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# Detecting potential regional effects of increased atmospheric $CO_2$ on growth rates of western juniper

PAUL A. KNAPP,* PETER T. SOULÉ† and HENRI D. GRISSINO-MAYER‡
**Department of Anthropology and Geography, Georgia State University Atlanta, GA 30303; †Department of Geography and Planning, Appalachian State University, Boone, NC 28608; ‡Department of Geography, The University of Tennessee, Knoxville, TN 37996, USA*

## Abstract

**Evidence of an atmospheric $CO_2$ fertilization effect on radial growth rates was uncovered by examining climate–growth relationships for seven western juniper tree-ring chronologies in central Oregon using multiple regression models. Consistent upward trends of the residuals from dendroclimatic models indicated a decreased ability for climate parameters to predict growth with time. Additionally, an assessment was made of whether enhanced growth was detectable under drought conditions, because a major benefit of elevated atmospheric $CO_2$ is the reduction of water stress. Mean ring indices were compared between ecologically comparable drought years, when atmospheric $CO_2$ was lower (1896–1949), and more recent drought years that occurred under higher atmospheric $CO_2$ concentrations (1950–96/98). The results presented herein show that: (i) residuals from climate/growth models had a significant positive trend at six of seven sites, suggesting the presence of a nonclimatic factor causing increased growth during recent decades; (ii) overall growth was 23% greater in the latter half of the 20th century; (iii) growth indices during matched drought and matched wet years were 63% and 30% greater, respectively, in the later 20th century than the earlier 20th century; and (iv) harsher sites had greater responses during drought periods between early and late periods. While it is not possible to rule out other factors, these results are consistent with expectations for $CO_2$ fertilization effects.**

*Keywords:* atmospheric $CO_2$ enrichment, climate–growth responses, western juniper

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## Introduction

The effects of elevated atmospheric $CO_2$ on plant growth in natural environments are unclear. While many laboratory studies have documented the positive responses of plants to elevated $CO_2$ levels, these studies primarily investigated short-term (often $<1$ y) responses of crop species, and typically under double ambient atmospheric $CO_2$ conditions (e.g. Kimball 1983; Idso 1989; Harley *et al*. 1992; Rozema 1993; Kimball *et al*. 1995). Fewer laboratory experiments have been conducted on tree species (e.g. Centritto *et al*. 1999), whose responses often differ from those of crops (Lee & Jarvis 1995), and may vary over the longer lifespans of trees (e.g. Idso & Kimball 1997). Studies examining the role of atmospheric $CO_2$ enrichment on trees growing under natural conditions are uncommon (Polley 1997; Idso 1999; Naidu & Delucia 1999). Results from these studies show relative increases in growth (e.g. standing biomass, ring widths) in response to elevated atmospheric $CO_2$ (Hattenschwiler *et al*. 1997; Idso & Kimball 1997; Tissue *et al*. 1997; Tewelski *et al*. 1999). Furthermore, Norby *et al*. (1999) have noted that the responses of field-grown trees under elevated atmospheric $CO_2$ (approximately 300ppm/v increase) suggest that increases in photosynthesis are 'continuous and surprisingly consistent,' and 'there is, at present, little reason to expect a long-term loss of sensitivity to $CO_2$', although exceptions exist (e.g. Griffin *et al*. 2000). Thus, the question arises: do natural trees benefit from more modest increases of atmospheric $CO_2$ that have occurred during the 20th century?

Correspondence: Paul A. Knapp, fax +1/404 651-3235, e-mail gegpak@langate.gsu.edu

Several dendroecological studies have investigated the possibility that tree growth has exceeded expected growth (given climatic conditions) during the 20th century (e.g. LaMarche *et al*. 1984; Kienast & Luxmoore 1988; Graumlich 1991; Briffa 1992; Graybill & Idso 1993; Nicolussi *et al*. 1995). These studies are valuable for examining natural responses of plants to rising atmospheric $CO_2$ because the length of tree-ring chronologies provides a long-term context for evaluating changes in growth. Several studies present evidence of a probable $CO_2$ enrichment effect on tree growth (e.g. LaMarche *et al*. 1984; Graybill 1987; Graybill & Idso 1993; Nicolussi *et al*. 1995; Feng 1999), while others have not (e.g. Kienast & Luxmoore 1988; Graumlich 1991; D'Arrigo & Jacoby 1993; Tognetti *et al*. 2000a).

Evaluating the effect of atmospheric $CO_2$ enrichment on plant growth in natural environments remains an inexact proposition. Current evidence supporting atmospheric $CO_2$-fertilization on tree growth is 'inconclusive' (Jacoby & D'Arrigo 1997) largely owing to difficulties in determining whether increased radial growth rates during the last century are a function of: (i) favourable climatic changes; (ii) anthropogenic atmospheric deposition (e.g. nitrogen); (iii) $CO_2$ fertilization; or (iv) the synergistic effects of some or all of these factors. Furthermore, growth responses can be confounded by a suite of environmental factors such as soil type, growing season length, and duration of exposure (Norby *et al*. 1999). However, examination of species that exhibit high sensitivity to precipitation variability, low sensitivity to temperature variability and nutrient deposition, and that grow under a variety of soil conditions may diminish this problem.

Western juniper (*Juniperus occidentalis* var. *occidentalis*), a woodland tree of arid California, Idaho, Nevada, Oregon, and Washington, may be an ideal candidate species to test for a $CO_2$ fertilization effect for two reasons: first, the primary effects of rising atmospheric $CO_2$ on tree growth may be most evident in arid to semiarid environments (Mayeux *et al*. 1991; Mooney *et al*. 1991; Polley 1997); second, western juniper growth exhibits great sensitivity to precipitation variability, but considerably less sensitivity to temperature variability (Grissino-Mayer 1993; Grissino-Mayer *et al*. 1997a) and nitrogen deposition (Miller *et al*. 1991). High growth sensitivity to precipitation allows testing of the effects of elevated atmospheric $CO_2$ on the amelioration of water stress during drought periods through increased water-use efficiency (Hogan *et al*. 1991; Idso & Idso 1994; Owensby *et al*. 1999; Tognetti *et al*. 2000b).

