

DETECTING THE AERIAL
FERTILIZATION EFFECT OF
ATMOSPHERIC CO₂ ENRICHMENT IN
TREE-RING CHRONOLOGIES

Donald A. Graybill

Laboratory of Tree-Ring Research, University
of Arizona, Tucson

Sherwood B. Idso

U.S. Water Conservation Laboratory
Agricultural Research Service
Phoenix, Arizona

Abstract. The growth-promoting effects of the historical increase in the air's CO₂ content are not yet evident in tree-ring records where yearly biomass additions are apportioned among all plant parts. When almost all new biomass goes into cambial enlargement, however, a growth increase of 60% or more is observed over the past two centuries. As a result, calibration of tree-ring records of this nature with instrumental climate records may not be feasible because of such growth changes. However, climate signals prior to about the mid-19th century may yet be discovered by calibrating such tree-ring series with independently derived proxy climate records for those times.

INTRODUCTION

In the most comprehensive review of the plant science literature ever conducted into the effects of atmospheric CO₂ enrichment on plant growth and development, Idso [1992] analyzed 342 peer-reviewed journal articles that reported

the findings of 1087 individual experiments. Averaged across all plant types, the mean growth enhancement resulting from a 300 $\mu\text{L/L}$ increase in the air's CO₂ content was found to be 52%; while in 181 experiments conducted on trees, the corresponding growth enhancement was 62%. In the vast majority of these studies, however, the experimental plants were grown in small pots or other root-restricting containers; and it has been demonstrated that this artifact considerably reduces plant response to CO₂ [Arp, 1991; Thomas and Strain, 1991]. CO₂ effects are also reduced when soil nutrients are meager [Norby et al., 1992]; but as nutrients are often less than optimal in nature, this response-restricting artifact has often been regarded as producing realistic results [Kramer, 1981; Jarvis 1989; Bazzaz and Fajer, 1992]. It can be effectively argued, however, that plants in the natural environment can increase their nutrient-gathering capacities at a rate sufficient to meet the real-world rate of rise in growth potential provided by the yearly incremental rise in atmospheric CO₂, which is about two orders of magnitude less than that imposed in most CO₂ enrichment studies [Idso, 1989a; Drake, 1992; Rogers et al., 1992]. Consequently, if one seeks knowledge about the likely response of plants, and especially trees, to the rising CO₂ content of Earth's atmosphere, it should be sought in specimens rooted in the natural soil of the

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outdoor environment and supplied with adequate nutrients.

Unfortunately, few such experiments have been conducted. One notable exception is the 5-year-and-running sour orange tree experiment of S.B. Idso and his colleagues, where measurements of photosynthetic rate [Idso et al., 1991a; Idso and Kimball, 1992a], trunk and branch volume [Idso et al., 1991b; Idso and Kimball, 1992b], and fine-root biomass [Idso and Kimball, 1991, 1992c] have demonstrated that sour orange trees (*Citrus aurantium* L.) exposed to air enriched with an extra 300 $\mu\text{L/L}$ of CO_2 may be capable of yearly sequestering about 2.8 times more carbon than control trees growing in ambient air. A similar study of two eucalyptus species and the Australian bottle tree has produced equivalent results [Idso and Kimball, 1992d]; and studies of the yearly increasing amplitude of the atmosphere's annual CO_2 cycle additionally suggest that this response may be typical of most of the world's forests [Idso, 1991a, b]. Hence, since the CO_2 content of the air has risen about 85 $\mu\text{L/L}$ over the past two centuries (Figure 1), there is reason to expect a manifestation of this "aerial fertilization effect" in tree-ring records of the same period.

During the past decade a wide-ranging network of subalpine tree-ring chronologies has been under development in the southwestern United States (Figure 2, Table 1). This effort was undertaken for potential detection of the regional extent of carbon dioxide fertilization of tree growth and for other environmental research [Graybill, 1987]. Stands of long-lived conifers were sought in high elevation, upper treeline settings where remarkable growth increases of 73-106 percent over the past century or more had previously been observed (MTJ, SHP, CAM), leading to the hypothesis that carbon dioxide fertilization of tree growth may be occurring [LaMarche et al., 1984]. Increasing water use efficiency [Percy and Bjorkman, 1983] may also be partially responsible for the observed growth increases, particularly in the arid western sectors of the study region.

Some investigators working in or near this region have also found growth increases that might be attributable to increasing CO_2 [Jacoby, 1986; Peterson et al., 1990], but others have not

[Kienast and Luxmoore, 1988; Graumlich, 1991], raising serious questions about this issue. In this communication we thus present an hypothesis that explains why the "biological greenhouse signal" should be evident in some data sets and not in others. We also present a regional tree-ring record of the former type that exhibits a CO_2 -induced growth stimulation in excess of 60% over the past 210 years, which is exactly what would be expected on the basis of the sour orange tree experiments and studies of the atmosphere's CO_2 cycle.

