Sensitivity of ring growth and carbon allocation to climatic variation vary within ponderosa pine trees

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Most dendrochronological studies focus on cores sampled from standard positions (main stem, breast height), yet vertical gradients in hydraulic constraints and priorities for carbon allocation may contribute to different growth sensitivities with position. Using cores taken from five positions (coarse roots, breast height, base of live crown, mid-crown branch and treetop), we investigated how radial growth sensitivity to climate over the period of 1895–2008 varies by position within 36 large ponderosa pines (Pinus ponderosa Dougl.) in northern Arizona. The climate parameters investigated were Palmer Drought Severity Index, water year and monsoon precipitation, maximum annual temperature, minimum annual temperature and average annual temperature. For each study tree, we generated Pearson correlation coefficients between ring width indices from each position and six climate parameters. We also investigated whether the number of missing rings differed among positions and bole heights. We found that tree density did not significantly influence climatic sensitivity to any of the climate parameters investigated at any of the sample positions. Results from three types of analyses suggest that climatic sensitivity of tree growth varied with position height: (i) correlations of radial growth and climate variables consistently increased with height; (ii) model strength based on Akaike’s information criterion increased with height, where treetop growth consistently had the highest sensitivity and coarse roots the lowest sensitivity to each climatic parameter; and (iii) the correlation between bole ring width indices decreased with distance between positions. We speculate that increased sensitivity to climate at higher positions is related to hydraulic limitation because higher positions experience greater xylem tensions due to gravitational effects that render these positions more sensitive to climatic stresses. The low sensitivity of root growth to all climatic variables measured suggests that tree carbon allocation to coarse roots is independent of annual climate variability. The greater number of missing rings in branches highlights the fact that canopy development is a low priority for carbon allocation during poor growing conditions.

Keywords: Arizona, climate sensitivity, missing rings, roots, tree rings.

Introduction

Climate frequently controls tree growth, and annual ring widths are often used to reconstruct climate (Fritts 1966, 1991, Schweingruber 1996, Cook et al. 2000, Hughes 2002). Wider rings form during years of good growing conditions, while narrow, incomplete or missing rings form during years of constrained growth caused by suppression, cold temperatures (Colenutt and Luckman 1991), drought (Fritts 1976, Kramer and Kozlowski 1979, Colenutt and Luckman 1991) and other factors. Due to the strong relationship between climate and growth, tree rings are commonly used to develop annual climate reconstructions (Fritts 1991, Schweingruber 1996, Cook et al. 2000, Hughes 2002). Dendroclimatic analyses have been used to reconstruct various hydroclimatic metrics (Meko et al. 1980, D’Arrigo and Jacoby 1991, Grissino-Mayer 1995, Cleaveland et al. 2003, Villanueva-Diaz et al. 2007). Dendroclimatological
reconstructions are almost exclusively based on ring widths sampled at tree breast height (~1.37 m) or lower on the bole. While ring widths are known to vary by sample height within trees (Duff and Nolan 1953, Fritts et al. 1965, Brookhouse and Brack 2008), the relationship between within-tree variability and climate sensitivity is less well understood.

Although the limiting growth factor usually determines tree ring sensitivity to climate, two additional factors, hydraulic limitation and basipetal, or top-down, carbon allocation, likely alter the strength of the sensitivity within trees. Gravitational effects on water transport up the bole reduce water availability at the top of a tall tree compared with its base (Ryan and Yoder 1997, Koch et al. 2004, Woodruff et al. 2004). This reduced water availability can limit growth in tall treetops by reducing stomatal conductance (Ryan and Yoder 1997), foliar cell turgor (Koch et al. 2004, Woodruff et al. 2004) and internal CO₂ diffusion (Mullin et al. 2009). Decreasing water availability with height suggests that sensitivity of tree growth to climate may also vary with height. It is possible that reduced water availability makes treetops more sensitive in the presence of climate fluctuations compared with lower positions in the tree. Alternatively, basipetal carbon allocation during the growing season (Myers 1963, Kozlowski 1971, Hansen et al. 1996, Pallardy 2008) possibly renders treetops less sensitive to climate than lower positions on the tree. In other words, the top-down distribution of newly fixed carbon results in less sensitive (more complacent) growth at the treetop compared with more sensitive growth at the base. By this second line of reasoning, treetops would be less sensitive to climatic variation than tree bases.