In this paper, western juniper growth rates are examined to determine whether growth responses are consistent with our current understanding of $CO_2$ fertilization. Graumlich (1991) suggested that if $CO_2$ fertilization is occurring, there should be a consistent upward trend of the residuals from climate–growth regression models, indicating a decreased ability for climate parameters to predict growth with time. Specifically, $CO_2$ fertilization would increase radial growth above levels predicted based on historical relationships between growth and climate (e.g. LaMarche *et al*. 1984). Additionally, enhanced growth should be more apparent under drought conditions than under nondrought conditions (e.g. Idso & Idso 1994), especially during the later part of this century when atmospheric $CO_2$ was higher than in the early 1900s. In order to address these questions seven western juniper chronologies from central Oregon were examined to determine whether: (i) residuals from climate/growth models exhibited significantly positive trends during the last century; (ii) mean growth rates from 1950 to 1996/98 increased relative to 1896–1949; (iii) growth indices during comparable drought years from post-1950 were greater than from pre-1950; (iv) mean growth index values were significantly greater for the 1986–94 drought compared to the 1929–37 drought; (v) site harshness and relative growth responses (when comparing pre- vs. post 1950 droughts) were positively correlated; and (vi) these growth patterns were consistent across multiple sites, indicating a common, macroscale causal mechanism.

## Methods

### *Data collection and processing*

Western juniper samples from seven sites in central Oregon were analysed (Fig. 1, see Table 1 for site key). All sites experienced substantially less domestic livestock grazing, organized fire suppression or woodcutting than most woodlands in central Oregon (BLM 1995; Knapp & Soulé 1996, 1998). Core samples were collected from junipers at IRN and HRN in summer 1997, from PBU and BNU in summer 1998, and HBU, GMU, and STU in summer 1999. Following standard techniques (Phipps 1985), two cores/tree were taken using increment borers at a height of approximately 30 cm above ground level; core sample sizes ranged from 54 trees (IRN) to 139 trees (HBU). Individual trees were selected using a random sampling plan designed primarily for another related study concerning establishment rates of western junipers on neighbouring grasslands. The design used at IRN and HRN is described by Soulé & Knapp (2000). For the remaining sites, 20 plots (0.05 ha) were established systematically along a transect, and samples taken from the 10 trees closest to the plot centre, regardless of age. To study the potential effects of $CO_2$ fertilization on tree growth rates, however, longer temporal records are desirable, thereby necessitating deliberate inclusion of older individual trees. When the random sampling design failed to include the potentially oldest trees on a site, additional trees with old-age characteristics were purposely selected (LaMarche 1982) to include in the samples for this study. For all sites, the cores with the clearest ring structures (to facilitate crossdating and measurement) and longest sequences (providing greater comparative analysis) were selected for chronology development.

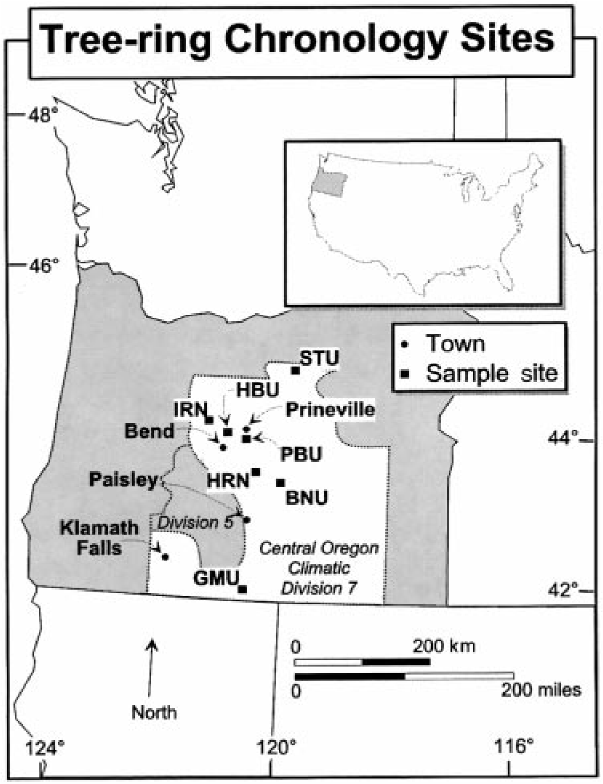

**Fig. 1** Location of sample sites and boundaries of selected climatic divisions.

All cores were mounted, sanded, and crossdated using standard techniques (Stokes & Smiley 1968). Crossdating and measurement accuracy were checked using COFECHA (Holmes 1983), and any errors in ring-width measurements subsequently corrected. Cores that could not be crossdated conclusively using graphical techniques (i.e. skeleton plots) and statistically confirmed using COFECHA were excluded from all further analyses. ARSTAN (Cook & Holmes 1997) was used for both ring-width standardization and chronology assembly and a standard index chronology was thereby developed for each site. All chronologies were produced using conservative standardization techniques (i.e. negative exponential curve, linear regression of negative slope, or horizontal line) to preserve the variance attributable to such low-frequency processes as climate variability and $CO_2$ fertilization. Use of more flexible standardization techniques (i.e. use of spline curves) would likely have removed many of the low-frequency $CO_2$ signals that were investigated in this study. The number of radii included in chronology development ranged from 29 (HRN) to 42 (BNU).

### Data analysis

For preliminary climatic analyses and regression modelling, monthly mean temperature and total precipitation data were used for the period 1903–96 from Prineville,

**Table 1** Site characteristics of seven western juniper chronologies

| Site code | Site name | Lat.(N) | Long. (W) | Altitude (m) | Slope |
|---|---|---|---|---|---|
| BNU | Benjamin Research Natural Area | 43°35′ | 120°21′ | 1510 | 1–2° |
| GMU | Goodlow Mountain Research Natural Area | 42°12′ | 121°11′ | 1555 | 1–2° |
| HBU | Haystack Butte Proposed Research Natural Area | 44°27′ | 121°09′ | 1185 | 30–44° |
| HRN | Horse Ridge Research Natural Area | 43°55′ | 121°02′ | 1300 | 0–9° |
| IRN | Island Research Natural Area | 44°34′ | 121°16′ | 730 | 0–3° |
| PBU | Powell Butte Research Natural Area | 44°09′ | 121°00′ | 1220 | 5–25° |
| STU | Sutton Mountain Proposed Research Natural Area | 44°41′ | 120°14′ | 800 | 16–40° |

OR (44°21′N 120°54′W, 866 m), Bend, OR (44°04′N 121°19′W, 1112 m), Paisely, OR (42°42′N, 120°32′W, 1329 m), Klamath Falls, OR (42°12′N, 121°47′W, 1249 m), the South Central Climate Division (SCOR), and the High Plateau Climate Division (HPOR) of Oregon (Fig. 1). The Bend and Prineville stations are centrally located and fall within the elevational range of all sites except GMU, which was matched to the Klamath Falls and Paisley station data (Fig. 1). Climate data from Bend, Klamath Falls, Paisley, and Prineville are part of the Historical Climatology Network (HCN), in which data are quality-controlled, with adjustments made for potential biases such as station moves, time of measurement, and urbanization effects (Karl *et al*. 1990). The regionally derived climatic division data also are quality-controlled and corrected for potential biases (Karl *et al*. 1986). While all seven sites fall within the boundaries of SCOR, GMU was near the boundary between SCOR and HPOR. We matched GMU with HPOR because our preliminary analyses revealed that growth rates at GMU were more closely matched to HPOR data than SCOR data. We also used climatic division-level Palmer Drought Severity Index (PDSI; Palmer 1965) data from SCOR & HPOR (1896–1996) to differentiate between drought and nondrought periods. The PDSI is a water-balanced measure of drought severity with a moderate rate of response to major changes in the evapotranspiration regime.

