Reports

Increasing Atmospheric Carbon Dioxide: Tree Ring Evidence for Growth Enhancement in Natural Vegetation

Abstract. *A response of plant growth to increased atmospheric carbon dioxide, which has been anticipated from laboratory data, may now have been detected in the annual rings of subalpine conifers growing in the western United States. Experimental evidence shows that carbon dioxide can be an important limiting factor in the growth of plants in this high-altitude environment. The greatly increased tree growth rates observed since the mid-19th century exceed those expected from climatic trends but are consistent in magnitude with global trends in carbon dioxide, especially in recent decades. If correctly interpreted, these findings have important implications for climate studies involving tree ring observations and for models of the global carbon dioxide budget.*

The amount of CO_2 in the earth's atmosphere has been increasing steadily over the past century because of human activities that release stored CO_2 from terrestrial reservoirs (*1–3*). The increase in CO_2 and other minor or trace gases may affect the radiation balance of the earth, with possible climatic consequences (*4*). In addition, rising atmospheric CO_2 may directly influence net photosynthesis, plant growth, and productivity (*5*). Termed the fertilization effect, enhanced growth in response to artificially elevated CO_2 has been observed in greenhouses and in limited field experiments (*6*). Large-scale effects may now be taking place in nature (*7*). In this report we present what appears to be the first direct evidence of CO_2-related growth enhancement in natural vegetation: increased widths of annual rings of trees in subalpine habitats in the western United States during recent decades.

Ring widths in subalpine bristlecone pines (*Pinus longaeva* D. K. Bailey and *Pinus aristata* Engelm.) at high-altitude sites from New Mexico and Colorado to California show increases from about 1840 to 1970. Physiological considerations and temperature records suggested that this positive growth trend was due to rising warm-season temperatures until about 1960 (*8*). Its persistence through the late 1960's without continuation of this climatic trend was originally interpreted as a lagging biological response to temporarily increased leaf area related to rising temperatures in the first half of the century because bristlecone pines commonly retain needles for 15 years or more (*9*). The increase in photosynthetic biomass could have resulted in higher growth rates despite stable or even cooling temperatures. However, more recent sampling of another subalpine conifer, *Pinus flexilis* James, in central Nevada (*10*), showed that the growth trend had continued or even accelerated during the 1970's (Fig. 1). Mechanisms other than, or in addition to, climatic factors must be invoked to explain this apparent anomalous regional trend.

In order to determine whether the recent growth increase in Nevada is a local phenomenon, or part of a regional or larger trend, and to clarify the role of climate we recently resampled bristlecone pines at two upper tree-line sites (3400 to 3500 m) in the White Mountains of eastern California (*11*). The sites lie between two high-altitude meteorological observatories (*12*). Ring width data on these samples were used to supplement existing ring width index chronologies (*13*) through the early 1980's, and are shown in Fig. 2 (*14*). Growth rates have remained very high through the early 1980's. Figure 3 shows climatic records combining data for the two stations for the period 1949 to 1980. No climatic trends are apparent that might explain the positive trends in tree growth, nor are such trends apparent in longer series of regional data (*15*).

In the absence of strong climatic forcing, alternative explanations for this positive regional growth anomaly must be considered. We believe, from the evidence now available, that subalpine vegetation generally, and upper tree-line conifers in particular, could now be exhibiting enhanced growth as a direct response to increasing concentrations of atmospheric CO_2. The basis for this hypothesis is the important effect that CO_2 concentration would be expected to have on net photosynthesis in this high-altitude environment.

Although there are systematic regional differences and regular seasonal fluctuations in CO_2 concentration of a few parts per million, as well as longer term global trends (*16*), the proportion of CO_2 in the atmosphere remains constant over a vertical range of at least 80 km (*17*). However, because the atmospheric pressure and thus the density of air decrease with increasing altitude, the partial pressure, or concentration of CO_2 per unit volume of air, also drops. For the standard atmosphere in July at 30°N (*18*), the density of air decreases from 1.159 kg/m^3 at sea level to 0.835 kg/m^3, or 72 percent of its sea-level value, at an altitude of 3500 m. As pointed out by Tranquillini (*19*), the change in CO_2 concentration reduces the diffusion gradient from atmosphere to plant leaf and thus could substantially reduce CO_2 uptake. Although theoretical calculations by Gale (*20*) suggested that there might be some compensating effects of lower partial pressure, such as increased diffusion coefficients, his own research did not demonstrate a major counteracting effect. Also, Tranquillini (*19*) estimated that the photosynthetic performance of trees at timberline in the Alps (1900 to 2600 m) may fall 10 to 20 percent below that at lower altitudes because of decreased availability of CO_2.

