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Available online: 28 Apr 2011

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Radial Growth and Increased Water-Use Efficiency for Ponderosa Pine Trees in Three Regions in the Western United States*

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We examined changes in and relationships between radial growth and intrinsic water-use efficiency (iWUE) of ponderosa pine (*Pinus ponderosa*) trees, climate, and atmospheric CO_2 in the western United States since the mid-nineteenth century. We developed tree-ring chronologies for eight sites in three climate regions and used carbon isotope data to calculate pentadal values of iWUE. We examined relationships among radial growth, climate, iWUE, and CO_2 via correlation and regression analyses. Significant upward trends in iWUE occurred at all sites, and despite an absence of climate changes that would favor growth, upward radial growth trends occurred at five sites. Our findings suggest that increased iWUE associated with rising CO_2 can positively impact tree growth rates in the western United States and are thus an evolving component of forest ecosystem processes. **Key Words: atmospheric CO_2, climate, drought, intrinsic water-use efficiency, *Pinus ponderosa*.**

我们研究了自十九世纪中叶以来美国西部的黄松（Pinus ponderosa）树的径向生长和内在水分利用效率之间的变化，以及它与气候和大气中二氧化碳变化的关系。我们在三个气候区八个站点建立了树木年轮年表，并用碳同位素数据来计算灌溉水利用效率的五年值。我们通过相关和回归分析研究径向生长，气候，灌溉水利用效率和二氧化碳的关系。尽管缺少有利于增长和向上径向生长的气候变化条件，灌溉水利用效率在所有的站点都出现显著的上升趋势。我们的研究结果表明，与不断上升的二氧化碳含量相关的增加的灌溉水利用效率可以对美国西部的树木生长率产生积极影响，因而是森林生态系统过程的一个不断进化的部分。关键词：大气二氧化碳，气候干旱，内在水分利用效率，黄松。

Examinamos los cambios entre crecimiento radial y la eficiencia intrínseca del uso del agua (iWUE, sigla en inglés) del pino ponderosa (*Pinus ponderosa*), y las relaciones con el clima y el CO_2 presente en la atmósfera del occidente de los Estados Unidos, desde mediados del siglo XIX. Desarrollamos cronologías basadas en los anillos del tronco de los árboles para ocho sitios de tres regiones climáticas y utilizamos datos de isótopos de carbono para calcular los valores pentadales de la iWUE. También, examinamos las relaciones entre crecimiento radial, clima, iWUE y CO_2, por medio de análisis de correlación y regresión. En todos los sitios se detectaron tendencias significativas de aumento de la iWUE y a pesar de la inexistencia de cambios climáticos que hubiesen favorecido el crecimiento, en cinco sitios se registraron tendencias de aumento en el crecimiento radial. Nuestros hallazgos sugieren que el incremento de la iWUE asociado con elevación del

CO₂ pueden impactar positivamente las tasas de crecimiento de los árboles en la región occidental de EE.UU. y son, por lo tanto, un componente en evolución de los procesos que ocurren en el ecosistema de bosque. **Palabras clave: CO₂ atmosférico, clima, sequía, eficiencia intrínseca del uso del agua, *Pinus ponderosa*.**

In 2008, atmospheric CO_2 concentrations (hereafter CO_2) from the Mauna Loa, Hawaii, Observatory records exceeded 385 ppmv (http://www.esrl.noaa.gov/gmd/ccgg/trends/ [last accessed 1 December 2009]), representing a 22 percent increase since 1959. In forested ecosystems, one of the primary effects related to higher levels of CO_2 on tree growth is decreased stomatal conductance (Tognetti et al. 1998). As CO_2 has increased, most tree species have been able to use water more efficiently as they experienced changes in stomatal conductance; that is, leaf stomatal apertures narrow during photosynthesis (Ainsworth and Rogers 2007). Consequently, the uptake of CO_2 during photosynthesis currently and in recent decades may have occurred at rates equivalent to a lower CO_2 environment but with less transpirational water loss per biomass gained. Thus, tree growth during periods of temporary moisture limitations in the twenty-first and late twentieth century should be greater than comparable periods prior to the 1950s because of increased water-use efficiency. Several studies have documented significant increases in intrinsic water-use efficiency (iWUE; i.e., the ratio of net CO_2 assimilation to stomatal conductance) for various tree species in many parts of the world (Bert, Leavitt, and Dupouey 1997; Feng 1999; Tang, Feng, and Funkhouser 1999; Arneth et al. 2002; Saurer, Siegwolf, and Schweingruber 2004; Waterhouse et al. 2004; Liu et al. 2007), and others (Soulé and Knapp 2006; Knapp and Soulé 2008) have documented radial growth rate increases and linked these increases to changing CO_2 concentrations, which in turn likely increased iWUE rates for those species.

