

## Tree ring evidence for limited direct CO<sub>2</sub> fertilization of forests over the 20th century

Ze'ev Gedalof<sup>1</sup> and Aaron A. Berg<sup>1</sup>

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[1] The effect that rising atmospheric CO<sub>2</sub> levels will have on forest productivity and water use efficiency remains uncertain, yet it has critical implications for future rates of carbon sequestration and forest distributions. Efforts to understand the effect that rising CO<sub>2</sub> will have on forests are largely based on growth chamber studies of seedlings, and the relatively small number of FACE sites. Inferences from these studies are limited by their generally short durations, artificial growing conditions, unnatural step-increases in CO<sub>2</sub> concentrations, and poor replication. Here we analyze the global record of annual radial tree growth, derived from the International Tree ring Data Bank (ITRDB), for evidence of increasing growth rates that cannot be explained by climatic change alone, and for evidence of decreasing sensitivity to drought. We find that approximately 20 percent of sites globally exhibit increasing trends in growth that cannot be attributed to climatic causes, nitrogen deposition, elevation, or latitude, which we attribute to a direct CO<sub>2</sub> fertilization effect. No differences were found between species in their likelihood to exhibit growth increases attributable to CO<sub>2</sub> fertilization, although Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*), the two most commonly sampled species in the ITRDB, exhibit a CO<sub>2</sub> fertilization signal at frequencies very near their upper and lower confidence limits respectively. Overall these results suggest that CO<sub>2</sub> fertilization of forests will not counteract emissions or slow warming in any substantial fashion, but do suggest that future forest dynamics may differ from those seen today depending on site conditions and individual species' responses to elevated CO<sub>2</sub>.

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### 1. Introduction

[2] Future rates of carbon sequestration and forest distributions depend on how trees will respond to elevated atmospheric CO<sub>2</sub>. Elevated CO<sub>2</sub> could stimulate growth of trees through two main mechanisms: First, direct CO<sub>2</sub> fertilization may occur because higher partial pressure of CO<sub>2</sub> increases the rate of CO<sub>2</sub> reactions with rubisco during photosynthesis, and inhibits photorespiration [Bazzaz, 1990]. Second, increasing water use efficiency may occur due to reduced stomatal conductance [Field *et al.*, 1995], leading to reduced sensitivity to drought and potentially allowing species to expand their distributions in xeric environments [Neilson and Drapek, 1998]. Most studies of the effects of elevated CO<sub>2</sub> have been undertaken on agricultural plant species [Bazzaz, 1990], and of the few analyses of tree species most have been undertaken on seedlings [Curtis and Wang, 1998]. Only the FACE experiments have attempted to quantify the effects of elevated CO<sub>2</sub> on mature trees [Okada

*et al.*, 2001], and these experiments have been poorly replicated and relatively short in duration.

[3] Long-term studies of CO<sub>2</sub> induced changes to growth rates are necessarily based on dendrochronological evidence. Radial growth is a relatively low priority for carbon allocation within trees, meaning that wide rings are typically only produced during years of unusually high photosynthate production [Fritts, 1976]. Consequently any CO<sub>2</sub> induced increases in productivity should be evident as an increase in mean growth rates. Dendrochronological analyses of CO<sub>2</sub> fertilization have generally been restricted to the analysis of a small number of sites, and have produced conflicting results [Graumlich, 1991; Graybill and Idso, 1993; Kienast and Luxmoore, 1988; Knapp *et al.*, 2001; LaMarche *et al.*, 1984; Soulé and Knapp, 2006; Tognetti *et al.*, 2000]. Here we evaluate the global tree ring record for evidence of (1) increasing growth trends that are not attributable to climatic trends; and (2) decreasing sensitivity of growth to drought. Tree rings are a particularly important indicator of CO<sub>2</sub> fertilization because tree boles are the most persistent biomass carbon pool in terrestrial vegetation, and so any detectable signal may indicate a change to long-term carbon storage dynamics [Körner, 2003]. Specifically, we test the following three hypotheses (stated as predictions):

<sup>1</sup>Department of Geography, University of Guelph, Guelph, Ontario, Canada.

