The δ^{13} C of tree rings in full-bark and strip-bark bristlecone pine trees in the White Mountains of California

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Abstract

Dendrochronological work at Sheep Mountain in the White Mountains, CA has demonstrated that bristlecone pine trees in two forms, full-bark and strip-bark, have experienced different cambial growth rates over the past century or longer. The stripbark trees showed a greater growth increase than the full-bark ones. A calculation of the plant water-use efficiency (W) in response to anthropogenic CO_2 released into the atmosphere shows that W of trees in both forms has increased for the past 200 years. However, there is no significant difference between the two tree forms in the rate of increase in W. This implies at least two possibilities with respect to the CO_2 fertilization effect. First, the biomass in both tree forms might have increased, but carbon distribution among different parts of a tree was different. Second, the biomass may increase without causing any corresponding change in the plant water-use efficiency.

Keywords: biomass, carbon, fertilization, isotope, tree ring, water use efficiency

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Introduction

To account for the missing carbon sink that has taken up about one third of anthropogenic carbon dioxide released to the atmosphere, a large amount of research has been generated to study CO2 fertilization, the effect of enhanced growth of terrestrial biosphere in response to increasing atmospheric CO₂ concentration (e.g. Mooney et al. 1991; Beerling & Woodward 1993; Friedlingstein et al. 1995; Kheshgi et al. 1996; Luo et al. 1996; and references therein). Experimental work has strongly demonstrated the positive response of photosynthesis and plant water use efficiency to increasing atmospheric CO₂ concentration (e.g. Strain & Cure 1985; Bazzaz 1990; Mooney et al. 1991; Idso 1992; Körner & Arnone 1992; Norby et al. 1992; Polley et al. 1993 ; Wullschleger et al. 1995) and the negative response of stomatal conductance of plant leaves (Woodward 1987; Beerling & Woodward 1993; Van de Water et al. 1994). For example, by studying a number of C3 and C4 species, Polley et al. (1993) showed that both plant water-use efficiency and biomass increased with increasing ambient CO₂ concentration. This led to the idea that CO2 fertilization may be evaluated

Correspondence: Kuilian Tang, tel. +1/(603)646-1712, fax: +1/(603)646-3922, e-mail Kuilian.Tang@Dartmouth.edu by measuring plant water-use efficiency (W). Recently, Feng (1998a) calculated the change in W for some sites over the past 100–200 years using carbon isotope treering time series, and pointed out that water-use efficiency of trees in at least some natural forests indeed increased during the studied time periods. There is little direct evidence for the response of biomass in natural forests to the release of anthropogenic CO_2 into the atmosphere (LaMarche *et al.* 1984; and Graybill & Idso 1993). We also have no knowledge about the relationship between a change in plant water-use efficiency and changes in rate of accumulation of biomass in natural forests.

Using tree-ring width measurements, Graybill & Idso (1993) studied growth rates of bristlecone pine trees (*Pinus longaeva*) on Sheep Mountain in the White Mountains, California. Sheep Mountain, with an elevation of about 3400–4000 m, is the upper treeline for bristlecone pine in this area. At this site, the trunk of a young bristlecone pine is completely covered with active ring-forming cambium (full-bark), but in an older bristlecone pine the zone of active cambial growth becomes restricted to a narrow band on one side of the trunk (strip-bark). Graybill and Idso found that full-bark and strip-bark trees both experienced an enhanced growth trend over the past



Fig. 1 Bristlecone pine tree-ring index chronologies of full-bark (dashed line) and strip-bark (solid line) growth forms from Sheep Mountain, California (Graybill & Idso 1993).

century or more, but the growth rate increased more for strip-bark than for full-bark trees (Fig. 1). We report the results of a study that intended to test, using carbon isotopes of tree rings, (i) whether the water-use efficiency of bristlecone pine trees at this site has increased, and (ii) whether the magnitude of any increase in W for these two tree forms corresponds to the rate of stem growth (and possibly rate of increase of stored biomass).

