

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

By Peter T. Soule and Paul A. Knapp

[Soulé, P.T.](#) and [Knapp, P.A.](#) 2011. Radial growth and increased water-use efficiency for ponderosa pine trees in three regions in the western United States. *The Professional Geographer*. 63(3) (August) <http://dx.doi.org/10.1080/00330124.2011.574088>

Made available courtesy of the Association of American Geographers: <http://www.aag.org/> and Taylor & Francis: <http://www.taylorandfrancis.com/>

**\*\*\*Reprinted with permission. No further reproduction is authorized without written permission from Taylor & Francis. This version of the document is not the version of record. Figures and/or pictures may be missing from this format of the document. \*\*\***

### **Abstract:**

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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> can positively impact tree growth rates in the western United States and are thus an evolving component of forest ecosystem processes.

**Keywords:** atmospheric CO<sub>2</sub> | climate | drought | intrinsic water-use efficiency | *pinus ponderosa* | geology

### **Article:**

In 2008, atmospheric CO<sub>2</sub> concentrations (hereafter CO<sub>2</sub>) 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<sub>2</sub> on tree growth is decreased stomatal conductance (Tognetti et al. 1998). As CO<sub>2</sub> 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<sub>2</sub> during photosynthesis currently and in recent decades may have occurred at rates equivalent to a lower CO<sub>2</sub> 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<sub>2</sub> 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; Arneeth 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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 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 using 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).

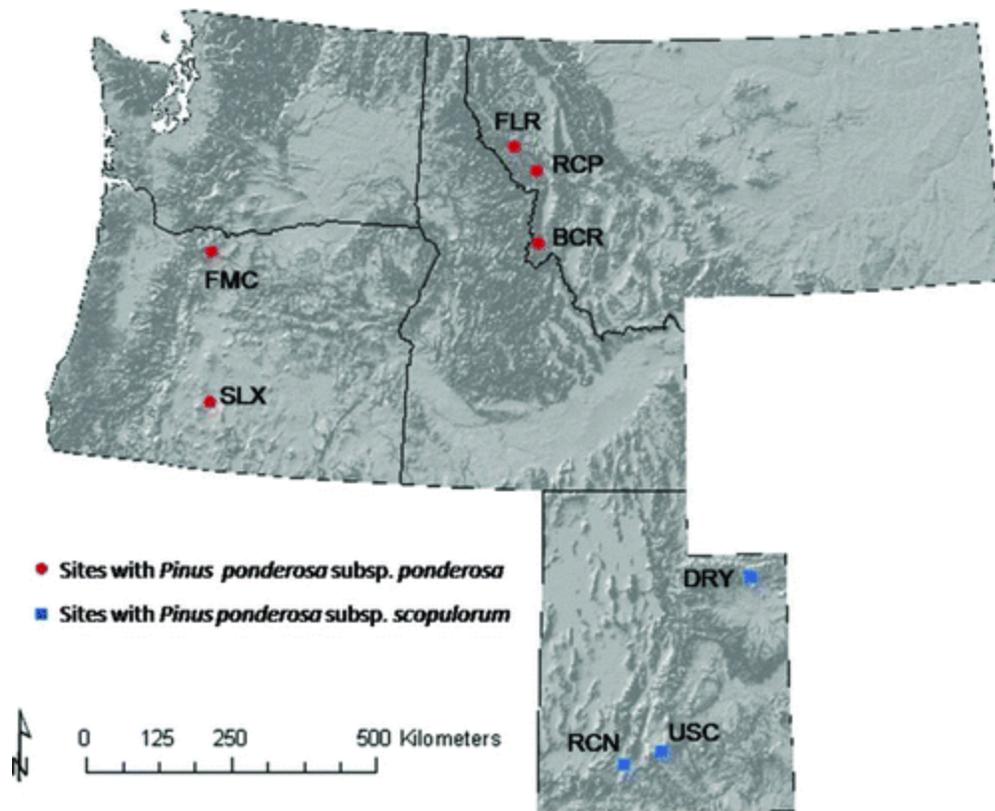


Figure 1 Location of the eight study sites.

**TABLE 1 IS OMITTED FROM THIS FORMATTED DOCUMENT**

### 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) 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,  $\delta^{13}\text{C}_{\text{plant}}$ , to calculate iWUE ( $\text{A/g H}_2\text{O}$ ) where  $\text{A}$  =  $\text{CO}_2$  assimilation uptake and  $g$  = by the following (Farquhar, Ehleringer, and Hubick 1989):

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

where  $\Delta$  is carbon isotopic discrimination expressed in parts per mille and  $\delta^{13}\text{C}_{\text{air}}$  and  $\delta^{13}\text{C}_{\text{plant}}$  are carbon isotopic composition of the atmosphere and tree rings, respectively.

