Climate variation and the stable carbon isotope composition of tree ring cellulose: an intercomparison of *Quercus robur*, *Fagus sylvatica* and *Pinus silvestris*

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ABSTRACT

The relationship between climate parameters and the carbon stable isotope composition, (δ^{13} C), of annual tree ring cellulose is examined for three native British tree species; Common beech (Fagus sylvatica L.), Pedunculate oak (Quercus robur L.) and Scots pine (Pinus sylvestris L.). The last 100 annual tree rings of six trees, two of each species, were cut into slivers and the α -cellulose extracted. Annual δ^{13} C values of each species were averaged to produce three species δ^{13} C chronologies. These were compared with climate parameters from a nearby meteorological station. The carbon stable isotope discrimination (Δ^{13} C) of pine is consistently lower, by approximately 2.5‰, than that of beech and oak. Although the exact cause of this offset cannot be identified, similar differences in carbon isotope ratios have been noted between other gymnosperm and angiosperm species and attributed to inherent physiological differences. As this offset is consistent, once centered around the same mean $\delta^{13}C$ and $\Delta^{13}C$ chronologies from these 3 species can be combined. $\Delta^{13}C$ chronologies of the three species demonstrate strong crosscorrelations in both high and low frequency fluctuations. Low frequency fluctuations, although consistent between species, show no direct climate relationship, and may be linked with physiological responses to increasing CO₂ concentrations. Significant correlations do exist between the high frequency δ^{13} C fluctuations and climate parameters. The high frequency δ^{13} C series of all three species are most significantly correlated with the same two climate parameters and have the same seasonal timing; July-October average maximum temperature and June-September average relative humidity. Pine δ^{13} C is the most responsive species to climate changes and displays the most significant correlations with all the climate parameters studied. However, an average series of all three high frequency species $\delta^{13}C$ series shows the most significant correlations with climate. Assuming these relationships are consistent spatially and temporally, high frequency δ^{13} C chronologies from the three species studied are climatically comparable and can be combined to reconstruct the same climatic information.

1. Introduction

There are relatively few proxy measures of climate change which reconstruct thousand year

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time scales at annual or decadal resolution, even though such resolution is necessary in order to understand well the more complex and subtle climate changes. Indeed, the International Geosphere-Biosphere Programme (IGBP-PAGES) has emphasised a need for such high resolution information about the last 2000 years

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to separate natural climate variability from anthropogenic impacts and provide accurate data for validation of predictive climate models (IGBP, 1990).

The stable isotope composition of annual tree ring cellulose is known to be influenced by climate (Wilson and Grinsted, 1977; Tans and Mook, 1980; Stuiver and Braziunas, 1987; Saurer and Siegenthaler, 1989; Lipp et al., 1991; Hemmann, 1993; Dupouey et al., 1993; White et al., 1994; Robertson et al., 1996; Switsur et al., 1996). Studies that have used this parameter for climate reconstruction have tended to focus on one tree species per reconstruction even though different species have been used successfully to reconstruct climate in different studies. Particular regions and time periods are dominated by specific tree species. To expand the tree ring stable isotope record significantly it is necessary to combine stable isotope chronologies from multiple species. However, it is unclear how isotope chronologies from different tree species can be compared. Here, we examine this problem using the carbon stable isotope ratio $(\delta^{13}C)$ of cellulose in the last 100 annual tree rings of three native British tree species: Common beech (Fagus sylvatica L.), Pedunculate oak (Quercus robur L.), and Scots pine (Pinus silvestris L.). The aim is to establish whether δ^{13} C results from these three species can be used to reconstruct the same climatic information or whether the δ^{13} C signal recorded in different species is forced by different climate variables or seasonal timings and must be regarded individually.

2. Method

The estate of Woburn Abbey, Bedfordshire, England is the site location for this study. The trees sampled are open canopy, planted for estate landscaping purposes, so experience very little inter-tree competition. They are in close proximity (no greater than 3 km apart) and are all over 150 years old. Therefore, any influences of microclimate are kept to a minimum, and the last century of tree rings can be sampled without including juvenile growth (Freyer, 1979). However, the location in central England means the trees may have been exposed to traffic and industrial air pollution, the amount of which cannot be adequately quantified. A 65-year meteorological record from a station within the estate was compared with a longer record (100 years for most parameters, 81 years for relative humidity) from IACR Rothamsted, which is 15 km south of Woburn Abbey. These records are highly correlated (r > 0.9 for most parameters, p < 0.01), and statistical robustness, the longer record was used for analysis with the cellulose δ^{13} C data. All statistics were completed using the Statistical Package for Social Scientists (SPSS), (Norusis, 1993).