[4] 1. The radial growth of trees should exhibit increases in mean growth rates over the 20th century that cannot be attributed to climatic variability;

[5] 2. Variability in growth rates should be more weakly correlated to drought in the latter portion of the 20th century than in the early portion;

[6] 3. Ring width chronologies will differ from each other in their likelihood to exhibit evidence of CO<sub>2</sub> induced growth changes based on their species and their geographic location.

## 2. Methods

[7] To evaluate the global importance of CO<sub>2</sub> fertilization of trees we used records from the International Tree Ring Data Bank (ITRDB) [Grissino-Mayer and Fritts, 1997]. From the ITRDB, all chronologies for which raw ring widths were available were extracted. Chronologies were developed using ARSTAN (ver. 40c) to fit either a negative exponential curve or a horizontal line to each measurement series [Cook *et al.*, 1990]. Individual series were combined to form site chronologies using a robust mean [Mosteller and Tukey, 1977]. This highly conservative approach to detrending should preserve virtually all of the low-frequency variability in the tree ring series, including trends in recent decades that might be removed by other methods due to end-fitting limitations. Palmer Drought Severity Index (PDSI) data were taken from Dai *et al.* [2004]. The PDSI is an index of meteorological drought that reflects antecedent moisture conditions and variability in supply and demand. Positive (negative) values indicate wetter (drier) than average conditions at a given location. Monthly PDSI measurements are available for the interval 1870 – 2003, on a 2.5 degrees latitude by 2.5 degrees longitude grid – although data continuity and completeness is highly variable in different regions of the Earth. From these data, mean growing season PDSI values were calculated (Dec. to Feb. for the southern hemisphere; June to Aug. for the northern hemisphere).

[8] To test for CO<sub>2</sub> fertilization and increasing water use efficiency we used two main analyses. First, simple linear regression was used to quantify the relationship between annual growth index and the nearest PDSI grid point. This climatically induced variability was then linearly removed from the tree ring chronology, and the regression residuals were then tested for an increasing trend in growth over time that cannot be attributed to climate by using Sen's method [Sen, 1968]. Sen's method is based on Kendall's Tau, and is a nonparametric trend estimator that is robust to outliers, non-normal distributions, and missing data points [Hess *et al.*, 2001; Kundzewicz and Robson, 2004]. This test is premised on the assumption that once the effects of climatic variability have been removed from the chronologies the residuals should exhibit an increasingly positive bias over time due to CO<sub>2</sub> growth stimulations. Field significance of the results was tested using a Monte Carlo simulation [Livezey and Chen, 1983]: Each tree ring series was randomly shuffled (with replacement) to generate a new tree ring time series. The corresponding time series of the PDSI was unaltered preserving the temporal and spatial trends in the data set. The new tree ring time series was then subjected to the

same analyses described above. This process was iterated 5,000 times for each site and the resulting statistics were used to estimate the 95 percent confidence limit on the number of significantly positive trends that would be expected randomly.