Climatic influences on ring-width measurements were first assessed using Pearson's product–moment correlation coefficients. Monthly precipitation and temperature data from May in the previous growing season through October of the current growing season were used as predictor variables. Because ring-widths may depend on precipitation and/or temperature data integrated over several months, composite variables were created that represented sums of consecutive months of precipitation or averages of consecutive months of temperature for analysis. Stepwise multiple regression was then used to calibrate climate-response models, with mean standardized ring indices as the dependent variable, and the combination of climate variables that best accounted for annual growth as the independent variables. Use of multiple regression models involves numerous assumptions that decrease model efficiency when violated (Clark & Hosking 1986). Accordingly, for each model we examined the significance of both $t$-values and $F$-values and examined the signs (+ or –) of the partial regression coefficients for logical consistency. Multicollinearity among the final model variables was also tested, and no significant ($P < 0.05$) relationships were found.

The 'studentized' residuals were plotted and Cook's $D$ statistic used to identify and remove outlier observations that added significantly to the error variance. First-order autocorrelation of the time-series residuals was checked using the Durbin–Watson test. The Durbin–Watson tests indicated that persistence was present in all the models. However, the Box–Jenkins class of ARIMA time-series models, which ensure randomness in the resulting residuals (Brocklebank & Dickey 1986), were not used herein because previous studies (e.g. Graumlich 1991; Briffa *et al*. 1996; Grissino-Mayer 1996) have shown that such techniques potentially remove the possible long-term (i.e. nonrandom) trends that are the focus of this study. The presence of autocorrelation, however, makes significance tests liberal for the entry level of variables into our models, so the significance level for entry of variables into the model was adjusted to $< 0.01$.

Several studies have selected 1950 as the time when the effects of atmospheric $CO_2$ enrichment would have most likely occurred (e.g. Kienast & Luxmoore 1988; Graumlich 1991). Atmospheric $CO_2$ concentrations were approximately 281 ppm in 1800, 300 ppm/v in 1900 (Neftel *et al*. 1994), 310 ppm in 1950, and 367 ppm in 1998 (Keeling & Whorf 2000). For comparison, this date was also used to determine whether long-term growth trends during the later period (from 1950 to 1996 for IRN and HRN; and from 1950 to 1998 for BNU, GMU, HBU, PBU and STU) were significantly different from the earlier period (1896–1949 for all sites) using a two-sample difference of means test.

In order to determine whether growth rates during drought years were significantly different between periods of lower and higher atmospheric $CO_2$ concentrations, a matched-pairs $t$-test was used to compare annual ring indices between comparable drought years before and after 1950 (Figs 2 and 3). Matched pairs were selected, using only years that matched two criteria: (i) those with similar mean PDSI values from October to June, the period when the moisture regime most strongly impacts radial growth at the study sites; (ii) those in a similar drought sequence, to ensure that the drought periods were as ecologically comparable as possible. For example, an isolated drought year preceded by a wet year prior to 1950 was matched with an isolated drought year preceded by a wet year post-1950, with 11 matched years meeting these criteria for the SCOR divisional data and 10 years for the HPOR divisional data (GMU). The same method was used for comparable wet years (Figs 2 and 3), with nine matched years identified at BNU, HBU, PBU and STU, but only eight matched years at HRN and IRN (the 1913/1997 comparison could not be included because these chronologies ended in 1996). For GMU, the paucity of comparable wet years was problematic when using the HPOR PDSI dataset. Alternatively, the 10 wettest years (October–June) were selected both pre- and post-1950 and these data were compared using a one-tailed, two sample means test.

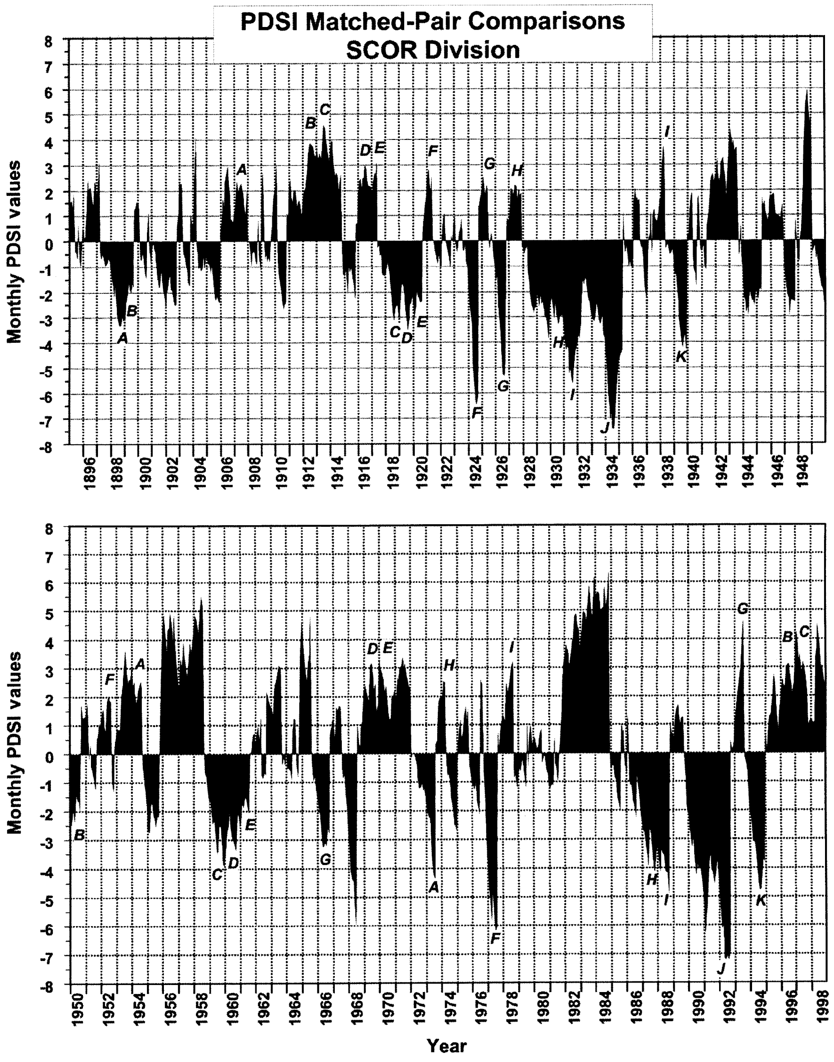

**Fig. 2** Matched drought years and matched wet years based on Palmer Drought Severity Indices from SCOR divisional data. Letters below show drought years while letters above show wet years that are ecologically comparable and were used in matched-pair *t*-tests.