For the western United States, the consensus of global circulation model predictions is for substantially warmer and drier summers (Christensen et al. 2007). Increasing aridity can cause a decline in forest productivity (Hanson and Weltzin 2000; Ciais et al. 2005; Bréda et al. 2006) or continue a trend of increasing tree mortality already observed in the region (van Mantgem et al. 2009). Increasing iWUE associated with rising CO_2 concentrations, however, could potentially help offset any declines associated with possible climate changes detrimental to tree growth and forest health. Examining the historical responses to changing atmospheric conditions such as CO_2 will help us understand how western conifers might respond if climate change results in an environment less favorable for growth. In this study we examined changes in iWUE, radial growth rates, and associated climate and atmospheric variables for ponderosa pine (*Pinus ponderosa*) trees growing in three distinct climatic regions of the western United States. Our objectives were to (1) determine if long-term (>100 years) trends exist for ponderosa pine for iWUE rates, radial growth rates, and the primary climatic drivers for radial growth of ponderosa pine; and (2) examine the relationships among these three variables.

Methods

Chronology Development

We selected ponderosa pine because it is an ecologically important species occurring throughout the American West with a geographical range exceeding 20° of latitude and longitude. Occupying over 10.9 million hectares (http://www.wpa.org/ppine.htm [last accessed 3 March 2010]), ponderosa pine is a major species for U.S. forestry (Western Wood Products Association 2007). Ponderosa pine forests are among the most valued in North America because of the diverse benefits they provide including "timber, forage, wildlife habitat, recreation . . . and scenic beauty" (Youngblood 2005, 49–50). Finally, ponderosa pine trees grow within semiarid sites where the combined effects of warmer and drier conditions might make them among the first species to be affected by climate variability.

We sampled live ponderosa pine from two subspecies (*P. ponderosa* var. *ponderosa* and *P. ponderosa* var. *scopulorum*) at eight sites in three regions of the western United States (Figure 1, Table 1). We selected open-canopy (i.e., park-like) woodland sites on federally owned lands with minimal anthropogenic disturbances from logging, domestic livestock grazing, fire
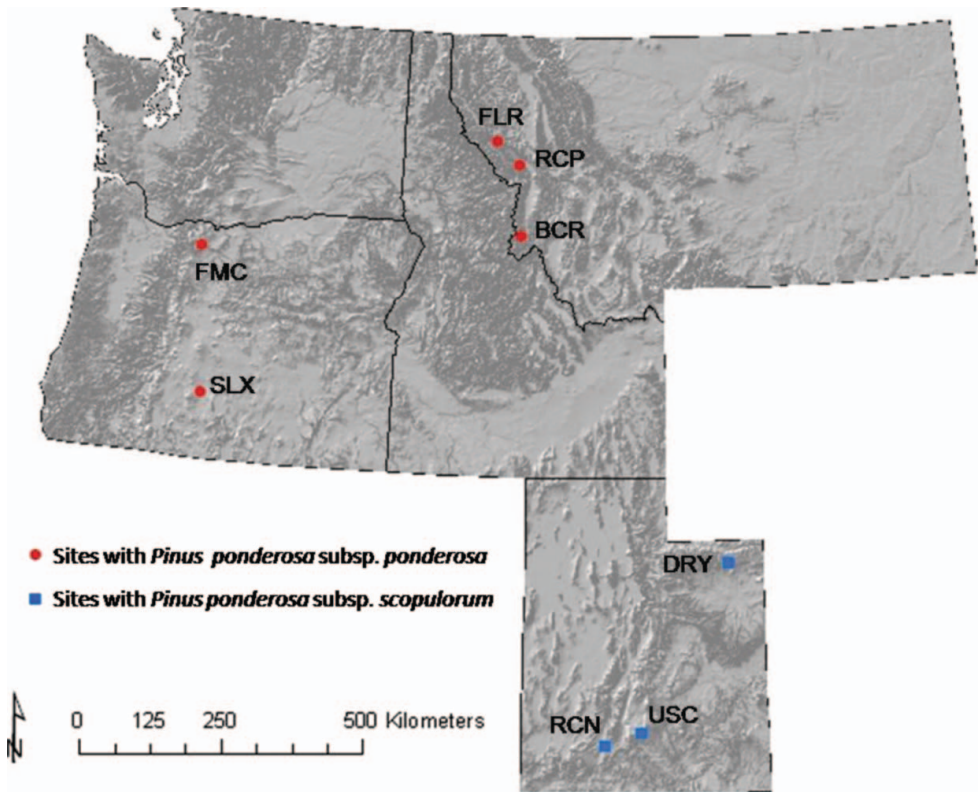
Figure 1 *Location of the eight study sites.*