Non-bole positions, such as coarse roots and branches, might also differ in climatic sensitivity to growth. Plant growth and survival strategies often involve changes in within-tree carbon sink strength, where growth is prioritized to the organ that acquires the most limiting resource (Chapin et al. 2002, Pallardy 2008). For example, water is often the most limiting resource to ponderosa pines (Pinus ponderosa Doug.) in the semi-arid Southwest (Fritts 1966, Adams and Kolb 2005). Given this, ponderosa pine roots, compared with the bole and branches, would be persistently stronger carbon sinks, making their growth less sensitive to variation in water availability. Branches might also differ from the bole in climate sensitivity because of reduced hydraulic conductance at branch junctions (Tyree and Alexander 1993, Spicer and Gartner 1998) and the slow arrest of growth associated with the natural branch pruning process (Andrews and Gill 1939, Reukema 1959, Pallardy 2008).

The pattern of missing rings can provide valuable insight on within-tree carbon allocation. Basipetal carbon allocation, the geometry of decreased bole area per unit carbon higher on the bole due to stem taper, and the younger cambium higher on the bole (Lindstrom 1997, Park et al. 2009), may reduce tree ring width from treetop to tree base in a given year (Myers 1963, Waring and O’Hara 2006) and suggest that higher positions have fewer incomplete or missing rings (Cherubini et al. 1996). In this scenario, carbon allocation to ring growth during years with poor growing conditions, such as drought, is prioritized to the upper crown, with the lower bole having more incomplete and/or missing rings due to insufficient carbon sink strength (Turberville and Hough 1939, Bormann 1965, Niklasson 2002, Waring and O’Hara 2006). Despite the potential use of missing rings as a proxy for whole-tree carbon allocation priorities, to our knowledge this subject has been little studied.

Southwestern ponderosa pine forests provide a model system to investigate the climate sensitivity of tree growth and carbon allocation. While ponderosa pine growth in this region is predominantly water-limited (Fritts 1966, Adams and Kolb 2005), the high altitude of northern Arizona, where cold winters and frigid soil profiles due to snowmelt commonly persist late into the spring, makes this environment potentially temperature-limited as well. Northern Arizona ponderosa pines have a well-established and successfully cross-dated chronology that has been used in earlier studies (Adams and Kolb 2005, Kolb et al. 2007). Furthermore, active restoration thinning and research within the region provides a framework to investigate the relationship between tree density and climatic sensitivity (Biondi 1996). Previous work indicates reduced climatic sensitivity with increased tree density (Cescatti and Piotti 1998, Gae-Isquierdo et al. 2009) or decreased tree density (i.e., thinning) in small trees (Martin-Benito et al. 2010); however, the strength of this relationship for large trees is not well known. Thus, due to their limiting growth factors and well-established chronologies, southwestern US ponderosa pine trees are particularly well suited to examine inter-annual climatic variability and carbon allocation patterns.

Using this model system, our study investigates the climatic sensitivity and carbon allocation patterns within large southwestern US ponderosa pine trees. We ask the following research questions: (i) Does climatic sensitivity of radial growth decrease with tree density? (ii) How does climatic sensitivity of radial growth vary with sample height and among roots, bole and branches? (iii) How does the number of missing rings vary with bole height and among roots, bole and branches? Improved understanding of both the climatic sensitivity of tree growth and carbon allocation patterns within ponderosa pine can potentially be used to optimize climate reconstruction and carbon sequestration models.

