

Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO₂ fertilization effect?

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Summary

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- The primary objective of this study was to determine if gradually increasing levels of atmospheric CO₂, 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 CO₂ 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 CO₂ fertilization is probably operative, having a positive effect on radial growth rates of ponderosa pine through increasing water-use efficiency. A CO₂-driven growth enhancement may affect ponderosa pine growing under both natural and controlled conditions.

Key words: CO₂ fertilization, ponderosa pine (*Pinus ponderosa*), site harshness, drought, interior Pacific Northwest.

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Introduction

Two major environmental issues have arisen regarding the increasingly CO₂-rich world of the late 20th and early 21st centuries: climatic change, and plant responses to the environment. While the implications of atmospheric CO₂ for potential climatic change have received the majority of attention, the potential role of atmospheric CO₂ 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 CO₂. 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 CO₂ conditions may be substantially different from step increases in CO₂ (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 CO₂

fertilization response of ponderosa pine (*Pinus ponderosa*) under natural conditions in the interior Pacific Northwestern USA.

Directly implicating atmospheric CO₂ 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 CO₂ 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 CO₂ 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 CO₂ fertilization effects. Second, we employ a series of tests to determine if a CO₂ 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 CO₂ levels were higher. Further, we hypothesize that site harshness will be positively related to enhanced radial growth rates caused by atmospheric CO₂ fertilization, and that atmospheric CO₂ 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 CO₂ fertilization (Knapp & Soulé, 1996, 1998; Knapp *et al.*, 2001a, 2001b; 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 CO₂ 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 CO₂ 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 CO₂ on mature ponderosa pine, tree growth-simulation models have demonstrated that ponderosa pine grown under elevated CO₂ conditions (550 µl 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 CO₂ conditions (500 µmol 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 CO₂ 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; Wullschlegel *et al.*, 2002). However, a meta-analysis of ecosystem Free Air CO₂ 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). 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 topographic conditions, ranging from extremely water-limiting environments such as QRY (southern exposure, low elevation)

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> , <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> , <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> , <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> , <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.

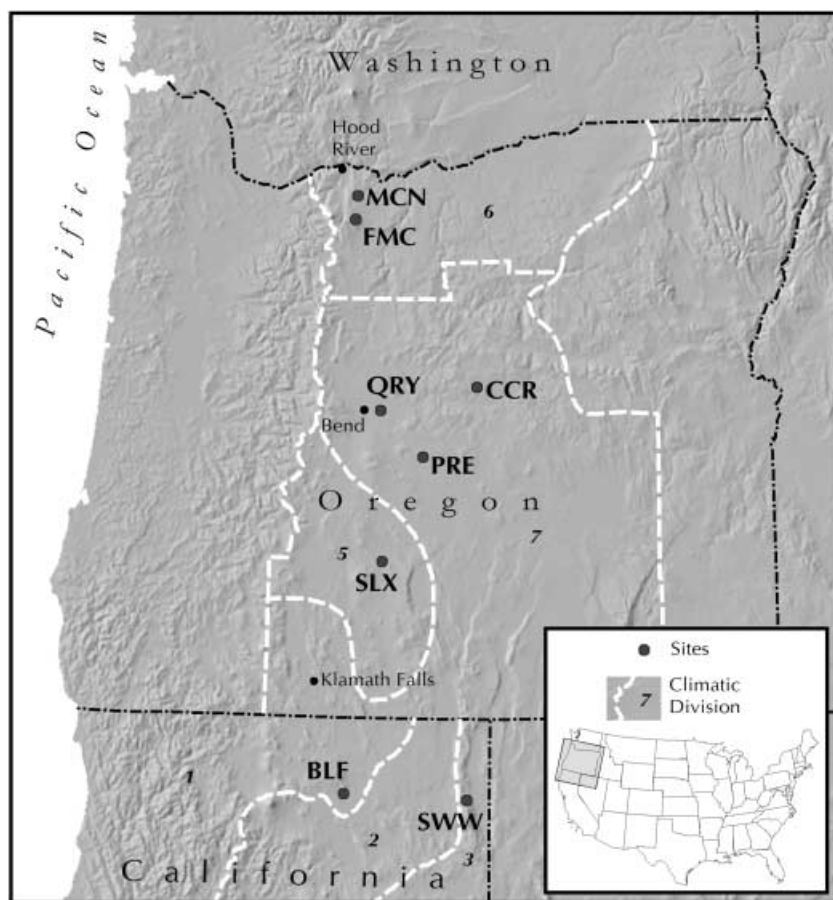


Fig. 1 Location of ponderosa pine (*Pinus ponderosa*) sampling sites and selected climatic divisions (see Table 1 for site descriptions).