management, and nitrogen deposition (Fenn et al. 2003). We sampled more than forty trees per site, taking two increment cores per tree at approximately 1.4 m above ground level (Phipps 1985). We used a selective sampling strategy to avoid as many site-related confounding influences to radial growth as possible and excluded trees with large fire scars, dead or damaged tops, and abnormal foliar growth associated with dwarf mistletoe (Stanton 2007). All cores were processed using standard laboratory techniques for sample preparation and sanding (Stokes and Smiley 1968). We used the list method for cross-dating (Yamaguchi 1991), a technique that allows for each ring on each core to be assigned an exact calendar date, which accounts for the possibility of missing rings (i.e., years with zero radial growth) or false rings. We measured ring widths on all cores to 0.001 mm precision using a linear encoder and developed the tree-ring chronology based on the measured values. We confirmed the accuracy of cross-dating at each site us-

ing the program COFECHA (Holmes 1983; Grissino-Mayer 2001) and developed a tree-ring chronology based on cores selected for isotopic analysis using the program ARSTAN (Cook 1985). A tree-ring chronology showed the average annual rate of growth for a study site. To account for age-related declines in radial growth we conservatively standardized the raw ring width measurements using negative exponential, negative linear, or line through the mean. We then selected the STANDARD chronology version for final analysis to preserve low-frequency growth variance needed to examine long-term relationships between radial growth and climate (Grissino-Mayer 1996).

Isotopic Analysis

All trees selected for isotopic analysis had (1) a clear ring structure and growth patterns closely matched to the full chronology pattern (i.e., they were included in the full chronology by virtue of their interseries correlation), (2)

Table 1 *Study site and tree-ring chronology information*

Site	Latitude/ longitude	Elevation (m)	Tree subspecies	Beginning year of tree-ring data	Ending year of tree-ring data[a]	Series intercorrelation/ mean sensitivity[b]
RCN	37.75 112.32	2,261	*scopulorum*	1480	2005	0.65 0.26
USC	37.95 111.6	2,528	*scopulorum*	1620	2005	0.74 0.36
DRY	40.65 109.75	2,736	*scopulorum*	1720	2005	0.75 0.25
FLR	47.33 114.87	1,214	*ponderosa*	1560	2004	0.61 0.26
RCP	46.95 114.33	1,683	*ponderosa*	1602	2007	0.65 0.28
BCR	45.83 114.25	1,555	*ponderosa*	1650	2004	0.62 0.26
SLX	43.05 121.1	1,486	*ponderosa*	1659	1999	0.72 0.30
FMC	45.35 121.43	1,265	*ponderosa*	1750	2000	0.53 0.24

[a]We collected all samples in the following year.
[b]The values are within the range of medians reported for this species by the NOAA Paleoclimatology Program (see http://www.ncdc.noaa.gov/paleo/treering/cofecha/speciesdata.html).

two cores available for destructive analysis, and (3) interior dates as old as possible (preferably pre-1800) at approximately 1.4 m above ground level. Using six matched tree cores per site (thus $n = 12$ cores, except for RCN where $n = 11$), we calculated iWUE by pentad from 1850 (i.e., 1850–1854) through 1995–1999 or 2000–2004 (depending on the length of the tree-ring record). The isotopic laboratory work was performed by the Environmental Isotope Laboratory of the Department of Geosciences at the University of Arizona using standard techniques (Sternberg 1989; Leavitt & Danzer 1993; Coplen 1996). The laboratory analyses provided us with pentadal measurements of carbon isotope composition ($\delta^{13}C$), a measure reflecting temporal variability or directional changes in physiological responses that include stomatal conductance (Seibt et al. 2008). We then used the $\delta^{13}C$ measurements derived from the core samples, $\delta^{13}C_{plant}$, to calculate iWUE ($A/g_{H_2 0}$) where $A = CO_2$ assimilation uptake and $g_{H_2 0} =$ by the following (Farquhar, Ehleringer, and Hubick 1989):

$$\Delta \text{‰} = \frac{\delta^{13}C_{air} - \delta^{13}C_{plant}}{1,000 + \delta^{13}C_{plant}} \times 1,000 \quad (1)$$