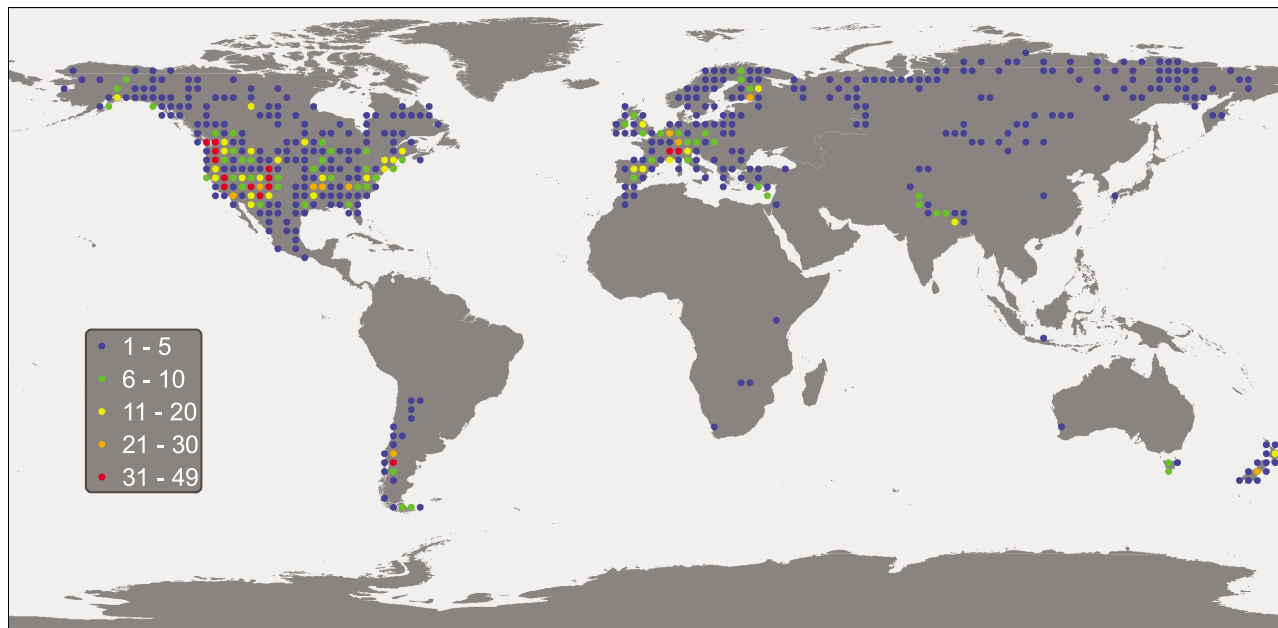
[9] To test whether species differed in their likelihood to exhibit positive residual growth trends we used a second Monte Carlo simulation. For this analysis, 10,000 pseudodata sets of species were created by sampling without replacement from the pool of candidate species. The size of this data set was equal to the number of sites that were found to have significant positive trends in their residuals. The resulting frequency statistics were used to calculate 95 percent confidence limits for the number of sites for a given species that would be expected to exhibit increasing trends in their regression residuals randomly.

[10] Second, we used superposed epoch analysis [von Storch and Zwiers, 2002] to test for a difference in the correlations between radial growth and drought under epochs of relatively lower and higher CO<sub>2</sub> concentrations. Because this test is very sensitive to data quality we restricted it to the interval after 1950, over which data coverage and quality is best [Dai *et al.*, 2004; Peterson and Vose, 1997]. For this test, Pearson's *r* was calculated for the intervals 1950 to 1969, and 1970 to 2003. Because very few of the tree ring chronologies extend to 2003, and most extend only to the early 1980s, these intervals result in an equal number of data points being included in each epoch. A paired *t*-test was then used to test the hypothesis that tree ring chronologies exhibit a decreased correlation to drought over the latter interval.

[11] Whereas the direct effects of CO<sub>2</sub> fertilization should be detectable in ring width series regardless of mean climatic conditions, increasing water use efficiency should be most evident at sites where moisture is limiting growth. Consequently each of the above analyses was run on four different subsets of the data set: (1) On the complete data set. This analysis seeks to assess the overall importance of CO<sub>2</sub> fertilization and changing water use efficiency on forests regardless of their climatic sensitivity; (2) On only those sites that exhibit a statistically significant correlation to mean growing season PDSI. This analysis is used to assess CO<sub>2</sub> fertilization and changing water use efficiency at locations where available moisture is limiting growth; (3) On only those sites where there is no statistically significant trend in PDSI over the interval common to the tree ring and drought data. This subset controls for spurious trends in the residuals that might be caused by a trend in the drought record itself; and (4) On sites that match both conditions (2) and (3). Because this last condition is the least likely to be affected by noise, and the most likely to contain a detectable signal, we analyze the results of this subset in more detail.

## 3. Results

[12] From the ITRDB, 2431 tree ring chronologies were calculated. Of these, 2302 had at least 20 years overlap in the tree ring and drought data and were retained for residuals analysis (Figure 1). For all four subsets, more sites exhibit a statistically significant positive trend in their residuals than



**Figure 1.** The locations and number of the tree ring chronologies used in this analysis, resampled to the same 2.5 degree grid as the PDSI data.

would be expected randomly (Table 1): Between 18 and 20 percent of all sites exhibit evidence of increasing growth relative to drought. While these results are highly statistically significant, they also suggest that CO<sub>2</sub>-induced growth increases are not universal. Over three-quarters of the sites assessed do not exhibit evidence for increasing growth in recent decades.