The possibility that changes in climate during the past century might be responsible for the unusual increases in ringwidth growth of our subalpine conifers was investigated extensively. Regression-based analyses were used to explore models of growth as it might be related to instrumented values of temperature, precipitation and computed drought values [Palmer, 1965]. Climate data were from single station records that in some cases reached back to the late 1800s, as well as state divisional averages since 1931 (Historical Climatology Network, [Quinlan et al., 1987], annual station summaries, U.S. Department of Agriculture and U.S. Commerce Department, NCDC state divisional averages [Karl et al., 1983]). It is notable that trends of the magnitude observed in 20th century ringwidth growth are conspicuously lacking in all of the time series of instrumented climatic variables that might reasonably be considered growth-forcing in nature. These modeling efforts were met with only limited success in establishing strong, temporally consistent relationships of tree-ring growth with monthly, seasonal or annual climatic values [Graybill 1993a, b]. None of the models are capable of describing the late 19th to 20th century growth increases.

One perplexing problem has been the lack of strong, consistent temperature responses in the subalpine chronologies. The elevational level of the stands is to some large degree controlled by growing season temperature in terms of limitations on germination and seedling survival [Daubenmire, 1954; Tranquillini, 1979]. A positive tree-ring width growth response to those temperatures might also be reasonably expected. LaMarche [1974a, b] examined this issue with data from some of the stands used here and hypothesized that upper treeline

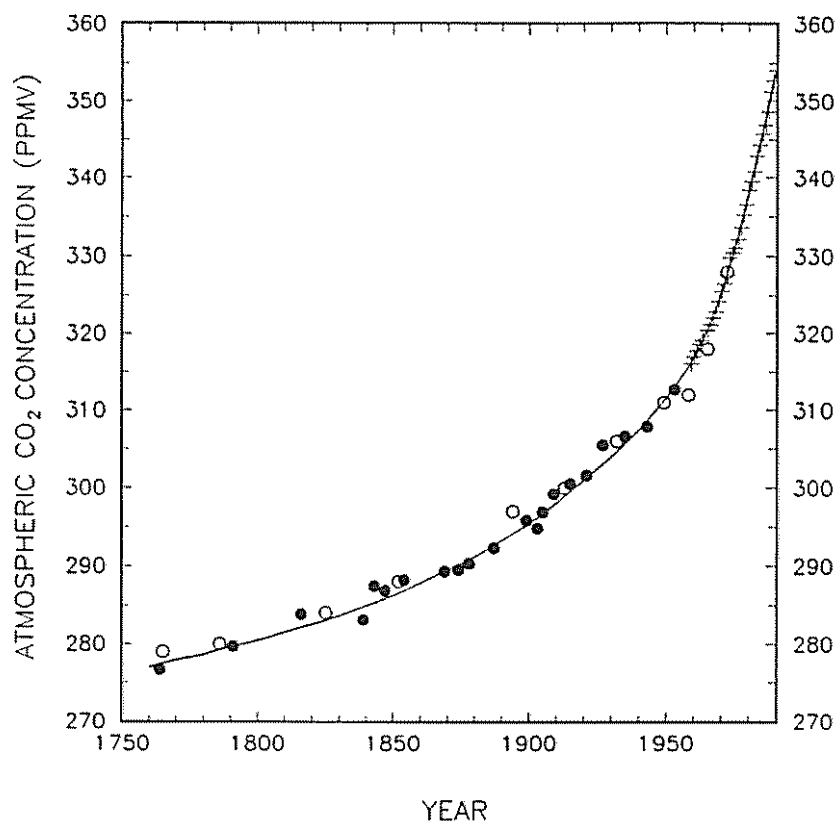


Fig. 1. Historical levels of atmospheric CO₂ concentration. Solid circles, Friedli et al. [1986]; open circles, Neftel et al. [1985]; pluses, Keeling and Whorf [1990].

bristlecone pine chronologies should provide records of warm season temperatures, at least at low frequencies. He did not, however, develop any reliable quantitative transfer functions between instrumental climate data and ringwidth growth that could support this notion. From other perspectives, an ecophysiological study of bristlecone pine in the White Mountains of California, that included the Sheep Mountain ("Patriarch") stand, reported no marked or direct correlation of summer temperature with ringwidth growth [Fritts, 1969]. Lack of success in establishing these relationships may in part reflect the limited amount of climatic data available at such high elevations, the possible inadequacy of using monthly climatic values, or, the possibility that climate-tree growth relationships are being obscured by growth responses to increasing CO₂.

Other lines of evidence suggest that variation

in precipitation or drought are not responsible for unusual century-scale tree-growth patterns in subalpine stands throughout the region. Foxtail pine and bristlecone pine chronologies from the western region that are near their lower elevational limits for growth (circa 2600-2900 m), and that are strongly sensitive to moisture deficit, do not show growth trends analogous to the subalpine chronologies that in several cases are only a few kilometers distant in the same mountain range (Sierra Nevada, Calif.; White Mountains, Calif.; Snake Range, Nev.; Ruby Mountains, Nev.; Spring Mountains, Nev. [LaMarche, 1974a; Graybill, 1987, 1993a]. Recent studies of pollution and tree-ring growth through the larger region (Colorado Front Range, Arizona-New Mexico, Sierra Nevada, California) developed numerous tree-ring chronologies from several coniferous species in settings that primarily ranged from forest interior to lower forest border. [Graybill et al.,