Materials and methods

Study site and trees

Our study sites are located in the Fort Valley Experimental Forest (USDA Forest Service, Rocky Mountain Research Station) 10 km northwest of Flagstaff, AZ, USA (N35°15′58″, W111°42′1″, elevation 2200 m). This ponderosa pine-dominated forest was experimentally thinned in 1998 to the following four
post-treatment average basal area densities: control 38.2 m² ha⁻¹, light thinning 22.4 m² ha⁻¹, moderate thinning 18.1 m² ha⁻¹ and heavy thinning 15.8 m² ha⁻¹ (Skov et al. 2005). Two cohorts of trees comprise the population of ponderosa pines in our study sites: one composed of older ponderosa pines established prior to European settlement in the 1890s, and a second composed of younger ponderosa pines predominantly established in 1919 when a large establishment event occurred (Savage et al. 1996). Overgrazing and fire suppression throughout most of the twentieth century promoted increased survival of the second cohort and greater intra-specific competition over the past 90 years (Covington et al. 1997). The soils are classified as basaltic, fine montmorillonitic complex of frigid Typic Argiborolls and Mollic Eutroboralfs (Mast et al. 1999). Eighteen (≥60 cm diameter at breast height) healthy and non-leaning presettlement ponderosa pine trees were selected from each of the four basal area treatments (control, light thinning, moderate thinning and heavy thinning) in the Fort Valley Experimental Forest, for a total of 72 trees. From these 72 trees, 9 were then randomly selected from each treatment, yielding 36 study trees in total. These 36 trees had an average height of 28.9 ± 0.76 m; a diameter at breast height of 73.8 ± 1.4 cm; an age of 219 ± 11 years; and a basal area density, as measured with a basal area factor 10 angle gauge, of 13.5 ± 1.2 m² ha⁻¹. The basal area density associated with each tree is a local measure of tree density that takes into consideration neighbor tree size. We therefore refer to this basal area density measure as ‘tree density’ throughout the paper.

Core collection and processing

We non-destructively sampled 36 study trees using arborist-style climbing techniques (Jepson 2000) in summer 2009. We collected tree cores from two radii at breast height (BH, 1.37 m), base of the live crown (BL, average height of 10.1 ± 0.6 m), mid-crown branch (BR, average height of 15.2 ± 0.6 m) and treetop (TT, average height of 22.1 ± 0.5 m). We also cored one radius in two coarse roots (CR) of each tree, for a total of 10 cores per study tree. Branch and root core locations were carefully selected to avoid potential anomalous growth sections, such as branch junctions, areas with compression wood or other visual irregularities. These 360 cores were prepared using standard dendrochronological techniques (Stokes and Smiley 1968, Fritts 1976) and were then digitally scanned at 2400 dpi. All scanned cores were visually cross-dated and annual ring widths were measured to the nearest 0.01 mm using WinDENDRO software (Regent Instruments, Inc., Quebec, Canada). We created separate ring width chronologies for each tree sample position and used COFECHA (Holmes 1983) to verify the cross-dating for each. Cores whose series intercorrelation was <0.35 were deemed unfeasible to confidently cross-date and were removed from our analysis. We averaged the ring widths measured for all trees that had more than one core (i.e., radii) per tree position, resulting in the following sample size for each position: CR n = 25, BH n = 31, LCR n = 31, BR n = 26 and TT n = 29. During cross-dating, we assigned missing rings to cores based on the absence of marker years typically found during extreme droughts. The cross-dated ring width series from each core was then standardized with a cubic smoothing spline function to remove allometric-related trends in growth with the program ARSTAN (Cook and Holmes 1986). After cross-dating and standardizing all cores, we truncated the series to 1895–2008 so that our sample depth was at least three trees in each of the five positions over the entire time period and also because instrumental climate data are available only after 1895. This truncation of the study period was necessary to ensure comparable sample sizes among positions, as treetops do not date back as far as lower positions and therefore limit the temporal scope of this study. We then used the standardized and truncated chronology from ARSTAN for each position. Chronology characteristics are provided in the Appendix (Figure A1 and Table A1). Lastly, we counted the number of missing rings, assigned through cross-dating, on each core for the years 1895–2008.