Materials and methods

We cored a number of trees of both full-bark and stripbark forms in June 1994, five of which were the same trees studied by Graybill & Idso (1993). Three or four cores of 4.3 mm diameter were drilled from three or four perpendicular directions of each tree. All cores were cross-dated dendrochronologically, but no attempt was made to determine the age of the trees. Four trees (two full-bark and two strip-bark) were analysed for carbon isotopic compositions. Tree cores of each tree were cut by individual rings and segments for the same year were pooled. Ground wood of at most every fifth ring from 1795 to 1993 was extracted for cellulose which was then oxidized into H₂O and CO₂ by combustion with CuO at 850 °C. The ${}^{13}C/{}^{12}C$ ratios were determined with a mass spectrometer and expressed as δ^{13} C values with respect to PDB standard. The analytical uncertainty is < 0.1% (1 σ).

The plant water-use efficiency, W, of C_3 species is defined by Farquhar *et al.* (1989) as the ratio of the net carbon fixed to the total water cost,

$$W = \frac{p_a(1 - p_i/p_a)(1 - \phi_c)}{1.6v(1 + \phi_w)},$$
 (1)

where p_i and p_a are the partial pressures of CO_2 in the intercellular space of leaves and in the atmosphere,

respectively. The parameter ϕ_c is the proportion of the fixed carbon that is lost from the plant (e.g. by respiration), ϕ_w is the unproductive water loss (e.g. water lost at night if stomata are not completely closed) as a proportion of productive water use, and v is the difference between water vapour pressure in the intercellular spaces, e_i, and in the atmosphere, e_a, i.e.

$$v = e_i - e_a. \tag{2}$$

Using (1) we can determine how W varies with changing CO_2 concentration in the atmosphere. For now, assume that only p_a and the p_i/p_a vary with time (this assumption will be discussed later), then from (1),

$$\frac{dW}{dt} = \frac{(1 - p_i/p_a)(1 - \phi_c)}{1.6\nu(1 + \phi_w)} \frac{dp_a}{dt} - \frac{p_a(1 - \phi_c)}{1.6\nu(1 + \nu_w)} \frac{d(P_i/p_a)}{dt}.$$
(3)

Dividing (3) by (1), the relative change in W can be expressed as:

$$\frac{1}{W}\frac{dW}{dt} = \frac{1}{p_{a}}\frac{dp_{a}}{dt} - \frac{1}{1-p_{i}P_{a}}\frac{d(p_{i}/p_{a})}{dt}.$$
 (4)

The first term on the right-hand side of (4) can be obtained from the CO₂ concentration record of the atmosphere (Keeling & Whorf 1994, 1996). Figure 2(a) shows the data and the regression curve, and p_a at sea level may be numerically expressed as (Feng 1998b),

$$p_a = 277.78 + 1.350 \exp(0.01572(t - 1740)), \tag{5}$$

where *t* is time in year AD. It is not necessary to correct for elevation, because $(1/p_a)dp_a/dt$ is independent of elevation.

The second term on the right-hand side of (4) can be calculated from the carbon isotope record of tree rings, $\delta^{13}C_{\text{plant}}$, and the carbon isotopic values of the

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Fig. 2 Observations (see references in the text) and regression (Feng 1998b) of the CO_2 concentration (a) and the $\delta^{13}C$ (b) of the atmosphere.