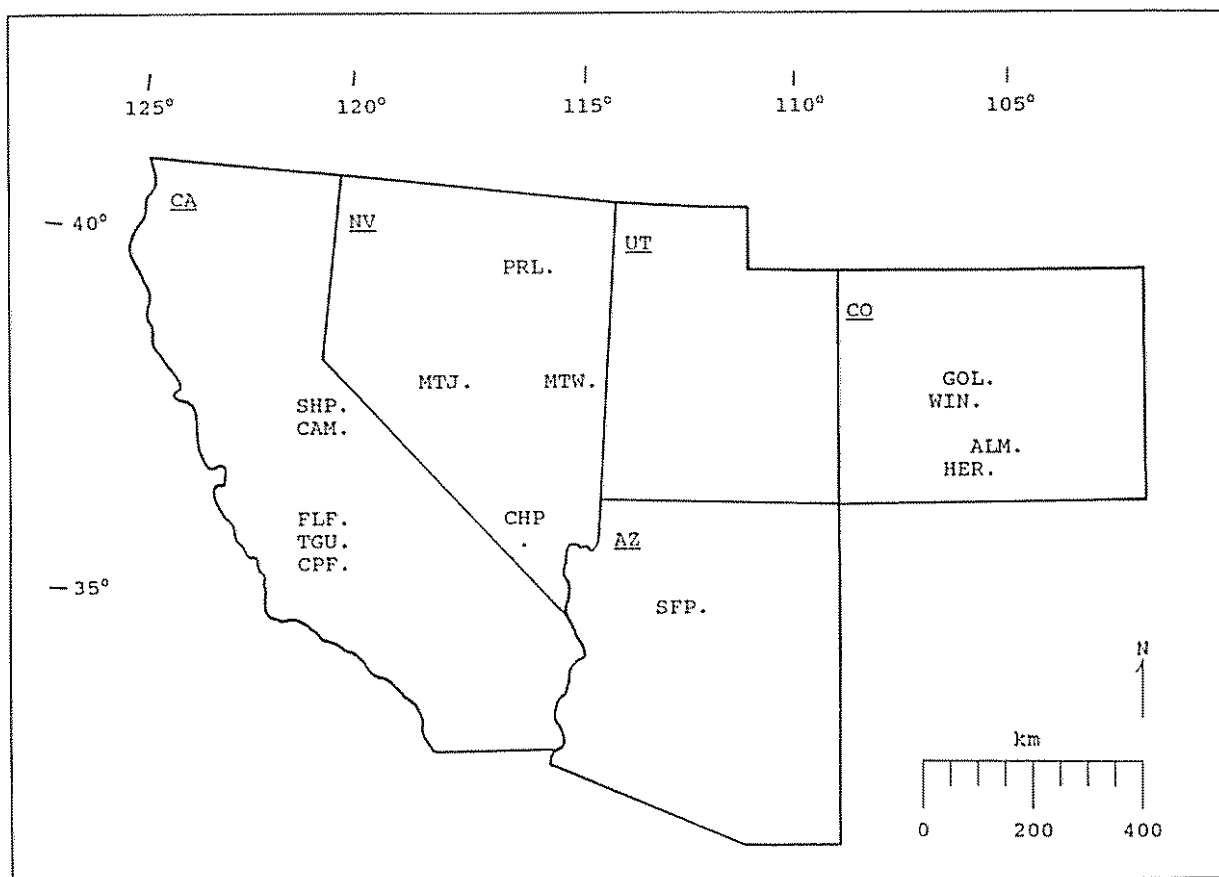


Fig. 2. Tree-ring chronology and stand information.

1992; Graybill and Rose, 1992; Peterson and Arbaugh, 1992]. Climatic sensitivity of the trees was predominantly moisture-related and no unexplainable growth increases were noted.

Given these observations, and what is thought to be nonclimatically induced growth increase in our chronologies from upper treeline settings over the past century or so, traditional calibration procedures with instrumental climatic data may not be feasible or productive [Lamarche et al., 1984; Idso, 1989b]. A different approach to discovery of temperature signals in these chronologies, and of the possibility of recent change in this growth sensitivity, is thus undertaken by comparing growth records from this region with independently derived dendroclimatic reconstructions that cover most of western North America [Fritts, 1991; Schweingruber et al., 1991; Briffa et al., 1992].

MATERIALS AND METHODS

Sour Orange Tree Studies

The sour orange tree studies cited in the Introduction are part of an ongoing long-term experiment that was begun in July of 1987, when several seedlings were planted directly into the ground at Phoenix, Arizona and surrounded in pairs by transparent walls of clear plastic film. Since November of that year, half of the trees, which now stand approximately 5 m in height, have been continuously exposed to a bottom-to-top flow of ambient air expelled through perforated plastic tubes lying upon the surface of the soil, while the other half have been similarly exposed to air containing an extra 300 $\mu\text{L/L}$ of CO_2 . Throughout the experiment, the trees have been manually flood-irrigated at periods deemed appropriate to preclude the

