

## Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO<sub>2</sub> fertilization effect?

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### **Summary:**

- The primary objective of this study was to determine if gradually increasing levels of atmospheric CO<sub>2</sub>, as opposed to 'step' increases commonly employed in controlled studies, have a positive impact on radial growth rates of ponderosa pine (*Pinus ponderosa*) in natural environments, and to determine the spatial extent and variability of this growth enhancement.
- We developed a series of tree-ring chronologies from minimally disturbed sites across a spectrum of environmental conditions. A series of difference of means tests were used to compare radial growth post-1950, when the impacts of rising atmospheric CO<sub>2</sub> are best expressed, with that pre-1950. Spearman's correlation was used to relate site stress to growth-rate changes.
- Significant increases in radial growth rates occurred post-1950, especially during drought years, with the greatest increases generally found at the most water-limited sites. Site harshness is positively related to enhanced radial growth rates.
- Atmospheric CO<sub>2</sub> fertilization is probably operative, having a positive effect on radial growth rates of ponderosa pine through increasing water-use efficiency. A CO<sub>2</sub>-driven growth enhancement may affect ponderosa pine growing under both natural and controlled conditions.

**Key words:** CO<sub>2</sub> fertilization, ponderosa pine (*Pinus ponderosa*), site harshness, drought, interior Pacific Northwest.

### **Article:**

#### ***Introduction***

Two major environmental issues have arisen regarding the increasingly CO<sub>2</sub>-rich world of the late 20th and early 21st centuries: climatic change, and plant responses to the environment. While the implications of atmospheric CO<sub>2</sub> for potential climatic change have received the majority of attention, the potential role of atmospheric CO<sub>2</sub> fertilization in plant growth and subsequent ecosystem dynamics may be equally important. Results from reviews of numerous controlled studies for agricultural crops (Kimball et al., 2002), ecosystems (Nowak et al., 2004) and trees (Norby et al., 1999; Ainsworth & Long, 2005) indicate consistently that most species respond significantly to 'step' increases in elevated CO<sub>2</sub>. Further, for many species/ecosystems these responses have been sustained in long-term experiments (Hättenschwiler et al., 1997; Idso & Kimball, 2001; Ainsworth et al., 2003; Rasse et al., 2005). In contrast, comparatively little is known about how tree species respond under natural conditions. Tree growth under long-term exposure to gradually increasing atmospheric CO<sub>2</sub> conditions may be substantially different from step increases in CO<sub>2</sub> (Klironomos et al., 2005), and further modified by different topographic and climatic conditions found at natural sites. These critical research needs are consistent with those identified by Saxe et al. (1998); Idso & Kimball (2001); and Gifford (2004). This study examines the possible CO<sub>2</sub> fertilization response of ponderosa pine (*Pinus ponderosa*) under natural conditions in the interior Pacific Northwestern USA.

Directly implicating atmospheric CO<sub>2</sub> enrichment as a cause of vegetation change in natural environments is

impeded by the scarcity of settings where the confounding influences of grazing, fire suppression, and other anthropogenic impacts are minimal. Thus, comparing the results of laboratory- and field-based CO<sub>2</sub> enrichment studies with plant responses under natural conditions is restricted to the few protected sites where these confounding influences are limited. In this study, we use two means to address this research gap between controlled and field-based studies through a nonlaboratory examination of the potential effects of increasing levels of atmospheric CO<sub>2</sub> on radial growth rates of the semiarid tree species ponderosa pine. First, our specific site selection allows for the minimization of confounding influences that may either bias or obfuscate possible CO<sub>2</sub> fertilization effects. Second, we employ a series of tests to determine if a CO<sub>2</sub> fertilization effect is operative. Thus, the primary objectives of this study were (1) to determine if the passive fertilization associated with the gradually increasing concentration of atmospheric carbon dioxide has a positive impact on radial growth rates of ponderosa pine in natural environments; and (2) to determine the spatial extent and variability of this potential growth enhancement. Our main hypothesis is that the relative effects of enhanced radial growth rates of ponderosa pine will be more evident during drought years in comparison with wet years during the latter half of the 20th century, when atmospheric CO<sub>2</sub> levels were higher. Further, we hypothesize that site harshness will be positively related to enhanced radial growth rates caused by atmospheric CO<sub>2</sub> fertilization, and that atmospheric CO<sub>2</sub> fertilization is having a positive effect on radial growth rates of ponderosa pine across a wide range of environmental (site-specific) conditions.

We selected ponderosa pine for three specific reasons. First, our earlier work in the interior Pacific Northwest examining possible atmospheric CO<sub>2</sub> fertilization (Knapp & Soulé, 1996, 1998; Knapp et al., 2001 a, 2001 b; Soulé et al., 2003, 2004) suggests that the effect is operative for the tree species western juniper (*Juniperus occidentalis* var. *occidentalis*). Our studies concluded that the 25% increase in atmospheric CO<sub>2</sub> during the past century, most of which occurred since 1950, contributed to both ecotonal expansion into drier areas and enhanced radial growth of western juniper. As western juniper and ponderosa pine are often found in association, we sought to determine if similar radial growth responses exist with ponderosa pine.

Second, controlled studies examining elevated interactions between atmospheric CO<sub>2</sub> and ponderosa pine seedlings consistently identify a growth-enhancement effect measured by photosynthesis (Pushnik et al., 1995; Tissue et al., 1999; Olszyk et al., 2001, 2002); biomass (Maherali & DeLucia, 2000; Olszyk et al., 2003); water-use efficiency (Olszyk et al., 2002); fine-root extent and intensity (Tingey et al., 2005); and trunk diameter (Walker et al., 2000). While less is known about the possible growth impacts of elevated CO<sub>2</sub> on mature ponderosa pine, tree growth-simulation models have demonstrated that ponderosa pine grown under elevated CO<sub>2</sub> conditions (550  $\mu\text{l l}^{-1}$ ) had a 3-yr biomass increase of 29% relative to initial conditions (Constable et al., 1996). Tingey et al. (2001) employed the same simulation model but incorporated the effects of seasonal drought, a common limiting factor for growth of ponderosa pine in late summer. Their results show that annual biomass increased under elevated CO<sub>2</sub> conditions (500  $\mu\text{mol mol}^{-1}$ ) at all their seven sites (range 28–50%), with the greatest increase at the driest site. Thus, we sought to determine what type of response is operative under natural conditions with mature trees.

Our final reason for selecting a species native to semiarid environments is that several studies (Idso, 1989; Mayeux et al., 1991, 1994; Mooney et al., 1991) have posited that species most likely to benefit from increasing atmospheric CO<sub>2</sub> would be located in drier environments, because of increased water-use efficiency. This effect is typically best expressed under stressful conditions such as drought (Idso & Idso, 1994; Pospisilova & Catsky, 1999; Wullschleger et al., 2002). However, a meta-analysis of ecosystem Free Air CO<sub>2</sub> Enrichment (FACE) studies (Nowak et al., 2004) suggests that the relationship between precipitation and the enhancement effect of above-ground primary productivity is limited to grasslands, and is maximized where annual precipitation is between 300 and 500 mm. As ponderosa pine trees are often found in woodland settings with comparable annual precipitation totals and frequent droughts, they too may benefit from increased water-use efficiency in water-limited environments.