where Δ is carbon isotopic discrimination expressed in parts per mille and $\delta^{13}C_{air}$ and $\delta^{13}C_{plant}$ are carbon isotopic composition of the atmosphere and tree rings, respectively. Using Equation 1, iWUE ($A/g_{H_2 0}$) can be determined:

$$\Delta(\text{‰}) = a + (b - a)(1 - 1.6A) \quad C_a g_{H_2 0} \quad (2)$$

where a and b represent fractionation through the stomata (4.4‰) and during carboxylation (27‰) for C_3 plants (Farquhar and Richards 1984), C_a is CO_2 concentration (Etheridge et al. 1998; Keeling and Whorf 2005), A is the CO_2 uptake rate, and $g_{H_2 0}$ is leaf conductance to water. Thus:

$$\text{iWUE} = A/g_{H_2 0} = c_a(b - \Delta)/1.6(b - a) \quad (3)$$

Although each chronology began in the eighteenth century or earlier (Table 1), some individual samples dated to the early 1800s. To avoid the "juvenile effect" that could artificially bias our results (McCarroll and Loader 2004,

789) we excluded from our analyses all pentadal data prior to 1850.

Statistical Analysis

We identified the dominant climatic drivers of radial growth using monthly climatic division-level data (NOAA-ESRL 2009) for temperature, precipitation, and the Palmer Drought Severity Index (PDSI; Palmer 1965). We examined concurrent relationships between annual radial growth and climate; lagged relationships up to one year; and relationships with monthly, annual, and multimonth averages using Pearson correlation. Once we identified the climate variable most strongly related to radial growth, we created bivariate regression models with radial growth as the dependent variable and climate as the independent variable. We examined the residuals from each model for temporal trends using Pearson correlation. The presence of residual trends has been used (Graumlich 1991; Knapp, Soulé, and Grissino-Mayer 2001) to suggest that either model over- or under-prediction is caused by a factor(s) not captured by the (climatic) variables considered. To determine the potential impact of CO_2 on radial growth we added annual CO_2 values as a second independent variable in the regression models and examined the partial R^2 values and residual trends. From 1959 through the end of the tree-ring record (Table 1), we obtained annual CO_2 data from the Mauna Loa record (Keeling and Whorf, 2005). For the period from 1895 through 1958 we obtained pentadal CO_2 data from the Law Dome ice cores (Etheridge et al. 1998) and used a linear interpolation to obtain annual values between pentadal values.

To identify possible significant ($p < 0.05$) temporal trends in radial growth and iWUE by pentad we used Pearson correlation over three time periods: 1850–1995/2000 pentads, 1850–1945 pentads, and 1950–1995/2000 pentads. We selected 1950 as a dividing point because the largest increases in CO_2 occurred during this period and prior studies have used the same threshold to analyze associated changes in CO_2 and plant growth (Kienast & Luxmoore 1988; Graumlich 1991; Knapp, Soulé, and Grissino-Mayer 2001; Soulé and Knapp 2006). We used Curve Estimation (SPSS 2009) to determine the best curve fit (e.g., linear, quadratic, power function) for trends in iWUE. We used

Pearson correlation to determine the relationship between iWUE and radial growth by pentad and to identify the presence of trends in the annual climate data, the annual radial growth data, and the residuals from the linear regression models.

We used pre- and post-1950 subsets to determine if radial growth responses during drought periods have changed through the instrumental time period (i.e., 1895–end). We tested for significant differences in radial growth and drought severity as measured by a twelve-month mean of PDSI from prior-year October to current-year September using Mann–Whitney tests. We retained years in each subset with PDSI values ≤ -1.0 (mild drought or worse) and tested for differences in radial growth and drought severity pre- and post-1949 for the drought years only.

Results

Changes in iWUE

A positive quadratic model provided the best fit for the significant positive trends from 1850 through 1995/2000 and the highest iWUE values were recorded during the last pentad at six of eight sites and during the last two decades at all eight study sites (Figure 2, Table 2). Fifty percent of the sites had significant positive trends in iWUE for the 1850 through 1945 pentads and all sites had significant positive trends for the 1950 through 1995/2000 pentads. The magnitude of the relationship also increased except for the SLX site in southern Oregon (Table 2). Because the significance, direction, and magnitude of temporal trends established by Pearson correlation followed those established by the nonparametric Spearman correlation (e.g., see Table 2 for 1850–end iWUE pentadal trends), we use only the Pearson results for consistency in determining the presence of trends.