Climate data

Climate parameters investigated in this study included annual Palmer Drought Severity Index (PDSI), water year (total precipitation from previous October through current September, WY), total monsoon precipitation (current July, August and September, MON), maximum annual temperature (Tₚₓₚ), minimum annual temperature (Tₚₚ), and average annual temperature (Tₚₑₑ). We generated mean values for each climate parameter using monthly data from 1895 to 2008. Local climate data from the Fort Valley weather station were assembled from the United States Historical Climatology Network (USHCN, http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html).

Data analysis

For our analysis on climate sensitivity, we calculated Pearson correlation coefficients (r) for the relationships between standardized ring width and all six climate parameters between 1895 and 2008 for each tree and tree position using R (R Foundation for Statistical Computing, Vienna, Austria). To answer our research questions of how radial tree growth climatic sensitivity varies with tree density and tree position, we used a one-way analysis of variance (ANOVA) with Tukey’s honestly significant difference (HSD) orthogonal contrast post hoc tests. Levine and Bartlett tests were used to test the assumption of homogeneous variance. For the density ANOVA, we grouped the 36 study trees into four basal area density classes (<10, 11–15, 16–20 and >20 m² ha⁻¹) and tested for differences among these density classes in radial tree growth climatic sensitivity at each position over the entire study period, 1895–2008, as well as the post-thinning period, 1999–2008. Significance was determined at the 95% confidence level.
We used three different analyses to address our research question about how sensitivity varies with height. First, we used linear regression to determine the relationship between height and climate sensitivity based on the correlation coefficients between annual ring width and each climate parameter at each position. Second, using these same correlation coefficients between annual ring width and each climate parameter, we then calculated Akaike's information criterion (AIC) in R to determine which position yields the best model for each of the climate parameters investigated (Burnham and Anderson 2002). For this AIC analysis we also calculated simple difference values (Δ) for each model; where simple difference values were greater than 10, models were considered to be poorer and had no statistical support (Burnham and Anderson 2002). Lastly, we investigated the inter-position correlation (r) of ring width indices among the three bole positions to see how annual growth relationships vary along the bole.

To determine whether the number of missing rings differed by position, we also used an ANOVA with Tukey’s HSD orthogonal contrast post hoc tests to determine which groups were significantly different. Levine and Bartlett tests were again used to test the assumption of homogeneous variance. Lastly, we used linear regression to examine the relationship between bole position height and the number of missing rings. We regressed the mean height for each bole position on the mean number of missing rings per tree.

**Results**

While standardized growth patterns were generally consistent among positions within a given year (Figure A1), in a handful of years growth increased or decreased along the bole. For example, in 1963, a dry year, annual growth increased slightly along the bole, while in 2006, another dry year, and 1908, a relatively wet year, annual growth decreased along the bole. Thus, there does not seem to be a consistent reason as to why growth trends occur along the bole in some years while in other years growth is more or less consistent among bole positions.

Overall, tree ring growth was well correlated to climatic variables. The best correlations were with the climate variables PDSI, WY and $T_{\text{max}}$, while poorer relationships were found with MON, $T_{\text{min}}$ and $T_{\text{avg}}$ (Figure 1). For most tree positions, PDSI

![Figure 1. Correlation coefficients (r) during 1895–2008 between standardized annual ring width and climatic parameters (a, Palmer Drought Severity Index (PDSI); b, water year (previous October through current September, WY); c, total monsoon precipitation (current July, August and September, MON); d, annual maximum temperature ($T_{\text{max}}$); e, annual minimum temperature ($T_{\text{min}}$); and f, annual average temperature ($T_{\text{avg}}$)) for five tree positions (coarse roots, CR; breast height, BH; base of live crown, BLC; mid-crown branch, BR; and treetop, TT). Positions with different letters are significantly different ($\alpha = 0.05$) according to ANOVA results. Aboveground positions do not differ from one another in sensitivity to climate. Coarse roots are less responsive to PDSI, water year and $T_{\text{max}}$ compared with aboveground positions.](https://academic.oup.com/treephys/article-abstract/32/1/14/1667992)
and WY had a positive relationship with tree growth, while $T_{\text{max}}$ was negatively correlated. Our ANOVA found no relationship between tree density and climatic sensitivity at any of the positions investigated during the entire study period, 1895–2008 (results not shown), nor during the post-thinning period, 1999–2008 (Table 1).