Tree coring took place between January and March 1995. Ring-width chronologies were constructed from approximately 20 trees of each species, using 5 mm diameter cores taken at 1.2 m above ground level. Two cores were taken from each oak and pine tree, usually at bearings 0° and 180° . Beech trees proved very difficult to core so were cored once only at the 0° bearing. Two trees from each species were randomly selected. From these, two vertically adjacent 12 mm cores ("isotope" cores) were taken at the 0° bearing and combined to provide sufficient cellulose for isotope analysis.

The last 100 annual rings of the "isotope" cores were sectioned into approximately 40 μ m slivers with a razor blade. Following consideration of results which show that significantly different isotope ratios can exist between early and late wood (Lipp and Trimborn, 1991; Hill et al., 1995; Robertson et al., 1996; Switsur et al., 1996), the late wood from the oak and pine was isolated for analysis. For beech the whole of the annual growth was used because clear identification of early and late wood was not possible.

A 2-stage chemical procedure (Loader et al., 1997) was used to isolate α -cellulose, the most abundant single chemical component of wood. This involved oxidation of lignins using a sodium chlorite and glacial acetic acid solution, followed by hydrolysis of hemicelluloses with aqueous sodium hydroxide. The resultant α -cellulose samples were vacuum dried and 1–2 mg loaded into tin-foil cups for carbon isotope ratio analysis. This was done using a Carlo Erba elemental analyser linked to a dual inlet VG ISOGAS Sira-II mass spectrometer. Isotopic compositions are recorded in parts per thousand (‰) relative to the Vienna Pee-Dee Belemnite (VPDB) standard, (Coplen, 1996), and expressed in delta notation:

$$\delta^{13}$$
C (‰) = (($R_{\text{sample}}/R_{\text{standard}})$ -1)×1000, (1)

where R_{sample} and R_{standard} are the ratios ${}^{13}\text{C}/{}^{12}\text{C}$ of the sample and standard respectively. The overall precision is less than $\pm 0.1\%$.

Each pair of isotope series from the same species have very similar means and standard deviations and could therefore be averaged, without prior standardisation, to produce three species chronologies.

3. Background

Between atmospheric CO₂ and cellulose, carbon stable isotopes undergo significant fractionation in favour of the lighter ¹²C atoms, mainly due to their more rapid diffusion into the leaf and preferential reactivity once at the site of carboxylation. The resultant difference between the δ^{13} C of atmospheric CO₂ and that of tree ring cellulose is approximately 20‰. The two major sources of fractionation are outlined in the following theoretical expression (Farquhar et al., 1982):

$$\delta^{13}C_{pl} = \delta^{13}C_{at} + a (1 - (c_i/c_a)) + b(c_i/c_a),$$
(2)

where pl and at refer to plant and atmosphere, respectively, a is fractionation due to diffusion of CO_2 into the leaves, b is fractionation caused by carboxylation and c_i and c_a represent the intercellular and atmospheric concentrations of CO₂ respectively. Although fractionation by diffusion and carboxylation both discriminate against ¹³C, and make the $\delta^{13}C$ value more negative, an increase in the fractionation of one of these factors occurs at the expense of the other. For example, when stomatal resistance to diffusion approaches its minimum; stomata are fully open and the laminar wind flow boundary layer over the leaf is narrow, c_i/c_a tends to 1 and fractionation approaches the carboxylation maximum $(b \approx -27\%)$. Alternatively, when stomatal resistance to diffusion tends towards its maximum; stomata are nearly closed and the laminar wind flow boundary layer is wide, c_i/c_a tends to 0 and fractionation tends toward the diffusional maximum ($a \approx -4.4\%$). Therefore, the link between climate and the δ^{13} C of tree ring cellulose is mainly through the relative response of c_i and c_a to climatic changes.

