

The climate-carbon isotope relationship in tree rings and the significance of site conditions

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(Manuscript received 5 April 1994; in final form 6 September 1994)

ABSTRACT

Considerable complexity exists regarding the relationship between tree ring $\delta^{13}\text{C}$ and climate. We proceed from the theoretically derived and experimentally confirmed finding that the relative humidity of the atmosphere but also the soil water content can influence the stomatal opening of plant leaves and consequently the $\delta^{13}\text{C}$ of photosynthetically fixed carbon. Therefore, the potential to reconstruct humidity variations by $\delta^{13}\text{C}$ in tree rings should depend on the water conditions at the site where the trees are growing. We analysed $\delta^{13}\text{C}$ series (3-year ring samples) of cellulose of beech trees (*Fagus sylvatica*) covering the time period from 1934 to 1989 for 3 sites in Switzerland: a relatively dry and a humid site close together and another dry site 30 km distant. The $\delta^{13}\text{C}$ series from the two dry sites are closely interrelated and are inversely correlated to the total precipitation amount of the months May + June + July. This is most expressed for first differences, i.e., differences of consecutive values, while the long-term trends are more strongly influenced by biological effects. A multivariate analysis shows that at the dry sites, $\delta^{13}\text{C}$ is relatively high for dry/warm summers and low for cool/wet summers. The respective correlations for the humid site are less distinct. In addition, we compared average $\delta^{13}\text{C}$ values for beech, pine and spruce trees from sites differing in soil moisture conditions. For all species we found that the drier the sites the more positive the tree $\delta^{13}\text{C}$ values are. We conclude that at relatively dry sites in temperate-moist climatic conditions, short-term precipitation variations can be reconstructed by $\delta^{13}\text{C}$ measurement on tree rings of beech and probably also of the conifers pine and spruce.

1. Introduction

The $^{13}\text{C}/^{12}\text{C}$ isotope ratio in plant matter is determined by the $\delta^{13}\text{C}$ of atmospheric CO_2 and by a number of environmental factors like, e.g., soil moisture, temperature, solar irradiation and nutrient availability (Francey and Farquhar, 1982). The latter factors have an influence on the isotopic composition via their effect on the intracellular CO_2 concentration which in turn influences the isotopic fractionation between

atmospheric CO_2 and plant matter (see Section 2). Therefore an environmental signal is recorded in the $\delta^{13}\text{C}$ of tree rings. Interpretation of this signal in terms of climatic or environmental variables is hampered because the processes involved are complex and not fully understood.

In studies relating the $\delta^{13}\text{C}$ of tree rings to climate, correlations with temperature have often been sought for and also been found, but there is no consensus about the magnitude of the temperature coefficient. Farmer (1979) and Grinstead et al. (1979) reported high negative coefficients of $-0.7\text{‰}/^\circ\text{C}$ and less, whereas in most other studies positive coefficients in the range from $0.18\text{‰}/^\circ\text{C}$ (Freyer and Belacy, 1983) to $0.48\text{‰}/^\circ\text{C}$ (Tans and Mook, 1980) have been found.

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Lipp et al. (1991) measured a $\delta^{13}\text{C}$ record of fir during the period from AD 1004 to AD 1980 and Stuiver and Braziunas (1987) presented a 2000-yr-long $\delta^{13}\text{C}$ record from coniferous trees. They interpreted their records mainly in terms of temperature using coefficients of $0.33^\circ/\text{‰}/^\circ\text{C}$ and $0.32^\circ/\text{‰}/^\circ\text{C}$, respectively, but they also found significant negative correlations with precipitation amount and with relative humidity during their calibration period. From a theoretical point of view (see Section 2) humidity conditions are expected to be an important factor influencing $\delta^{13}\text{C}$ variations in tree rings, because water stress can induce stomatal closure and thus increase the $\delta^{13}\text{C}$ of the incorporated carbon. According to this simple model, both low soil moisture content and low air humidity influence $\delta^{13}\text{C}$, though the reaction of plants on these two stress factors is not the same. In fact some recent $\delta^{13}\text{C}$ tree ring studies emphasise the prime influence of water conditions: Saurer and Siegenthaler (1989) find a strong influence of relative air humidity from April to September for beech trees ($r = -0.74$, $n = 18$). The results of Dupouey et al. (1993), also for beech trees, point to the importance of July soil water content ($r = -0.77$, $n = 40$), which the authors calculated from a bioclimatic water balance model. Leavitt and Long (1988) found a correlation of $\delta^{13}\text{C}$ with a drought index for pine chronologies in the southwestern United States, significant with a confidence level of 95% for 5 out of 12 sites.