Radial Growth

Using the pentadal averages over the full study period (i.e., 1850–end), four sites had significant positive trends in radial growth, with two sites having positive trends in the early (1850–1945) and late (1950–1995/2000) pentadal periods. Using yearly data (1895–end), we
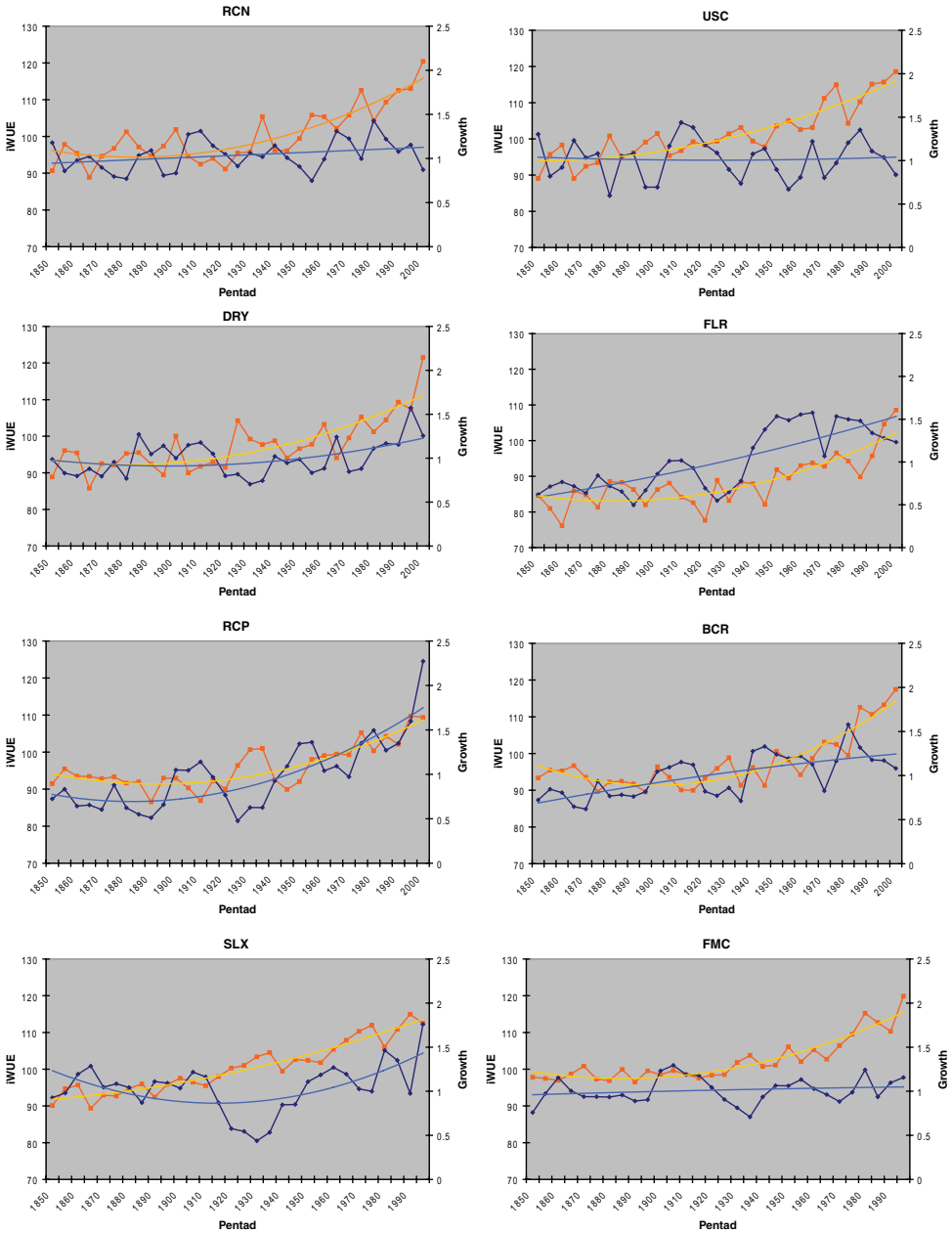
Figure 2 *Pentadal values of intrinsic water-use efficiency (iWUE; orange squares) and radial growth (blue diamonds) from 1850 to end. The trend lines represent a second-order polynomial (gold for iWUE; light blue for radial growth).*

found positive radial growth trends at five sites (Table 3), and two and three sites had positive trends in the last fifty and thirty years, respectively (Table 3). At FLR (Montana), the long-term positive trend in growth was replaced with a negative trend over the last fifty- and thirty-year periods, even though radial growth indexes remained above 1.0 since 1945 (Figure 2).

