}}$ 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 $\Delta^{3}{\text{C}}$ ($r = 0.5$, $p < 0.01$). 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 $\Delta^{3}{\text{C}}$ and may in part be driven by environmental variability in climatic water deficit (Figure 4).

**Effect of environmental variables on $\Delta^{3}{\text{C}}$**

The response of $\Delta^{3}{\text{C}}$ to environmental variables (i.e. climate, CO$_2$) differed across elevations and transects (Table 2). Linear mixed-effects models indicated that temporal changes in $\Delta^{3}{\text{C}}$ 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 $\Delta^{3}{\text{C}}$ response at the low and mid elevations of the west transect where temporal changes in $\Delta^{3}{\text{C}}$ 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 $t_{\text{max}}$ 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 $t_{\text{max}}$, 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 $t_{\text{max}}$ of the current year. Across the east transect, BAI was strongly negatively associated with August $t_{\text{max}}$ of the previous year at all elevations, and positively associated with December $t_{\text{max}}$ 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 $t_{\text{max}}$, increasing January, March, and June through September $t_{\text{min}}$, 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 $t_{\text{min}}$ and $t_{\text{max}}$, as well as increasing July $t_{\text{min}}$, 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 $p_{\alpha}$-$p_i$ (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 $p_{\alpha}$-$p_i$ are likely a response of trees to concurrent increases in CO$_2$ and summer VPD. Despite increasing $p_{\alpha}$-$p_i$ over time across all sites, growth increases were only related to greater $p_{\alpha}$-$p_i$ at the lowest elevation of the west transect where temperature and CWD were greatest and increase of $p_{\alpha}$-$p_i$ most substantial (Table 1; Figure 3). Variability in the relationship between BAI and $p_{\alpha}$-$p_i$ is likely in part driven by environmental variability in water deficit, where a positive relationship between BAI and $p_{\alpha}$-$p_i$ is more likely where CWD is greater (Figure 4). I therefore posit that strong increases in $p_{\alpha}$-$p_i$ 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 $p_{\alpha}$-$p_i$ do not translate to greater growth*

This study finds that increases in $p_{\alpha}$-$p_i$ (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 CO₂ 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\textsubscript{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\textsubscript{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\textsubscript{2} due in part to some other environmental factor constraining photosynthesis more than CO\textsubscript{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\textsubscript{2} over the study period may contribute to the relatively strong increases in p\textsubscript{a}-p\textsubscript{i} observed at the low and mid elevations of the west transect, while p\textsubscript{a}-p\textsubscript{i} at other sites is primarily being driven by changes in CO\textsubscript{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\textsubscript{a}-p\textsubscript{i} with monthly climate variables also indicate a particularly strong importance of summer temperature and VPD on p\textsubscript{a}-p\textsubscript{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 $p_{c} - p_{i}$ 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. $p_{c} - p_{i}$, $\Delta^{13}C$) 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.
### 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.

<table>
<thead>
<tr>
<th></th>
<th>Elevation (m a.s.l)</th>
<th>T$_{\text{min}}$ (°C)</th>
<th>T$_{\text{max}}$ (°C)</th>
<th>T$_{\text{avg}}$ (°C)</th>
<th>VPD (kPa)</th>
<th>CWD (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>West</td>
<td>Low</td>
<td>1290 (3.2)</td>
<td>3.7 (0.1)</td>
<td>24.9 (0.2)</td>
<td>14.3 (0.1)</td>
<td>0.63 (0.06)</td>
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<td>Mid</td>
<td>1630 (29.4)</td>
<td>8.4 (1.4)</td>
<td>23.1 (1.4)</td>
<td>14.4 (0.9)</td>
<td>0.48 (n/a)</td>
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<tr>
<td></td>
<td>High</td>
<td>2130 (28.3)</td>
<td>7.8 (1.4)</td>
<td>17.9 (0.3)</td>
<td>12.2 (0.2)</td>
<td>0.55 (0.01)</td>
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<tr>
<td>East</td>
<td>Low</td>
<td>1830 (19.9)</td>
<td>4.6 (0.6)</td>
<td>22.5 (0.3)</td>
<td>13.3 (0.1)</td>
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<tr>
<td></td>
<td>Mid</td>
<td>2170 (17.8)</td>
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<td>19.3 (0.2)</td>
<td>10.9 (0.1)</td>
<td>0.54 (n/a)</td>
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<tr>
<td></td>
<td>High</td>
<td>2510 (23.7)</td>
<td>4.6 (0.2)</td>
<td>17.6 (0.5)</td>
<td>10.1 (0.1)</td>
<td>0.59 (0.01)</td>
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</table>
Figure 1. Trends in discrimination (Δ^{13}C), p_o-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_o-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 $p_0 - p_1$ (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~p~ 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.

<table>
<thead>
<tr>
<th>Model fixed effects</th>
<th>Low</th>
<th>Mid</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CO$_2$</strong></td>
<td>6.15</td>
<td>0</td>
<td>15.11</td>
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<tr>
<td>Temperature</td>
<td>37.25</td>
<td>25.08</td>
<td>45.59</td>
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<td>Precipitation</td>
<td>91.57</td>
<td>45.57</td>
<td>99.87</td>
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<td>VPD</td>
<td>64.06</td>
<td>25.15</td>
<td>71.25</td>
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<tr>
<td>CO$_2$ + Temp</td>
<td>3.70</td>
<td>3.83</td>
<td>8.42</td>
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<tr>
<td>CO$_2$ + Prcp</td>
<td>15.78</td>
<td>10.24</td>
<td>18.93</td>
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<tr>
<td>CO$_2$ + VPD</td>
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<td>1.95</td>
<td>0.97</td>
</tr>
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<td>15.45</td>
<td>14.85</td>
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<td>4.25</td>
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<td>10.44</td>
<td>12.66</td>
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<tr>
<td>CO$_2$ + Temp + Prcp + VPD</td>
<td>11.57</td>
<td>16.76</td>
<td>16.88</td>
</tr>
</tbody>
</table>
Figure 5. Relationships between interannual climatic variability and radial growth. Colors correspond to Pearson’s correlation coefficients between detrended BAI and monthly climate variables ($T_{\text{max}}$, 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 (mm²) 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).
REFERENCES


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