atmospheric CO₂, $\delta^{13}C_{airr}$ using the following equation (Farquhar *et al.* 1982):

$$\delta^{13}C_{\text{plant}} = \delta^{13}C_{\text{air}} - a - (b - a) p_i/p_a$$
(6)

or

$$p_i/p_a = \frac{\delta^{13}C_{plant} - \delta^{13}C_{air} + a}{-(b - a)},$$
(7)

where a (= 4.4) and b (= 29) are constants that characterize the isotopic fractionation of diffusion of CO₂ from the atmosphere into the intercellular space of leaves, and the isotopic discrimination against ¹³CO₂ by carbon fixation, respectively. In (6), $\delta^{13}C_{\text{plant}}$ is the carbon isotopic composition of whole-tissue leaves. Woody materials of a tree are often about 2–4 per mil higher in $\delta^{13}C$ than the leaves (Leavitt & Long 1982, Francey *et al.* 1985). Using $\delta^{13}C$ values of tree rings as $\delta^{13}C_{\text{plant}}$ in (6) would cause some difference in the calculated change of W, but the main feature of the variation in W is preserved and so does not affect our interpretation (Feng 1998a).

Direct measurements of the atmospheric δ^{13} C, δ^{13} C_{atm}, are available for 1956, 1957 (Keeling 1958, 1961; Keeling *et al.* 1989) and between 1978 and 1988 (Keeling *et al.*

1989). The δ^{13} C values of CO₂ separated from air bubbles in ice samples provide a δ^{13} C_{atm} record between 1744 and 1953 (Friedli *et al.* 1986). The nonlinear regression curve (Fig. 2b) for the δ^{13} C of CO₂ in the atmosphere,

 $\delta^{13}C_{atm} = -\ 6.429 - 0.0060 exp(0.0217(t\ -\ 1740)) \eqno(8)$ is used.

In order to use (7), we assume that $\delta^{13}C_{air}$ equals $\delta^{13}C_{atm}$. This means that the CO₂ in the open atmosphere is the sole source for the carbon fixation of the trees considered and the contribution of respired CO₂ for assimilation is ignored. This is justified by the fact that the study site is in an arid, alpine environment where the vegetation is sparse and the soil is thin (Feng & Epstein 1995; Feng 1998b).

Results

Given (5), (7), and (8), we only need a proper time series of $\delta^{13}C_{\text{plant}}$ to calculate the change in water use efficiency using (4).

The results of carbon isotopic analyses are shown in Table 1 and Fig. 3. It is well known that δ^{13} C is a function of precipitation and light intensity (Feng & Epstein 1995). However, we are interested only in its dependency on the CO₂ concentration of the atmosphere. To separate the atmospheric CO₂ signal from the climatic noise, we assume that the variation of δ^{13} C with CO₂ concentration is long-term and of low frequency, while climatic and other environmental factors contribute only to high frequency fluctuations in a δ^{13} C tree-ring series. This assumption has been shown to be essentially valid for this site (Feng & Epstein 1995; Feng 1998b).

The superposition of high frequency with low-frequency variations can be easily identified from the $\delta^{13}C$ time series in Fig. 3. The long-term trends mimic the trend of $\delta^{13}C_{atm}$ (Fig. 2b) and form a mirror image compared with the CO₂ concentration of the atmosphere (Fig. 2a). We consider that the trends of carbon isotopes of tree rings contain the signal of atmospheric conditions for the past 200 years. The highfrequency variations of δ^{13} C of tree rings for trees in an arid environment often correlate with the amount of annual precipitation. Feng & Epstein (1995) showed that, in southern California, precipitation during one rainy reason can affect tree growth for the next 1-3 growing seasons. They also showed that for a bristlecone pine of the White Mountains, California the best correlation between δ^{13} C and ring width (both of which are sensitive to precipitation) is found using a 15-year running average of both records. In this study, the high frequency variations of the four trees correlate in general with each other (Fig. 4), indicating that common variables (climate) controlled the carbon isotopic variations over an approximately decadal time-scale. Therefore, we removed the high-frequency