TABLE 1. Tree-Ring Chronology and Stand Information

Region/Site	Species ^a	Latitude, Longitude (°N, °W)	Elevation m	Primary Aspect	Dates AD
Colorado					
Almagre Mountain (ALM)	Pa	38°46', 104°59'	3536	N	560 - 1983
Mount Goliath (GOL)	Pa	39°38', 105°35'	3535	SE	525 - 1983
Hermit Lake (HER)	Pa	38°06', 105°38'	3660	S	1048 - 1983
Windy Ridge (WIN)	Pa	39°19', 106°05'	3570	S,E	1050 - 1985
Great Basin					
Campito Mountain (CAM)	Pl	37°30', 118°13'	3400	W	150 - 1983
Charleston Peak (CHP)	Pl	36°16', 115°42'	3425	S	800 - 1984
Mount Jefferson (MTJ)	Pf	38°47', 116°57'	3300	S,W	1300 - 1980
Mount Washington (MTW)	Pl	38°54', 114°19'	3415	S	700 - 1983
Pearl Peak (PRL)	Pl	40°14', 115°32'	3170	S	320 - 1985
San Francisco Peaks (SFP)	Pa	35°30', 111°40'	3535	S	548 - 1983
Sheep Mountain (SHP)	Pl	37°22', 118°13'	3475	S,E	150 - 1990
Sierra Nevada					
Cirque Peak (CPF)	Pb	36°27', 118°13'	3505	S	917 - 1987
Flower Lake (FLF)	Pb	36°46', 118°36'	3291	SW	898 - 1987
Timber Gap Upper (TGU)	Pb	36°27', 118°36'	3261	W	699 - 1987

^a Pa: *Pinus aristata* (Engelm.), Rocky Mountain bristlecone pine; Pb: *Pinus balfouriana* (Grev. and Balf.), foxtail pine; Pf: *Pinus flexilis* (James), limber pine; and Pl: *Pinus longaeva* (D.K. Bailey), Great Basin bristlecone pine.

development of significant water stresses; and they have been supplied with a commercial citrus fertilizer at rates that should also have precluded the development of significant nutrient stresses.

The findings of this experiment that are pertinent to the current study are the following: (1) total tree biomass, both above- and below-ground, has been increased by a factor of 2.77 in the CO₂-enriched open-top chambers, while (2) trunk cross-sectional areas at a height of 45 cm above the ground have been increased by a factor of 1.77.

Tree-Ring Studies

These endeavors focused exclusively on five-needled pines (Table 1) because they are the most widespread group with relatively great age potential. Age is an important factor because it provides perspective on how common or unique the recent growth changes are with respect to growth variation during the past one or two millennia, when levels of atmospheric CO₂ were less than those of recent times and relatively stable [Oeschger and Stauffer, 1986].

Stands were selected for sampling when they appeared to be undisturbed by obvious factors such as fire, logging or road construction in order to limit extraneous disturbance signals in ringwidth growth. Relatively open stand growth was also sought, which minimizes, if not precludes, the effects that competition between trees may have on their ringwidth growth variation. The sites in the Sierra Nevada and the Great Basin were generally bereft of substantial soils, well-drained and xeric. Sites in Colorado exhibited limited soil development and were somewhat more mesic than those in the western part of the network.

Trees within stands were selected for sampling if they did not have obvious signs of disease or major injury such as that sustained from lightning. Another tree selection factor that is crucial to our findings involves tree form. Experience has indicated that many of the oldest five-needled pines have experienced cambial dieback to varying degrees. This appears to begin after several hundred years of growth and is progressive. These so-called "strip-bark" trees can have active cambium that is only a few centimeters in width. Foliage and cones are also accordingly limited. Trees of

this nature were the primary focus of investigation whenever possible. They were most commonly found and sampled in stands of bristlecone pine and limber pine in the Great Basin, and in stands of foxtail pine in the Sierra Nevada. A separate set of full-bark trees growing among strip-bark forms was also recently sampled in the Sheep Mountain stand for comparative purposes. All tree-ring samples in the study were taken at breast height with 4.5-mm-diameter increment borers. One or more increment core samples were normally taken from each of 15 to 30 trees per stand.

Tree-ring series were crossdated and assigned calendar dates [Stokes and Smiley, 1968]. All dating was independently verified by at least two dendrochronologists. The rings were then measured to the nearest 0.01 mm. Visual comparison of time series plots with the actual ringwidths, as well as the use of computer-assisted procedures, provided further checks on the quality of measurement and dating [Holmes, 1983].

The measured ringwidth series were subjected to the process of standardization to remove age-related growth trends [Fritts, 1976; Graybill, 1979, 1982]. An appropriate curve was fit to each series to model this variation. Simple deterministic models such as negative exponential curves or straight lines were used in almost all cases. These conservative methods do not normally remove climatic or other environmental growth forcing trends that are of lesser duration than the length of each individual series. Perhaps more importantly in this study, the use of these methods did not introduce spurious upward trends near the ends of the series. Dimensionless tree-ring indices were computed by dividing the actual growth by the expected growth for each year per series, where expected growth was determined by model fit. The indices for individual series were then averaged to form a composite tree-ring index chronology for each stand (Table 1.) In addition to the Sheep Mountain strip-bark chronology, another chronology was developed from full-bark trees for 1680-1990.

Climate Data and Dendroclimatic Reconstructions

Major differences were found in recent growth trends of the strip- and full-bark tree

growth forms at Sheep Mountain. The possibility that they represent different climate responses was considered by first reviewing Pearson correlations of seasonal climate with the chronologies from the two forms. Multiple regression of the chronologies with seasonal climate data was also undertaken. This is particularly feasible here, because there are two monthly temperature and precipitation series from high elevations in the White Mountains. The Sheep Mountain and nearby Campito Mountain stand are the only ones in the entire network with instrumental climate data in such close proximity to the trees (less than 10 km). One record from Crooked Creek (White Mountain 1 - NOAA 04079633, 37°35' N, 118°14' W, 3094 m) includes data from 1949 to 1977. Another station on Mount Barcroft (White Mountain 2, NOAA 04079632, 37°30' N, 118°11' W, 3801 m) has data from 1953 to 1980. The elevation of the Sheep Mountain stand is intermediate between the stations. Consequently, a composite station record was developed for 1949-1980. Appropriate estimates of the few years' difference in each station record were made with the available data, and the composite record is a simple average.