It is necessary to take account of changes in

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atmospheric δ^{13} C to differentiate between those changes in cellulose δ^{13} C caused by tree discrimination (Δ^{13} C) in response to climate and environmental changes and those caused by changes in the "base level" of atmospheric CO₂ entering the tree. Early in the 20th century the $\delta^{13} C$ value of atmospheric CO_2 was approximately -6.5%(Friedli et al., 1986) (Fig. 1). However, since the middle of the century, as a result of anthropogenic activity introducing isotopically light CO₂ into the atmosphere, this value has fallen dramatically to $-7.55\pm0.15\%$ in 1980 at Mauna Loa (Friedli et al., 1986) and $-8.5\pm0.25\%$ in 1996 in eastern England (Hemming, unpublished data). The atmospheric δ^{13} C trend generally mirrors the increasing trend in atmospheric CO₂ concentration (Fig. 1). Using the definition of $\delta^{\bar{13}}C$ in equation 1, plant isotopic discrimination is defined by the following equation (Farquhar et al., 1982):

$$\Delta^{13}C = (\delta^{13}C_{s} - \delta^{13}C_{p})/$$
(1+(\delta^{13}C_{s}/1000)), (3)

where $\delta^{13}C_s$ values refer to the $\delta^{13}C$ composition of atmospheric CO₂, (Fig. 1), and $\delta^{13}C_p$ refers to the raw cellulose $\delta^{13}C$ values. Annual resolution atmospheric $\delta^{13}C$ data were determined by taking the yearly values of the 6th order polynomial curve fit of Antarctic ice core and flask-sampled European measurements. Using eq. (2), it should be noted that isotopic discrimination by trees ($\Delta^{13}C$) is positive whereas $\delta^{13}C$ composition is negative.

At present, the Antarctic/European composite record is the most suitable record of atmospheric δ^{13} C available that covers the last 100 years. Clearly, this is not an ideal approximation of the annual atmospheric δ^{13} C in central England. Indeed, the fitted values of the composite atmospheric δ^{13} C record for 1995 and 1996 are approximately 0.5% heavier than average summer atmospheric δ^{13} C values measured in eastern England (100 km east of Woburn Abbey) in 1995 and 1996 (Fig. 1). If the lighter values measured in England represent the bulk air this would suggest our atmospheric $\delta^{13}C$ correction is not accurate for the study site. However, the air samples from England in 1995 and 1996 were taken for a completely different experiment at 1 m and 5 m respectively above ground height from a region of intense crop production. In such a



Fig. 1. Atmospheric CO₂ concentration (circles) and carbon isotope (δ^{13} C) composition (triangles). CO₂ concentration data is from the Siple ice-core, Antarctica; filled circles, 1899–1953 (Friedli et al., 1986), South Pole summer average (April–September) air flask measurements; filled circles, 1957–1988 (Keeling and Whorf, 1996) and Schauinsland, Germany summer average air flask measurements; open circles 1972–1992. δ^{13} C data is from the Siple ice core; filled triangles, 1895–1953 (Friedli et al., 1986), Vermunt, Austria summer average air flask measurements; filled triangles, 1966–1974 (Levin et al., 1994), Schauinsland summer average air flask measurements; filled triangles, 1977–1992 (Levin et al., 1996), and Brooms Barn Research Station, eastern England summer average air flask measurements; open triangles, 1995–1996 (Hemming, unpublished data). A 6th order polynomial fitted to the δ^{13} C data (excluding the eastern England measurements) is assumed to be the general atmospheric δ^{13} C trend over the last 100 years.

location respired CO₂ from plant, soil and organic fertilizers introduces unusually high concentrations of lighter carbon into the atmosphere which may explain the more negative values at this site compared to those of the polynomial trend line fitted through the Antarctic/European composite δ^{13} C record. Until an accurate proxy measure of atmospheric δ^{13} C can be identified the available data are used with caution.

4. Results and discussion

It is clear from the raw δ^{13} C and the Δ^{13} C series, (Figs. 2a, b), that both high and low frequency fluctuations occur synchronously between species. This coherency is confirmed by crosscorrelation analysis of the high frequency δ^{13} C series (Table 1). There is a consistent offset, of approximately -2.5%, between the average Δ^{13} C series of the pine compared to those of the oak and beech. This lower discrimination has been noted in other studies of gymnosperm and angio-

Table 1. Cross-correlation coefficients between the high frequency $\delta^{13}C$ series; all correlations are significant at the p<0.01 level (two tailed)

High frequency δ^{13} C series	Oak	Pine
beech	0.40	0.57
pine	0.43	1.00

sperm species (Leavitt and Newberry, 1992), but the cause is not known and cannot be linked to a single physiological factor. Instead it was attributed to many interacting factors, including; lower mean annual stomatal conductance of gymnosperm due to photosynthesis during the colder times of the year and deeply sunken stomata; and differences in xylem cell and canopy structure which affect leaf water potential and photosynthetic rates. As the offset is consistent it is possible to combine the Δ^{13} C chronologies from these three species by adjusting for this difference. However, statistical regression and correlation analyses



Fig. 2. (a) Raw carbon isotope (δ^{13} C) data of beech, oak and pine, with trends lines fitted using a 30 year Gaussian filter; and (b) carbon isotope discrimination (Δ^{13} C) data, calculated using eq. (1).

consider relative variations, making such absolute adjustments unnecessary.

