The $\delta^{13}C$ 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 strip-bark 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

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 CO$_2$ fertilization, the effect of enhanced growth of terrestrial biosphere in response to increasing atmospheric CO$_2$ 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 CO$_2$ 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. 1997) 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 CO$_2$ concentration. This led to the idea that CO$_2$ fertilization may be evaluated 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 tree-ring 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...
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 strip-bark 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 $\text{H}_2\text{O}$ and $\text{CO}_2$ by combustion with $\text{CuO}$ at 850 °C. The $13\text{C}/12\text{C}$ ratios were determined with a mass spectrometer and expressed as $^{\delta}13\text{C}$ values with respect to PDB standard. The analytical uncertainty is $0.1\%$ ($1\sigma$).

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,

$$W = \frac{p_a(1 - p_i/p_a)(1 - \phi_e)}{1.6\nu(1 + \phi_w)},$$  \hspace{1cm} (1)

where $p_i$ and $p_a$ are the partial pressures of $\text{CO}_2$ in the intercellular space of leaves and in the atmosphere, respectively. The parameter $\phi_e$ is the proportion of the fixed carbon that is lost from the plant (e.g. by respiration), $\phi_w$ 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 $\nu$ is the difference between water vapour pressure in the intercellular spaces, $e_i$, and in the atmosphere, $e_a$, i.e.

$$\nu = e_i - e_a.$$  \hspace{1.5cm} (2)

Using (1) we can determine how $W$ varies with changing $\text{CO}_2$ 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),

$$\frac{dW}{dt} = \frac{(1 - \phi_e/\phi_w) \frac{dp_a}{dt}}{1.6\nu(1 + \phi_w)} - \frac{p_a(1 - \phi_e)}{1.6\nu(1 + \phi_w)} \frac{d(p_i/p_a)}{dt}.$$  \hspace{1cm} (3)

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

$$\frac{1}{W} \frac{dW}{dt} = \frac{1}{p_a} \frac{dp_a}{dt} - \frac{1}{1 - p_i/p_a} \frac{d(p_i/p_a)}{dt}.$$  \hspace{1cm} (4)

The first term on the right-hand side of (4) can be obtained from the $\text{CO}_2$ 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),

$$p_a = 277.78 + 1.350\exp(0.01572(t - 1740)),$$  \hspace{1cm} (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, $\delta^{13}\text{C}_{\text{plant}}$, and the carbon isotopic values of the

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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).
\[ \delta^{13}C_{\text{plant}} = \delta^{13}C_{\text{air}} - a - (b - a) \frac{p_t}{p_a} \] (6)

or

\[ \frac{p_t}{p_a} = \frac{\delta^{13}C_{\text{plant}} - \delta^{13}C_{\text{air}} + a}{-(b - a)}, \] (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 \( ^{13}\text{CO}_2 \) 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 does not affect our interpretation (Feng 1998a).

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 \( \delta^{13}C \) 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 \( \delta^{13}C \) with CO2 concentration is long-term and of low frequency, while climatic and other environmental factors contribute only to high frequency fluctuations in a \( \delta^{13}C \) 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 \( \delta^{13}C_{\text{atm}} \) (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 high-frequency variations of \( \delta^{13}C \) 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 \( \delta^{13}C \) 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
signals by fitting the δ¹³C 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 \( p_c \) (eqn 5) and \( \delta^{13} \text{C} \text{ atm} \) (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 \( (1/W)\frac{dW}{dt} \) is positive, and decreases when \( (1/W)\frac{dW}{dt} \) is negative. Figure 5 shows that for all trees and for the entire time period studied, \( (1/W)\frac{dW}{dt} \) 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 \( \phi_c \), \( \phi_w \) 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 \( \phi_c \), \( \phi_w \) 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. 1993). With these small climatic variations, change in \( \phi_c \) and \( \phi_w \) 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, \( e_c \). It has been shown that an increase in air temperature will also cause an increase in the atmospheric water vapour pressure, \( e_a \). Models of changes in atmospheric water vapour 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 $\delta^{13}C$ 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.
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 $\nu$ would have stayed 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 CO2 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 CO2 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


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