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 CO₂, we accounted for this possibility through the selection of a species that responds significantly to CO₂ 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 CO₂ 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 CO₂ levels, but where growth, particularly post-1950, has occurred under increasing and substantially higher atmospheric CO₂ 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.

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 CO₂-caused vegetation change in nonlaboratory settings (Kienast & Luxmoore, 1988; Graumlich, 1991; Knapp *et al.*, 2001a, 2001b) because it marks an inflection point in rising CO₂ levels. Similarly to Knapp *et al.* (2001a), 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 ≤ -1 and ≤ -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 ≤ -2.0 , ≤ -1.0 , < 0 , ≥ 0 , ≥ 1.0 and ≥ 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.* (2001a). 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.

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

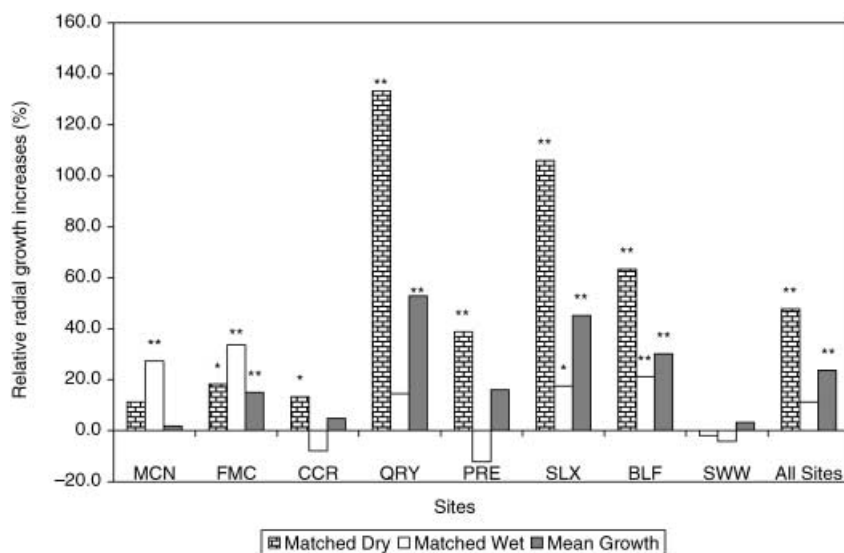


Fig. 2 Ponderosa pine (*Pinus ponderosa*) increases in radial growth rates post-1950 relative to pre-1950 during ecologically comparable drought years and wet years, and between all years. **, *, Significant differences from a one-tailed matched-pairs test at $P < 0.01$ and $P < 0.05$, respectively.

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).

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 , ≤ -1 and ≤ -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 $PDSI \geq 0$ and ≥ 1 , and 25% of the sites with $PDSI \geq 2$. The

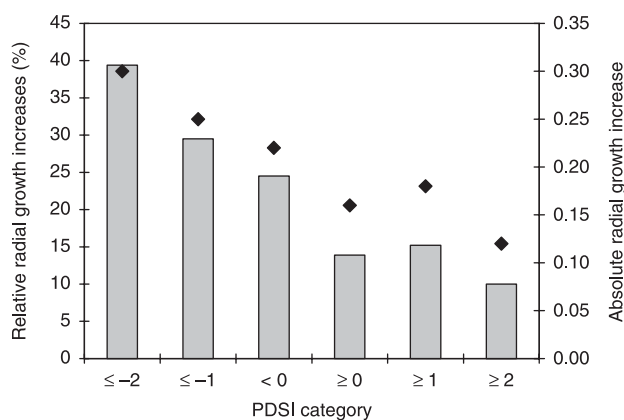


Fig. 3 Ponderosa pine (*Pinus ponderosa*) relative (horizontal bars) and absolute (diamonds) radial growth increases post-1950 compared with pre-1950 during years falling into various Palmer Drought Severity Index (PDSI) categories of drought (wet) severity.