[13] There are no obvious defining features among the sites that do exhibit increasing trends in their regression residuals: Those sites with positive trends in their residuals do not exhibit a higher correlation to drought than those that do not ( $p = 0.699$ ) [Soulé and Knapp, 2006], and they are located at the same mean elevation ( $p = 0.490$ ) [c.f. LaMarche et al., 1984]. Angiosperms are just as likely to exhibit increasing residual growth trends as gymnosperms ( $p = 0.568$ ). Examining the spatial distribution of these sites reveals no obvious patterns (Figures 2 and 3): Sites are not clustered in regions of high nitrogen deposition, such as eastern North America or central and northern Europe, or regions that are particularly arid, such as the U.S. Southwest and Mediterranean Europe.

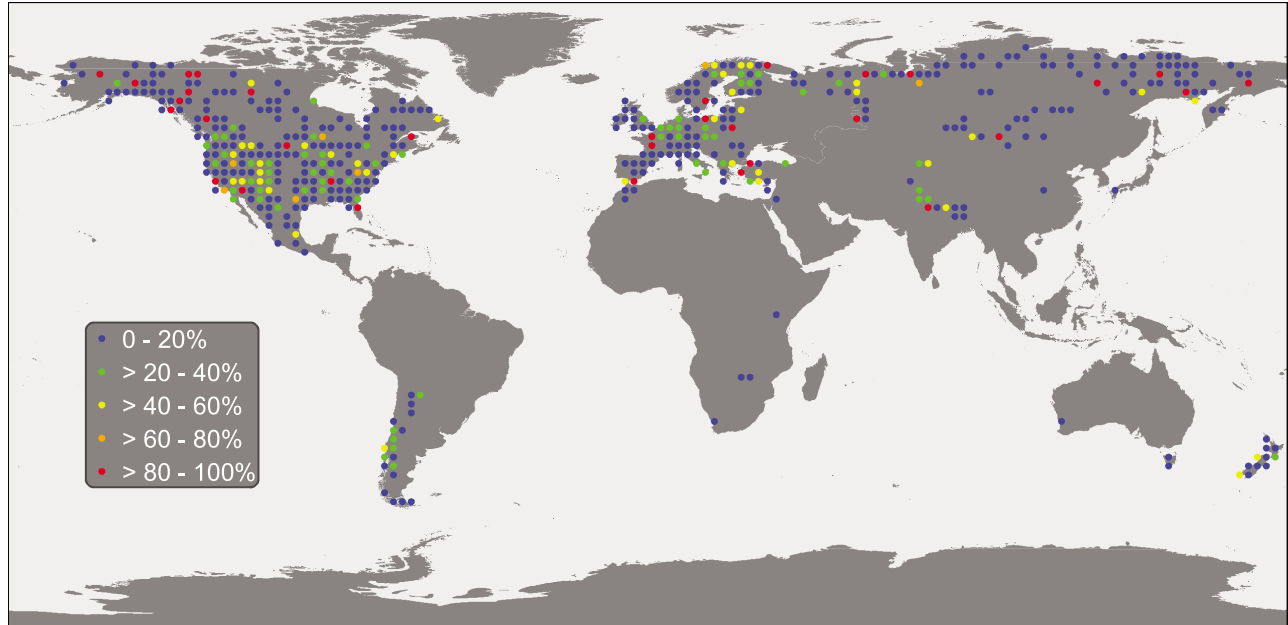
[14] Similarly, the Monte Carlo simulation indicates that there are no species that are statistically over- or underrepresented in the population of sites in subset (4) that exhibit increasing trends in their regression residuals, and for a large