Data from this study were compared with two dendrochronological reconstructions of temperature in western North America that were developed for 1602-1962 [Fritts, 1991] and 1600-1982 [Schweingruber et al., 1991; Briffa et al., 1992]. Those studies were based on chronologies from different stands and neither used trees from stands in the current network of five-needled pines.

The former study focused on arid-site or generally lower forest border conifers that can have both precipitation and temperature signals. An annual as well as four seasonal temperature reconstructions were based on quantitative calibration of a network of 65 tree-ring width index chronologies and 77 temperature station records. The seasonal periods reconstructed were winter (December-February), spring (March-June), summer (July-August), and fall (September-November); while the annual period was from December-November.

Stands in the latter study were selected near the timberline on shady sites with moist soils to

minimize precipitation signals and maximize temperature signals. The reconstruction of average April-September temperature was based upon variation in maximum latewood density measurements of samples from 53 stands of various coniferous species. All species are different from those used in the current study. Calibrations and reconstructions were accomplished for 23 points in the region that are part of a 5° latitude by 10° longitude grid of northern hemispheric temperatures [Jones et al., 1985]. Most of the grid point temperature reconstructions are essentially devoid of autocorrelation, and Fritts' [1991] reconstructions generally have limited persistence; but this is not true for the chronologies in our tree-ring network [Graybill, 1985]. Prewhitened series were therefore developed for these comparisons. The ARMA models [Box and Jenkins, 1976] were established with data only through 1859 in order to limit the potentially overwhelming effects of recent trends on model parameters.

Simple averages of temperature grid point reconstructions, or of temperature station reconstructions, were made that corresponded to the areas respectively covered by the eastern and western sectors of our tree-ring network. Visual comparison of time series plots of the average of the tree-ring series per subregion and the various temperature reconstruction averages was first used to screen and isolate potentially important correspondences. Bivariate correlation was then used to describe them.

RESULTS AND DISCUSSION

Growth trends in the tree-ring chronologies are presented for major subareas of the study region (Figure 3). A large growth increase since about the mid-1800s is widespread and common to all but two of the chronologies (SFP, GOL). Examination of the yearly values for all chronologies (not shown), and of the filtered 20-year averages (Figure 3), indicates that none have growth increases of such magnitude in earlier years. These observations indicate that one or more growth-forcing factors operating on a pan-regional scale began to have a new and substantial effect on subalpine radial tree growth in these stands during at least the

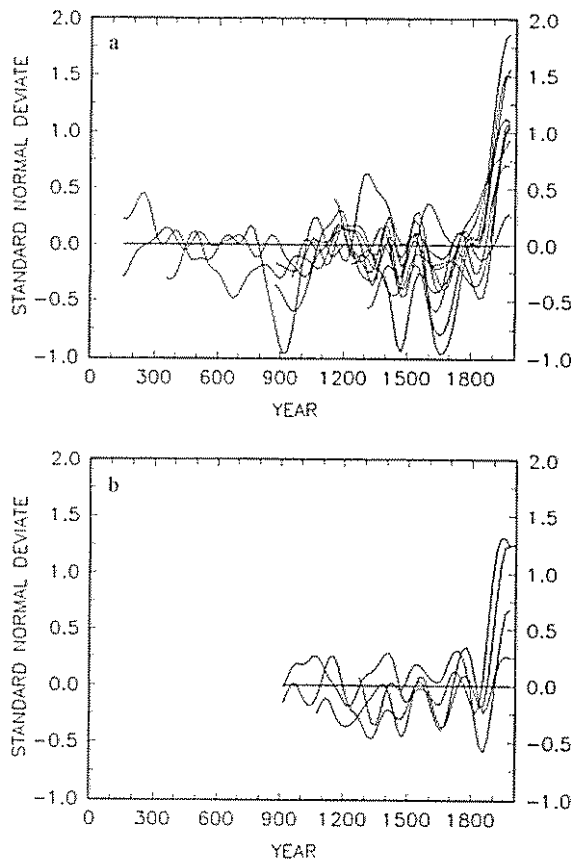


Fig. 3. Growth trends in subalpine tree-ring chronologies from (a) Great Basin and Sierra Nevada and, (b) Colorado. Twenty-year nonoverlapping averages for each chronology were smoothed with an 8-point low-pass filter.

past century. A model of growth changes derived from experimental CO_2 fertilization studies supports the notion that one such factor, and perhaps the only factor, has been increasing atmospheric CO_2 .