Two additional relationships were explored between stress and growth responses. First, a difference of means test was used (except at GMU) to compare mean index values between 1928 and 1937 and 1985–94, the longest periods of extreme drought within the instrumental record (post-1895 for climatic division data). It was hypothesized that if elevated atmospheric CO$_2$ increased water-use efficiency in western juniper, then the mean growth rate would be greater during the later drought period compared to the earlier period. The periods before these drought sequences were different, with the 1928–37 drought preceded by alternating wet and dry years and the 1985–94 drought preceded by three consecutive years of above-average moisture conditions (Fig. 2). While these differences make the extended drought periods less ecologically comparable than the drought years in the matched pairs analysis, the possible radial growth inertia of prior wet years was minimized by starting analyses in the second sustained year of drought (i.e. 1929 and 1986). Secondly, the relationship between growth responses during matched dry years and site harshness was examined, using percentage of absent rings (common period of 1750–1998) as a measure of site harshness. In this way it could be determined whether differences between matched dry years (early vs. late period) index values were influenced by the severity of the site conditions. If no relationship existed between a drought and the growth responses of these trees, then this would suggest that site harshness does not influence the sensitivity of western juniper growth responses to elevated atmospheric CO$_2$.

## Results

### General statistics

The seven chronologies varied in length from 264 years to 714 years. Mean sensitivity, standard deviation, and first-order autocorrelation for each chronology all suggest that these chronologies are well suited for examining relationships between growth and climatic variability (Table 2). Mean sensitivity, indicating year-to-year variability (Fritts 1976), ranged from 0.28 to 0.70. The higher values are exceptional for arid site conifers and represent some of the highest mean sensitivities yet reported. Standard deviation values, which describe overall variability, were also high, ranging from 0.33 to 0.41. First-order autocorrelation, indicating the interdependence between tree growth for successive years, ranged from 0.32 to 0.63. In general, most standard tree-ring chronologies (as opposed to residual chronologies) exhibit such autocorrelation because climate considered over longer periods (as opposed to intra-annual timescales) is often serially correlated in its year-to-year persistence.

**Table 2** General descriptive statistics for western juniper tree-ring chronologies

| Study site | Period | MS | SD | R1 |
|---|---|---|---|---|
| BNU | 1682–1998 | 0.38 | 0.34 | 0.6 |
| GMU | 1285–1998 | 0.28 | 0.33 | 0.63 |
| HBU | 1596–1998 | 0.67 | 0.36 | 0.48 |
| HRN | 1613–1996 | 0.5 | 0.37 | 0.46 |
| IRN | 1733–1996 | 0.63 | 0.37 | 0.41 |
| PBU | 1665–1998 | 0.7 | 0.41 | 0.32 |
| STU | 1709–1998 | 0.6 | 0.39 | 0.44 |

MS, mean sensitivity; SD, standard deviation; R1, first-order autocorrelation

### *Climate–growth analyses*

Climate–growth relationships were similar at each of the seven sites when using the six different climate datasets, but the strongest correlations and greatest amount of explained variance consistently occurred when using the divisional data (extending back to winter 1896). Thus, only the SCOR data were used in climate–growth models, PDSI analyses, and growth rate comparisons for all sites except GMU where the HPOR dataset was used.

Multiple regression analyses revealed that much of the variance in the ring-width chronologies could be explained by climatic variables (Table 3). October–June precipitation was the sole variable that entered into the regression models for BNU, HBU, HRN, IRN and PBU, thus accounting for the majority of variability in tree growth rates. The relationship was also positive, i.e. increased growth was associated with wetter periods, and *vice versa*. The regression model for STU was similar, except that additional predictive power was provided by the influence of lower spring temperatures (April and May) during the current growing season. For GMU, three variables were included in the final model, with May precipitation having the largest model contribution, and lesser contributions from warmer and wetter conditions in January. In several instances, the $R^2$ values generated by the regression models were higher when a single outlier year was omitted. Thus, for PBU and STU, data for 1897 were omitted, and for HRN and IRN data for 1950 were omitted. Omitting these years increased the model $R^2$ values by 0.02 for PBU and STU and by 0.03 for HRN and IRN. Antecedent climatic conditions (i.e. > 1 y) were insignificant in affecting radial growth of our sampled sites.

Bivariate regression models between studentized residuals (from the multiple regression models) and time revealed significant upward trends in the residuals for all sites except GMU (Fig. 4 and Table 3). These results, showing actual growth exceeding predicted growth, suggest that some factor not included in the regression model has systematically increased radial growth. Similarly, the mean of the studentized residuals from 1950 to 1996/98 was significantly greater than zero at all sites except GMU and STU (Fig. 4; Table 3).

### *Growth rate comparisons*

For all sites except GMU, mean standardized ring index values in the later period (1950–96/98) were significantly greater ($P < 0.05$) than from 1896 to 1949. The greatest difference between mean indices was for HBU (52%), and the least for GMU (1%). For all sites combined, mean ring indices were 23% greater in the later period. October–June precipitation during the same periods (based on divisional data, two-sample means test) was not significantly different for SCOR, but was significantly less for HPOR (matched with GMU) during the later period. The greatest growth increase between the early and later periods occurred during drought conditions. When the matched drought years were compared between pre- and post-1950 periods, the average relative increase was 63% (Fig. 5). Differences in mean ring indices between ecologically comparable drought periods were significant ($P < 0.05$) at all sites except STU and for all sites combined ($P < 0.01$). Among matched wet year comparisons, significant increases ($P < 0.05$) were found in the later period at all sites, and as a group, except GMU and STU (Fig. 6). For both matched drought year and matched wet year comparisons, differences between mean PDSI values were insignificant ($P > 0.05$) between early and late-period groups.