number of the species considered, this test has weak statistical power due to the small numbers of chronologies available in the ITRDB. For the 22 species that have ten or more sites represented in the subset all are within the 95 percent confidence limits. However, this analysis does indicate that the two most common species in the data set, *Pinus ponderosa* and *Pseudotsuga menziesii*, both occur at frequencies very near to the limits expected randomly. *P. ponderosa* exhibits a significant positive trend in its residuals at 18 sites, with an expected frequency of 15 to 30, and *P. menziesii* exhibits a significant positive trend at 23 sites, with an expected frequency of 11 to 24. These two species often co-occur at warm dry sites in western North America, and if *P. menziesii* is more likely to exhibit CO<sub>2</sub> related growth stimulations than *P. ponderosa* this difference may alter future competitive interactions, and lead to a reduction in their range overlap.

[15] The superposed epoch analysis reveals no evidence for increasing water use efficiency by trees (Table 2). The mean correlation to drought remains virtually unchanged between the two intervals, regardless of the subset used. For example, the mean correlation to PDSI for the quartile of sites that are most sensitive to drought (defined by  $R > 0.387$  over the post-1950 interval) changes from 0.532 to 0.527; the mean correlation of the top ten percent most sensitive sites (defined

**Table 1.** Number of Sites Exhibiting a Significant Trend in Regression Residuals

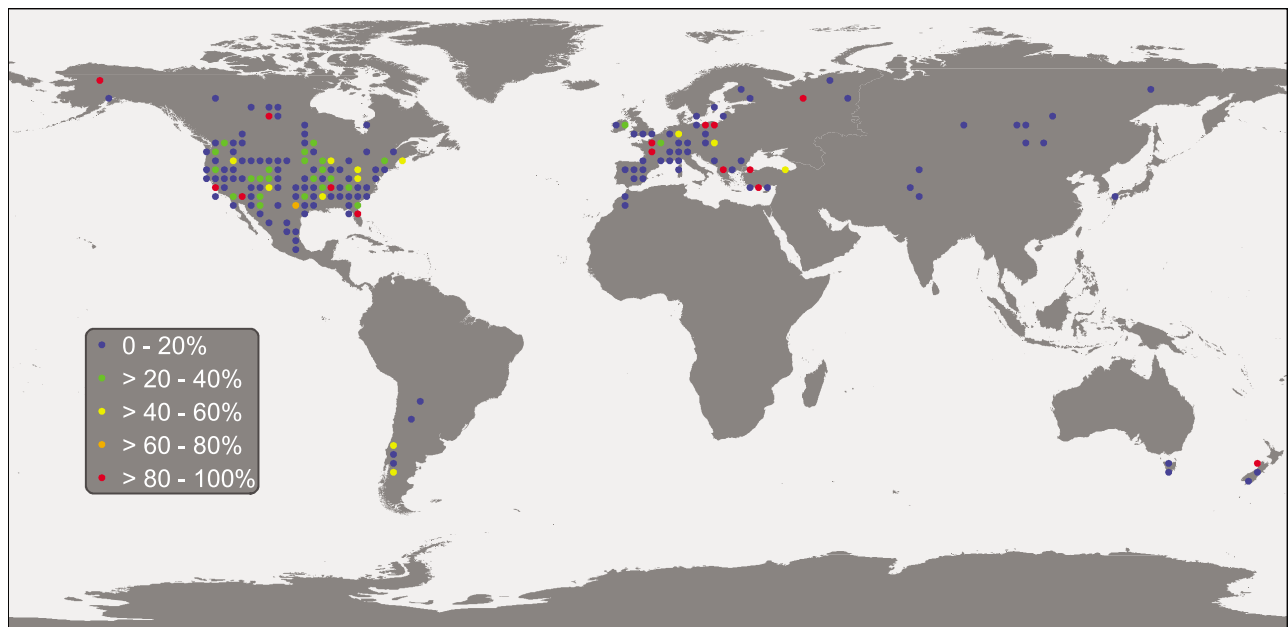
Conditions Required for Inclusion	Number of Sites	Number With Significant Positive Trend in Residuals	Percentage With Significant Positive Trend in Residuals	Percentage Required for Field Significance
(1) None	2302	448	19	10.2
(2) Significant Positive R to PDSI	1098	224	20	4.8
(3) No trend in PDSI	1501	281	19	4.9
(4) Significant R to PDSI and no trend in PDSI	752	154	18	5.1



