Post-drought growth responses of western juniper (*Juniperus occidentalis* var. *occidentalis*) in central Oregon

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Abstract. Increased atmospheric CO_2 may affect the physiological response of natural trees to drought. We examined radial growth rates developed from five western juniper chronologies to determine if post-drought growth responses have changed. Using prior year October to current year June precipitation from 1896-1998, we identified drought recovery years as having standardized scores (z-scores) > 0 and preceded by a year with a z-score <-0.6. We defined our analysis by an early period, 1896-1930, when atmospheric CO_2 concentrations were close to preindustrial levels, and a late period, 1964-1998, when concentrations were substantially higher. Mean growth index values of recovery years between early and late periods were significantly greater ($p < 0.05$) for four of the five sites, and for all sites combined. These results are consistent with the drought-ameliorating effects of CO_2 shown by controlled laboratory studies and suggest that rising levels of atmospheric CO_2 may impact western juniper growth rates.

Introduction

Rises in atmospheric CO_2 levels may alter plant community composition and distributions via changes in climate, differential plant responsiveness to elevated CO_2, or both [*Polley* 1997; *Osborne et al.*, 2000]. Overall rises in atmospheric temperature and the increased likelihood of more frequent droughts [*Easterling et al.*, 2000] raises the question of how well species respond to drought as well as whether their physiological response has changed during the 20th century.

Laboratory studies have shown that environmental stresses (e.g., water and temperature stress) are ameliorated when plants grow under elevated atmospheric CO_2 relative to those that grow under ambient conditions [*Idso and Idso*, 1994]. When water is limiting, the growth benefits of elevated CO_2 are often related to reductions in stomatal conductance that in turn reduce transpirational loss without an equal reduction in rates of CO_2 assimilation [*Eamus*, 1991]. Thus, water-use efficiency (WUE) increases, causing a smaller relative decrease in photosynthetic activity. Considerably less is known about the changes in WUE for trees in natural conditions as a consequence of rising atmospheric CO_2. However, several studies that examined $\delta^{13}C$ in tree rings showed that intrinsic WUE also has increased during the past 100-200 years [*Bert et al.*, 1997; *Duquesnay et al.* 1998; *Feng* 1999; *Tang et al.*, 1999]. Further, these increases were most rapid during the last fifty years, paralleling increases in atmospheric CO_2, generating discussion that anomalous 20th century tree growth (relative to tree growth during other centuries) may be responding to a CO_2 fertilization effect [*Briffa*, 2000].

If CO_2 fertilization is an operative driving force for enhanced tree growth, its effects should be detected best in water-stressed environments. For example, *Hattenschwiler et al.*, [1997] and *Tognetti et al.*, [2000] found that the effects of drought on the Mediterranean oak, *Quercus ilex*, and Mediterranean juniper, *Juniperus communis*, respectively, were reduced under elevated CO_2 compared to the same species growing under ambient conditions. Similarly, *Osborne et al.*, [2000] modeled recent CO_2 impacts on Mediterranean sclerophyllous shrubland vegetation and determined that despite long-term trends of increasing aridity, "rising CO_2 [had] already led to significant stimulation of NPP [net primary productivity] and LAI [leaf area index]." Further, they noted that the effects of elevated CO_2 on Mediterranean shrub NPP during the last 50 years is approximately twice the estimated global total, possibly because water-limited ecosystems appear to benefit the most from increased WUE.

Western juniper (*Juniperus occidentalis* var. *occidentalis*) is a long-lived xeric tree species that grows in California, Idaho, Nevada, Oregon, and Washington in areas that typically receive less than 35 cm annual precipitation. The mean sensitivity of western juniper tree-ring data is among the highest of all tree species, with annual rings strongly reflecting interannual changes in climate. In addition, annual growth rates are largely determined by October-June precipitation amounts, with variability in temperature and summer rainfall contributing little additional influence to ring widths [*Knapp and Soulé*, 1999]. Thus, it is an ideal species to study the possible effects of CO_2 fertilization. In this paper, we examine post-drought recovery responses of western juniper from 1896-1998. We hypothesize that in response to the ameliorating effects of elevated atmospheric CO_2 on tree water relations during drought stress, radial growth rates following a drought should have significantly increased during the latter half of the 20th century when atmospheric CO_2 concentrations have risen rapidly.