Table 2 *Temporal trends of intrinsic water-use efficiency (iWUE) and radial growth based on pentadal averages and relationships between iWUE and radial growth*

Site	iWUE with time All pentads 1850– (SLX, FMC n = 30; all others n = 31)	iWUE with time[a] All pentads 1850– (SLX, FMC n = 30; all others n = 31)	iWUE best regression model with time[b,c] All pentads 1850– (SLX, FMC n = 30; all others n = 31)	iWUE with time All pentads 1850–1945 (n = 20)	iWUE with time All pentads 1950– (SLX, FMC n = 10; all others n = 11)	Radial growth with time All pentads 1850– (SLX, FMC n = 30; all others n = 31)	Radial growth with time All pentads 1850–1945 (n = 20)	Radial growth with time All pentads 1950– (SLX, FMC n = 10; all others n = 11)	iWUE and growth All pentads 1850– (r value; p value, n) (SLX, FMC n = 30; all others n = 31)
RCN	0.79**	0.74**	0.76**	0.24	0.84**	0.31	0.28	0.26	−0.05
USC	0.88**	0.89**	0.82**	0.67**	0.82*	0.00	0.06	0.39	−0.25
DRY	0.74**	0.75**	0.66**	0.45**	0.82**	0.39*	0.00	0.69**	0.28
FLR	0.76**	0.78**	0.7**	0.22	0.74**	0.79**	0.49*	−0.51	0.57**
RCP	0.73**	0.63**	0.74**	0.16	0.89**	0.75**	0.28	0.63**	0.62**
BCR	0.73**	0.66**	0.83**	−0.02	0.87**	0.70**	0.57**	0.02	0.38*
SLX	0.94**	0.95**	0.91**	0.87**	0.85**	0.22	−0.62**	0.42	0.14
FMC	0.83**	0.86**	0.87**	0.59**	0.84**	0.19	0.03	0.18	0.18

Note: All values represent Pearson r values except as footnoted.
[a]Spearman correlation r-values.
[b] R^2 values.
[c]All best models quadratic in form.
* $p < 0.05$.
** $p < 0.01$.

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Table 3 Radial growth/climate relationships and linear trends of radial growth, climate, and residuals from the growth/climate and growth/climate + CO_2 regression models

Site	Climate variable	Best growth-climate relationship[a]	Linear trend of climate variable[b]	Linear trend of climate variable (last 50 years)	Linear trend of climate variable (last 30 years)	Growth-time relationship 1895–end	Growth-time relationship Last 50 years	Growth-time relationship Last 30 years	Linear trend of residuals for the growth-climate regression model	Growth-climate + CO_2 relationship[a]	Linear trend of residuals for the growth-climate + CO_2 model[a]	Improvement in R^2 for the +CO_2 model
RCN	Annual[c] PDSI	0.37** 110	0.14 110	0.25 50	0.06 30	0.15 111	0.07 50	−0.28 30	0.08 110	0.37 110	0.04 110	0.00
USC	July PDSI	0.31** 111	0.11 111	0.22 50	0.04 30	0.02 111	0.23 50	−0.16 30	−0.05 111	0.31 111	−0.03 111	0.00
DRY	January + May + June precipitation	0.17** 111	0.11 111	0.14 50	0.20 30	0.27** 111	0.53** 50	0.45* 30	0.12 111	0.3** 111	−0.13 111	0.13
FLR	Annual PDSI	0.13** 109	−0.12 109	−0.42** 50	−0.38** 30	0.59** 110	−0.29* 50	−0.45* 30	0.68** 109	0.38** 109	0.21* 109	0.25
RCP	April + May + June + July precipitation	0.1** 113	0.05 113	0.14 50	−0.16 30	0.67** 113	0.75** 50	0.72** 30	0.64** 112	0.64** 113	−0.04 113	0.54
BCR	May + June + July precipitation	0.24** 110	−0.01 110	0.12 50	−0.04 30	0.34** 110	0.05 50	−0.32 30	0.39** 110	0.31** 110	0.12 110	0.07
SLX	Prior November to current August PDSI	0.36** 104	0.06 104	−0.08 50	−0.02 30	0.38** 105	0.27 50	0.4* 30	0.43** 104	0.54** 104	−0.06 104	0.18
FMC	May + June + July precipitation	0.13** 106	0.17 106	0.15 50	0.37* 30	−0.04 106	0.16 50	0.33 30	−0.09 106	0.13 106	−0.10 106	0.00

Note: PDSI = Palmer Drought Severity Index.

[a] R^2 values and all relationships are positive.