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| Year | Strip-Bark Trees | | Full-Bark Trees | |
|------|------------------|---------|-----------------|--------|
| | SM-83158 | SM83162 | SM9544 | SM9184 |
| 1795 | -18.17 | -19.47 | -18.88 | -18.95 |
| 1800 | -18.58 | -19.59 | -18.69 | -18.92 |
| 1805 | -18.46 | -19.53 | -18.71 | -19.02 |
| 1810 | -18.16 | -19.90 | -19.17 | -19.68 |
| 1815 | -18.17 | -19.42 | -18.44 | -19.13 |
| 1820 | -18.09 | -19.69 | -18.36 | -19.23 |
| 1825 | -18.24 | -19.26 | -18.14 | -19.31 |
| 1830 | -18.70 | -20.11 | -18.68 | -19.33 |
| 1835 | -18.19 | -19.19 | -18.30 | -18.93 |
| 1840 | -18.74 | -19.79 | -18.96 | |
| 1845 | -19.21 | -19.38 | -18.99 | -19.45 |
| 1850 | -19.00 | -19.03 | -19.03 | -18.98 |
| 1855 | -18.35 | -18.41 | -18.88 | -18.85 |
| 1860 | -18.82 | -19.42 | -19.27 | -19.78 |
| 1865 | -18.62 | -19.70 | -19.31 | -19.52 |
| 1870 | -19.06 | -19.68 | -19.47 | -19.85 |
| 1875 | -19.20 | -19.57 | -19.10 | -19.30 |
| 1880 | -18.71 | -19.04 | -18.75 | -19.71 |
| 1885 | -19.00 | -19.52 | -19.07 | -19.93 |
| 1890 | | -20.11 | -19.91 | -20.20 |
| 1895 | -19.04 | -19.95 | -18.91 | -19.97 |
| 1900 | -19.45 | -19.90 | -18.88 | -19.64 |
| 1905 | -19.34 | -20.14 | -18.58 | -19.29 |
| 1910 | -19.31 | -20.55 | -18.99 | -19.98 |
| 1915 | -18.99 | -20.20 | -19.39 | -20.09 |
| 1920 | -19.31 | -20.26 | -19.12 | -19.92 |
| 1925 | -19.81 | -20.98 | -19.92 | -20.06 |
| 1930 | -19.12 | -20.25 | -19.60 | -20.07 |
| 1935 | -19.29 | -19.65 | -19.80 | -20.20 |
| 1940 | -19.36 | -20.13 | -19.98 | -20.13 |
| 1945 | -20.11 | -20.77 | -20.64 | -20.74 |
| 1950 | -19.34 | -20.06 | -19.85 | -20.05 |
| 1955 | -19.92 | -20.89 | -19.81 | -19.96 |
| 1960 | -19.74 | -19.88 | -19.59 | -19.50 |
| 1962 | -20.29 | | | -20.24 |
| 1965 | -20.69 | -21.60 | -20.51 | -20.80 |
| 1970 | -20.49 | -21.50 | -20.38 | -20.65 |
| 1973 | -20.70 | | | -20.65 |
| 1975 | -20.02 | -21.77 | -20.60 | -19.63 |
| 1980 | -20.73 | -21.95 | -20.99 | -20.69 |
| 1983 | -21.33 | | | -21.49 |
| 1985 | -20.92 | -22.07 | -21.56 | -20.93 |
| 1988 | -20.84 | | • • | -21.09 |
| 1990 | -21.30 | -21.86 | -21.73 | -21.30 |
| 1993 | -21.15 | | | -20.71 |

Table 1 δ^{13} C values of tree rings of bristlecone pine trees from Sheep Mountain, White Mountains, California

signals by fitting the δ^{13} C data to a smooth exponential curve, and in doing so we do not significantly alter the low-frequency signal of the atmosphere. We chose an exponential form because it is the form of equations for p_a (eqn 5) and δ^{13} C $_{atm}$ (eqn 8). Regression curves along with the time series are also shown in Fig. 3.