range of response across the eight sites in absolute growth-rate changes are: 0.0–0.69 for $PDSI \leq -2$; 0.02–0.54 for $PDSI \leq -1$; 0.02–0.49 for $PDSI < 0$; 0.01–0.4 for $PDSI \geq 0$; –0.06 to 0.42 for $PDSI \geq 1$; –0.18 to 0.26 for $PDSI \geq 2$.

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 ≤ -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

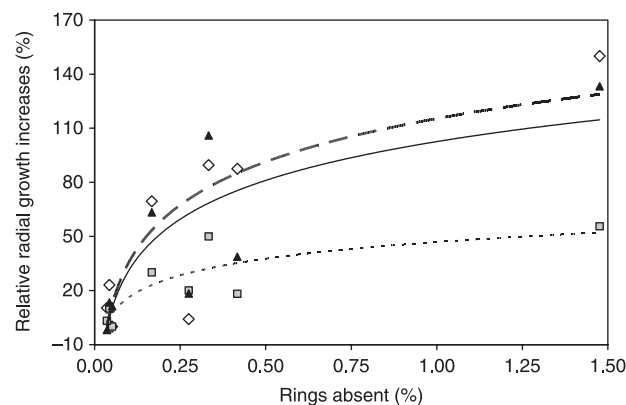


Fig. 4 Comparison of site harshness (measured as percentage missing rings) and radial growth increases of ponderosa pine (*Pinus ponderosa*) post-1950 relative to pre-1950 during ecologically comparable drought years (triangles, solid line); years with $PDSI \leq -2$ (diamonds, long dashed line); and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

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 (<i>n</i> = 54)	0.0	–0.4	0.1	–0.4
Mean PDSI 1950–99 (<i>n</i> = 50)	–0.2	0.2	0.2	0.4
<i>P</i>	0.85	0.16	0.83	0.02
<i>r</i> , PDSI/year (1896–1999, <i>n</i> = 104)	0.02	0.08	–0.10	0.20
<i>P</i>	0.86	0.44	0.92	0.04
<i>r</i> , Annual precipitation/year (1896–1999, <i>n</i> = 104)	–0.02	0.12	–0.05	0.12
<i>P</i>	0.87	0.22	0.64	0.22
<i>r</i> , Annual temperature/year (1896–1999, <i>n</i> = 104)	0.17	0.22	0.10	0.07
<i>P</i>	0.08	0.02	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.

≤ –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.

We found no relationship between the age structure of a site (Fig. 5; Table 3) and radial growth-rate changes (Fig. 2). For

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.