Using Equation 1, iWUE ( $\text{A/gH}_2\text{O}$ ) can be determined:

$$\Delta(\text{‰}) = a + (b - a)(1 - 1.6A) \quad C_a g_{\text{H}_2\text{O}} \quad (2)$$

where  $a$  and  $b$  represent fractionation through the stomata ( $4.4\frac{1}{2}$ ) and during carboxylation ( $27\frac{1}{2}$ ) for  $\text{C}_3$  plants (Farquhar and Richards 1984),  $C_a$  is  $\text{CO}_2$  concentration (Etheridge et al. 1998; Keeling and Whorf 2005),  $A$  is the  $\text{CO}_2$  uptake rate, and  $g_{\text{H}_2\text{O}}$  is leaf conductance to water.

Thus:

$$\text{iWUE} = \text{A/g}_{\text{H}_2\text{O}} = c_a(b - \Delta)/1.6(b - a) \quad (3)$$

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 underprediction is caused by a factor(s) not captured by the (climatic) variables considered. To determine the potential impact of  $\text{CO}_2$  on radial growth we added annual  $\text{CO}_2$  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  $\text{CO}_2$  data from the Mauna Loa record (Keeling and Whorf, 2005). For the period from 1895 through 1958 we obtained pentadal  $\text{CO}_2$  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

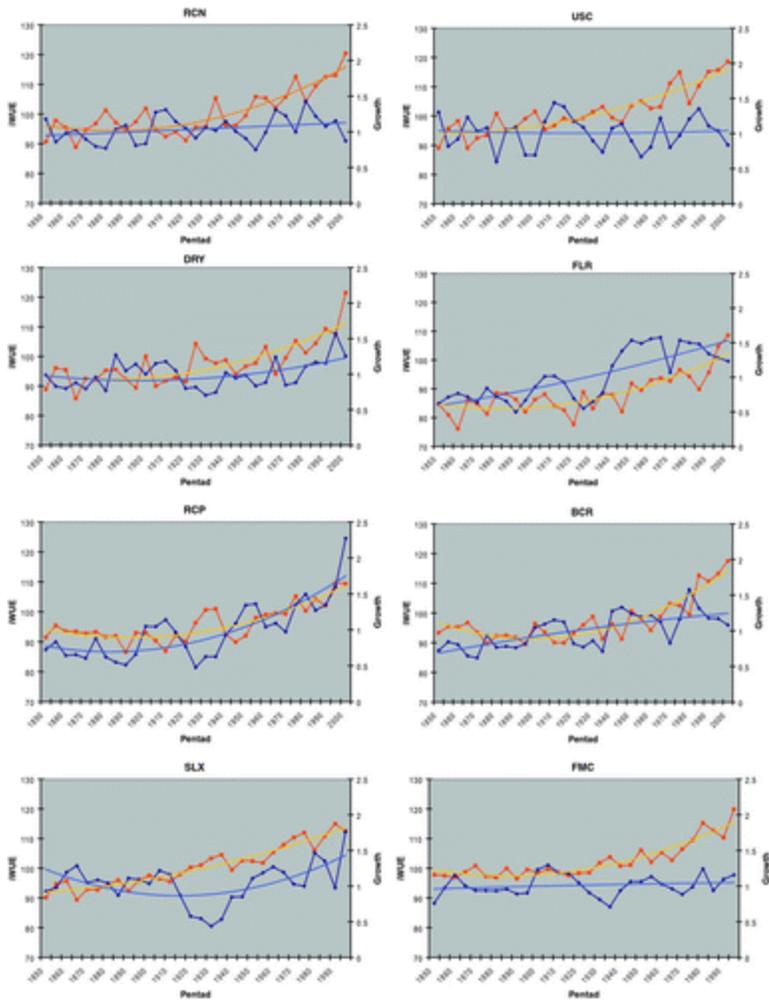
pentads, and 1950–1995/2000 pentads. We selected 1950 as a dividing point because the largest increases in CO<sub>2</sub> occurred during this period and prior studies have used the same threshold to analyze associated changes in CO<sub>2</sub> and plant growth (Kienast & Luxmoore 1988; Graumlich 1991; 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  $\leq -1.0$  (mild drought or worse) and tested for differences in radial growth and drought severity pre- and post-1949 for the drought years only.