On the basis of atmospheric CO_2 trend of Figure 1, we have developed two different CO_2 -induced growth enhancement histories, as shown in Figure 4. One is based upon the trunk cross-sectional area response of the sour orange trees to atmospheric CO_2 enrichment, while the other comes from the trees' total biomass response to CO_2 . Both histories assume a linear response of tree growth to CO_2 enrichment extrapolated back to pre-industrial CO_2 values and were calculated as follows. First, a growth rate of unity was assigned to the current atmospheric CO_2 concentration (360

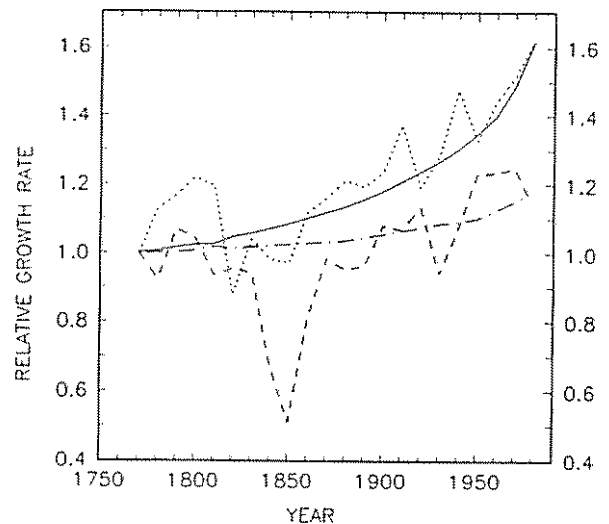


Fig. 4. Relative growth rates of sour orange trees and subalpine conifers. (Solid) sour orange tree total biomass; (dashed and dotted) sour orange tree trunk cross-sectional area; (dotted) Great Basin and Sierra Nevada tree-ring chronologies; (dashed) Colorado tree-ring chronologies. Tree-ring curves are decadal ratios of average index values per subregion for 1761-1980, where 1761-1770 is 1.0.

$\mu\text{L/L}$). Then, a growth rate of 1.77 for the trunk cross-sectional area response and a growth rate of 2.77 for the total biomass response was assigned to a CO_2 concentration of 660 $\mu\text{L/L}$. Straight lines connecting these latter two points with the current growth rate of unity were next constructed and extrapolated back to the atmospheric CO_2 concentration characteristic of 1770, i.e., 278 $\mu\text{L/L}$. The CO_2 history of Figure 1 then allowed growth rate histories to be calculated from these two lines, after which they were renormalized to a value of unity at 1770. Also included in Figure 4 are decadal ratios of the observed relative growth rates obtained from the upper treeline data sets over the same time interval.

The actual tree-ring data exhibit two types of variability: (1) mean upward trends across the 210-year period and, (2) natural variability about those mean trends induced by variation in other factors (Figure 4). The upward trend of the tree-ring data from the western part of the grid is described almost perfectly by our total-biomass-based prediction of CO_2 -induced

growth enhancement, while the trend in the eastern series is more similar to that of the trunk cross-sectional area predictions from the sour orange tree data. We think these correspondences provide some of the first empirical evidence of similar growth responses to increasing CO_2 by rather different kinds of trees, respectively growing in controlled and natural environments.

Observed differences in subregional tree-ring growth trends may be due to species differences, but more importantly we think, they are probably due to tree form. All of the eastern series are based on Rocky Mountain bristlecone pine. The SFP series that had the most limited (but increasing) recent growth trend in the western region is also of this species. The strip-bark form of growth, however, is less common in this species than in others that were sampled. We hypothesize that observed growth level differences are a result of differential allocation of increasingly available carbon by the two tree forms. An evaluation of our hypothesis is provided by a simple comparison of two tree-ring chronologies developed from the Great Basin bristlecone pine stand at Sheep Mountain, California. Since tree form is considered the critical issue, rather than species, we think this is a pertinent exercise. One chronology is based exclusively on strip-bark forms while the other includes only full-bark trees (Figure 5).

The two chronologies are almost indistinguishable until about 1870, when the

one based on strip-bark trees begins a sustained, low-frequency trend of radial growth increase. A more limited low frequency upward trend is also present in the full-bark chronology since about 1890. Since carbon availability as well as other environmental factors affecting tree growth are similar, if not the same, for all trees here, we suggest that the strip-bark forms are incorporating newly fixed carbon primarily into cambial growth. The full-bark forms may also be doing so to some degree, but they are likely using a substantial fraction of their fixed carbon for foliage and reproductive growth. Increased carbon allocation to roots is likely involved in both cases, as below-ground growth is generally stimulated to at least the same degree as above-ground growth [Idso et al., 1988]. However, we suspect that the full-bark trees have a larger, more active root system than do the strip-barks, which would provide a somewhat greater sink for new carbon in the former trees as opposed to the latter [Norby et al., 1992]. Consequently, detection of radial tree growth change in response to carbon dioxide fertilization may be significantly obscured in full-bark trees when it is readily evident in strip-bark specimens.