## Materials and Methods

We collected core samples during the summers of 2000 and 2001, and developed standardized tree-ring

chronologies from eight sites in the Pacific Northwest (Fig. 1; Table 1). The study sites fit several criteria designed to limit potential confounding influences associated with anthropogenic disturbance. We intentionally avoided areas that had experienced active fire suppression and/or logging to eliminate or minimize any nonnatural changes in growth (e.g. a growth surge caused by selective logging of a site and the subsequent increases in light, water and nutrients).

**Table 1** Study site characteristics and selection criteria

| Site code | Site name          | Site description   | Latitude/longitude | Elevation (m) | Associated tree species*   | Annual PDSI measure† |
|-----------|--------------------|--|--------------------|---------------|--|----------------------|
| MCN       | Mill Creek         | Research natural area (protected)                        | 45°30'/121°25'     | 1002          | <i>Pseudotsuga menziesii</i> ,<br><i>Abies grandis</i> , <i>Larix occidentalis</i> | Jul–Jun Oregon 6‡    |
| FMC       | Fifteen Mile Creek | Topographic isolation (historically minimally disturbed) | 45°21'/121°26'     | 1265          | <i>Juniperus occidentalis</i>  | Jul–Jun Oregon 6     |
| CCR       | Committee Creek    | Topographic isolation (historically minimally disturbed) | 44°13'/120°08'     | 1297          | <i>Juniperus occidentalis</i>  | Aug–Jul Oregon 7     |
| QRY       | Quarry             | Topographic isolation (disjunct stand)                   | 44°04'/121°09'     | 1128          | <i>Juniperus occidentalis</i>  | Aug–Jul Oregon 7     |
| PRE       | Pine Ridge East    | Topographic isolation (disjunct stand)                   | 43°45'/120°42'     | 1459          | <i>Juniperus occidentalis</i>  | Aug–Jul Oregon 7     |
| SLX       | Silver Lake        | Research natural area (protected)                        | 43°03'/121°06'     | 1486          | <i>Juniperus occidentalis</i> ,<br><i>Cercocarpus ledifolius</i>                   | Aug–Jul Oregon 7§    |
| BLF       | Burnt Lava Flow    | Topographic isolation (trees within lava flow)           | 41°29'/121°29'     | 1543          | <i>Pinus lambertiana</i> ,<br><i>Abies concolor</i>                                | Jun–May California 1 |
| SWW       | South Warner       | Wilderness area (protected)                              | 41°27'/120°14'     | 2078          | <i>Abies concolor</i> , <i>Pinus albicaulis</i> ,<br><i>Cercocarpus ledifolius</i> | Apr–Mar California 3 |

\*Tree species co-occur with ponderosa pine (*Pinus ponderosa*) within the study sites.

†PDSI, annual Palmer Drought Severity Index measurement (month of prior year through month of annual ring width growth year) used to determine the matched dry and wet year pre-1950 to post-1950 and in all statistical analyses.

‡Climatic division matched with study site for data analyses.

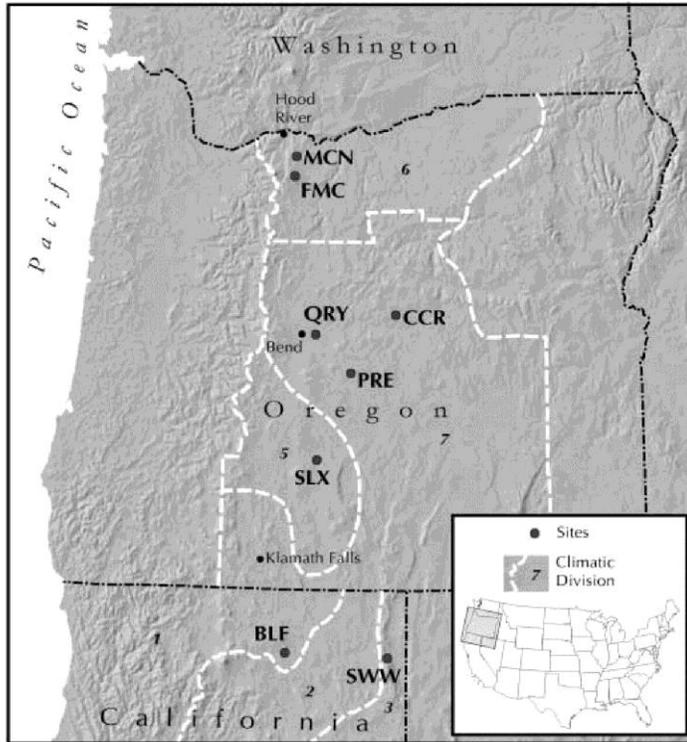
§Silver Lake is located within Oregon Climatic Division 5, but radial growth matched more closely with PDSI values from Division 7, which surrounds it.

Conversely, we selected areas that have been historically protected, either by governmental decree (e.g. research natural areas such as MCN or wilderness areas such as SWW) or naturally through topographic isolation. As an example of what we looked for in terms of minimal disturbance from topographic isolation, the BLF site had stands of ponderosa pine growing within a large lava flow. Thus, we were assured that direct human disturbance (such as logging and fire suppression) was either minimized or not a factor. We selected sites with a variety of climatic and topoedaphic conditions, ranging from extremely water-limiting environments such as QRY (southern exposure, low elevation) to areas where soil moisture should be a limiting factor for growth only during extreme drought years (e.g. SWW). All sites were in areas where ozone concentrations (Lee & Hogsett, 2001) and nitrogen deposition (Fenn et al., 2003) are typically low because of the distance from urban areas and point sources of pollutants, and are located east of the Cascade Mountains. Further, while Luo et al. (2004) suggest that insufficient soil N availability may limit the potential response of ecosystems to elevated CO<sub>2</sub>, we accounted for this possibility through the selection of a species that responds significantly to CO<sub>2</sub> fertilization under low soil N levels (Olszyk et al., 2003). We selected only trees that were growing in open-canopy conditions. All cores were collected from *Pinus ponderosa* Laws. var. *ponderosa*. This subspecies was selected because it occurs east of the Cascade Range crest and thus is typically found in semiarid environments.

Each site included trees from multiple age classes, one of the main determinants used to classify ponderosa pine forests as old growth (Youngblood et al., 2004). Our selection process was selective rather than random to ensure that the potentially oldest trees on each site were sampled, and to ensure that tree growth had not been confounded by a variety of ecological factors, including canopy infilling that could create either intra- or interspecific competition. Our core definition for open canopy was that there could be no overlap in canopy for sampled trees. We sampled c. 40 mature trees per site using standard dendroecological field techniques (Phipps, 1985). Because we sought to examine potential changes in growth rates across the timespan of human-caused CO<sub>2</sub> enrichment (pre- and post-1950), we avoided sampling juvenile ponderosa pine (< 50 yr old). Thus, our results indicate the response of mature, naturally occurring ponderosa pine trees that germinated before anthropogenically elevated CO<sub>2</sub> levels, but where growth, particularly post-1950, has occurred under increasing and substantially higher atmospheric CO<sub>2</sub> concentrations. We collected a minimum of two increment cores from the stem of each tree at a height of approx. 1.5 m. We sampled parallel to slope contours to avoid problems associated with reaction wood. While obtaining the core samples, we recorded additional information about each tree, including basal diameter.