Climatic sensitivity of tree growth differed by within-tree position, being significantly lower in coarse roots compared with all aboveground positions for PDSI ($F = 17.17, P < 0.0001$), WY ($F = 12.36, P < 0.0001$), $T_{\text{max}}$ ($F = 9.86, P < 0.0001$) and $T_{\text{min}}$ ($F = 15.80, P < 0.0001$). Correlation between growth and PDSI for all aboveground positions ranged between 0.36 and 0.47, while for coarse roots was 0.09. Sensitivity to $T_{\text{avg}}$ was significantly higher in coarse roots ($r = 0.22, F = 19.08, P < 0.0001$) than in aboveground positions ($-0.08 \leq r \leq -0.01$, Figure 1), although the low value of this root correlation coefficient suggests that roots are relatively insensitive to average air temperature.

Climate sensitivity varied with height within trees. Using three lines of evidence, we found a small but consistent trend for increased sensitivity of tree growth to climate with position height. First, sensitivity to the six climate parameters increased with height between coarse roots and treetops (Table 2). On average, the climate sensitivity correlation was 0.13 (CR), 0.25 (BH), 0.25 (BLC), 0.23 (BR) and 0.28 (TT). This trend was largely driven by the insensitivity of coarse roots to any of the climatic factors investigated. For instance, treetops averaged a 54% higher climate sensitivity compared with coarse roots across all climate parameters. Second, model selection results (AIC values) consistently showed that treetops had the best-performing models for the six climate parameters, while coarse roots consistently had the worst-performing models (Table 3). Additionally, the simple difference values of all models, except the treetop position, were greater than 10, suggesting little to no support for models of all other positions (Table 3). Lastly, the inter-position correlation among the three bole positions showed that as the distance between two positions increases, the annual ring width correlation between them decreases (Table 4). For instance, the annual ring width correlation between breast height and base of live crown was 0.54. This pattern indicates a decreased relationship between growth and climatic variation based on distance between bole positions and likely reflects variability in climatic sensitivity over bole positions.

The mean number of missing rings differed by within-tree position and decreased with height along the bole. Branches had significantly more missing rings between 1895 and 2008 compared with any of the other four positions investigated ($F = 9.29, P < 0.0001$, Figure 2) and these missing ring years corresponded with regional drought years (PDSI $< -2$), with the most common being 2002, 1996, 2000 and 2007. Coarse roots had about one missing ring per tree while branches were missing the most with an average of two and a half rings per tree. Along the bole there was a trend for the number of missing rings to decrease with height ($r^2 = 0.99, P = 0.02$, number of missing rings $= -0.0265 \times \text{height} + 1.3145$), so that treetops had fewer missing rings ($0.6 \pm 0.18$) than breast height measures ($1.3 \pm 0.23$), representing a 130% increase in missing rings between the two positions.

Table 1. Analysis of variance results for the relationship between basal area ($m^2 \text{ha}^{-1}$) density class (<10, 11–15, 16–20, >20) and climatic sensitivity to six climate parameters: Palmer Drought Severity Index (PDSI), water year (previous October through current September, WY), total monsoon precipitation (current July, August and September, MON), maximum annual temperature ($T_{\text{max}}$), minimum annual temperature ($T_{\text{min}}$) and average annual temperature ($T_{\text{avg}}$) during 1999–2008. Results are given for each position: coarse roots (CR), breast height (BH), base of live crown (BLC), mid-crown branch (BR) and treetop (TT). Overall, tree density does not affect climatic sensitivity at any position.