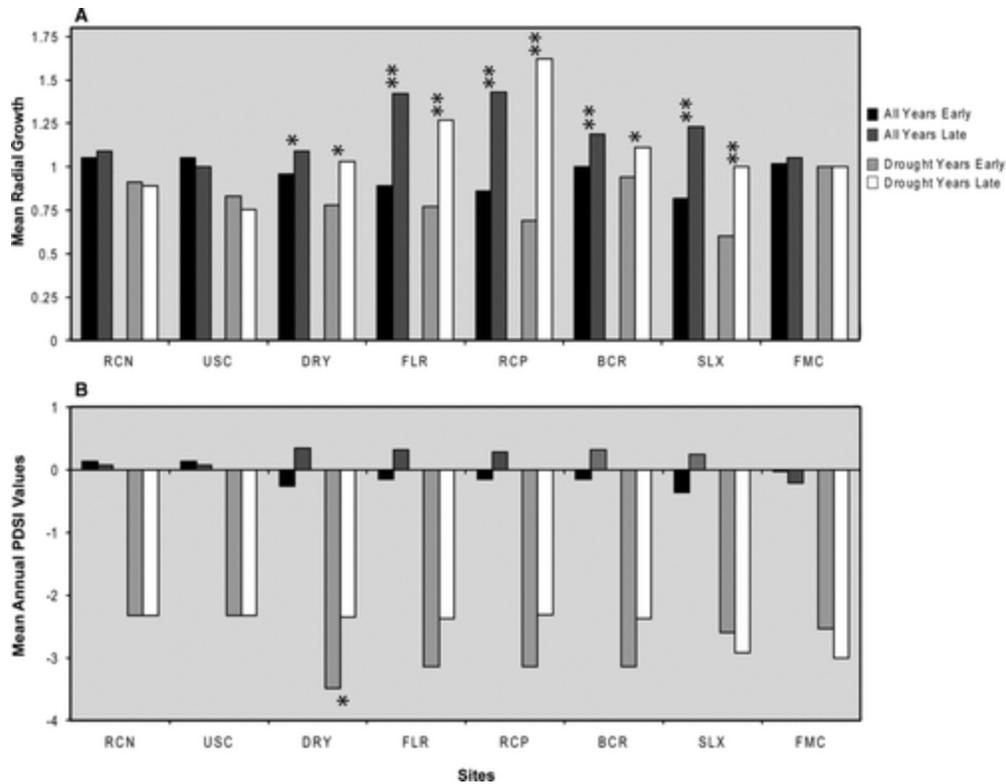
## **Results**

### **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.



**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).



**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  $\leq -1.00$  (moderate drought severity). Significant differences based on a Mann–Whitney  $U$  test are highlighted ( $*p < 0.05$ ;  $**p < 0.01$ ).

**TABLE 2 IS OMITTED FROM THIS FORMATTED DOCUMENT**

### 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 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 3 IS OMITTED FROM THIS FORMATTED DOCUMENT**

## **Relationships Among Radial Growth and Climate, CO<sub>2</sub>, 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<sub>2</sub> 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<sub>2</sub> 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 –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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>, 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>.

#### Acknowledgments

PETER T. SOULÉ is Professor in the Department of Geography and Planning at Appalachian State University, Boone, NC 28608. E-mail: soulept@appstate.edu. His primary research focus deals with understanding the linkages between changing climate and atmospheric conditions on forest ecosystems.

PAUL A. KNAPP is Professor in the Department of Geography at the University of North Carolina Greensboro, Greensboro, NC 27412. E-mail: paknapp@uncg.edu. His research interests focus on climatology, biogeography, and tree-ring science projects in the American West.

#### Notes

\*This project was funded by the USDA NRI Competitive Grant Program, Plant Adaptations to the Environment #2005-35100-15226, and Faculty Research Grants from both Appalachian State University and the University of North Carolina at Greensboro. The Environmental Isotope Laboratory at the Laboratory of Tree-Ring Research, University of Arizona, conducted the isotopic analyses for use under the guidance of Dr. Steve Leavitt. Steve Shelly, USDA Forest Service Region 1 RNA coordinator, helped us identify study sites and helped us in the field. Also assisting in field and laboratory work were Justin Maxwell, Jason Ortegren, Ian Snider, William Tyminski, and Philip White. We thank all of these individuals and the two anonymous reviewers of the article.