Substituting the time derivatives of (5), (6) and (8) into

(4), the relative rate of change in W can be calculated; results are shown in Fig. 5. The plant water-use efficiency, W, increases when the value of (1/W)dW/dt is positive, and decreases when (1/W)dW/dt is negative. Figure 5 shows that for all trees and for the entire time period studied, (1/W)dW/dt increases, first very gradually from a near zero value to about 0.06%/year in the nineteenth century, and then increasingly rapidly for the most part of the twentieth century. There is no significant difference between full-bark and strip-bark tree forms in the change of W.

Discussion

In the following, we first discuss the influence of sources of uncertainty on the calculations and then discuss implications of the results shown in Fig. 5.

Errors may be introduced when we assume constant physiological and/or environmental conditions for situations which are not truly constant. These include ϕ_{cr} , ϕ_w and v. We stress that because we are interested in long-term variations in *W*, only low-frequency changes of these parameters are of importance for our analysis.

There is very little information on how ϕ_c , ϕ_w and v might have varied over the past 200 years. All three parameters may be functions of climate. The increase in temperature at this site over the past two hundred years is probably around 0.7 °C (Hansen & Lebedeff 1987). There is some suggestion that in California the June to August precipitation increased since the turn of the century, but no significant trend appears in annual precipitation totals (Karl *et al.* 1983). With these small climatic variations, change in ϕ_c and ϕ_w are probably small, but v is more likely to be significant and needs to be examined carefully.

Recall that v is the difference in water vapour pressure between intercellular spaces and the atmosphere (2), and is sensitive to temperature. On Sheep Mountain, the current average temperature for the growing season is about 12 °C (Powell & Klieforth 1984). We assume that the temperature at this site has increased by 1 °C over the past two hundred years. Given that intercellular air spaces are saturated with water vapour, an increase in leaf temperature from 11 to 12 °C would result in a 9% increase in water vapour pressure in intercellular spaces, e_i. It has been shown that an increase in air temperature will also cause an increase in the atmospheric water vapour pressure, ea. Models of changes in atmospheric water vapor pressure for the atmosphere with doubled the levels of the CO₂ concentration show that, for temperature increase of about 3.5 °C, global water vapor pressure would increase by about 20-33% (Trenberth et al. 1987; Hansen et al. 1984). Hence, a 1 °C change in temperature over the past 200 years would likely cause a 6% to 10%

Fig. 3 Carbon isotopic compositions of tree rings for bristlecone pine trees from Sheep Mountain of the White Mountains, CA. The δ^{13} C values were obtained from each tree for at most every fifth ring from 1795 to 1995. The smooth solid lines are modelled curves assuming exponential trends.

Fig. 4 Correlation of high-frequency variations among four bristlecone pine trees. The detrended value of $\delta^{13}C$ represents the difference between the measured $\delta^{13}C$ values of a given ring of a given tree and the value of the exponential trend (see modelled curves in Fig. 3) at that year for the tree.

Fig. 5 The relative rate of change in water-use efficiency (% per year) for the full-bark (solid lines) and strip-bark (dashed lines) bristlecone pine trees on Sheep Mountain of the White Mountains, CA. There is no significant difference in the relative rate of change in W between full-bark and strip-bark forms.





Fig. 6 Comparison of change in water use efficiency determined in this study with those reported in previous studies (Epstein & Krishnamurphy 1990 and Leavitt & Long 1992) on bristlecone pine trees from the White Mountains area.

increase in atmospheric water vapour. As a result, both e_i and e_a might have increased at approximately the same rate. If so, the vapour pressure difference v would have staved more or less constant.

When we compare results of the two types of tree forms, many errors can be ignored. This is because these trees, full-bark or strip-bark, were within a few hundreds meters from one another, and thus grew under the same climatic conditions. All parameters that vary with climate should affect both types of trees identically.

Figure 5 indicates that for all trees analysed, plant water-use efficiency increased with concentration of atmospheric CO_2 increased. This may be related to the increase in the growth rate observed from tree-ring widths by Graybill & Idso (1993) for bristlecone pine on Sheep Mountain and earlier by LaMarche *et al.* (1984) in the White Mountains.