We processed and crossdated core samples using standard laboratory procedures for dendroecological samples

(skeleton plots, Stokes & Smiley, 1968; Swetnam et al., 1985; and the list method, Phipps, 1985; Yamaguchi, 1991). Once crossdated, we measured the individual ring widths to an accuracy of 0.01 mm using a linear encoder, and a tree-ring chronology was constructed. We used the COFECHA program (Holmes, 1983) to check the accuracy of crossdating, and the program ARSTAN (Cook & Holmes, 1997) to develop the standardized chronology for each site. Because flexible standardization techniques (e.g. spline curves) may remove low-frequency signals, we used conservative standardization techniques such as negative exponential curve fitting or negative linear in the development of our chronologies.



**Fig. 1** Location of ponderosa pine (*Pinus ponderosa*) sampling sites and selected climatic divisions (see Table 1 for site descriptions).

We present information on the age structure and growth patterns for each site. We calculated the percentage of sample sharing an interior date (the oldest dated tree ring) by decade. Because we sampled trees above ground level and did not obtain pith for every core sample, the tree ages are estimates, with actual ages always older, as the time required for each tree to grow to sampling height (1.5 m) is unknown. We used the actual interior dates to calculate mean age, median age and standard deviation of age for each site. We used Spearman's correlation to examine the relationship between mean age and radial growth-rate changes. In addition, we show the standardized chronology (average radial growth per year) for each site through a common ending year of 1999.

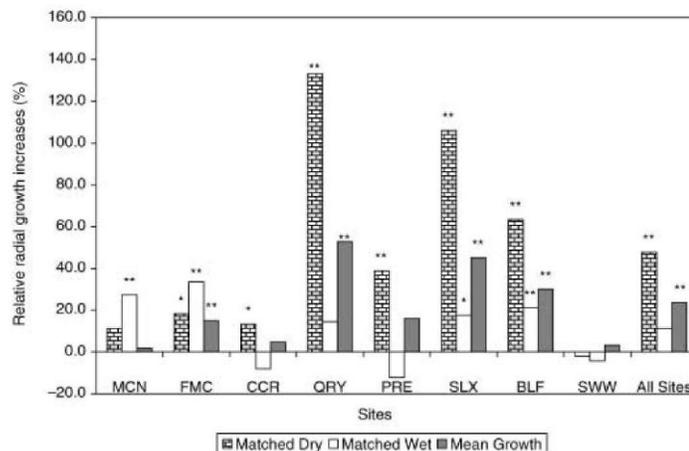
We used a one-tailed Wilcoxon matched pairs signed-rank test (McGrew & Monroe, 2000) to determine if radial growth-rate differences exist during ecologically comparable drought years and wet years pre- and post-1950 (is post-1950s growth greater than pre-1950s growth?). The 1950 divide is often used in studies addressing CO<sub>2</sub>-caused vegetation change in nonlaboratory settings (Kienast & Luxmoore, 1988; Graumlich, 1991; Knapp et al., 2001 a, 2001 b) because it marks an inflection point in rising CO<sub>2</sub> levels. Similarly to Knapp et al. (2001 a), we identified ecologically comparable drought years (wet years) using the Palmer Drought Severity Index (PDSI) (Palmer, 1965; NCDC, 2004), a monthly, water balance-based measure of drought severity commonly linked to tree growth (Pohl et al., 2002). The basic inputs into the PDSI calculation are local temperature and precipitation data, and a suite of water-balance measures (e.g. actual and potential evapotranspiration, soil-water recharge). The PDSI is standardized on zero by location, with negative PDSI values indicating soil moisture deficits relative to normal, and positive values moisture surpluses (Palmer, 1965). Values  $\leq -1$  and  $\leq -2$  represent mild and moderate drought, respectively, with similar descriptors for wet spells (Palmer, 1965). Comprehensive discussions of the methods used to calculate the PDSI are found in various sources (Palmer, 1965; Alley, 1984; Karl, 1986).

We used PDSI data for Climatic Divisions in Oregon and California over a common period for our eight sites (1896– 1999). We first tested various annual measures of the PDSI (e.g. prior-year August to current-year July) to see which measure most closely matched the annual growth index at each site (Table 1). Using this annual measure, we matched years with comparable levels of drought severity (wet severity) and that fell in a similar position during a drought (wet spell) sequence. For example, we matched the second year (mean PDSI =  $-2.0$ ) of a drought sequence pre- 1950 with the second year (mean PDSI =  $-2.1$ ) of a drought sequence post-1950. We also used the Wilcoxon test on the PDSI values to ensure there were no significant ( $P < 0.05$ , two-tailed) differences between matched drought (wet) years between pre- and post-1950 periods. We computed the mean (relative) radial growth-rate differences at each site and across all sites for all matched drought (wet) years pre- and post-1950, and compared these graphically. To determine if growth differences occurred across all sites combined, we calculated the mean radial growth during matched dry (wet) years at each site and compared these mean values using a one-tailed Wilcoxon test to determine if mean radial growth in the post-1950 period is greater than mean growth in the pre-1950 period.

We compared mean growth for all years pre-1950 with mean growth post-1950 using a one-tailed Mann–Whitney U test (is mean growth post-1950 greater than pre-1950?) (McGrew & Monroe, 2000). We used the same test, but two-tailed, on the PDSI data to determine if any significant ( $P < 0.05$ ) differences in moisture regime existed between the two periods. We used simple correlation to test for temporal trends in climatic division-level PDSI data, annual mean temperature, and annual total precipitation data (NCDC, 2004).

We divided the mean radial growth data into pre- and post-1950 subsets, then sorted the subsets by PDSI categories. We calculated mean radial growth for all years with PDSI values  $\leq -2.0$ ,  $\leq -1.0$ ,  $< 0$ ,  $\geq 0$ ,  $\geq 1.0$  and  $\geq 2.0$  for the pre- and post-1950 periods at each site, and compared these values using a one-tailed Mann–Whitney U test (is mean growth post-1950 greater than pre-1950?). We then calculated the difference between the pre- and post-1950 years, and averaged these across all eight sites. These mean differences are presented in raw form and as relative changes where the difference is divided by the pre-1950 mean then multiplied  $\times 100$ .

We calculated a measure of site harshness using procedures outlined by Knapp et al. (2001 a). Specifically, we used a common period (1800 –1999) across all eight sites to calculate the percentage of missing rings for each chronology. Missing rings are typically associated with extremely stressful (dry) years. Thus, more missing rings suggest a harsher growing site. We then compared site harshness with the relative radial growth rate increase (or decrease) in the post-1950 period to the percentage of missing rings, graphically and via Spearman’s correlation. As stressed sites should also produce trees with smaller diameter, basal diameter was used as a secondary measurement of site stress and compared with radial growth rates changes via Spearman’s correlation.

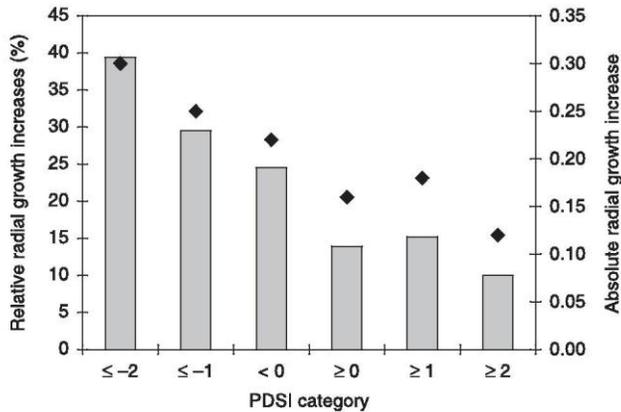


**Fig. 2** Ponderosa pine (*Pinus ponderosa*) increases in radial growth rates post-1950 relative to pre-1950 during ecologically comparable drought years and wet years, and between all years. \*\*, \*, Significant differences from a one-tailed matched-pairs test at  $P < 0.01$  and  $P < 0.05$ , respectively.