<table>
<thead>
<tr>
<th>Position</th>
<th>Climate parameter</th>
<th>$F$</th>
<th>$P$</th>
<th>($\alpha = 0.05$)</th>
</tr>
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<tr>
<td>CR</td>
<td>PDSI</td>
<td>0.405</td>
<td>0.751</td>
<td></td>
</tr>
<tr>
<td></td>
<td>WY</td>
<td>0.281</td>
<td>0.839</td>
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<tr>
<td></td>
<td>MON</td>
<td>0.446</td>
<td>0.722</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$T_{\text{max}}$</td>
<td>0.383</td>
<td>0.766</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$T_{\text{min}}$</td>
<td>0.212</td>
<td>0.887</td>
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<tr>
<td></td>
<td>$T_{\text{avg}}$</td>
<td>0.774</td>
<td>0.522</td>
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<td>PDSI</td>
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<td>$T_{\text{avg}}$</td>
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Climatic sensitivity and carbon allocation of ponderosa pines

Table 2. Linear regression equations and statistics for the relationship between standardized annual ring width and bole height for six climate parameters: Palmer Drought Severity Index (PDSI), water year (previous October through current September, WY), total monsoon precipitation (current July, August and September, MON), maximum annual temperature ($T_{\text{max}}$), minimum annual temperature ($T_{\text{min}}$) and average annual temperature ($T_{\text{avg}}$). Sensitivity to all investigated climate parameters increases with height.

| Climate parameter | Equation | $R^2$ | $p$  
|-------------------|----------|-------|-----
| PDSI              | $y = 0.0102x + 0.2606$ | 0.38  | 0.0010 |
| WY                | $y = 0.0077x + 0.2981$ | 0.36  | 0.0005 |
| MON               | $y = -0.0043x + 0.1610$ | 0.81  | 0.0112 |
| $T_{\text{max}}$  | $y = -0.0089x - 0.1616$ | 0.46  | 0.0023 |
| $T_{\text{min}}$  | $y = -0.0114x - 0.0569$ | 0.51  | <0.0001 |
| $T_{\text{avg}}$  | $y = -0.0099x + 0.1034$ | 0.57  | <0.0001 |

Table 3. Akaike's information criterion (AIC) and simple difference values ($\Delta$) for the best positional (treetop (TT), base of live crown (BLC), breast height (BH), mid-crown branch (BR) and coarse root (CR)) model to explain each climate parameter (Palmer Drought Severity Index (PDSI), water year (previous October through current September, WY), total monsoon precipitation (current July, August and September, MON), maximum annual temperature ($T_{\text{max}}$), minimum annual temperature ($T_{\text{min}}$) and average annual temperature ($T_{\text{avg}}$)) investigated. Treetops were the most sensitive to all six climate parameters, as represented by the highest AIC and lowest $\Delta$ values (Burnham and Anderson 2002). For each parameter, the order of most to least sensitive position is consistent: TT, BLC, BH, BR, CR.

<table>
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<th>Climate parameter</th>
<th>AIC</th>
<th>$\Delta$</th>
<th>AIC</th>
<th>$\Delta$</th>
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<td>CR</td>
<td>142.11</td>
</tr>
<tr>
<td>MON</td>
<td>TT</td>
<td>54.29</td>
<td>0.00</td>
<td>TT</td>
</tr>
<tr>
<td>BLC</td>
<td>76.07</td>
<td>21.78</td>
<td>BLC</td>
<td>76.39</td>
</tr>
<tr>
<td>BH</td>
<td>90.51</td>
<td>36.22</td>
<td>BH</td>
<td>91.78</td>
</tr>
<tr>
<td>BR</td>
<td>106.84</td>
<td>52.55</td>
<td>BR</td>
<td>106.94</td>
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<tr>
<td>CR</td>
<td>142.58</td>
<td>88.29</td>
<td>CR</td>
<td>144.56</td>
</tr>
</tbody>
</table>

Discussion

Our study repeatedly shows that within-tree positions did not respond similarly to inter-annual variation in water availability and temperature in old-growth ponderosa pines of the southwestern USA. Additionally, the prevalence of missing rings also varied within trees. These results provide important insights into dendrochronology and carbon allocation within trees.