Field and laboratory experiments were

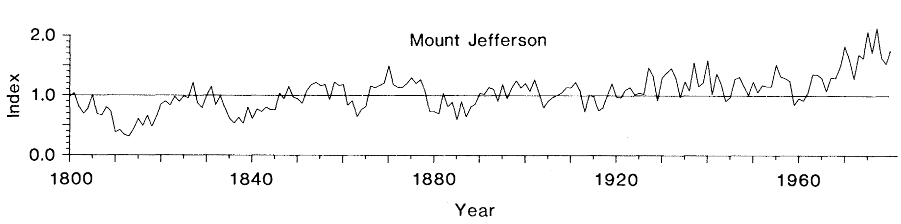

Fig. 1. Ring width indices for limber pine, Mount Jefferson, Nevada, showing rapidly increasing growth since the 1960's.

conducted at reduced CO_2 concentrations on herbaceous plants, woody perennials, and shrubs native to the White Mountains near sea level and at about 3100 m by Mooney and co-workers (*21*). They estimated that photosynthetic rates for these species in the field at 3900 m, somewhat above the local tree line, average about 70 percent of those under standard laboratory conditions near sea level because of differences in the concentration of CO_2. Although data are not available for the photosynthetic performance of bristlecone pine at reduced CO_2 concentrations, the CO_2 response seems to be shared by a broad range of subalpine taxa. For example, measurements made at lower altitudes on another subalpine conifer (*Abies alba*) by Koch (*22*) also showed a nearly linear decrease in net assimilation with decreasing CO_2 concentration in the range 50 to 350 ppm under moderate light (1×10^4 lux). Thus an atmosphere like that of the early 1960's, containing 310 to 320 ppm CO_2 at sea level (*16*), would have had volumetric concentrations in the July standard atmosphere at 3500 m equivalent to 223 to 230 ppm, which is well within the linear portion of the net assimilation versus CO_2 response curve for *Abies* and probably for *P. longaeva* as well.

The reduction in photosynthetic efficiency would thus be directly proportional to the decrease in the partial pressure of CO_2 with increasing altitude if the proportion of CO_2 remained constant. Therefore, whether due directly to higher CO_2 concentrations or to less direct physiological effects, photosynthetic efficiency in high-altitude plants could be increasing with time as the concentration of CO_2 in the atmosphere increases.

If we use a value for the preindustrial CO_2 concentration of about 270 ppm (*23*) and a modern value of 340 ppm (*24*), we find a 26 percent increase in the concentration of CO_2 from 1850 to 1983. A corresponding increase in the average growth rate of high-altitude bristlecone and limber pine would be consistent with an increase in CO_2 of this magnitude.

In addition to the direct effects on net photosynthesis that would be expected at high altitudes because of increased assimilation rates, increasing CO_2 might have longer term effects on radial growth by influencing plant growth and development, anatomical features, and flowering and fruiting patterns (*25*). For example, in bristlecone and limber pine the number of needle primordia and the rate of needle elongation might be positively influenced by CO_2, leading to large long-term gains in exposed photosynthetic surface and in biomass that could reinforce the direct effects of CO_2 (*26*).

Although high-altitude subalpine forests constitute only a small fraction of the earth's standing biomass, increased CO_2 uptake and storage could now be occurring in these habitats. This could modify projected future increases in atmospheric CO_2. Estimates of the "beta factor" (*2*) in some global carbon-balance models reflecting growth enhancement by elevated CO_2 concentrations may now need to be reconsidered.