Average drought severity (October–June) was similar between the 1929–37 and 1985–94 periods, with mean monthly PDSI values of $-2.59$ for the early period and $-2.16$ for the later drought. Mean winter precipitation

**Table 3** Regression models for western juniper chronologies predicting ring width measurements as a function of climatic variability

| Chronology<br>Regression model | $F$ | $R^2$ | Residuals | |
|---|---|---|---|---|
| | | | Slope[a] | Mean[b] |
| BNU | | | | |
| Width = 0.132 + 0.089(Oct–Junppt[c])<br>(0.29[d]) | 41.38** | 0.29 | 1.70** | 0.64** |
| GMU | | | | |
| Width = 0.203 + 0.079(Mayppt[e]) + 0.022(Jantmp[f]) + 0.032(Janppt[g])<br>(0.15) (0.13) (0.07) | 17.36** | 0.35 | –0.03 | –0.04 |
| HBU | | | | |
| Width = −0.074 + 0.168(Oct–Junppt)<br>(0.39) | 64.48** | 0.39 | 1.51** | 0.50** |
| HRN | | | | |
| Width = −0.404 + 0.147(Oct–Junppt)<br>(0.44) | 77.47** | 0.44 | 0.72* | 0.26 |
| IRN | | | | |
| Width = −0.631 + 0.163(Oct–Junppt)<br>(0.51) | 100.20** | 0.51 | 0.69* | 0.29* |
| PBU | | | | |
| Width = −0.511 + 0.151(Oct–Junppt)<br>(0.42) | 71.87** | 0.42 | 0.82* | 0.39** |
| STU | | | | |
| Width = 2.322 + 0.095(Oct–Junppt) – 0.023(Sprtmp[h])<br>(0.23) (0.05) | 29.83** | 0.28 | 0.82* | 0.23 |

[a] Slope of linear regression line fit to studentized residuals for 103-y period (1896–1998), all sites except IRN and HRN where slope was based on a 101-y period (1896–1996).

[b] Mean of studentized residuals (1950–96/98) and significance ($P < 0.05$*, $P < 0.01$**) for a one-tailed $t$-test with $H_o$: mean of studentized residuals is not significantly different from zero.

[c] Oct–Junppt: sum of monthly precipitation from October of previous year through June of current year.

[d] Partial $R^2$ is shown parenthetically below regression coefficients.

[e] Mayppt: May precipitation in the current year.

[f] Jantmp: mean January temperature in the current year.

[g] Janppt is the sum of January precipitation in the current year. [h] Sprtmp: the average of April and May temperature for the current year.

(SCOR divisional data) during the same periods was 24.6 cm for both periods. Differences between means were insignificant (two-sample means test, $P > 0.05$) for either measure of drought. Mean radial growth indices during the 1986–94 drought at all sites except GMU (excluded from analysis) were significantly greater ($P < 0.05$) than ring indices during the 1929–37 drought. As a group, radial growth from 1986 to 1994 was 127% greater ($P < 0.01$) than for the earlier period. Patterns among the chronologies between the early and late periods (Fig. 7) show a pronounced decline in radial growth occurring during the 1930s at all sites except GMU. These declines are among the greatest for the entire record, and likely reflect the cumulative effects of extended drought between 1928 and 1937. Site harshness was significantly correlated ($P < 0.05$) with growth responses (pre- vs. post-1950) during matched drought years (Fig. 8). Thus, these results suggest that the harsher the site, the larger the difference between mean growth indices from the earlier vs. later period drought years.

## Discussion

October–June precipitation is the most important variable affecting growth of western juniper at six of the seven sites, and accounts for at least one-third of the total variance in ring indices at four sites. These results are in general agreement with other western juniper studies that have shown that winter and/or spring precipitation is critical (e.g. Earle & Fritts 1986; Fritts & Wu 1986; Graumlich 1991; Grissino-Mayer *et al.* 1997a). Results from the present study suggest that temperature has little effect on growth with the exceptions of GMU (warmer Januarys) and STU (cooler springs). Again, these findings are in agreement with other western juniper studies

(Earle & Fritts 1986; Fritts & Wu 1986; Grissino-Mayer *et al.* 1997a) which determined that warm winter temperatures and/or mild winters and cool springs positively affected growth.

One of the commonest signatures of elevated atmospheric $CO_2$ on plant growth is an increase in water-use efficiency that often becomes most apparent during periods of water stress (Idso 1989; Idso & Idso 1994; Kimball *et al.* 1995; Arp *et al.* 1998; Owensby *et al.* 1999). In an examination of 43 experiments in which atmospheric $CO_2$ concentrations were increased by 300 ppm/v, but where water was limiting, Idso & Idso (1994) found an average increase in plant biomass of 62% over control plants grown at ambient atmospheric $CO_2$ concentrations (and a 31% increase when water was not limiting). These values are nearly identical to the increases of 63% and 30% reported herein, comparing matched dry and wet years, respectively, suggesting that even under modest atmospheric $CO_2$ increases stressed plant responses are roughly twice that of nonstressed plants. This $CO_2$ fertilization effect also has been measured under natural conditions. For example, Hättenschwiler *et al.* (1997) found that, for *Quercus ilex* trees growing near natural $CO_2$ springs that emit approximately 650 ppm/v, the relative stimulation of radial growth by elevated atmospheric $CO_2$ increased when precipitation was limited. Similar conclusions were drawn by Oechel *et al.* (1995) regarding biomass increases of several chaparral shrubs during drought periods, while Tognetti *et al.* (2000b) determined that *Juniperus communis* shrubs exposed to elevated atmospheric had higher turgor potentials under drought stress. Additionally, Feng (1999) documented increases in intrinsic water-use efficiency for natural trees (mostly