[b] Determined via Pearson correlation (r value and sample size).

[c] Annual calculated as the 12-month average of prior-year October to current-year September values.
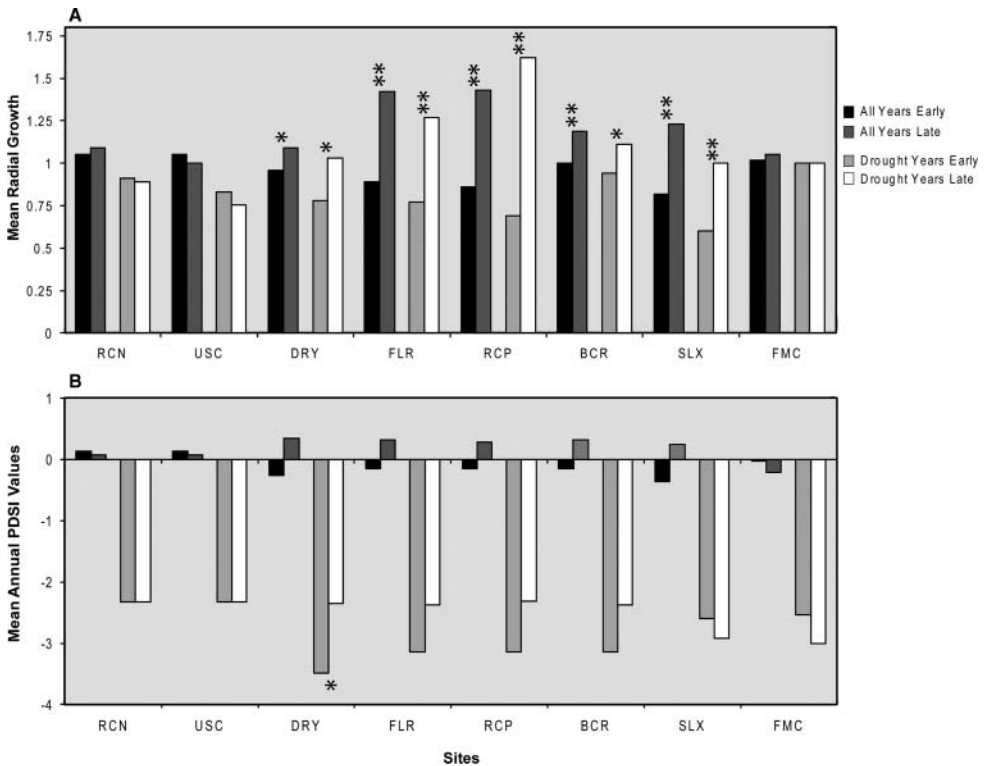
* $p < 0.05$.

** $p < 0.01$.

Figure 3 *A comparison of radial growth and annual Palmer Drought Severity Index (PDSI) values (prior-year October through current-year September) between the early (1896–1949) and late (1950–end) periods using all annual data and data from years when annual PDSI values were ≤ -1.00 (moderate drought severity). Significant differences based on a Mann–Whitney U test are highlighted (* $p < 0.05$; ** $p < 0.01$).*

Relationships Among Radial Growth and Climate, CO_2, and iWUE

The primary climatic drivers of radial growth were site specific but included the impacts of moisture during the growing season at all sites (e.g., July PDSI in southern Utah [USC]; May–July precipitation at BCR [southwestern Montana] and FMC [northern Oregon]) and moisture extending to the prior calendar year at others (e.g., prior-year October to current-year September [i.e., Annual] PDSI values at RCN [southern Utah] and FLR [Montana]; Table 3). Radial growth variance explained by the primary climate variables ranged from 10 to 37 percent (Table 3). At four sites, significant positive trends exist in residuals from the growth/climate regression

model, indicating that the climate variables alone underpredict observed radial growth in the later portion of the study. Adding annual CO_2 as a second variable in the regression models revealed that it influences radial growth at five of the eight study sites significantly (Table 3) and increased explained variance at these sites by an average of 23.4 percent.

None of the climate variables displayed long-term temporal trends, but May through July precipitation in northern Oregon (FMC) increased during the last thirty years, and annual PDSI for FLR (Montana) decreased for the last fifty- and thirty-year periods (Table 3). Annual CO_2 values trend positively through time ($R^2 = 0.99$ for a cubic model), and there are significant, positive relationships between iWUE and radial growth at three of the sites over the

full study period when using the pentadal data (Table 2).