There is no significant difference between full-bark and strip-bark trees in the rate of increase in water-use efficiency. This indicates that the relationship between increase in the rate of cambial growth and in water-use efficiency is complicated. Assuming that an increase in water-use efficiency can produce a corresponding change in biomass for this site, the discrepancy between the same rate of increase in W and different rates of cambial growth for the two different tree forms may reflect a difference in carbon partitioning among different parts of a tree. There have been intensive studies of the response of whole-plant carbon partitioning to elevated CO2 concentration (Hollinger 1987; Norby et al. 1987; Chu et al. 1992; Larigauderie et al. 1994; Rouhier et al. 1994; Vivin et al. 1995). Although the results are controversial, many studies suggested that, at an elevated atmospheric CO2 concentration, an increase in biomass allocation to roots is generally expected (Chu et al. 1992 and references within). To compensate for an increase in leaf photosynthesis, large roots are required for acquiring nutrients

and water. Therefore, biomass ratio of root to shoot (R/S) may increase. By examining juvenile Douglas fir [Pseudotsuga menziesii (Mirb.) Franco] under elevated CO₂ concentrations, Gorissen et al. (1995) showed that the effect of CO₂ on the R/S ratio may depend on the age of a tree. Younger trees seem to translocate relatively more carbon to the roots, resulting in a relative increase in R/S ratio in comparison with older trees. Unfortunately, all these experiments are short-term, 14 months at most. They may not be applicable to physiological adjustment of bristlecone pine trees over periods of 100-200 years. It is possible, however, that the partitioning of biomass between roots and shoots was systematically different for the full-bark than for the strip-bark trees. For young, full-bark trees, to maintain foliage and reproductive growth, much assimilated carbon is allocated to the root system. Older, strip-bark trees may also be doing this to some degree, but they use a substantial fraction of fixed carbon for cambial growth (Graybill & Idso 1993). It would be helpful to do a systematic analysis of stem growth rates for trees of difference ages.

Another possibility is that the relative increase in the photosynthetic rate of strip-bark trees is greater than that of full-bark trees, but such a difference is not related to the adjustment of water-use efficiency. There are no data to evaluate this hypothesis. The set of experiments reported in this paper indicates that neither water-use efficiency nor cambial growth rate can be a sufficient indicator for changes in the biomass of natural forests. However, studies of this sort may provide some information for long-term physiological responds of trees in natural forests to increasing atmospheric CO_2 concentration.

Our results compare well with previously published results. Using carbon isotope data of tree rings from the White mountains area published by Epstein & Krishnamurthy (1990) and Leavitt & Long (1992), we have calculated water use efficiency for these trees and found that the water use efficiency shows the same trends as trees we present in this study (Fig. 6). Most of these trees grew in lower elevations (2800–3500 m) than the trees we studied, but there is no information about whether these trees are in full-bark or strip-bark form.