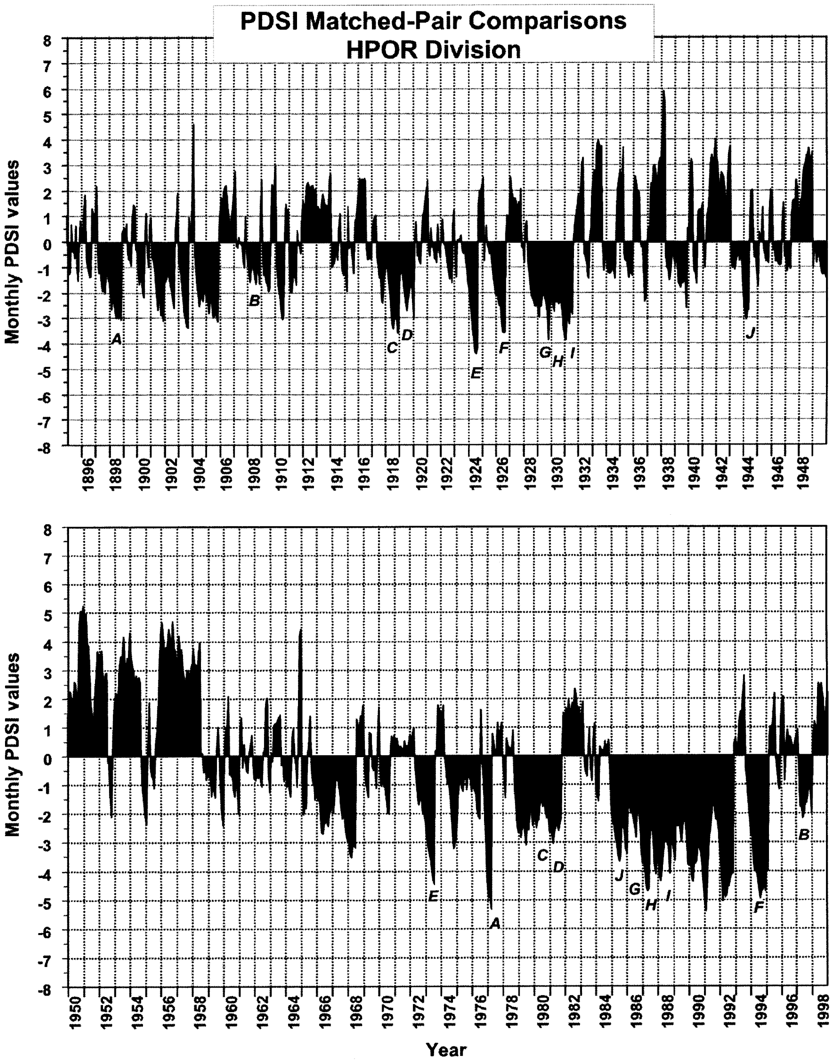

**Fig. 3** Matched drought years based on Palmer Drought Severity Indices from HPOR divisional data. Letters show years that are ecologically comparable and were used in matched-pair *t*-tests.

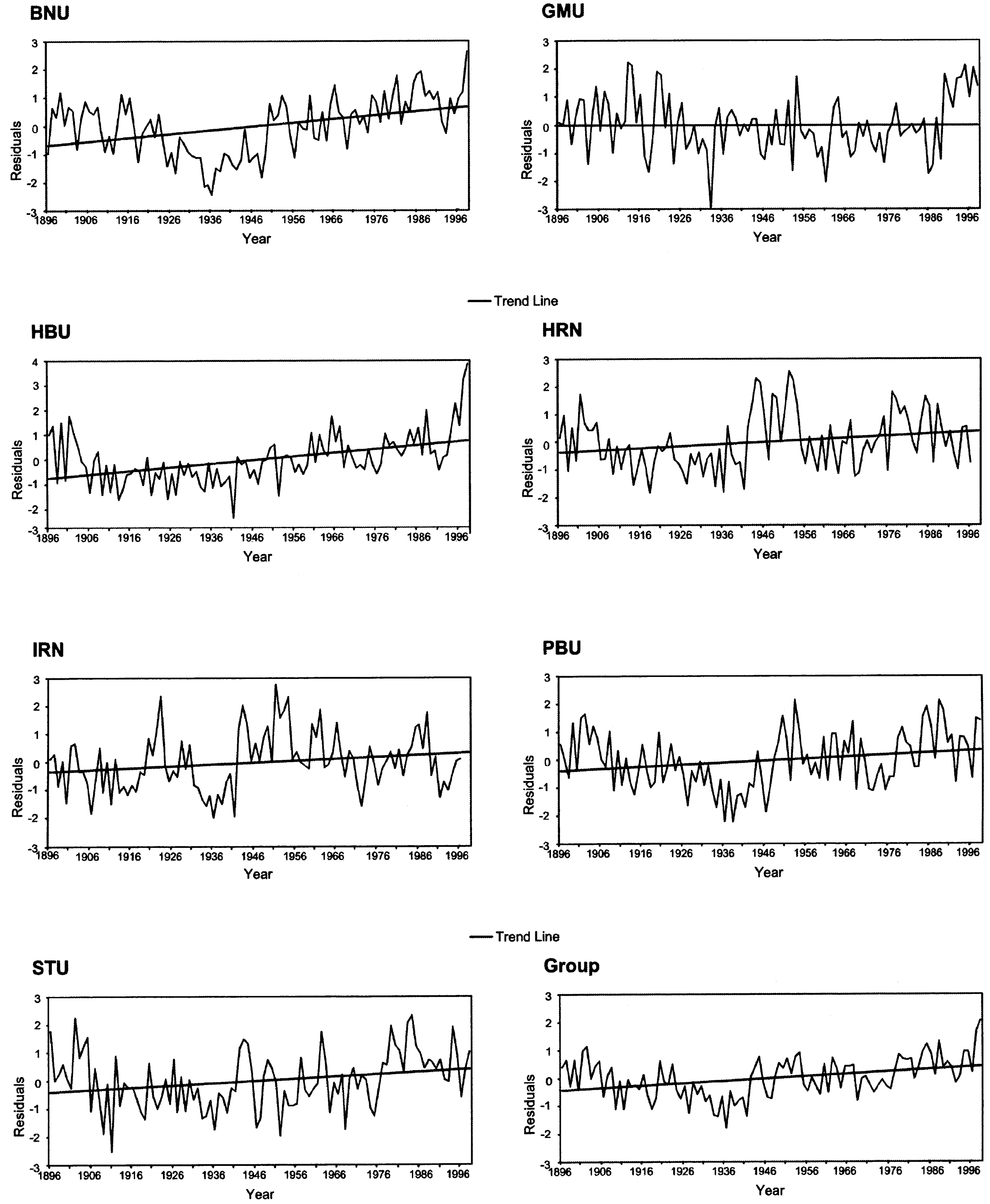

**Fig. 4** Studentized residuals and trend lines for seven chronologies and as a group. Trend lines are significant ($P < 0.05$) except for GMU.

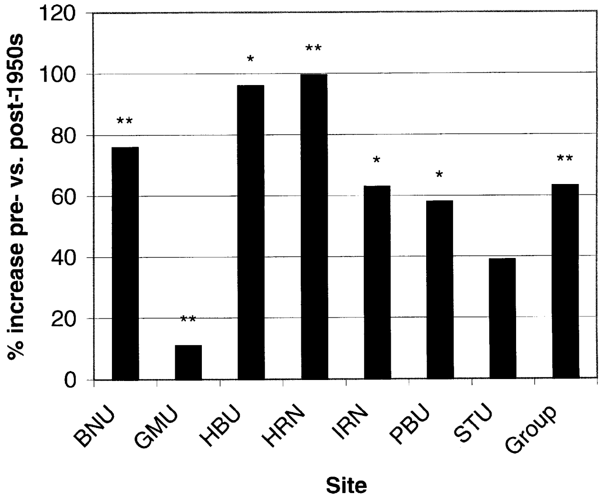

**Fig. 5** Relative growth increases pre- vs. post-1950 for ecologically matched drought years. Significance (one-tailed, difference of means test) is at * $P < 0.05$ and ** $P < 0.01$.