Radial Growth Comparisons During Drought Years

Mean radial growth was significantly greater in the post-1950 period compared to the pre-1950 period at five sites. The increases occurred absent significant differences in moisture conditions, with all sites recording mean annual PDSI values in the near normal range (0.49 to –0.49). Further, using a subset of drought years produced similar results, with four sites recording significantly greater radial growth in the post-1950 period despite no significant differences in drought conditions. At these four sites, the mean radial growth was at or above normal (1.0) despite average drought conditions classified as moderate or worse (PDSI $\leq$ –2.0). At DRY (northern Utah), there was a significant difference in both radial growth rates and drought severity. Radial growth at DRY increased post-1950 when drought conditions were less severe than the pre-1950 period.

Discussion

Our results demonstrate that trends toward higher rates of iWUE for ponderosa pine are panregional, occurring at eight sites within three distinct climatic regimes and for two subspecies (Figure 1). The increasing trends in iWUE at our sites are similar to those reported by Feng (1999) for several coniferous tree species found throughout western North America, and increasing iWUE has been reported for conifers at other northern hemisphere locations (e.g., Bert, Leavitt, and Dupouey 1997; Saurer, Siegwolf, and Schweingruber 2004). Further, our results showing the highest iWUE were recorded in the last pentad at six of eight sites and follow a positive quadratic progression at all sites (Figure 2), suggesting that future increases in iWUE are likely for ponderosa pine within our study regions as CO_2 levels increase.

Five of the eight sites display long-term positive trends in annual radial growth rates post-1895, which have occurred absent long-term trends toward more favorable climate conditions (Table 3). Pairing CO_2 with the climate

variables results in a significant improvement in the explanatory power of the model at five sites. At all but one site, the positive temporal autocorrelation of residuals disappears with the inclusion of CO_2, and at three sites a significant relationship between pentadal iWUE and radial growth exists. We also found significant improvements in radial growth rates during drought years after 1950. In a prior study that included the full chronologies for FMC and SLX plus six additional sites in the Pacific Northwest, Soulé and Knapp (2006) found similar improvements in radial growth during drought periods of the late twentieth to early twenty-first century and concluded that CO_2 enrichment was likely operative. This prior study lacked the empirical evidence provided by the iWUE data, however, which were derived from collected tree-ring samples.

For three sites (RCN, USC in southern Utah, and FMC in northern Oregon), we found no evidence of significant radial growth increases despite significant increases in iWUE. As the RCN and USC chronologies were developed from *P. ponderosa* var. *scopulorum* (Figure 1), we posited that different genotypes might vary in their responses to increased iWUE, but a similar response occurs with the FMC chronology developed from *P. ponderosa* var. *ponderosa* that otherwise was responsive to increased iWUE, and the DRY (northern Utah) chronology was also developed from *P. ponderosa* var. *scopulorum*. Alternatively, we also speculated that the timing of precipitation might be influential, as RCN and USC experience a late-summer maximum, but FMC has a late-summer minima of precipitation and also lacks long-term trends in radial growth.

Although microscale environmental factors undetected by our analysis could override the potentially positive impacts of increasing iWUE on radial growth in some locations, the theoretical progression that increased CO_2 improves iWUE is supported by our results. In concert, these findings lead us to conclude that, for open-canopy ponderosa pine trees growing in locations with limited anthropogenic disturbance, increased iWUE associated with rising CO_2 might be a contributing factor to observed increases in radial growth rates through time. That said, we caution that these conclusions are based on a limited sample size for each site

and focus on one of many potential vectors of change for western U.S. forests.

Multiple, synergistic linkages exist between forest processes and climate change (Bonan 2008) and between climate change and forest processes (Ollinger et al. 2008). For example, future increases in CO_2 should lead to increasing rates of net primary productivity (NPP) in a variety of forested ecosystems because "the photosynthetic uptake of carbon that drives NPP is not saturated at current levels" (Norby et al. 2005, 18052). In turn, this can potentially impact rates of carbon sequestration and feedback mechanisms between the biosphere and atmosphere that control CO_2 concentrations. Globally, about one third of the carbon released by humans from fossil fuel combustion and land clearing is removed from the atmosphere by trees, and forests can impact climatic conditions through changes in surface albedo, evapotranspiration, and runoff (Bonan 2008; Ollinger et al. 2008). If potential climate changes lead to increasing aridity in the western United States, additional increases in iWUE associated with future increase in CO_2 might ameliorate growth declines associated with drought conditions. As iWUE changes are recognized as a potentially important component of global environment change processes (Aber et al. 2001), it is likely that forest ecosystems will continue to be influenced by rising CO_2. ∎

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