Climate parameters show no significant long term trends during the last 100 years. There is certainly no trend in climate parameters which corresponds with the prominent increasing $\delta^{13}C$ (decreasing discrimination) trend in the series of all three species between 1930 and 1975 (Fig. 2). However, similar increasing long term trends in tree ring carbon isotope records, at approximately this time, have been noted in several species from Arizona, North Carolina, Wisconsin, Netherlands and USSR, mainly between 1920 and 1960 (Freyer, 1986), also in Pinus sylvestris from Scotland between 1930 and 1970 (Loader, 1995), in Quercus robur from East Anglia between 1930 and 1970 (Field, 1994) and in Pinus sylvestris from Finland between 1910 and 1940 (Jungner and Sonninen, 1995). There is no clear cause for this widespread common carbon isotope signal, which is not directly related to a corresponding long term climate change; furthermore, there are studies that show no trend in tree ring carbon isotopes during this time (Freyer, 1986). The fact that the 1930-1975

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period was one of considerable change in the concentration and isotopic composition of atmospheric CO₂, implies that, either the atmospheric δ^{13} C correction curve adopted is inappropriate during this period, or a link exists between increasing CO₂ concentration and decreasing discrimination. The correction curve is clearly prone to inaccuracies. However, it is unlikely that the difference of ~1.5‰ between the Δ^{13} C values in 1930 and 1975 can be completely explained by errors in the atmospheric δ^{13} C trend which shows a total 1.5‰ decrease during this period.

Regarding the link between discrimination and CO_2 concentration, discrimination has actually been shown to increase in *Quercus robur* leaves exposed to higher CO_2 concentrations (Picon et al., 1996). However, it is unclear how trees maintain an optimal balance between water loss and CO_2 uptake, especially with respect to small CO_2 increases over many years (Mott, 1990). It has been shown that stomatal aperture and density changes display an inverse relationship with CO_2 concentration, (Beerling et al., 1995; Field et al., 1995; Wagner et al., 1996; Van de Water et al.,

1994; Woodward, 1987). A decrease in leaf stomatal apertures in the trees at Woburn Abbey during the 1930–1975 period in response to the rising CO₂ concentration would decrease the flux of CO₂ in to and out of leaves and reduce c_i/c_a (see eq. (2)). This may account for the decreasing trend in discrimination. The extreme dry, hot summer of 1976 may have been responsible for a change in the relationship between CO₂ and Δ^{13} C resulting in the observed change in the Δ^{13} C trend, possibly due to excessive die-back reducing assimilation capacity in the following years.

It must not be forgotten that there are also other factors that became increasingly significant during this period, including pollution and crop fertilization. These may be responsible for the observed Δ^{13} C trend (Freyer, 1979; Martin and Sutherland, 1990). Future comparisons with oxygen and hydrogen stable isotopes from the same trees will provide more information which may indicate the cause of these common longterm trends.

The high frequency δ^{13} C series display significant cross-correlations (Table 1) associated with climatic forcing. Specific climate "marker" years such as 1921, 1933/4, 1976 and 1990, which were exceptionally dry and warm summers in this region, correspond to notably high δ^{13} C values and low discrimination, (Fig. 2), and significant correlations exist between climate parameters and the individual and averaged high frequency $\delta^{13}C$ series (Table 2). Of the three species, the pine shows the most significant correlations with all of the climate parameters examined and has a higher variance (0.60) compared to those of beech (0.42)and oak (0.44), which indicates it is the most responsive of the 3 species to climatic changes. Pine and beech are more highly correlated with

relative humidity and rainfall than oak which may be indicative of the relatively shallow rooting systems of these 2 species, making them more responsive to and dependent on rapid changes in near surface water availability than the oak with its deep tap root.

The months during which the most significant correlations occur between the high frequency δ^{13} C series and climatological parameters vary according to the climate parameter studied, although, as would be anticipated, all occur during the period when trees are photosynthetically most active (June to October). Fig. 3 shows the typical seasonal cycle of correlation between climate, in this instance relative humidity, and high frequency δ^{13} C of all 3 species. It is clear that the timing of the seasonal response of δ^{13} C to climate is also comparable between species.