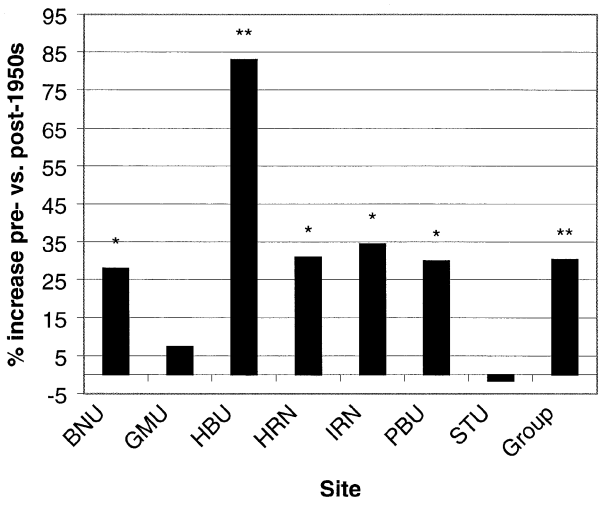

**Fig. 6** Relative growth increases pre- vs. post-1950 for ecologically matched wet years. Significance (one-tailed, difference of means test) is at * $P < 0.05$ and ** $P < 0.01$.

western North America conifers) during the last two centuries that paralleled increases in atmospheric $CO_2$, and suggested that this 'would have caused natural trees growing in arid environment[s] to grow more rapidly'.

The substantially increased growth during drought years of the later periods in comparison to the early periods, and increased growth in the 1986–94 drought period in comparison to a similar drought period from 1929 to 1937, reported herein, are consistent with the hypothesis that elevated $CO_2$ increases water-use efficiency and therefore alleviates drought stress. Reduced water stress, in turn, delays the onset of reduced photosynthesis caused by stomatal closure (Owensby *et al.* 1999), allowing plant species to have an extended growing season. If applicable to western juniper, a delay in water stress-induced photosynthesis reduction would allow the species to grow later into the summer, a major benefit given the consistently dry summer conditions of central Oregon. In addition, it is noteworthy that the site with the least radial growth increases during drought, GMU, was the highest and wettest site, and hence the least likely to benefit from elevated atmospheric $CO_2$, while the sites with the harshest conditions (HBU, HRN), had the greatest radial growth increases during drought periods (Fig. 8). These results are in agreement with Graumlich (1991), who suggested that arid sites (e.g. LaMarche *et al.* 1984; Graybill 1987) might be more likely to show a $CO_2$-fertilization effect.

By nearly all criteria used in this study, tree-ring growth since 1950 has increased significantly at all sites (except GMU) compared to the earlier period. The evidence does not, however, suggest that a sustained trend toward more favourable climatic conditions is a major driving force behind this growth enhancement. Studies of western juniper expansion suggest that this species is most viable during periods when soil moisture availability is above average (e.g. Miller & Wigand 1994; Miller & Rose 1995). If conditions post-1950 were abnormally wet, a positive response in the growth indices would be expected. While the October–June precipitation data from SCOR showed no significant temporal trend (1896–1998), no significant changes occurred in radial growth at GMU (HPOR data), despite a significant decrease in precipitation since 1950.

Residuals produced from climate–growth regression models can be influenced by long-term trends in the climatic variables affecting growth, and by the timing and severity of drought events. In the absence of long-term trends in precipitation, one would expect no trend in the residuals unless an exogenous factor (e.g. atmospheric $CO_2$) was operative. Accordingly, the possibility was explored that unexplained growth after 1950 (i.e. a high percentage of positive residuals) was caused simply by a large number of drought/wet years pre-/post-1950, respectively. Climatic records from SCOR do not show the pre-1950s period as having an exceptional number of dry years. Seven of the 10 driest October–June periods in the instrumental record occurred after 1950, and the years after 1950 were divided evenly between above-average and below-average October-June precipitation years. Furthermore, HPOR divisional data show exceptionally dry conditions dominated after 1950.

It is possible that the positive trend in the residuals could be caused by a nonlinear climate–growth relationship (Van Deusen 1990). While the western juniper trees sampled herein could have been responding to different (and undetected) climate variables post-1950s, the results (excluding the GMU/HPOR comparison) do show that the relationship between winter precipitation and growth strengthened when climate–growth regression models were run separately for the 1896–1949 and 1950–98 periods, despite no change occurring in mean October-June precipitation values. In addition, the temperature variable for STU (spring) dropped from the regression model while the temperature variable for GMU (January) decreased. These results are thus consistent with the concept of increasing WUE, as western juniper should become more sensitive to precipitation amounts and concurrently less sensitive to temperature variability, because water availability, not temperature, is the primary controlling factor to growth.

Nonclimatic causative mechanisms of increased radial growth were explored, including the effects of logging, road building, grazing, fire, and nutrient deposition (Fritts 1976; Wigley *et al.* 1984; Johnson *et al.* 1998). Any of these events, either operating individually or together, can alter the surrounding environment of trees by affecting amounts of light, nutrients, and soil-water availability. Sampling only on established and proposed Research Natural Area has limited the potential effects