References

- Bazzaz FA (1990) The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics*, 21, 167–196.
- Beerling DJ, Woodward FI (1993) Ecophysiological responses of plants to global environmental change since the Last Glacial Maximum. *New Phytology*, **125**, 641–648.
- Chu CC, Coleman JS, Mooney HA (1992) Controls of biomass partitioning betweenroots and shoots: Atmospheric CO₂ enrichment and the acquisition and allocation of carbon and nitrogen in wild radish. *Oecologia*, **89**, 580–587.
- Epstein S, Krishnamurthy RV (1990) Environmental information in the isotopic record in trees. *Philosophical Transactions of the Royal Society of London Series A*, **330**, 427.
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology Plant Molecular Biology, 40, 503–537.
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration of leaves. *Australian Journal of Plant Physiology*, 9, 121–137.
- Feng X (1998a) Trends in intrinsic water-use efficiency of natural trees for the past 100–200 years: a response to atmospheric CO₂ concentration. *Geochimica et Cosmochimica Acta*, in press.
- Feng X (1998b) Long-term C_i/C_a responses of trees in Western North America to atmospheric CO₂ concentration derived from carbon isotope chronologies. *Oecologia*, in press.
- Feng X, Epstein S (1995) Carbon isotopes of trees from arid environments and implications for reconstructing atmosphere CO₂ concentration. *Geochimica et Cosmochimica Acta*, **59**, 2599–2608.
- Francey RJ, Gifford RM, Sharkey TD, Weir B (1985) Physiological influences on carbon isotope discrimination in huon pine (Lagarostrobos franklinii). Oecologia, 66, 211–218.
- Friedli H, Lötscher H, Oeschger H, Seigenthaler U, Stauffer B (1986) Ice core record of the ${}^{13}C/{}^{12}C$ ratio of atmospheric CO₂ in the past two centuries, *Nature*, **324**, 237–238.
- Friedlingstein P, Fung I, Holland E, John J, Brasseur G, Erichson D, Schimel D (1995) On the contribution of CO₂ fertilization to the missing biospheric sink. *Global Biogeochemical Cycles*, 9, 541–556.
- Gorissen A, Kuikman PJ, Beek VD (1995) Carbon allocation and water use in juvenile Douglas fir under elevated CO₂. *New Phytology*, **129**, 275–282.
- Graybill DA, Idso SB (1993) Detecting the aerial fertilization effect of atmospheric CO₂ enrichment in tree-ring chronologies. *Global Biogeochemical Cycles*, **7**, 81–95.
- Hansen JE, Lacis A, Rind D, Russel G, Stone P, Fung I, Rudy R, Lerner J (1984) Climate sensitivity: analysis of feedback
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mechanisms. In: *Climate Processes and Climate Sensitivity* (eds Hansen JE, Takahashi T). *Geophysical Monograph*, **29**, .

- Hansen JE, Lebedeff S (1987) Global trends of measured surface air temperature. *Journal of Geophysical Research*, 92, 13, 345–13,372.
- Hollinger DY (1987) Gas exchange and dry matter allocation responses to elevation of atmospheric CO₂ concentration in seedlings of three tree species. *Tree Physiology*, **3**, 193–202 1987.
- Idso KE (1992) Plant responses to rising levels of atmospheric carbon dioxide: A compilation and analysis of the results of a decade of international research into the direct biological effects of atmosphere CO₂ enrichment. Climatol. Pub. Sci.23, Office of Climatology, Arizona State University, Tempe, AZ.
- Karl TR, Metcalf LK, Nicodemus ML, Quayle RG (1983) Historical Climatology Series 6–1. National Climate Data Center, Asheville, NC.
- Keeling CD (1958) The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. *Geochemica Cosmochemica Acta*, **13**, 322–334.
- Keeling CD (1961) The concentration and isotopic abundances of atmospheric carbon dioxide in rural and marine air, *Geochemica Cosmochemica Acta*, 24, 277–298.
- Keeling CD, Bacastow RB, Carter AF, Piter SC, Whorf TP, Heimann M, Mook WG, Roeloffzen H (1989) A threedimensional model of atmospheric CO₂ transport based on observed winds: 1. Analysis of observational data. In: Aspects of Climate Variability in the Pacific and the Western Americas (ed. Peterson DH). Geophysical Monograph, 55, 165–236.
- Keeling CD, Whorf TP (1994) Atmospheric CO₂ records from sites in the SIO air sampling network. In: *Trends '93: A Compendium of Data on Global Change* (eds Boden TA, Kaiser DP, Sepanski RJ, Stoss FW), ORNL/CDIAC-65. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN.
- Keeling CD, Whorf TP (1996) Atmospheric CO₂ records from sites in the SIO air sampling network. In: *Trends: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN.
- Kheshgi HS, Jain AK, Wuebbles DJ (1996) Accounting for the missing carbon-sink with the CO2-fertilization effect. *Climatic Change*, **33**, 31–62.
- Körner C, Arnone JA (1992) Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science*, 257, 1672– 1675.
- LaMarche VC Jr, Graybill DA, Fritts HC, Rose MR (1984) Increasing atmospheric carbon dioxide: Tree ring evidence for growth enhancement in natural vegetation. *Science*, **225**, 1019–1021.
- Larigauderie A, Reynolds JF, Strain BR (1994) Root response to CO₂ enrichment and nitrogen supply in loblolly pine. *Plant* and Soil, 165, 21–32.
- Leavitt SW, Long A (1982) Evidence for ¹³C/¹²C fractionation between tree leaves and wood, *Nature*, **298**, 742–744.
- Leavitt SW, Long A (1992) Altitudinal differences in δ^{13} C of bristlecone pine tree rings. *Naturwissenschaften*, **79**, 178–180.
- Luo Y, Sims DA, Thomas RB, Tissue DT, Ball JT (1996) Sensitivity of leaf photosynthesis to CO₂ concentration is an invariant function for C₃ plants: A test with experimental data and global applications. *Global Biogeochemical Cycles*, **10**, 209–222.