The high frequency δ^{13} C series of all three species are correlated most significantly with the same two climate parameters; average relative humidity during June–September and average maximum temperature during July–October (Table 2). The relationships between these climate



Fig. 3. Correlation coefficients between the monthly averages of relative humidity and the high frequency δ^{13} C series of beech, oak and pine. Relative humidity data is from 1915 to 1994.

Table 2. Correlation coefficients between specific climate parameters and high frequency $\delta^{13}C$ of the beech, oak and pine series; all correlations are significant at the p < 0.01 level (two tailed)

High frequency $\delta^{13}C$ series	July-October average maximum temperature (°C)	August Palmer drought severity index	June-August average rainfall (mm)	June-September average relative humidity (%)	March-October total sunshine hours	July-September average temperature (°C)
beech	0.52	-0.44	-0.52	-0.62	0.48	0.40
oak pine average	0.51 0.67 0.71	-0.42 -0.62 -0.62	-0.44 -0.65 -0.67	-0.52 -0.67 -0.73	0.42 0.57 0.61	0.49 0.59 0.62

parameters and the $\delta^{13}C$ series are linear. The pine δ^{13} C series has steeper regression slopes with both climate parameters than those of the beech or oak δ^{13} C series. This is in agreement with the observations that the pine δ^{13} C series has a higher variance and more significant correlation with climate parameters than the oak or beech series, and emphasises the relatively more responsive nature of the pine to climate changes. Although Scots pine appears to be the most appropriate of the three species studied here for climate reconstruction, a series composed of the average of the three species high frequency $\delta^{13}C$ series displays more significant correlations with the climate parameters than any of the individual species series, and it, therefore, provides the most accurate climate reconstruction available with these data (Fig. 4).

A strong relationship between δ^{13} C and relative humidity is not a surprise and has been observed in many other studies, including Stuiver and Braziunas, 1987; Saurer and Siegenthaler, 1989; Lipp et al., 1991; Robertson et al., 1996, Switsur et al., 1996. It is well understood, theoretically, for C₃ plants, (White et al., 1994; Figge and White, 1995), through the link between the regulation of stomatal aperture, to prevent excessive transpirational water loss, and the effect these changes have on the ratio of internal to external CO₂ concentration (c_i/c_a), which in turn influences plant δ^{13} C (see eq. (3)). Although statistical relationships have been found with other climate parameters, especially temperature, (Wilson and Grinsted, 1977; Tans and Mook, 1980; Lipp et al., 1991; Hemmann, 1993; Dupouey et al., 1993), such associations may be indirect, as a result of the cross-correlation between these other climate parameters and relative humidity (Schleser, 1995). More isotope studies are required in regions where individual climate parameters are limiting tree growth to examine the role of these different climate parameters on the stable isotope signal recorded in tree rings.

5. Conclusions

The three species; Fagus sylvatica, Quercus robur and Pinus silvestris have similar responses to climatic forcing. The annual timing of the δ^{13} C response to climate is comparable between the three species, although the pine δ^{13} C values are more responsive to changes in all the climate parameters and therefore likely to yield more climate information than studies using just the oak or beech. Average June-September relative humidity and average July-October maximum temperature correlate significantly with high frequency δ^{13} C fluctuations in the cellulose of all three species. However, these correlations are enhanced, and a more accurate climate reconstruction is possible, when an average series is produced from the high frequency series of all three species. This result shows that it is not only possible for



Fig. 4. Reconstructed and actual relative humidity (average June-September). The high frequency $\delta^{13}C$ series is the average of the three species' high frequency $\delta^{13}C$ series. Reconstructed values are obtained using the equation cited on the graph, x=relative humidity and $y = \delta^{13}C \times -1$. $\delta^{13}C$ values are multiplied by -1 to graphically emphasise the similarities.

carbon isotope series from different species to be combined to reconstruct climate parameters, in this case it is an advantage to do so.

There are no clear long term trends in the climate parameters over the 100 years of this study and, although a 30 year Gaussian filter appears to remove non-climatic trends whilst retaining the climatic signal, for this data and during this time period, it would not be possible to reconstruct long term climate changes by simply applying this filtering technique. It is hoped that future examination of oxygen and hydrogen stable isotopes in the same cellulose will allow differentiation of climatically forced δ^{13} C changes from those caused by other influences such as atmospheric CO₂ concentration or δ^{13} C composition variations.

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