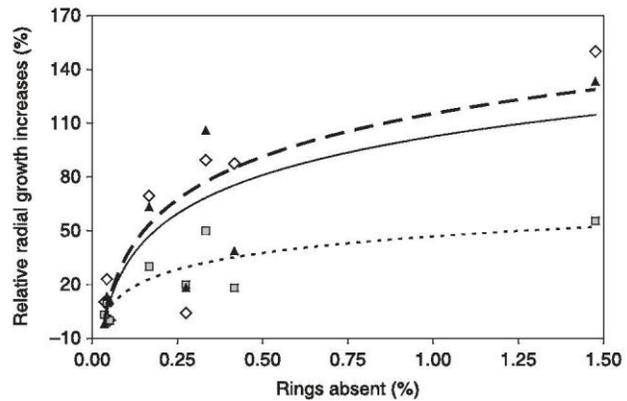
## Results

Mean radial growth values post-1950 were significantly greater ( $P < 0.05$ ) at six of the eight sites and across all sites combined during matched drought years (Fig. 2). Mean radial growth rates during matched wet years post-1950 were significantly greater ( $P < 0.05$ ) at four of the eight sites, but not across all sites combined ( $P = 0.054$ )

(Fig. 2). For all years post-1950, mean radial growth rates were significantly greater ( $P < 0.05$ ) at four of the eight sites (PRE was not significant,  $P = 0.052$ ), and across all sites combined (Fig. 2). Overall, radial growth enhancement was more pronounced during drought years compared with wet years, and the greatest response occurred at the most stressed site (QRY).



**Fig. 3** Ponderosa pine (*Pinus ponderosa*) relative (horizontal bars) and absolute (diamonds) radial growth increases post-1950 compared with pre-1950 during years falling into various Palmer Drought Severity Index (PDSI) categories of drought (wet) severity.



**Fig. 4** Comparison of site harshness (measured as percentage missing rings) and radial growth increases of ponderosa pine (*Pinus ponderosa*) post-1950 relative to pre-1950 during ecologically comparable drought years (triangles, solid line); years with PDSI ≤ -2 (diamonds, long dashed line); and all years (squares, short dashed line).

The analyses of radial growth differences pre- and post-1950 by PDSI category suggest there is a strong relationship between climatic harshness and radial growth-rate response. The greatest absolute and relative increases in radial growth in the post-1950s period are associated with those years with the lowest PDSI values (Fig. 3). During years with PDSI values  $< 0$ ,  $\leq -1$  and  $\leq -2$ , 62.5% of the study sites had significant ( $P < 0.05$ ) increases in radial growth in the post-1950 period. For the wetter years, 50% of sites had significant increases with  $\text{PDSI} \geq 0$  and  $\geq 1$ , and 25% of the sites with  $\text{PDSI} \geq 2$ . The range of response across the eight sites in absolute growth-rate changes are: 0.0–0.69 for  $\text{PDSI} \leq -2$ ; 0.02–0.54 for  $\text{PDSI} \leq -1$ ; 0.02–0.49 for  $\text{PDSI} < 0$ ; 0.01–0.4 for  $\text{PDSI} \geq 0$ ; -0.06 to 0.42 for  $\text{PDSI} \geq 1$ ; -0.18 to 0.26 for  $\text{PDSI} \geq 2$ .

**Table 2** Results of climatic comparisons based on climatic divisions in Oregon and California

| Climatic parameter compared                             | Oregon Climatic Division |                        | California Climatic Division |             |
|---|--------------------------|------------------------|------------------------------|-------------|
|   | 6 (MCN, FMC)             | 7 (CCR, QRY, PRE, SLX) | 1 (BLF)                      | 3 (SWW)     |
| Matched PDSI mean, dry years 1896–1949                  | -2.5                     | -2.6                   | -1.5                         | -1.5        |
| Matched PDSI mean, dry years 1950–99                    | -2.5                     | -2.6                   | -1.8                         | -2.1        |
| <i>P</i>  | 0.88                     | 0.36                   | 0.67                         | 0.29        |
| Sample size   | 12                       | 13                     | 8                            | 8           |
| Matched PDSI mean, wet years 1896–1949                  | 2.6                      | 2.3                    | 2.0                          | 1.1         |
| Matched PDSI mean, wet years 1950–99                    | 2.2                      | 2.3                    | 1.9                          | 1.3         |
| <i>P</i>  | 0.18                     | 0.95                   | 0.86                         | 0.30        |
| Sample size   | 7                        | 9                      | 7                            | 9           |
| Mean PDSI 1896–1949 ( $n = 54$ )                        | 0.0                      | -0.4                   | 0.1                          | -0.4        |
| Mean PDSI 1950–99 ( $n = 50$ )                          | -0.2                     | 0.2                    | 0.2                          | 0.4         |
| <i>P</i>  | 0.85                     | 0.16                   | 0.83                         | <b>0.02</b> |
| $r$ , PDSI/year (1896–1999, $n = 104$ )                 | 0.02                     | 0.08                   | -0.10                        | 0.20        |
| <i>P</i>  | 0.86                     | 0.44                   | 0.92                         | <b>0.04</b> |
| $r$ , Annual precipitation/year (1896–1999, $n = 104$ ) | -0.02                    | 0.12                   | -0.05                        | 0.12        |
| <i>P</i>  | 0.87                     | 0.22                   | 0.64                         | 0.22        |
| $r$ , Annual temperature/year (1896–1999, $n = 104$ )   | 0.17                     | 0.22                   | 0.10                         | 0.07        |
| <i>P</i>  | 0.08                     | <b>0.02</b>            | 0.31                         | 0.46        |

Values in bold type significant at  $P < 0.05$ .  
PDSI, Palmer Drought Severity Index.  
See Table 1 for site code descriptions.

The comparison of site harshness with relative radial growth rate increases (only SWW had reduced growth) during matched drought years in the post-1950s period for the eight sites was significant ( $r_s = 0.86$ ,  $P = 0.007$ ,  $n = 8$ ). Similarly, mean radial growth increases for all years pre- and post-1950 ( $r_s = 0.76$ ,  $P = 0.028$ ), and those

years with PDSI values  $\leq -2.0$  ( $r_s = 0.71$ ,  $P = 0.047$ ) had positive relationships with site harshness (Fig. 4). For matched wet years, there was no relationship ( $r_s = -0.02$ ,  $P = 0.955$ ). Removing the data from the high-stress QRY site that exhibited the largest relative radial growth increases (therefore  $n = 7$ ), the relationships remain positive but are reduced in both strength and significance (matched drought years,  $r_s = 0.79$ ,  $P = 0.036$ ; all years,  $r_s = 0.64$ ,  $P = 0.119$ ; PDSI  $\leq -2$  years,  $r_s = 0.57$ ,  $P = 0.18$ ). Thus, the overall results are not unduly influenced by a single site. Additionally, we found a significant relationship between radial growth-rate changes during matched drought years and a secondary measure of site stress: mean basal diameter of trees ( $r_s = -0.91$ ,  $P = 0.002$ ,  $n = 8$ ).