Our findings also have important implications for paleoclimatic reconstruc-

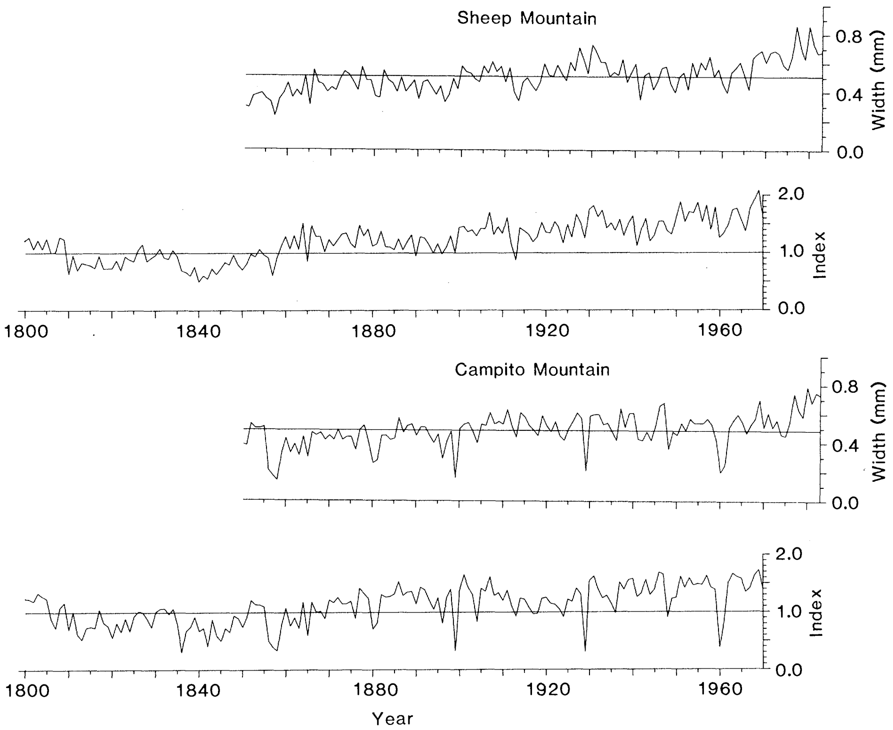

Fig. 2. Bristlecone pine growth records, White Mountains, California. Width index series for 1800 to 1970 are supplemented by average ring width data from recent sampling (*14*). Growth rates increased from 0.34 to 0.70 mm/year (106 percent) between 1850 to 1859 and 1974 to 1983 at the Sheep Mountain site and from 0.37 to 0.64 mm/year (73 percent) during the same interval at the Campito Mountain site.

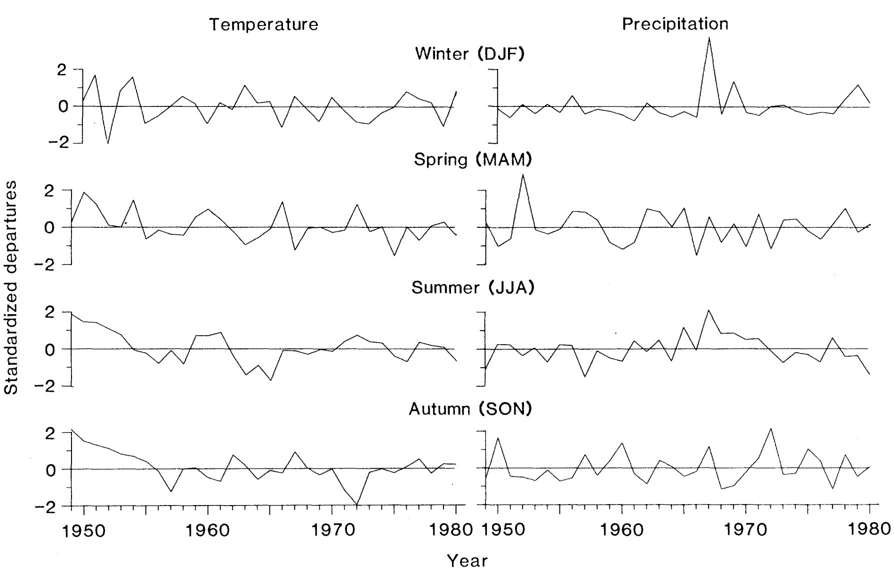

Fig. 3. Seasonal climatic data, White Mountains, California, 1949 to 1980. The data are seasonally averaged monthly mean daily average temperatures and total monthly precipitation values. The values in each series were reduced to standard scores or *Z* scores before being combined in order to eliminate the effects of differences in means and variances between the two stations. Only Crooked Creek Station is represented before 1953 and only Barcroft Station after 1977 (*12*).

tions involving certain kinds of tree ring data. Changing atmospheric CO_2 could introduce nonclimatic growth fluctuations that could interfere with calibration of climate and its reconstruction. Techniques like those now applied to remove biological age trends or effects of ecological factors (*27*) would have to be developed to separate such effects from the climate signal in tree ring data. Conversely, the climatic and ecological information in tree rings could be applied to isolate and enhance the apparent CO_2 signal. Such enhanced proxy records of atmospheric CO_2 might be developed at different localities from the beginning of the industrial era.

It will be necessary to determine the geographic extent of the postulated fertilization effect and to test high-altitude growth trends against longer and geographically more representative sets of climatic data. In addition, the effects of changing CO_2 concentrations on productivity, growth, and development of conifers growing under high-altitude conditions should be determined experimentally.