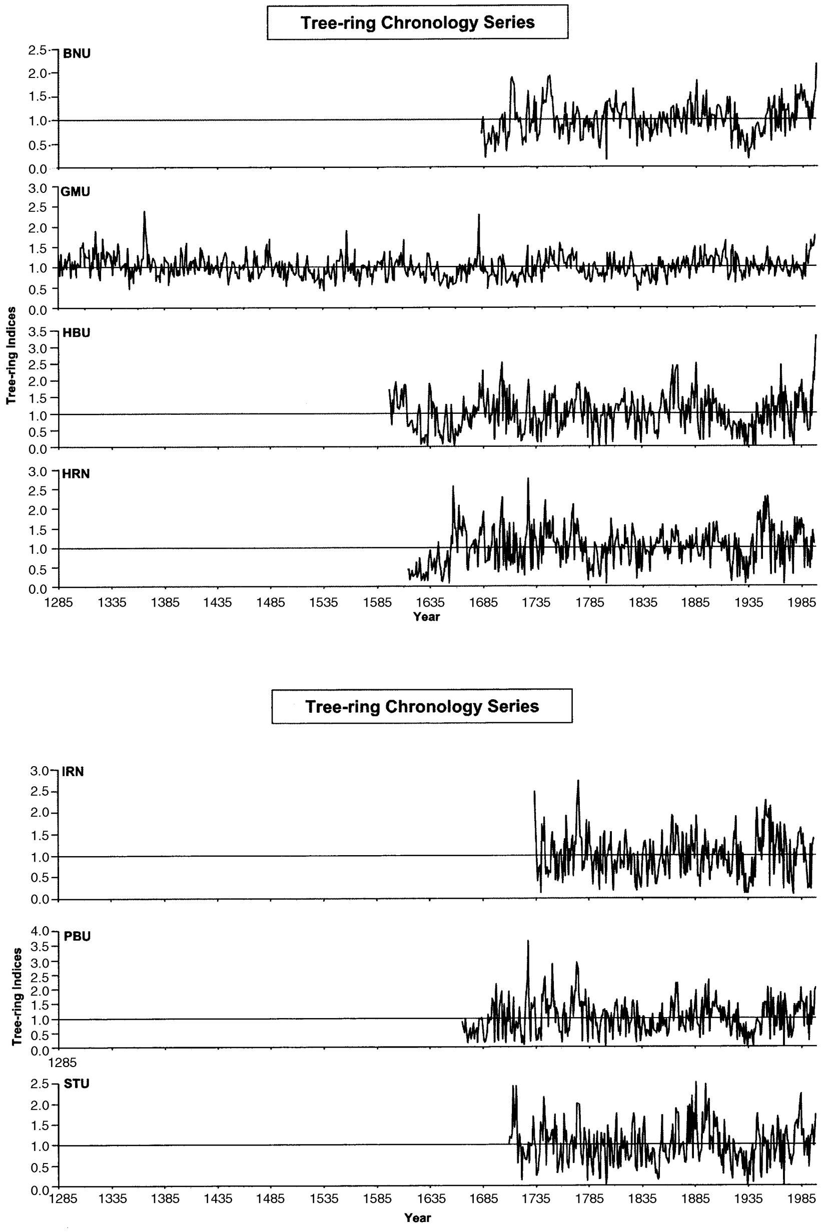

**Fig. 7** Tree ring chronology series for the seven sites showing annual growth index values. All chronologies ended in 1998 except HRN and IRN, which ended in 1996.

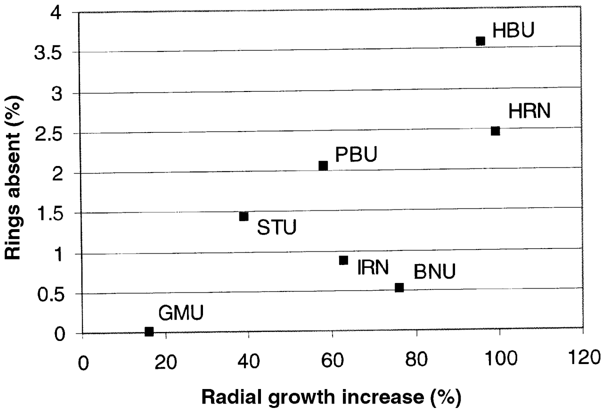

**Fig. 8** Correlation ($r = 0.72$, $P < 0.05$) between site harshness and radial growth increases during drought years pre- vs. post-1950.

of human activities on growth (i.e. logging, road building, domestic livestock grazing), and there is no evidence that fire has altered any of these ecosystems in a manner that would either substantially enhance or diminish growth. Furthermore, all sites represent open-canopy woodlands, areas unlikely to be subjected to changes in high light intensity. The influence of atmospheric nutrient deposition on growth rates is uncertain. On a central Oregon rangeland site, Miller *et al.* (1991) determined that growth rates of 'naturally established' juvenile and young adult western juniper (as measured by basal diameter) did not appear to be sensitive to elevated levels of either $NO_3$ or $NH_4$. Soil nitrogen levels for soils were not determined at our study sites, and thus the possible influence on growth remains undetermined.

The comparison of growth responses of these seven chronologies is an additional complicating factor in assessing the driving forces affecting radial growth. At four sites – BNU, HBU, PBU, and STU – there appears to be a systematic, upward trend in the residuals following the 1930s drought sequence (Fig. 4). At BNU and HBU, the residuals in the last year (1998) are the largest during the 103-year record. These trends are consistent with the hypothesis that the effects of atmospheric $CO_2$ fertilization would be most pronounced in the later period when atmospheric $CO_2$ concentrations have been highest. Furthermore, since 1977, almost all the residuals for these sites have been positive, despite a severe, sustained drought from 1985 to 1994 (Figs 2 and 4). At BNU and HBU, only one year at each site (since 1977) had a negative residual, while two years and four years had negative residuals at STU and PBU, respectively. At GMU, there is a sustained spike in the residuals (the greatest on record) beginning in 1989 (Figs 3 and 4). This chronology is more difficult to assess, however, since a long-running severe drought has impacted the site since 1979 and negative PDSI values have dominated since the late 1950s. At the remaining two sites, HRN and IRN, there has also been an upward trend in the residuals following the 1930s drought, but the largest residuals on record occurred in the early 1950s (Fig. 4). Although each year from 1951 to 1954 produced above-average amounts of October–June precipitation and available moisture (Fig. 2), the amount of water available for growth was less than that during other wet periods (e.g. 1982–84) and thus seems inadequate to fully account for the spike in residuals at IRN and HRN. We are uncertain why the climate/growth responses are not stronger (i.e. climate/growth models typically indicate that $>50\%$ of the variance is unexplained), or why the overall upward trend in residuals does not systematically match the upward trend in atmospheric $CO_2$ levels more closely at these sites. Numerous environmental site factors (i.e. soil, slope, aspect, microclimatic variability), and/or tree physiognomy could have affected growth responses. The chronologies with the greatest upward trends in the residuals (particularly BNU and HBU) consisted almost entirely of older strip-bark trees that often have substantially fewer living branches and active roots (Fritts 1976), and may be more responsive to the benefits of elevated atmospheric $CO_2$ (Graybill & Idso 1993). Conversely, the IRN and HRN chronologies were developed almost entirely from sampling full-bark trees, or an approximately even sampling of strip- and full-bark trees, respectively. In summary, given the suite of potential driving forces affecting western juniper growth, the relationships between unexplained growth and atmospheric $CO_2$ are unlikely to be inherently linear in nature, but rather patterns emerge that are generally in agreement with $CO_2$ fertilization. This latter point is shown by examination of the residuals as a group where there is a consistent upward trend following the 1930s drought sequence.

## Conclusions

This study has documented evidence of increased growth of western juniper that is consistent with the current understanding of $CO_2$ fertilization effects on tree growth. Specifically, it was determined that: (i) residuals from climate/growth models showed a significantly positive trend at all sites except GMU; (ii) growth was significantly greater in the latter half of the 20th century at all sites except GMU; (iii) growth indices during drought years were significantly greater post-1950 than pre-1950 at all sites (except STU) and when all study sites were combined; (iv) for matched wet years, significant differences existed at all sites except GMU and STU; (v) comparison of growth index values during two comparably long droughts during pre- and post-1950 also showed significantly greater growth in the later period; and (vi) growth responses were positively correlated with site harshness. While other environmental factors cannot be precluded, such as an increase in nutrients because of atmospheric deposition, an undetected change in climate, or simply recovery from the 1930s drought, little evidence was found to support them in this study. Thus, these results of enhanced growth, particularly during periods of drought stress, suggest atmospheric CO$_2$ fertilization has likely affected growth rates of western juniper in central Oregon during the 20th century.

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