All the comparisons of PDSI values for the matched dry and matched wet years were insignificant (Table 2), indicating that soil moisture conditions were similar for the selected years pre- and post-1950. For the comparison of mean PDSI values (all years pre- 1950 compared with all years post-1950), the only significant difference was for SWW (matched with California Division 3), which had wetter mean conditions post-1950 (Table 2). The trend analyses of mean annual temperature, annual precipitation and PDSI values for the four climatic divisions matched to our eight sites reveal a significant upward trend in temperature at Oregon 7 (matched with CCR, PRE, QRY and SLX), and a significant upward trend in PDSI values for California Division 3 (SWW), but no significant trends in precipitation (Table 2). Thus, only at SWW have the climatic conditions become more favorable for growth.

**Table 3** Age and basal diameter for samples within each chronology

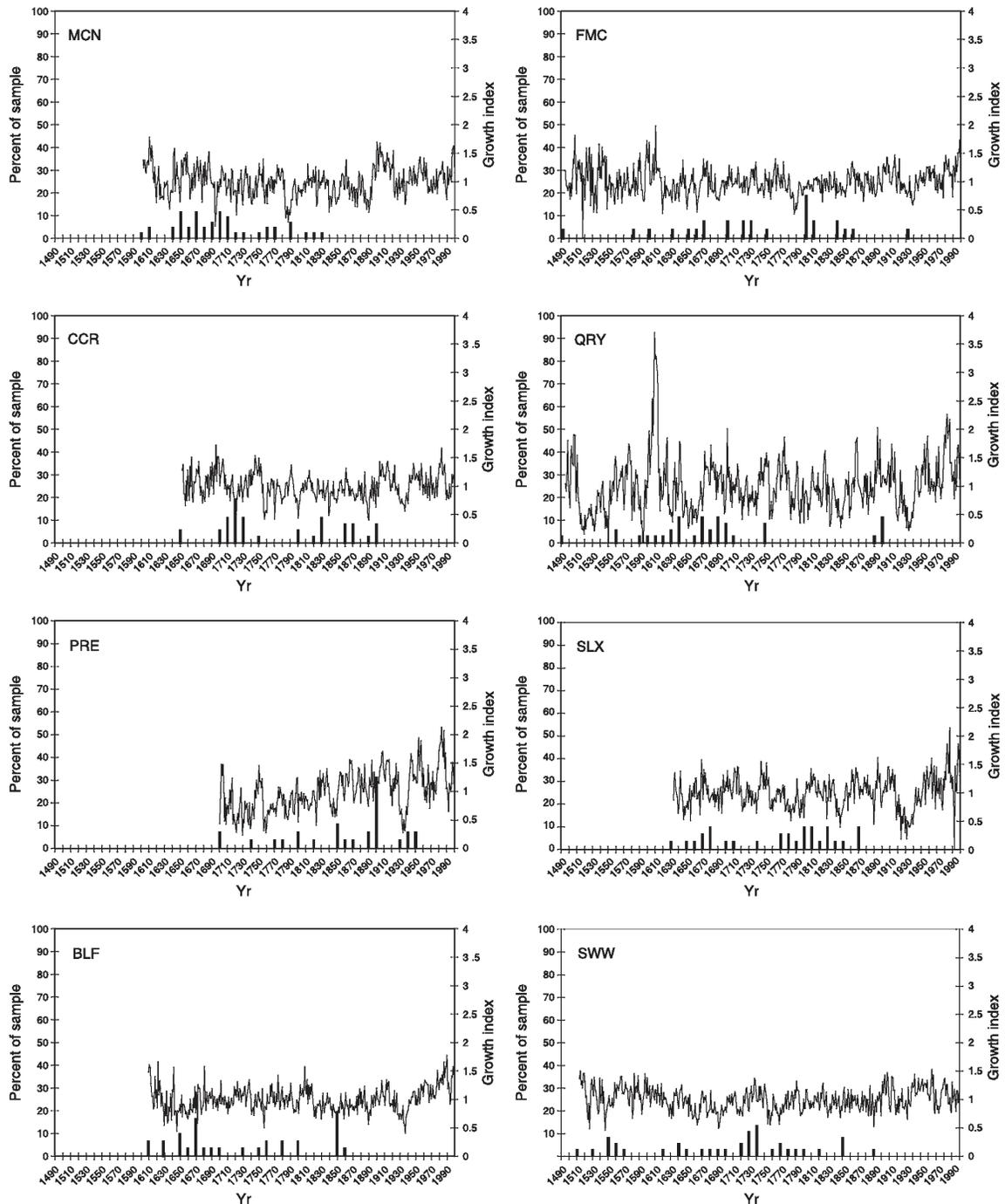
| Site code* | <i>n</i> | Age (yr) |       |        |         |         | Basal diameter (cm) |      |
|------------|----------|----------|-------|--------|---------|---------|---------------------|------|
|            |          | Mean     | SD    | Median | Maximum | Minimum | Mean                | SD   |
| MCN        | 44       | 293      | 58.3  | 300    | 399     | 162     | 120.8               | 22.6 |
| FMC        | 27       | 260      | 98.7  | 267    | 506     | 71      | 102.3               | 19.7 |
| CCR        | 37       | 220      | 76.5  | 263    | 349     | 99      | 109.8               | 32.2 |
| QRY        | 36       | 305      | 100.8 | 320    | 506     | 94      | 65.3                | 16.0 |
| PRE        | 29       | 137      | 69.5  | 101    | 301     | 50      | 115.6               | 20.7 |
| SLX        | 31       | 232      | 72.5  | 210    | 368     | 123     | 96.2                | 22.5 |
| BLF        | 31       | 267      | 85.7  | 300    | 391     | 141     | 85.6                | 34.1 |
| SWW        | 38       | 295      | 100.5 | 270    | 488     | 105     | 122.9               | 15.4 |
| All sites  | 34       | 251      | 82.8  | 254    | 414     | 106     | 102.3               | 22.9 |

\*See Table 1 for site description.

We found no relationship between the age structure of a site (Fig. 5; Table 3) and radial growth-rate changes (Fig. 2). For example, the two oldest sites have similar mean ages and variability (Table 3), with QRY having a substantial growth change through time, and SWW having virtually no change. The relationship between mean age and relative growth-rate changes during matched drought years was insignificant ( $r_s = -0.02$ ,  $P = 0.955$ ,  $n = 8$ ).

## Discussion

Previous research has shown that the comparative effects of elevated atmospheric CO<sub>2</sub> on both herbaceous and woody plant growth are commonly evident during water stress (see reviews by Idso & Idso, 1994; Pospisilova & Catsky, 1999; Poorter & Perez-Soba, 2001; Wullschleger et al., 2002). The effects, exhibited either individually or collectively during drought, have been reductions in stomatal conductance (thus transpiration) (Tognetti et al., 1998); higher leaf water potential (Polley et al., 1999; Wall, 2001); increased photosynthesis (Centritto et al., 1999; Palanisamy, 1999); increased biomass (Hättenschwiler et al., 1997; Schulte et al., 1998; Owensby et al., 1999; Knapp et al., 2001 a); extension of the active photosynthetic period (Owensby et al., 1997); and greater recovery following drought stress (Ferris et al., 1998; Hamerlynck et al., 2000; Knapp et al., 2001b). Our comparison of the growth responses during matched dry and wet years pre- and post-1950 are consistent with these findings, as the relative change in growth is upward at seven of our sites, ranging from 1 to 133% (Fig. 2), with responses during matched wet years less pronounced. Further, we found similar results when analysing the data by PDSI category, with the greatest absolute and relative increases in radial growth post-1950 occurring during the years when soil moisture was most limiting (Fig. 3).