**Figure 2.** The proportion of the 2302 sites in Figure 1 that exhibit a significant positive trend in their residual time series after the variability in growth that is related to drought has been linearly removed.

by  $R > 0.555$ ) actually increases from 0.624 to 0.642. Most importantly, the proportion of sites exhibiting positive regression residuals remains unchanged between locations where drought is and is not limiting to growth [Soulé and

Knapp, 2006]. Restricting the superposed epoch analysis to only those sites from subset (4) that exhibit a statistically significant increasing trend in their residuals reveals a decrease in mean correlation to PDSI from 0.486 to 0.456,



**Figure 3.** The locations of the 752 sites (resampled to the same 2.5 degree grid as the PDSI data) that meet condition (4): At least 20 years of overlapping tree ring and drought data, a significant correlation between radial growth index and PDSI, and no significant trend in the PDSI record. The color of the symbol indicates the proportion of the tree ring chronologies at a given grid point that exhibit a significant positive trend in their residual time series after the variability in growth that is related to drought has been linearly removed.

**Table 2.** Results of the Superposed Epoch Analysis, Testing for Changes in Tree Ring Sensitivity to Drought

Conditions Required for Inclusion	Number of Sites	Mean R (1950–1969)	Mean R (1970–2003)	P-Value (Paired t-Test, 1-Tailed Sig.)
(1) None	1808	0.166	0.150	0.020
(2) Significant R to PDSI	586	0.494	0.478	0.076
(3) No trend in PDSI	1387	0.151	0.140	0.112
(4) Significant R to PDSI and no trend in PDSI	493	0.449	0.451	0.443

a change in correlation that is not statistically significant ( $p = 0.146$ ).

#### 4. Discussion

[16] Our results suggest that CO<sub>2</sub> fertilization affects only about 20 percent of sites globally, but that it may be very important locally. We attribute the observed growth increases principally to a direct CO<sub>2</sub> fertilization effect (i.e., stimulation in photosynthesis) rather than to increasing water use efficiency for several reasons. In addition to the fact that no change over time in the sensitivity of trees to drought was detected, there was no difference in the proportion of sites exhibiting growth increases between drought-limited and non-drought-limited sites. While the number of sites exhibiting a CO<sub>2</sub> fertilization signal is substantially larger than would be predicted due to random variability alone, the overall proportion is still relatively modest. There are at least six reasons that the proportion of sites exhibiting CO<sub>2</sub>-induced growth increases might be as small as are seen here: (1) The drought records used are coarsely resolved, and may not be representative of the climate at the locations of the tree ring chronologies. However, because the disparity between large-scale and local climates is unbiased, and given that virtually identical results were found at sites where drought was and was not limiting to growth, this explanation is unlikely. (2) The total magnitude of atmospheric CO<sub>2</sub> change that has occurred over the analyzed period is relatively small compared to that expected to occur over the next century, and that used in most CO<sub>2</sub> enrichment studies. Over the period covered by the residuals analysis atmospheric CO<sub>2</sub> increased from 290 to 375 ppm, and over the period covered by the superposed epoch analysis CO<sub>2</sub> increased from an average of 317 to 339 ppm [Keeling and Whorf, 2004]. For comparison, pre-industrial CO<sub>2</sub> levels were 275 to 285 ppm, and projected CO<sub>2</sub> levels in the year 2100 range from 730 to 1020 ppm [Meehl et al., 2007]. Most open-top chamber and FACE experiments are run at levels of at least 550 ppm [Norby et al., 2005], and most closed growth chamber experiments have typically used treatments of 700 ppm or more [Curtis and Wang, 1998]. (3) Alternatively, CO<sub>2</sub>-induced increases in photosynthetic rates may not be directly linked to production rates [Körner, 2003]. That is, although photosynthesis may have increased the additional carbon assimilated is not being allocated to radial growth. (4) Trees growing in natural settings may not be carbon limited. Soil nutrients and direct impacts of drought on tree physiology may potentially limit growth rates and preclude CO<sub>2</sub> responses of trees [Körner et al., 2007]. Similarly, tree growth may already be carbon saturated under some natural growth conditions, such as at nutrient-limited sites or in regions where temperature is most limiting to growth [Körner, 2003]. In this respect, the ITRDB