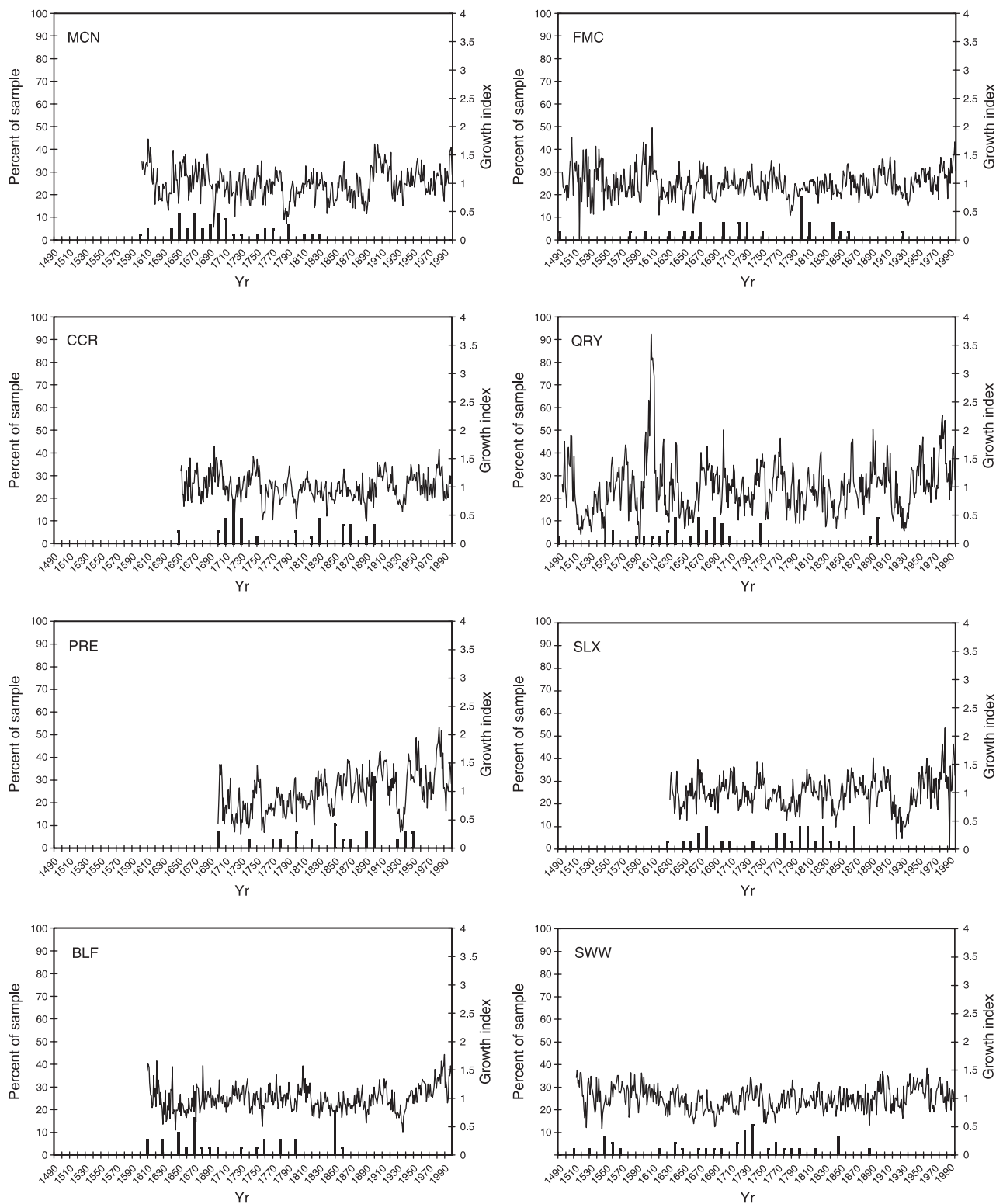


Fig. 5 Percentage of ponderosa pine (*Pinus ponderosa*) trees within each chronology established, by decade (vertical bars); standardized (mean = 1.0) yearly radial growth index values (continuous line) (see Table 1; Fig. 1 for site descriptions and locations).

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 CO₂ 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; Wullschlegel *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.*, 2001a); 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 11 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).

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 (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 CO₂ enrichment, while the same stresses produce smaller-diameter trees.

In contrast, an atmospheric CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ vent) of the potential growth enhancement effects of elevated CO₂ on trees (Hättenschwiler *et al.*, 1997, 2002; Norby *et al.*, 1999; Idso & Kimball, 2001; Adam *et al.*, 2004), as we detected the greatest potential CO₂-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 evergreen (Oren *et al.*, 2001) forest species have zero to limited stem-growth responses to elevated atmospheric CO₂, 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 CO₂ conditions have gradually increased.

In summary, we explored whether the observed physiological responses of plants exposed to step increases of atmospheric CO₂ in laboratory, open-top chamber, FACE and CO₂-vent settings also exist over: (1) large geographical areas; (2) extended time periods; (3) different climates; and (4) under modest increases in atmospheric CO₂ 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 CO₂ 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 CO₂-driven growth-enhancement effect exists for ponderosa pine growing under specific natural conditions within the interior Pacific Northwest.

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