**Fig. 5** Percentage of ponderosa pine (*Pinus ponderosa*) trees within each chronology established, by decade (vertical bars); standardized (mean = 1.0) yearly radial growth index values (continuous line) (see Table 1; Fig. 1 for site descriptions and locations).

The spatial pattern of relative growth responses is closely and positively related to site stress (Fig. 4). QRY, for example, is a disjunct stand of ponderosa pine in an ecosystem otherwise dominated by western juniper and sagebrush. QRY also has the second lowest elevation of the study sites (Table 1), a southern exposure, and estimated annual precipitation of  $< 30 \text{ cm yr}^{-1}$  (SCAS, 2004). Similarly, trees at SLX had large relative growth increases; this site is also characterized by dry conditions ( $\text{ppt} < 32 \text{ cm annually}$ ; SCAS, 2004). At SLX we sampled on a western juniper/ponderosa pine ecotone, thus ponderosa pine trees were growing near their minimal precipitation limit. In addition, sites with smaller diameter trees (e.g. QRY, BLF, SLX) experience larger changes in radial growth. Although the relationship between basal diameter and percentage missing rings is not significant ( $r_s = -0.61$ ,  $P = 0.108$ ,  $n = 8$ ), it is of sufficient magnitude to suggest an indirect relationship, as sites experiencing higher levels of stress experience the greatest growth enhancement effects from  $\text{CO}_2$  enrichment, while the same stresses produce smaller-diameter trees.

In contrast, an atmospheric CO<sub>2</sub> effect was not detected at SWW. SWW receives nearly double the annual precipitation of QRY/SLX (SCAS, 2004), and its high elevation assures comparatively cooler temperatures throughout the summer, thus soil moisture limitations are less common. A similar growth response to that at SWW is present at MCN, another comparatively wet site with less soil moisture stress. Although BLF receives roughly the same amount of annual precipitation as SWW (SCAS, 2004), it is lower in elevation and probably experiences extreme surface temperatures on sunny summer days, as the trees are growing within a low-albedo lava field that effectively absorbs heat energy. The trees here are probably rooted in poorly developed soils, which would further limit soil moisture retention.

Several studies have suggested that elevated atmospheric CO<sub>2</sub> has a positive effect on radial growth rates of naturally occurring trees (LaMarche et al., 1984; Graybill, 1987; Graybill & Idso, 1993; Nicolussi et al., 1995; Hättenschwiler et al., 1997; Knapp et al., 2001a, 2001b; Bunn et al., 2003). Further, a physiological mechanism to explain enhanced relative growth under more stressful conditions for ponderosa pine exists, as Feng (1999) has shown that the species, growing under natural conditions, has experienced increased intrinsic WUE during the last century. Conversely, other studies of naturally occurring conifers have either shown no detectable CO<sub>2</sub> enhancement effect for ponderosa pine (Kienast & Luxmoore, 1988), or have attributed anomalous post-1950s growth rates of high-elevation species (bristlecone and foxtail pines and Sierra juniper) to increasing temperatures (Bunn et al., 2005).

Our findings provide further insight on the variety of responses reported so far. Our results, showing that radial growth has increased in the post-1950s period at all sites, and significantly at 50% of the sites, while climatic conditions have generally been unchanged (Table 2), suggest that nonclimatic driving forces are operative. Our data collection from natural field sites precludes absolute control over the multiple driving forces that can affect radial growth rates. However, our specific selection of study localities that either minimize or eliminate anthropogenic influences on radial growth rates reduces these potentially confounding influences. Further, these radial growth responses are generally consistent with what has been shown in long-term open-top chamber (Idso & Kimball, 2001) and FACE studies (see review by Ainsworth & Long, 2005). These findings suggest that elevated levels of atmospheric CO<sub>2</sub> are acting as a driving force for increased radial growth of ponderosa pine, but that the overall influence of this effect may be enhanced, reduced or obviated by site-specific conditions.

We suggest that an atmospheric CO<sub>2</sub> response exists for ponderosa pine, as measured by radial growth, and that site-specific conditions probably have an impact on the influence of this effect. However, our study was based on a sample of trees selected principally from open-canopy stands as an artefact of minimizing confounding influences, and we do not know if similar responses would occur for ponderosa pine in closed-canopy environments, where both intra- and interspecific competition would be greater. Our results are consistent with results from various controlled studies (open-top chamber, FACE and CO<sub>2</sub> vent) of the potential growth enhancement effects of elevated CO<sub>2</sub> on trees (Hättenschwiler et al., 1997, 2002; Norby et al., 1999; Idso & Kimball, 2001; Adam et al., 2004), as we detected the greatest potential CO<sub>2</sub>-related growth enhancements, after controlling for other factors, on the most stressed sites. However, other FACE studies under closed-canopy conditions have shown that both deciduous (Norby et al., 2004; Körner et al., 2005) and coniferous ever-green (Oren et al., 2001) forest species have zero to limited stem-growth responses to elevated atmospheric CO<sub>2</sub>, and that a variety of conditions, including soil fertility (Oren et al., 2001), tree species and intra-annual climatic variability (Körner et al., 2005), and fine-root production (Norby et al., 2004), could affect tree-growth responses. Interesting questions arise as to whether a suite of responses would also occur for different species growing under natural conditions where atmospheric CO<sub>2</sub> conditions have gradually increased.

In summary, we explored whether the observed physiological responses of plants exposed to step increases of atmospheric CO<sub>2</sub> in laboratory, open-top chamber, FACE and CO<sub>2</sub>-vent settings also exist over: (1) large geographical areas; (2) extended time periods; (3) different climates; and (4) under modest increases in atmospheric CO<sub>2</sub> concentrations. We hypothesized that ponderosa pine, a widespread species in the American west that has great ecological and economic value, would respond to gradual increases in atmospheric CO<sub>2</sub> over

the past 50 yr, and that these effects would be most apparent during drought stress and on environmentally harsh sites. Overall, our results support these hypotheses. We conclude that it is likely an atmospheric CO<sub>2</sub>-driven growth-enhancement effect exists for ponderosa pine growing under specific natural conditions within the interior Pacific Northwest.