data may not be representative of forests in general, since most tree ring studies have specifically targeted sites where growth is sensitive to environmental variability. Nonetheless, trees are presently growing at CO<sub>2</sub> levels that are double what they were 18 000 years ago [Neffel et al., 1988], and that are higher than they have been at any point in the last 650 thousand years [Siegenthaler et al., 2005]. Additional increases in CO<sub>2</sub> may therefore not stimulate trees growing in natural conditions [Körner, 2003]. (5) Similarly, down-regulation of photosynthesis may have occurred following initial CO<sub>2</sub> fertilization effects due to changes in sink strength (the ability of trees to utilize photosynthate outside of leaves), or nutrient limitations [Field et al., 1995; Gunderson and Wullschlegel, 1994; Körner, 2003]. (6) Last, long-term gradual increases in CO<sub>2</sub> may differ in their effects from the short-term step-increases used in most experiments [Klironomos et al., 2005; Luo and Reynolds, 1999]. The magnitude of CO<sub>2</sub> fertilization is determined by processes that occur in leaves. Foliage longevity in trees rarely exceeds 25 years, and most species retain their foliage for one to six years [Chabot and Hicks, 1982]. Leaf properties such as size, number, thickness, position, longevity, stomatal density, and nitrogen allocations may vary in response to ambient CO<sub>2</sub> at the time of leaf formation [Gunderson and Wullschlegel, 1994]. Therefore leaves formed under ambient CO<sub>2</sub> but subsequently exposed to elevated CO<sub>2</sub> (as is the case in most CO<sub>2</sub> enrichment experiments) may differ in their rates of photosynthesis from leaves that are formed and that photosynthesize under relatively constant CO<sub>2</sub> levels.

[17] Of these possible explanations, the first two derive from data limitations and the last four from physiological differences between trees growing in natural settings and most of the manipulative experiments undertaken to date. Most critically, only explanations (2) and (3) suggest that the real magnitude of CO<sub>2</sub> fertilization may be larger than was found here. Even if one of these explanations proves to be true, the results found here suggest that the total magnitude of actual CO<sub>2</sub> fertilization is relatively small, and that any CO<sub>2</sub>-induced growth increases do not result in carbon allocations to persistent carbon pools. Consequently there are important implications for climate change science and policy development: First, because the majority of chronologies exhibit no evidence for CO<sub>2</sub> fertilization, forests cannot be relied upon to increase their rates of carbon assimilation, and thus offset emissions or reduce the rate of warming that is expected [Körner, 2000]. Second, models that assume increasing water use efficiency by trees are likely unreliable in their forecasts of future range shifts, particularly in xeric environments [Grünzweig et al., 2003; Neilson and Drapek, 1998]. Third, in addition to between-species differences in the effects of CO<sub>2</sub> fertilization [Körner, 2000], there are undoubtedly within-species differences. The causes of these

differences are not clear from this analysis, but cannot be reliably linked to either site moisture stress or elevation. Soil properties, competition and stand dynamics, disturbance history, and microclimatic effects may all contribute to these differences. Fourth, because there are both between- and within-species differences in CO<sub>2</sub> fertilization effects, future interspecific competitive interactions will be intrinsically unpredictable, and will vary in a manner that may be very different from that seen today. Last, these results suggest that CO<sub>2</sub> fertilization effects probably exert a relatively minor influence on tree ring-based reconstructions of climate that use large numbers of chronologies, though such efforts could benefit from a careful screening of chronologies for increasing trends in growth over the 20th century that cannot be attributed to climatic change [e.g., Salzer *et al.*, 2009].

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A. A. Berg and Z. Gedalof (corresponding author), Department of Geography, University of Guelph, Guelph, ON N1G 2W1, Canada. (zgedalof@uoguelph.ca)