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- Mooney HA, Drake BG, Luxmoore RJ, Oechel WC, Pitelka LF (1991) Predicting ecosystem responses to elevated CO₂ concentrations. *BioScience*, **41**, 96–104.
- Norby RJ, Gunderson CA, Wullschleger SD, O'Neill EG, McCracken MK (1992) Productivity and compensatory responses of yellow-poplar trees in elevated CO₂. Nature, 357, 322–324.
- Norby RJ, O'Neill EG, Hoo WG, Luxmoore RJ (1987) Carbon allocation, root exudaton and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO₂ enrichment. *Tree Physiology*, **3**, 203–210.
- Polley HW, Johnson HB, Marino BD, Mayeux HS (1993) Increase in C3 plant water-use efficiency and biomass over Glacial to present CO₂ concentrations. *Nature*, **361**, 61–64.
- Powell DR, Klieforth HE (1984) Weather and climate. In: Natural History of the White-Info Range, Eastern California (ed. Hall C. A. Jr), pp. 3–24. University of California Press, La Jolla, CA.
- Rouhier H, Billes G, Kohen AE, Mousseau M, Bottner P (1994) Effect of elevated CO₂ on carbon and nitrogen distribution within a tree (*Castanea sativa* Mill.) – soil system. *Plant and Soil.*, **162**, 281–292.

- Strain BR, Cure JD (1985) Direct Effects of Increasing Carbon Dioxide on Vegetation. U.S. Department of Energy, DOE/Er-0238, Washington, D.C.
- Trenberth KEChr, isty JR, Olson JG (1987) Global atmospheric mass, surface pressure and water vapor variations. *Journal of Geophysics Research*, 92, 14,815–14,826.
- Van de Water PK, Leavitt SW, Betancourt JL (1994) Trends in stomatal density and ¹³C/¹²C ratios of Pinus flexilis needles during alst Glacial-Interglacial cycle. *Science*, 264, 293–243.
- Vivin P, Gross P, Aussenac G, Guehl J (1995) Whole-plant CO₂ exchange, carbon partitioning and growth in *Quercus robur* seedlings exposed to elevated CO₂. *Plant Physiological Biochemistry*, 33, 201–211.
- Woodward FI (1987) Stomatal numbers are sensitive to increases in CO₂ from pre-industrial levels. *Nature*, **327**, 617–618.
- Wullschleger SD, Post WM, King AW (1995) On the potential for a CO₂ fertilization effect in forest: Estimates of the biotic growth factor based on 58 controlled-exposure studies. In: *Biotic Feedbacks in the Global Climatic System, Will the Warming Feed the Warming?* (eds Woodwell G., Mackenzie F.), pp. 85– 107. Oxford University Press, New York.