#### References:

1. Aber, J., Neilson, R. P., McNulty, S., Lenihan, J. M., Bachelet, D. and Drapek, R. J. 2001. Forest processes and global environmental change: Predicting the effects of individual and multiple stressors. *BioScience*, 51: 735–51.
2. Ainsworth, E. A. and Rogers, A. 2007. The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]; mechanisms and environmental interactions. *Plant, Cell and Environment*, 30: 258–70.
3. Arneeth, A., Lloyd, J., Santruckova, H., Bird, M., Girgoryev, S., Kalaschnikov, Y. N., Gleixner, G. and Schulze, E. 2002. Response of central Siberian Scots pine to soil water deficit

and long-term trends in atmospheric CO<sub>2</sub> concentration. *Global Biogeochemical Cycles*, 16: 5.1–5.13.

4. Bert, D., Leavitt, S. and Dupouey, J.-L. 1997. Variations of wood  $\delta^{13}\text{C}$  and water-use efficiency of *Abies alba* during the last century. *Ecology*, 78: 1588–96.

5. Bonan, G. B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, 320: 1444–49.

6. Bréda, N., Huc, R., Granier, A. and Dreyer, E. E. 2006. Temperate forest trees and stand under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63: 625–44.

7. Christensen, J., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I. and Jones, R. 2007. “Regional climate predictions”. In *Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Edited by: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M. and Miller, H. L. 847–940. New York: Cambridge University Press.

8. Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V. and Aubinet, M. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437: 529–33.

9. Cook, E. 1985. A time series analysis approach to tree-ring standardization, Tucson, AZ: PhD thesis, University of Arizona.

10. Coplen, T. 1996. New guidelines for reporting stable hydrogen, carbon and oxygen isotope-ratio data. *Geochimica. et Cosmochimica Acta*, 60: 3359–60.

11. Etheridge, D., Steele, L., Langenfelds, R., Francey, R., Barnola, V. and Morgan, J.-M. 1998. “Historical CO<sub>2</sub> records from the Law Dome DE08, DE08–2, and DSS ice cores”. In *Trends: A compendium of data on global change.*, Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy.

12. Farquhar, G. D., Ehleringer, J. R. and Hubick, K. T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40: 503–37.

13. Feng, X. 1999. Trends in intrinsic water-use efficiency of natural trees for the past 100–200 years: A response to atmospheric concentration. *Geochimica et Cosmochimica Acta*, 63: 1891–1903.

14. Fenn, M., Baron, J., Allen, E., Rueth, H., Nydick, K., Geiser, L., Bowman, W., Sickman, J., Meixner, T., Johnson, D. and Neitlich, P. 2003. Ecological effects of nitrogen deposition in the western United States. *BioScience*, 53: 404–20.

15. Graumlich, L. 1991. Subalpine tree growth, climate, and increasing CO<sub>2</sub>: An assessment of recent growth trends. *Ecology*, 72: 1–11.
16. Grissino-Mayer, H. D. 1996. “A 2129-year reconstruction of precipitation for northwestern New Mexico, USA”. In *Tree-rings environment and humanity*, Edited by: Dean, J. S., Meko, D. M. and Swetnam, T. W. 191–204. Tucson: Department of Geosciences, The University of Arizona.
17. Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, 57: 205–21.
18. Hanson, P. and Weltzin, J. 2000. Drought disturbance from climate change: Response of United States forests. *The Science of the Total Environment*, 262: 205–20.
19. Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43: 69–78.
20. Keeling, C. and Whorf, T. 2005. “Atmospheric CO<sub>2</sub> records from sites in the SIO air sampling network”. In *Trends: A compendium of data on global change.*, Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy.
21. Kienast, F. and Luxmoore, R. 1988. Tree-ring analysis and conifer growth responses to increased atmospheric CO<sub>2</sub> levels. *Oecologia*, 76: 487–95.
22. Knapp, P. and Soulé, P. 2008. Use of atmospheric CO<sub>2</sub>-sensitive trees may influence dendroclimatic reconstructions. *Geophysical Research Letters*, 35 doi:10.1029/2008GL035664
23. Knapp, P., Soulé, P. and Grissino-Mayer, H. 2001. Detecting the potential regional effects of increased atmospheric CO<sub>2</sub> on growth rates of western juniper. *Global Change Biology*, 7: 903–17.
24. Leavitt, S. and Danzer, S. 1993. Method for batch processing small wood samples to holocellulose for stable-carbon isotope analysis. *Analytical Chemistry*, 65: 87–89.
25. Liu, X., Shao, X., Liang, E., Zhao, L., Chen, T., Qin, D. and Ren, J. 2007. Species dependent responses of juniper and spruce to increasing CO<sub>2</sub> concentration and to climate in semi-arid and arid areas of northwestern China. *Plant Ecology*, 193: 195–209.
26. McCarroll, D. and Loader, N. 2004. Stable isotopes in tree rings. *Quaternary Science Reviews*, 23: 771–801.
27. NOAA-ESRL. 2009. US Climate Division: Temperature, precipitation and Palmer Drought Severity Index (PDSI). <http://www.esrl.noaa.gov/psd/data/timeseries/> (last accessed 1 December 2009).