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10. D.A.G. and M.R.R. collected tree ring samples at 3325 m on Mount Jefferson, Toquima Range, Nevada, on 11 August 1981.
11. D.A.G. and M.R.R. collected samples from 13 trees at Campito Mountain (3400 m) and from 15 trees at Sheep Mountain (3500 m) on 31 October 1983.
12. Crooked Creek Station (3094 m) was established in 1948 and discontinued in 1977; Barcroft Station (3801 m) was established in 1953 and discontinued in 1981. Early observations are summarized by N. Pace, D. W. Kiepert, and E. M. Nissen [*Climatological Data Summary for the Crooked Creek Laboratory, 1949–1967, and the Barcroft Laboratory, 1953–1967* (White Mountain Research Station, University of California, Berkeley, 1968)]. Instrument relocation in 1954 may have affected minimum temperatures at the lower station [V. C. LaMarche, Jr., *Quat. Res. (N.Y.)* **3**, 632 (1973)]. From 1955 on, data for these stations were published in *Climatological Data: California* (U.S. Weather Bureau and National Oceanographic and Atmospheric Administration, Washington, D.C.).
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14. Recent growth rate data are presented as simple average ring widths (i) to avoid creating any artificial trends in the critical recent decades which could possibly be introduced by the standardization process normally used to transform ring widths to dimensionless growth indices and (ii) in order that absolute growth rate changes could be calculated. Published indices are presented in original form only to provide basic documentation of growth fluctuations before the beginning of the postulated CO_2 effect. The disparity in units does not affect the comparison of long-term trends in the two sets of data.
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23. This is a consensus value reported by R. Kerr [*Science* **222**, 1107 (1983)]; the range cited is from about 270 ppm (ice core data) to 260 to 276 ppm (tree ring isotope results).
24. This is based on the 1980 Mauna Loa value of 238 ppm given by C. D. Keeling, R. B. Bacastow, and T. P. Whorf [in (*1*), p. 377], adjusted for an annual increase of about 1 ppm.
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26. A further possibility is that there are other morphological, physiological, or metabolic effects of elevated CO_2 that in some way preferentially enhance growth in plants limited to subalpine or other cold habitats and that these effects are operating in addition to the postulated direct fertilization effect.
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28. We thank M. McCarthy for aid in sampling, F. Telewski for helpful discussions, M. Harrington and A. Allen for manuscript preparation, and the National Science Foundation for partial support under grant EAR 8018687.

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Periodic Interfacial Precipitation in Polymer Films

Abstract. *Interfacial precipitation of silver halides in water-swollen polymer films occurred in complex, multilayered patterns if the concentrations of counterdiffusing reactants were unequal or decreased at different rates. Development of the rapidly forming Liesegang rings, which extend the phenomenon of periodic precipitation to the submicrometer range, is attributable to the combined effect of a moving reaction zone and periodic immobilization of colloidal silver halide.*

When solutions of electrolytes in which all convection has been eliminated—for example, $0.01M$ $Pb(NO_3)_2$ and $0.1M$ NaI in 1 percent agar or gelatin gels—are placed side by side in a test tube or petri dish, PbI_2 precipitates on interdiffusion of Pb^{2+} and I^- in the form of separate layers that are parallel to the diffusion front and 0.01 mm to several millimeters thick. This periodic precipitation, known as the Liesegang phenomenon (*1*), has been investigated intensively (*2–4*). During research on interfacial reactions in polymer films (*5*), I was able to produce a similar effect in a much denser matrix, down to 0.1 μm in thickness and with excellent resolution, when silver and halide ions were allowed to diffuse against each other in a water-swollen polyvinyl alcohol (PVA) film.

Two types of experiments were carried out. In the first, heat-sealed pouches of commercial PVA film (thickness, 0.11 mm when dry and 0.18 mm when wet; water content, 57 percent) were filled with silver nitrate solution and immersed in much larger volumes of equimolar sodium halide solutions. Because of their unequal volumes, both solutions were self-diluting at different rates during the reaction, and the ion concentration difference $D = [X^-] - [Ag^+]$ and the ion concentration ratio $R = [X^-]/[Ag^+]$ changed at a rate dependent on the volume difference. In the second type of experiment, water-swollen PVA film was used to separate equal volumes of anion and cation solutions in a diffusion cell. This allowed D and R to be kept constant or to be changed at any rate desired by diluting one compartment.

Precipitation began to show in the films within seconds. Reactions were terminated by emptying the pouches or cells and rinsing the films in distilled water for 1 hour. The films were then dried at 50°C in a vacuum. Cross sections were viewed through a microscope in both the dry and water-swollen states.

In the pouch-forming PVA films all silver halides precipitated in a complex, multilayered pattern (Fig. 1). Usually a strong, primary band of precipitate formed first, closer to the surface contacting the halide solution but separated from it by a precipitate-free zone. Ex-