Methods

Tree-ring index chronologies were developed from western juniper stands in four Research Natural Areas (RNAs) and
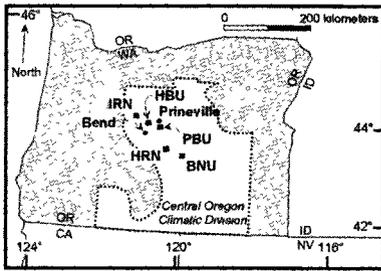
Figure 1. Location of sampling sites (squares), HCN stations (circles) and boundary of Oregon Climatic Division 7. Research Natural Area names and elevations (m) are: BNU (Benjamin, 1510); HBU (Haystack Butte [Proposed], 1185); HRN (Horse Ridge, 1109); IRN (The Island, 730); and PBU (Powell Butte, 1220).

one proposed RNA in central Oregon (Figure 1). These sites were selected to minimize the effects of non-climatic, human-related growth factors (e.g., wood cutting, road building, livestock grazing and fire suppression), and because they represent western juniper growth responses under a host of topoedaphic conditions [BLM, 1995]. With the exception of IRN, we selected trees using a random sampling design and collected cores from 54 trees (IRN) to 139 trees (HBU) per site. At IRN, 67% of the trees were selected randomly, while the remaining trees were selected based on morphological characteristics that suggested exceptional longevity [LaMarche, 1982]. From each tree, we obtained a minimum of two cores using increment borers and standard dendroecological field techniques [Phipps, 1985]. The cores were then mounted and sanded to ensure the cellular structure of the tree rings was visible at standard 10X magnification. We crossdated all tree rings using both skeleton plots [Stokes and Smiley, 1968; Swetnam et al., 1985] and the extreme-ring match-mismatch method [Phipps, 1985; Yamaguchi, 1991]. We developed chronologies using those cores with the longest, clearest record for measurement. Sample sizes for individual chronologies ranged from 29 radii to 42 radii. These chronologies consist of indices of tree growth (mean = 1.0) after age and size related trends have been removed during the standardization process [Fritts, 1976]. We used conservative standardization techniques (i.e., negative exponential curve) to ensure that low-frequency, long-term trends would be preserved in each chronology.

Using multiple regression, we constructed climate growth models with growth index values as the dependent variable and a suite of monthly and seasonal precipitation and temperature measurements (including lagged values up to two years) as the explanatory variables. We examined climatic data from individual stations (e.g., Historical Climatology Network data from Bend and Prineville, Oregon [Karl et al., 1990] and Oregon Climatic Division 7 (South-central). Because of the near singular response of western juniper radial growth to previous year October to current year June (i.e., winter/spring) total precipitation, and the level of agreement between models developed using individual station and climatic division data, the functional form of the final climate growth models was consistent across all sites. It includes data from the period 1895-1998 and has winter/spring precipitation as the sole independent variable. Similarly, we used regression to determine if a significant trend in winter/spring precipitation had occurred between 1895-1998, or over the periods 1896-1930 and 1964-1998.

Atmospheric CO_2 levels increased slightly from the beginning of the Industrial Revolution until the mid 20th

century. Since the 1950s, CO_2 levels have increased at an exponential rate. Thus, 1950 is sometimes chosen as a dividing point for statistical analyses of the potential effects of an enriched CO_2 atmosphere on vegetation growing in natural (non-laboratory) environments (e.g., Kienast and Luxmoore, 1988; Graumlich, 1991]. We chose to be more conservative in our analyses, separating our data sets into three periods. The period 1896-1930 represents a more stable, steady state CO_2 environment, while the period 1964-1998 represents a CO_2-enriched environment. Beginning and ending CO_2 levels were 295/306 ppm for 1896-1930, and 319.5/366.7 ppm for 1964-1998 [Neftel et al. 1994; Keeling and Whorf, 2000].

For drought response analyses, we converted the winter/spring precipitation values from 1896-1998 for Oregon Climatic Division 7 into standardized scores (z-scores) with a mean of 0 and a standard deviation of 1. Within each period (1896-1930, "early"; 1964-1998, "late"), we then selected any year with a positive z-score (recovery year) that was preceded by a year with a z-score <-0.6 (a drought year that was within the top one-third driest of all years). We used a two-sample means test (one-tailed, unequal variance, $\alpha=0.05$) to determine significance within a chronology between growth index values for the recovery years between early and late periods and likewise for the data as a group (all chronologies). We also used a two-sample means test (two-tailed, unequal variance, $\alpha=0.05$) to compare overall mean z-score values between early and late periods, and for comparison of drought and recovery years. We considered comparing the actual increases between drought years and recovery years, but did not because elevated atmospheric CO_2 levels during the later 20th century appear to ameliorate drought stress to western juniper [Knapp and Soulé, 1999]. Thus, this latter comparison would be an inadequate means by which to determine if elevated CO_2 has promoted a physiological response in western juniper in the post-drought year.