Pearson correlations of the two Sheep Mountain tree-ring index chronologies with average seasonal temperature, total seasonal precipitation and seasonal values of the Palmer drought severity index (PDSI) do not indicate major differences in their climate growth

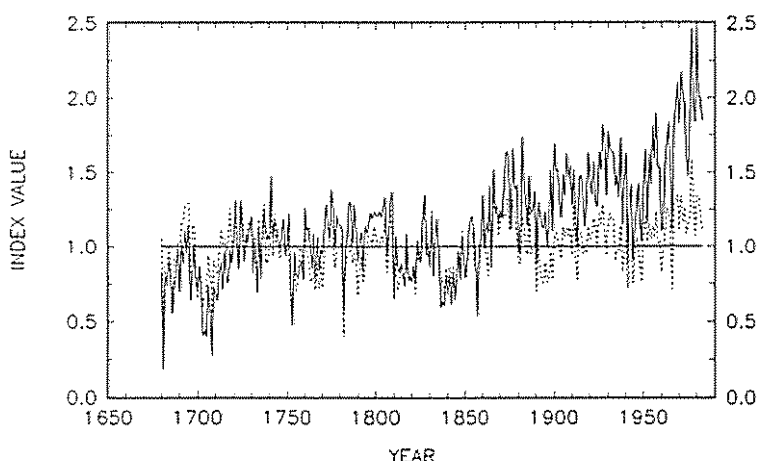


Fig. 5. Bristlecone pine tree-ring index chronologies from Sheep Mountain, California for strip-bark growth forms (solid) and full-bark growth forms (dotted).

responses (Table 2). The significance of those correlations is difficult to evaluate because of autocorrelation in the tree-ring indices that is significant to several lags. Therefore, prewhitened versions of the chronologies were developed over their common period (1680-1983) with standard Box and Jenkins [1976] protocol. Correlations with the climate data were recomputed and, again, these values do not indicate major differences in growth response to climate by the two tree forms (Table 2).

Stepwise multiple linear regression [Draper and Smith, 1981] was also used in evaluation of the climate-tree growth relationship. There were ten independent variables in each analysis that included the five seasonal values of both temperature and precipitation (Table 2). A significance level of 0.05 for F-test values was used to control the inclusion of variables. The only variable that entered in the analyses using indices of the full- and strip-bark series was spring temperature and the respective amounts of variance explained were 0.27 and 0.14. Winter temperature was the only variable selected to describe variation in the white noise residual series of the strip bark series ($r^2 = 0.11$). Spring, winter, and summer temperature were selected in that order during analysis with the full-bark residual series and the adjusted r^2 values by step were 0.22, 0.33, and 0.46.

The particular responses observed here are similar to those discovered in the ecophysiological study of bristlecone pine in this vicinity by Fritts [1969]. The positive responses to winter temperature probably reflect the importance of maintaining or increasing food reserves since cold winter temperatures at these elevations can limit or inactivate photosynthesis [Schulze et al., 1967]. High temperatures during the spring result in drought conditions during succeeding months that are apparently limiting to growth processes. Summer temperature appears to have limited impact on growth.

There are, however, consistent differences in the strengths of the more important climate responses by the two tree forms. For example, the strip-bark series have less variance in common with winter and spring temperatures and with the summer drought regime than do the full-bark series (Table 2). This may reflect the differential impact of the hypothesized atmospheric CO₂ effect on growth and climatic sensitivity of these forms.

Tree-Ring Growth Forcing Factors

Comparison of the average of the four prewhitened Colorado tree-ring series with the average seasonal and annual temperature reconstructions for three of Fritts' [1991]

TABLE 2. Pearson Correlations of Full Bark and Strip Bark Tree Ring Indices and White Noise Residuals From Sheep Mountain California With White Mountain California Seasonal Climate Data, 1949-1980

	Full-Bark Indices			Strip-Bark Indices		
	T	P	PD	T	P	PD
Prior Summer	-0.08	0.12	0.11	0.23	0.15	0.22
Prior Fall	0.04	0.01	0.12	-0.16	0.03	0.18
Winter	0.33*	0.22	0.20	0.20	0.23	0.26
Spring	-0.52***	0.28	0.36*	-0.41**	0.11	0.31
Summer	-0.25	0.21	0.47**	-0.27	0.09	0.38*
	Full-Bark Residuals			Strip-Bark Residuals		
	T	P	PD	T	P	PD
Prior Summer	0.04	0.05	-0.06	-0.12	0.14	0.09
Prior Fall	0.20	0.04	0.08	0.20	-0.02	0.12
Winter	0.42**	0.21	0.13	0.38**	0.19	0.13
Spring	-0.49***	0.28	0.32	-0.36**	0.15	0.26
Summer	-0.14	0.29	0.48**	-0.18	0.24	0.43**

T: temperature, P: precipitation, PD: PDSI; Summer is June-August, Fall is September-November, Winter is December-February, Spring is March-May; *, **, *** = 0.10, 0.05, 0.01 levels of significance.

stations in the area (numbers 1, 8, 9) showed no clear correspondences. An average of the ten Great Basin and Sierra Nevada series also showed no close correspondence with various subsets of his reconstructions, although this fact may reflect limited spatial overlap of our series. Fritts' tree-ring grid contains little data in the Great Basin and Southern Sierra region. A comparison of our Colorado upper treeline average with an average of two of the Briffa et al. [1992] April-September grid point reconstructions (latitude 35° and 40°N, longitude 100°W) was also unsuccessful. This fact may be related to the limited number of densitometric series in this area. Additionally, this area is near the southeastern edge of the grid where reconstructed seasonal temperature signals are not as strong as those for grid points further to the west [Briffa et al., 1992]. There are, however, strong but temporally restricted similarities in growth patterns of tree-ring series from the western sector of our network and an average of two of the closest grid point temperature reconstructions of average April-September temperature (latitude 35° and 40°N, longitude 120°W, Figure 6). Cross-spectral analysis [Jenkins and Watts, 1968] indicates relatively strong coherence between the two series for periods greater than 8 years so the data were filtered to emphasize this commonality. A striking correspondence is

apparent in the two series from about 1635 to 1845, but after that time they bear almost no resemblance to each other. Correlations between the series during those time periods are, respectively, 0.73 ($p < 0.001$) and -0.02 ($p = 0.83$), although the significance levels cannot be readily evaluated. Correlations of the unfiltered data (not shown) for those respective time periods are 0.37 ($p < 0.001$) and 0.21 ($p = 0.01$). The lack of correspondence in the two series before 1635 may result from declining numbers of samples in the densitometric data.