## References

- Adam N, Wall GW, Kimball BA, Idso SB, Webber AN. 2004. Photosynthetic down regulation over long-term CO<sub>2</sub> enrichment in leaves of sour orange (*Citrus aurantium*) trees. *New Phytologist* 163: 341–347.
- Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist* 165: 351–372.
- Ainsworth EA, Davey PA, Hymus GJ, Osborne CP, Rogers A, Blum H, Nosberger J, Long SP. 2003. Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with *Lolium perenne* grown for 10 years at two nitrogen fertilization levels under Free Air CO<sub>2</sub> enrichment (FACE). *Plant, Cell & Environment* 26: 705–714.
- Alley WM. 1984. The Palmer Drought Severity Index: limitations and assumptions. *Journal of Applied Meteorology* 23: 1100–1109.
- Bunn AG, Graumlich LJ, Urban DL. 2005. Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. *Holocene* 14: 481–488.
- Bunn AG, Lawrence RL, Bellante GJ, Waggoner LA, Graumlich LJ. 2003. Spatial variation in distribution and growth patterns of old growth strip-bark pines. *Arctic, Antarctic and Alpine Research* 35: 323–330.
- Centritto M, Magnani F, Lee HSJ, Jarvis PG. 1999. Interactive effects of elevated [CO<sub>2</sub>] and drought on cherry (*Prunus avium*) seedlings. II. Photosynthetic capacity and water relations. *New Phytologist* 141: 141–153.
- Constable JVH, Taylor GE Jr, Lawrence JA, Weber JA. 1996. Climatic change effects on the physiology and growth of *Pinus ponderosa*: expectations from simulation modeling. *Canadian Journal of Forest Research* 26: 1315–1325.
- Cook ER, Holmes RL. 1997. ARSTAN: Chronology development. In: Grissino-Mayer HD, Holmes RL, Fritts HC, eds. *The International Tree-Ring Data Bank Program Library Version 21: User's Manual*. Tucson, AZ, USA: University of Arizona Laboratory of Tree-Ring Research, 75–92.
- 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.
- Fenn ME, Haeuber RE, Tonnesen GS, Baron JS, Grossman-Clarke S, Hope D, Jaffe DA, Copeland S, Geiser L, Rueth HM, Sickman JO. 2003. Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience* 53: 1–13.
- Ferris R, Wheeler TR, Hadley P, Ellis RH. 1998. Recovery of photosynthesis after environmental stress in soybean grown under elevated CO<sub>2</sub>. *Crop Science* 38: 948–955.
- Gifford RM. 2004. The CO<sub>2</sub> fertilizing effect — does it occur in the real world? *New Phytologist* 163: 221–225.
- Graumlich LJ. 1991. Subalpine tree growth, climate, and increasing CO<sub>2</sub>: an assessment of recent growth trends. *Ecology* 72: 1–11.
- Graybill DA. 1987. A network of high elevation conifers in the western United States for detection of tree-ring growth response to increasing atmospheric carbon dioxide. In: Jacoby GC, Hornbeck JW, eds. *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*. Report DOE/CONF-8608144. Washington, DC, USA: US Department of Energy, 463–474.
- Graybill DA, Idso SB. 1993. Detecting the aerial fertilization of atmospheric CO<sub>2</sub> enrichment in tree-ring chronologies. *Global Biogeochemical Cycles* 7: 81–95.
- Hamerlynck EP, Huxman TE, Loik ME, Smith SD. 2000. Effects of extreme high temperature, drought and elevated CO<sub>2</sub> on photosynthesis of the Mojave Desert evergreen shrub. *Plant Ecology* 148: 183–193.
- Hättenschwiler S, Miglietta F, Raschi A, Körner C. 1997. Thirty years of in situ tree growth under elevated CO<sub>2</sub>: a model for future forest responses. *Global Change Biology* 3: 464–471.
- Hättenschwiler S, Handa T, Egli L, Asshoff R, Ammann W, Körner C. 2002. Atmospheric CO<sub>2</sub> enrichment of alpine treeline conifers. *New Phytologist* 156: 363–375.
- Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*

43: 69–78.

Idso SB. 1989. Carbon dioxide and global change: Earth in transition. Tempe, AZ, USA: IBR Press.

Idso KE, Idso SB. 1994. Plant responses to atmospheric CO<sub>2</sub> enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agricultural and Forest Meteorology* 69: 153 – 203.

Idso SB, Kimball BA. 2001. CO<sub>2</sub> enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* 46: 147–153.

Karl TR. 1986. The sensitivity of the Palmer Drought Severity Index and Palmer's Z-Index to their calibration coefficients including potential evapotranspiration. *Journal of Climate and Applied Meteorology* 25: 77–86.

Kienast F, Luxmoore RJ. 1988. Tree-ring analysis and conifer growth responses to increased atmospheric CO<sub>2</sub> levels. *Oecologia* 76: 487–495.

Kimball BA, Kobayashi K, Bindi M. 2002. Responses of agricultural crops to free-air CO<sub>2</sub> enrichment. *Advances in Agronomy* 77: 293–368.

Klironomos JN, Allen MF, Rillig MC, Piotrowski J, Makvandi-Nejad S, Wolfe BE, Powell JR. 2005. Abrupt rise in atmospheric CO<sub>2</sub> overestimates community response in a model plant–soil system. *Nature* 433: 621–624.

Knapp PA, Soulé PT. 1996. Vegetation change and the role of atmospheric CO<sub>2</sub> enrichment on a relict site in central Oregon: 1960–1994. *Annals of the Association of American Geographers* 86: 387–411.

Knapp PA, Soulé PT. 1998. Recent expansion of western juniper on near-relict site in central Oregon. *Global Change Biology* 4: 347–357.

Knapp PA, Soulé PT, Grissino-Mayer HD. 2001 a. Detecting the potential regional effects of increased atmospheric CO<sub>2</sub> on growth rates of western juniper. *Global Change Biology* 7: 903–917.

Knapp PA, Soulé PT, Grissino-Mayer HD. 2001b. Post-drought growth responses of western juniper (*Juniperus occidentalis* var. *occidentalis*) in central Oregon. *Geophysical Research Letters* 28: 2657–2660.

Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Peláez-Riedl S, Pepin S, Siegwolf RTW, Zotz G. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO<sub>2</sub>. *Science* 309: 1360–1362.

LaMarche VC, Graybill DA, Fritts HC, Rose MR. 1984. Increasing atmospheric carbon dioxide: tree-ring evidence for growth enhancement in natural vegetation. *Science* 225: 1019–1021.

Lee EH, Hogsett WE. 2001. Interpolation of temperature and non-urban ozone exposure at high spatial resolution over the western United States. *Climate Research* 18: 163–179.

Luo YQ, Su B, Currie WS, Dukes JS, Finzi A, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ, Pataki DE, Shaw MR, Zak DR, Field CB. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54: 731–739.

Maherali H, DeLucia EH. 2000. Interactive effects of elevated CO<sub>2</sub> and temperature on water transport in ponderosa pine. *American Journal of Botany* 87: 243–249.

Mayeux HS, Johnson HB, Polley HW. 1991. Global change and vegetation dynamics. In: James LF, Evans JO, Ralphs M, Child R, eds. *Noxious range weeds*. Boulder, CO, USA: Westview Press, 62–74.

Mayeux HS, Johnson HB, Polley HW. 1994. Potential interactions between global change and intermountain annual grasslands. In: Monsen SB, Kitchen S G, eds. *Proceedings of the Symposium on Ecology, Management and Restoration of Intermountain Annual Rangelands*. General Technical Report INT-GTR 313. Ogden, UT, USA: US Department of Agriculture, Forest Service, 95–100.

McGrew JC Jr, Monroe CB. 2000. *Statistical problem solving in geography*, 2nd edn. Boston, MA, USA: McGraw-Hill.

Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF. 1991. Predicting ecosystem responses to elevated CO<sub>2</sub> concentrations. *Bioscience* 41: 96–104.

NCDC. 2004. National Climatic Data Center. Time bias corrected divisional temperature-precipitation-drought index: dataset TD-9640. Asheville, NC, USA: National Climatic Data Center. <http://www1.ncdc.noaa.gov/pub/data/cirs/>.

Nicolussi K, Bortenschlager S, Körner C. 1995. Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO<sub>2</sub>-related. *Trees* 9: 181–189.

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R. 1999. Tree responses to rising CO<sub>2</sub> in field experiments: implications for the future forest. *Plant, Cell & Environment* 22: 683–714.

Norby RJ, Ledford J, Reilly CD, Miller NE. 2004. Fine-root production dominates response of a deciduous

forest to atmospheric CO<sub>2</sub> enrichment. PNAS 101: 9689–9693.

Nowak RS, Ellsworth DS, Smith SD. 2004. Functional responses of plants to elevated atmospheric CO<sub>2</sub>— do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* 162: 253–280.

Olszyk DM, Johnson MG, Phillips DL, Seidler RJ, Tingey DT, Watrud LS. 2001. Interactive effects of CO<sub>2</sub> and O<sub>3</sub> on a ponderosa pine plant/litter/soil mesocosm. *Environmental Pollution* 115: 447–462.

Olszyk D, Tingey D, Wise C, Davis E. 2002. CO<sub>2</sub> and O<sub>3</sub> alter photosynthesis and water vapor exchange for *Pinus ponderosa* needles. *Phyton* 42: 121–134.

Olszyk D, Johnson M, Tingey D, King G, Storm M, Plocher M. 2003. Effects of carbon dioxide and ozone on growth and biomass allocation in *Pinus ponderosa*. *Ekológia (Bratislava)* 22: 265–276.

Oren R, Ellsworth DS, Johnsen KH, Phillips N, Ewers BE, Maier C, Schäfer KVR, McCarthy H, Hendrey G, McNulty SG, Katul G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO<sub>2</sub>-enriched atmosphere. *Nature* 411: 469–472.

Owensby CE, Ham JM, Knapp AK, Bremer D, Auen LM. 1997. Water vapor fluxes and their impact under elevated CO<sub>2</sub> in a C<sub>4</sub> tallgrass prairie. *Global Change Biology* 3: 189–195.

Owensby CE, Ham JM, Knapp AK, Auen LM. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO<sub>2</sub>. *Global Change Biology* 5: 497–506.

Palanisamy K. 1999. Interactions of elevated CO<sub>2</sub> concentration and drought stress on photosynthesis in *Eucalyptus cladocalyx* F. Muell. *Photosynthetica* 36: 63–68.

Palmer W. 1965. Meteorological drought. Washington, DC, USA: US Government Printing Office.

Phipps RL. 1985. Collecting, preparing, crossdating, and measuring tree increment cores. United States Geological Survey Water Resources Investigations Report 85-4148. Reston, VA, USA.

Pohl KA, Hadley KS, Arabas KB. 2002. A 545-year drought reconstruction for central Oregon. *Physical Geography* 23: 302–320.

Polley HW, Tischler CR, Johnson HB, Pennington RE. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO<sub>2</sub> enrichment. *Tree Physiology* 19: 359–366.

Poorter H, Perez-Soba M. 2001. The growth responses of plants to elevated CO<sub>2</sub> under non-optimal environmental conditions. *Oecologia* 129: 1–20.

Pospisilova J, Catsky J. 1999. Development of water stress under increased atmospheric CO<sub>2</sub> concentration. *Biologia Plantarum* 42: 1–24.

Pushnik JC, Demaree RS, Houppis JLJ, Flory WB, Bauer SC, Anderson PD. 1995. The effect of elevated carbon dioxide on a Sierra–Nevadan dominant species: *Pinus ponderosa*. *Journal of Biogeography* 22: 249–254.

Rasse DP, Peresta G, Drake BG. 2005. Seventeen years of elevated CO<sub>2</sub> exposure in a Chesapeake Bay wetland: sustained but contrasting responses of plant growth and CO<sub>2</sub> uptake. *Global Change Biology* 11: 1–9.

Saxe H, Ellsworth DS, Heath J. 1998. Tansley Review 98. Tree and forest functioning in an enriched CO<sub>2</sub> atmosphere. *New Phytologist* 139: 395–436.

SCAS. 2004. Spatial Climate Analysis Service. Corvallis, OR, USA: Oregon State University.  
<http://www.ocs.orst.edu/prism/>

Schulte M, Herschbach C, Rennenberg H. 1998. Interactive effects of elevated atmospheric CO<sub>2</sub>, mycorrhization and drought on long-distance transport of reduced sulphur in young pedunculate oak trees (*Quercus robur* L.). *Plant, Cell & Environment* 21: 917–926.

Soulé PT, Knapp PA, Grissino-Mayer HD. 2003. Human agency, environmental drivers, and western juniper establishment during the late Holocene. *Ecological Applications* 14: 96–112.

Soulé PT, Knapp PA, Grissino-Mayer HD. 2004. Comparative rates of western juniper afforestation in south-central Oregon and the role of anthropogenic disturbance. *Professional Geographer* 55: 43–55.

Stokes MA, Smiley TL. 1968. Introduction to tree-ring dating. Chicago, IL, USA: University of Chicago Press.

Swetnam TW, Thompson MA, Sutherland EK. 1985. Using dendrochronology to measure radial growth of defoliated trees. USDA Forest Service Agricultural Handbook no. 639. Washington, DC, USA.

Tingey DT, Laurence JA, Weber JA, Greene J, Hogsett WE, Brown S, Lee EH. 2001. Elevated CO<sub>2</sub> and temperature alter the response of *Pinus ponderosa* to ozone: a simulation analysis. *Ecological Applications* 11:

412–1424.

- Tingey DT, Johnson MG, Phillips DL. 2005. Independent and contrasting effects of elevated CO<sub>2</sub> and N-fertilization on root architecture in *Pinus ponderosa*. *Trees* 19: 43–50.
- Tissue DT, Griffin KL, Ball JT. 1999. Photosynthetic adjustment in field-grown ponderosa pine trees after six years exposure to elevated CO<sub>2</sub>. *Tree Physiology* 19: 221–228.
- Tognetti R, Longobucco A, Miglietta F, Raschi A. 1998. Transpiration and stomatal behaviour of *Quercus ilex* plants during the summer in a Mediterranean carbon dioxide spring. *Plant, Cell & Environment* 21: 613–622.
- Walker RF, Johnson DW, Geisinger DR, Ball JT. 2000. Growth, nutrition, and water relations of ponderosa pine in a field soil as influenced by long-term exposure to elevated atmospheric CO<sub>2</sub>. *Forest Ecology and Management* 137: 1–11.
- Wall GW. 2001. Elevated atmospheric CO<sub>2</sub> alleviates drought stress in wheat. *Agriculture, Ecosystems and Environment* 87: 261–271.
- Wullschlegel SD, Tschaplinski TJ, Norby RJ. 2002. Plant water relations at elevated CO<sub>2</sub>— implications for water limited environments. *Plant, Cell & Environment* 25: 319–331.
- Yamaguchi DK. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21: 414–416.
- Youngblood A, Max T, Coe K. 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. *Forest Ecology and Management* 199: 191–217.