We found no effect of tree density on climatic sensitivity at any sample position during the entire study period, nor during the 10 post-thinning years. This lack of a relationship between tree density and sensitivity is surprising as other studies have shown that trees growing in high competition are less sensitive to climate (Fritts 1966, Cescatti and Piutti 1998, Martin-Benito et al. 2010). It is likely that the large, dominant status of our study trees rendered them immune to competitive effects on sensitivity regardless of local tree density. Our failure to find a relationship between tree density and climatic sensitivity could also stem from a methodological error. Perhaps estimating basal area density at each study tree with an angle gauge was too coarse a measurement, and a more precise approach such as the use of Thiessen polygons (Mithen et al. 1984, Kenkel et al. 1989, Hurteau et al. 2007) to approximate local crowding for each study tree might be more informative.

We found that sensitivity to six climate parameters increased with height and was strongest at the treetop (Table 2). Increased sensitivity with height identifies gravitational and/or path length hydraulic limitations, rather than basipetal carbon allocation, as a potential mechanism driving this trend. This information suggests that an improved climate reconstruction, one that explains slightly more of the variance, may be obtained.
by coring higher on the bole. Hydraulic limitation has been shown to occur in ponderosa pine (Hubbard et al. 1999, Skov et al. 2004), Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) (McDowell et al. 2002), coast redwood (Sequoia sempervirens (D. Don.) Endl.) (Koch et al. 2004, Ishii et al. 2008) and other tree species (Ryan and Yoder 1997). Therefore, it is reasonable to expect that hydraulic limitation may promote greater climate sensitivity to water availability in the tops of other large tree species. Since greater sensitivity has been associated with improved climate reconstructions (Schulman 1956, Fritts 1976, Stahle et al. 1998, Díaz et al. 2001), dendroclimatologists interested in producing slightly better climate reconstructions should core study trees as high on the bole as possible where a long enough time series is still obtainable.

In addition to increased climate sensitivity with height, we found that growth in roots is less sensitive to PDSI, WY, \( T_{\text{max}} \) and \( T_{\text{min}} \) compared with all aboveground positions (Figure 1). This apparent lack of sensitivity of coarse root growth suggests that ponderosa pines in northern Arizona prioritize carbon allocation to root growth regardless of inter-annual variation in climate. This pattern of complacency with respect to precipitation is consistent with the expectation that plants generally prioritize growth to the organ that acquires their most limiting resource (Chapin et al. 2002, Pallardy 2008). In the case of ponderosa pines in the arid Southwest, it seems that water and nutrient availabilities are consistently limiting enough to warrant carbon allocation to roots, the organ responsible for acquiring these resources, a persistent carbon sink independent of water availability. Root complacency with respect to temperature is surprising given that persistent cold soil temperatures late into the spring typically delay the onset of root growth relative to shoot growth (Harris et al. 1995). Our use of air temperature, a highly variable parameter, rather than soil temperature, a more buffered parameter, might explain the root insensitivity observed.

Branches had significantly more missing rings between 1895 and 2008 than any of the other four positions investigated (Figure 2). A higher proportion of missing rings in branches compared with the bole has been previously observed in ponderosa pine (Andrews and Gill 1939) as well as in Douglas-fir (Reukema 1959). The greater number of drought-related missing rings in branches suggests that canopy development is a lower priority for carbon allocation during years with poor growth conditions. More expectedly, we also found a decreased number of missing rings along the bole between breast height and treetop positions. This pattern confirms findings from other studies that basipetal carbon allocation (Myers 1963, Kozlowski 1971, Cherubini et al. 1996, Hansen et al. 1996, Pallardy 2008) is acting as a buffer against missing rings higher on the bole in years with poor growing conditions (Niklasson 2002, Waring and O’Hara 2006). This observation may be more pronounced in larger trees due to the greater discrepancy in circumferential area within an annual ring between bole top and base. Finally, it is possible that by removing uncross-datable cores from this study, we introduced bias into the missing ring analysis as these uncross-datable cores likely had a high frequency of missing rings. However, we felt that it was more important to obtain the most accurate chronology for each position so that we had the best possible ‘sample’ to test our main hypothesis regarding climate sensitivity.