These new observations are provocative, and permit two inferences: (1) there probably are regional temperature signals at low frequencies in some of the upper treeline data before the mid-19th century but, (2) these signals become obscure as atmospheric CO₂ has increased. While these relationships deserve further study, they initially appear to explain difficulties experienced in attempts to calibrate some of these data with instrumental records.

Relationships to Other Studies

Our hypothesis regarding differences in recent carbon allocation by tree form may be pertinent for explaining different growth trends from those we have observed in this region. A study of tree-ring chronologies from three

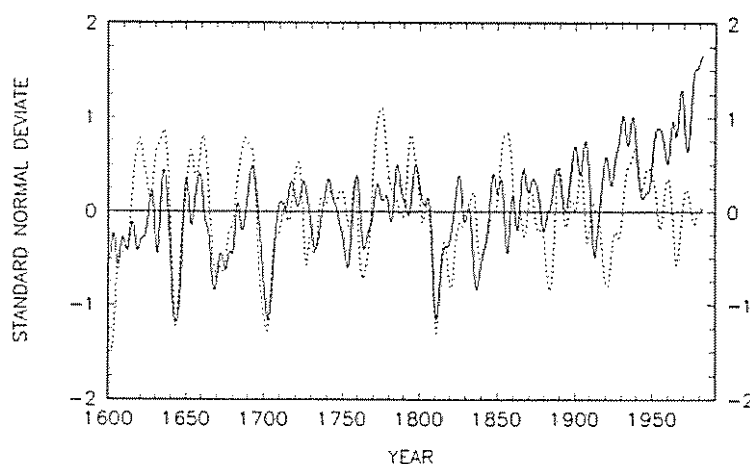


Fig. 6. Maximum late wood density reconstruction of average April-September temperature (dotted) and average of Great Basin and Sierra Nevada subalpine strip-bark tree-ring chronologies (solid). Standard normal deviates of both series were smoothed with an 8-year low-pass filter. Tree-ring chronologies were prewhitened before averaging.

stands of subalpine foxtail pine and one of lodgepole pine (*Pinus contorta*) from the southern Sierra Nevada reported no extraordinary growth increase over the past century [Graumlich, 1991]. Those stands are within 25 km of the three foxtail pine stands used in the current study (CPF, FLF, TGU) and are located at similar elevations. Climate differences are probably minimal in this small area. Methods of standardization used in the two studies were essentially identical and cannot be considered a cause for observed growth differences. The tree forms that we sampled, however, were different. Graumlich's samples were almost entirely from mature full-bark individuals with substantial foliage [L. J. Graumlich, personal communication, 1991]. Our samples of foxtail pine were predominantly from strip-bark forms.

The nature of the subalpine tree forms sampled in Colorado for the Kienast and Luxmoore [1988] study are not described, and their analyses focused primarily on growth and climate trends since 1950. Therefore it is difficult to comment or elaborate on the growth differences found in our studies.

A second hypothesis regarding the cause of recent tree-ring growth or biomass increase that should also be given consideration is the possibility that urban-industrial pollution has recently been fertilizing trees [Kauppi et al., 1992]. Studies by P. Hari and his colleagues in Finland, for example, initially indicated that increases in both atmospheric CO₂ and nitrogen deposition might be responsible for otherwise unexplained tree-ring width growth increases there [Hari et al., 1984], but more recently they have suggested that nitrogen may not be as important as CO₂ fertilization [Hari and Arovaara, 1988]. In addition, a summary of numerous studies that used tree-ring growth to analyze the effects of pollution on forest health in the United States and Canada did not report increases in growth that corresponded with areas of high pollution [Barnard and Lucier, 1990]. Some of those studies were conducted in areas that correspond with much of the subalpine tree-ring network used here (Colorado Front Range, north central Arizona, Sierra Nevada, California) [Graybill et al., 1992; Graybill and Rose, 1992; Peterson and Arbaugh, 1992].

CONCLUSIONS

Our research supports the hypothesis that atmospheric CO₂ fertilization of natural tree growth has been occurring from at least the mid- to late-19th century. This enhanced growth is most apparent in high elevation subalpine conifers where newly fixed carbon is primarily allocated to cambial growth rather than to other parts of the tree, as in the case of the strip-bark growth forms sampled here. These results, in tandem with studies of changes in the amplitude of the annual CO₂ cycle cited by Idso [1991a, b], also suggest that growth increases due to CO₂ fertilization are widespread. That they have not been commonly detected as ringwidth increases is likely due to the fact that most trees do not exhibit the form and growth behavior of those sampled in this study.

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- D. A. Graybill, Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ 85721.
- S. B. Idso, U.S. Water Conservation Laboratory, 4331 E. Broadway, Phoenix, AZ 85040.

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