Results

The chronology lengths varied from 264 (IRN) to 403 years (HBU). The HRN and IRN chronologies ended in 1996 while the BNU, HBU, and PBU chronologies dated through 1998. Mean sensitivities ranged from 0.38 for BNU to 0.70 for PBU.

R^2 values generated by the climate-growth models for the five chronologies were 0.29, 0.39, 0.41, 0.41, and 0.48 for BNU, HBU, HRN, PBU, and IRN, respectively. These values indicate that winter/spring precipitation accounts for approximately one-third to one-half of the variance in annual radial growth. No significant trend (p>0.05) existed for
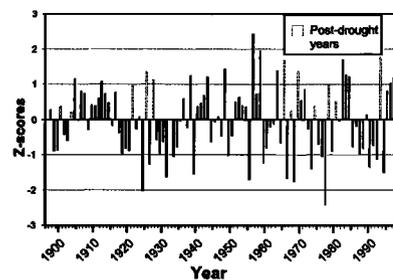

Figure 2. Z-scores based on October-June precipitation for south-central Oregon climatic division and selected post-drought years (open bars) used for analysis.

Table 1. Raw data, means, and significance (two-sample means test) between early and late periods for z-scores (two-tailed) and index values (one-tailed). Index values are for recovery years. Z-scores are based on a 103-year record (1896-1998).

Drought/Recovery Year	Dry-year z-score	Wet-year z-score	HBU Index	BNU Index	PBU Index	IRN Index	HRN Index	Index Mean
Early Period								
1899/1900	-0.88	0.37	0.73	1.08	1.00	0.63	0.95	0.88
1902/1903	-0.61	0.19	1.40	0.76	1.38	1.04	1.36	1.19
1920/1921	-0.88	0.99	0.75	1.34	1.09	1.54	1.34	1.21
1924/1925	-2.04	1.34	0.70	0.86	1.49	1.23	1.20	1.10
1926/1927	-1.29	1.11	0.78	0.74	0.78	1.28	0.92	0.90
Means	-1.14	0.80	0.87	0.96	1.15	1.14	1.15	1.05
Late Period								
1964/1965	-0.65	1.68	2.44	1.63	1.86	1.75	1.63	1.86
1966/1967	-1.67	0.26	1.61	1.31	1.57	1.12	1.35	1.39
1968/1969	-1.77	1.37	1.80	1.18	1.81	1.70	1.13	1.52
1973/1974	-1.42	0.37	1.31	1.05	1.06	1.34	1.26	1.20
1977/1978	-2.41	0.98	1.60	1.70	1.44	1.13	1.75	1.52
1979/1980	-0.90	0.52	1.52	1.52	1.46	1.15	1.74	1.48
1989/1990	-0.83	0.14	1.04	1.36	1.71	0.78	1.23	1.22
1992/1993	-1.14	1.76	1.65	1.36	1.89	1.18	1.42	1.50
1994/1995	-1.52	0.81	2.22	1.27	1.35	1.18	1.42	1.49
Means	-1.37	0.88	1.69	1.38	1.57	1.26	1.44	1.47
Significance	0.48	0.80	0.001	0.01	0.01	0.27	0.02	0.0001

winter/spring precipitation for the 1896-1998 period, or for the early and late periods.

Five early period recovery years and nine late period recovery years met the selection criteria (Figure 2; Table 1). The mean of winter/spring precipitation z-scores for the drought years indicate that years in the late period experienced more extreme negative deviations from normal precipitation than years in the early period (Table 1). However, the two-sample means test shows the difference in z-score values for drought years to be non-significant. We found no significant differences between the early and late period recovery years, or between the periods when using all data. Both the early and late periods had 17 years with above normal winter/spring precipitation, and 18 years below normal.

Mean growth index values of recovery years between early and late periods were significantly greater ($p<0.05$) for four of the five sites, and for all sites combined (Table 1). At the fifth site, IRN, mean index values were also greater, but not significant (Table 1).