28. Norby, R. J., Delucia, E. H., Glelen, B., Calfapletra, C., Giardina, C. P., King, J. S., Ledford, J. 2005. Forest response to elevated CO<sub>2</sub> is conserved across a broad range of productivity. *Proceedings of the National Academy of Science*, 102: 18052–56.
29. Ollinger, S. V., Goodale, C. L., Hayhoe, K. and Jenkins, J. P. 2008. Potential effects of climate change and rising CO<sub>2</sub> on ecosystem processes in northeastern U.S. forests. *Mitigation and Adaptation Strategies for Global Change*, 13: 467–85.
30. Palmer, W. 1965. *Meteorological drought*, Washington, DC: U.S. Government Printing Office.
31. Phipps, R. 1985. *Collecting, preparing, crossdating, and measuring tree increment cores*, Reston, VA: Water Resources Division. U.S. Geological Survey Water-Resources Investigations Report 85-4148.
32. Saurer, M., Siegwolf, R. and Schweingruber, F. 2004. Carbon isotope discrimination indicates improving water-use efficiency of trees in northern Eurasia over the last 100 years. *Global Change Biology*, 10: 2109–20.
33. Seibt, U., Rajabi, A., Griffiths, H. and Berry, J. A. 2008. Carbon isotopes and water use efficiency: Sense and sensitivity. *Oecologia*, 155: 441–54.
34. Soulé, P. and Knapp, P. 2006. Radial growth rate increases in naturally-occurring ponderosa pine trees: A late 20th century CO<sub>2</sub> fertilization effect. *New Phytologist*, 171: 379–90.
35. SPSS. 2009. *SPSS for Windows, Rel. 17.0.0*, Chicago: SPSS.
36. Stanton, S. 2007. Effects of dwarf mistletoe on climate response of mature ponderosa pine trees. *Tree Ring Research*, 63: 69–80.
37. Sternberg, L. 1989. “Oxygen and hydrogen isotope measurements in plant cellulose”. In *Modern methods in plant analysis*, Edited by: Linskens, H. F. and Jackson, J. F. 89–98. New York: Springer-Verlag.
38. Stokes, M. and Smiley, T. 1968. *Introduction to tree-ring dating*, Chicago: University of Chicago Press.
39. Tang, K., Feng, X. and Funkhouser, G. 1999. The  $\delta^{13}\text{C}$  of trees in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. *Global Change Biology*, 5: 33–40.
40. Tognetti, R., Longobucco, A., Miglietta, F. and Raschi, A. 1998. Transpiration and stomatal behaviour of *Quercus ilex* plants during the summer in a Mediterranean carbon dioxide spring. *Plant, Cell and Environment*, 21: 613–22.

41. van Mantgem, P., Stephenson, N., Byrne, J., Daniels, L., Franklin, J., Fulé, P., Harmon, M., Larson, A., Smith, J., Taylor, A. and Veblen, T. 2009. Widespread increase of tree mortality rates in the Western United States. *Science*, 323: 521–24.
42. Waterhouse, J., Switsur, V., Barker, A., Carter, A., Hemming, D., Loader, N. and Robertson, I. 2004. Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews*, 23: 803–10.
43. Western Wood Products Association. 2009. Ponderosa pine species facts. <http://www2.wwpa.org/SPECIESPRODUCTS/PonderosaPine/tabid/298/Default.aspx> (last accessed 1 December 2009).
44. Yamaguchi, D. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research*, 21: 414–16.
45. Youngblood, A. 2005. Silvicultural systems for managing Ponderosa pine, Albany, CA: Pacific Southwest Research Station. USDA Forest Service Technical Report PSW-GTR-198, U.S. Department of Agriculture.