**Conclusion**

Dendrochronology is a useful tool for climate reconstructions, particularly when meteorological records are temporally and/or spatially sparse. Achieving the best understanding of tree response to climate in both the past and present is of particular importance in the southwestern US as this region experiences a warmer and drier climate (Seager et al. 2007). Our failure to find a relationship between tree density and climatic sensitivity in our study trees suggests that large dominant trees are usable in climatic studies even when growing in dense forests, as competition does not affect their sensitivity. Our findings of increased sensitivity with height identify gravitational and/or path length hydraulic limitation as a potential mechanism driving this trend, and thereby provide new insight into ponderosa pine physiology. Moreover, our finding of increased climatic sensitivity of tree ring growth with bole height offers a potential method to improve the accuracy and precision of dendroclimatological reconstructions by coring higher up on the tree bole. This increased precision comes at the expense of reducing the temporal depth and requires more effort, experience and time to collect core samples. While this tradeoff of a slightly better correlation between annual ring width and climate is unlikely worth the additional effort, cost and reduced sample depth associated with coring higher on the bole, we show with this study that whole-tree investigations of annual growth provide useful information on sensitivity and carbon allocation. Furthermore, coring different positions within trees can improve understanding of whole-tree carbon allocation patterns, and thereby strengthen stand-level carbon sequestration models. Greater missing rings at lower bole positions may decrease the accuracy of carbon storage estimates at the tree level, thereby underestimating the importance of southwestern US forests’ terrestrial carbon sink strength and their potential to mitigate atmospheric CO₂. Additionally, dendrochronological analyses of coarse roots and branches will potentially yield novel information about carbon prioritization strategies at the individual-tree level.

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Appendix

Chronology characteristics are provided in Figure A1 and Table A1.
Table A1. Chronology statistics, including sample size, mean annual growth, mean sensitivity, series intercorrelation, first-order autocorrelation and expressed population signal (EPS; Wigley et al. 1984), for cores taken from five tree positions: coarse roots (CR), breast height (BH), base of live crown (BLC), mid-crown branch (BR) and treetop (TT). Chronologies based on the time period 1895–2008.

<table>
<thead>
<tr>
<th>Position</th>
<th>n</th>
<th>Growth¹</th>
<th>Sensitivity¹</th>
<th>Series intercorrelation¹</th>
<th>Autocorrelation²</th>
<th>EPS²</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR</td>
<td>25</td>
<td>0.98</td>
<td>0.42</td>
<td>0.52</td>
<td>0.54</td>
<td>0.87</td>
</tr>
<tr>
<td>BH</td>
<td>30</td>
<td>1.18</td>
<td>0.39</td>
<td>0.68</td>
<td>0.34</td>
<td>0.950</td>
</tr>
<tr>
<td>BLC</td>
<td>31</td>
<td>1.22</td>
<td>0.34</td>
<td>0.70</td>
<td>0.34</td>
<td>0.96</td>
</tr>
<tr>
<td>BR</td>
<td>26</td>
<td>0.48</td>
<td>0.44</td>
<td>0.58</td>
<td>0.34</td>
<td>0.9</td>
</tr>
<tr>
<td>TT</td>
<td>29</td>
<td>1.08</td>
<td>0.39</td>
<td>0.72</td>
<td>0.24</td>
<td>0.94</td>
</tr>
</tbody>
</table>

¹Denotes values taken from COFECHA (Holmes 1983).
²Denotes values taken from ARSTAN (Cook and Holmes 1986).

Figure A1. The standardized 1895–2008 annual ring width chronologies from ARSTAN for each of the five positions: (a) treetops, (b) mid-crown branches, (c) base of live crowns, (d) breast heights and (e) coarse roots.