Discussion

The post-drought index values of these five chronologies indicate radial growth rates of western juniper were greater in the later half of the 20th century, suggesting that these trees resume higher rates of photosynthesis following stress periods. Differences in post-drought index values between periods were greatest for HBU and least for IRN. These growth increases for western juniper occurred in the absence of significant trends in winter precipitation during the entire length of record, and in the absence of significant differences in precipitation between the selected early and late drought/recovery years.

Our results are in agreement with several controlled studies that have directly examined the effects of elevated atmospheric CO_2 in ameliorating water stress in trees. For example, *Polley et al.,* [1999] examined the effects of drought on growth, water relations, and seedling survival of *Prosopis glandulosa* under CO_2 enrichment of 700ppm. Their results showed that transpiration rates decreased while both root and stem biomass and survival percentage increased in comparison to seedlings grown under drought conditions in ambient CO_2. Similarly, *Palanisamy* [1999] found that photosynthetic rates for drought-stressed *Eucalyptus cladocalyx* seedlings exposed to 800 ppm CO_2 were greater and stomatal conductance was less (indicating an increase in WUE) than those drought-stressed seedlings grown under ambient conditions. Finally, *Tognetti et al.,* (1998: 620) found that adult *Quercus ilex* growing near a natural CO_2 spring had less reduction in hydraulic resistance when compared to control trees growing under ambient conditions which they noted might "prolong photosynthesis during dry periods."

Greater recovery following drought in the late period is consistent with the expected ameliorating influences of atmospheric CO_2 under stressful conditions. For example, *Tuba et al.,* [1998: 39] determined that exposure of the dessication-tolerant woody shrub, *Xerophyta scabria,* to elevated CO_2 prolonged photosynthesis during desiccation periods by 300%. They suggested the benefits of elevated CO_2 were "that the carboxylating enzymes must still have been active...to allow appreciable photosynthetic activity." Similarly, *Ferris et al.,* [1998] determined that recovery (i.e., photosynthesis) of soybean, *Glycine max,* following the cessation of drought occurred only under elevated atmospheric CO_2 conditions because leaf water potential dropped below the threshold for chloroplast damage under ambient atmospheric CO_2 conditions. For trees, *Fritts* [1976: 244] has noted that effects of droughts "can reduce ring width for that year and for several years thereafter."

We suspect that enhanced growth during recovery years in the late period is likely caused by two features. First, the actual detrimental effects of droughts (e.g., top dieback, dessication/death of shaded leaves, tissue damage; [Fritts, 1976]) that would reduce ring width appear to be mitigated for western juniper under higher atmospheric CO_2 conditions because of increased WUE [*Knapp and Soulé,* 1999]. Thus, the residual effects of drought on photosynthetic rates following the return to favorable soil moisture conditions would not be as pronounced. Our results support this, as the mean index values were all greater than 1.25 for the late period, while no mean index value exceeded 1.15 for the early period. Further, both HBU and BNU early period mean index values show reduced growth (index < 1) existed during the recovery year. Second, elevated CO_2 appears to stimulate growth (compared with ambient CO_2) even under favorable conditions [*Knapp et al.,* 2000], although this influence is considerably less than for drought conditions.

We were uncertain why no significant differences existed between early and late periods for the post-drought response at IRN. This chronology, however, was the youngest and most cores used in chronology development were from full-bark trees. The remaining four chronologies were developed from sampling of older, and typically strip-bark, trees. Examination of radial growth responses of high elevation western (USA) conifers by *Graybill and Idso* [1993] suggest

that strip-bark trees may be more sensitive to elevated atmospheric CO_2.

We cannot eliminate the possible role of additional factors. Growth surges following droughts can occur because the mortality of some trees release resources (i.e., water, light, and nutrients) for surviving individuals. While this is a possible scenario across our study sites, it is not probable as western juniper has continued to expand its range during the 20th century [Miller et al., 1987; Bedell et al., 1993; Soulé and Knapp, 1999]. Additionally, though our comparison of drought events based on winter/spring precipitation captures the single dominant factor affecting western juniper growth, this variable accounts for less than 50% of the total ring width index variance. Thus, subtle climatic (or other environmental) changes may have occurred between our selected early and late periods that are responsible for the significant differences in growth. Nonetheless, our results suggest the ability of western juniper to recover from drought during the 20th century has increased. Though the causes for these changes cannot be pinpointed with certainty, the results are consistent with the ameliorating effects of elevated atmospheric CO_2 on plant growth during stress periods.

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