We make the hypothesis that a major reason for the problems in interpreting $\delta^{13}\text{C}$ variations in tree rings is the neglected influence of site conditions. As is well-known from classical dendroclimatology using ring width or density, the potential to reconstruct climate strongly depends on site characteristics (Schweingruber, 1988). It has been found that palaeoclimatic information can mainly be gained at sites where growth is influenced by one dominant factor, like, e.g., precipitation in arid regions. In temperate-moist regions, not much variance of classical tree ring parameters can be explained by climate (Z'Graggen, 1992). It seems plausible that site conditions play an important role also for the environmental signal in carbon isotopes. From the above discussion it becomes clear that the moisture conditions of a site should be considered: The stomata of leaves have to react more frequently to a water deficit at a relatively dry site than at a humid site. Accordingly, carbon

isotope variations should record humidity variations better on a dry site than on a humid site. To test the validity of this hypothesis, we compare here the $\delta^{13}\text{C}$ tree ring series from a dry site (Saurer and Siegenthaler, 1989) to a $\delta^{13}\text{C}$ series from a nearby humid site, as well as to a series from another dry site in a distance of 30 kilometres to test the reproducibility on regional scale. These sites are situated in Switzerland and climate is temperate-moist.

As a complementary approach to investigate site influences we determined average site $\delta^{13}\text{C}$ values for beech, pine and spruce for sites differing in their soil moisture conditions. With this second experiment we wanted to find out if a similar dependence of $\delta^{13}\text{C}$ on humidity conditions as for beech also exists for conifers. Further it is interesting to see if there are systematic differences in $\delta^{13}\text{C}$ between species. If so this would question the lumping of $\delta^{13}\text{C}$ results from different species as has sometimes been made (Stuiver and Braziunas, 1987).

2. Theory

The $^{13}\text{C}/^{12}\text{C}$ discrimination between atmospheric CO_2 and plant material is $\delta_a - \delta_p$, where δ_a refers to atmospheric CO_2 and δ_p to photosynthetically fixed carbon. Farquhar et al. (1982) derived an expression for C_3 -plants for the dependency of this discrimination on c_i/c_a , the ratio of the CO_2 concentration in the intercellular air spaces (c_i) to the CO_2 concentration in the atmosphere (c_a), yielding:

$$\delta_p \cong \delta_a - a - (b - a) c_i/c_a, \quad (1)$$

whereby a is the discrimination by the diffusion through the stomatal pores ($a = 4.4^\circ/\text{‰}$, Lehmann, 1987) and b is the discrimination by the ribulose-biphosphate carboxylase-oxygenase ($b \approx 27^\circ/\text{‰}$), the enzyme which catalyses carbon-fixation. c_i and therefore δ_p are determined by the ratio of the diffusion resistance to the carboxylation resistance to photosynthesis. The interaction of factors which determine c_i is complex. A change in environmental conditions may have no effect on c_i and δ_p if the resulting shifts in stomatal and carboxylation resistance are in the same direction and of similar strength. For instance, no generally valid statement about the effect of a temperature change on

c_i can be made (Wong et al., 1979). On the other hand, water stress tends to reduce the stomatal conductance more strongly than the photosynthetic capacity, thereby decreasing c_i and leading to more positive $\delta^{13}\text{C}$ values of the incorporated carbon. Applying this model to tree rings it should be possible to reconstruct water stress variations. Beech trees for instance can be expected to be well suited for such a study, because their stomatal apparatus is known to be sensitive to humidity conditions (Schulze, 1970).

3. Material and methods

The 3 investigated sites are situated in the Swiss Central Plateau (see Fig. 1). Climate is temperate-moist with a mean annual precipitation amount of ca. 1000 mm and a mean annual temperature of ca. 9°C. Two sites are situated close together at the southeastern border of the Jura mountain chain, near Twann (600 m a.s.l.): a dry site (Twann Dry = TWD) on a southeastern slope and a humid site (Twann Humid = TWH) in a nearby gorge. The terms dry and humid refer to differences in the plant community, in soil characteristics and in bioclimate (Z'Graggen, 1992). The two sites were chosen to maximize the difference in moisture conditions. At the dry site, the growth of the beech

trees is limited by the poor water supply (a few steps down the slope they can not survive and are replaced by oak trees) whereas at the humid site water is abundant (and the trees are much larger). Another relatively dry site (Hub Dry = HUD) was selected in a distance of approximately 30 kilometers (700 m a.s.l.). 4 beech trees (*Fagus sylvatica*) per site were selected. At each site care was taken to use only trees which apparently had similar growth conditions (adult trees of similar height and exposition to light, stemming from an area smaller than 50 m × 50 m). 2 cores per tree from opposite sides of the stem were taken and cut into pieces including three tree rings each. The three rings were lumped together to yield enough material and to reduce processing time. At the beginning of the investigated period (1934) no tree was younger than 30 years. This is important because a so-called "juvenile effect", an increasing $\delta^{13}\text{C}$ trend with time, has sometimes been observed for young trees (Francey and Farquhar, 1982; Freyer, 1979). Whereas individual $\delta^{13}\text{C}$ series were measured for every tree for the TWD and the TWH site, the samples from the four trees of the HUD site were pooled before the $\delta^{13}\text{C}$ analysis. Ring width was measured on separate cores.

For the second kind of study, 5 sites were selected in a west-east valley of the Jura near Court (see Fig. 1) which differ greatly in soil moisture conditions. The sites are situated on a transverse axis to the valley (i.e., two sites on the southern slope, one in the valley-bottom and two on the northern slope). Cores from beech (*Fagus sylvatica*), pine (*Pinus silvestris*) and spruce (*Picea abies*) trees (6 trees from each species per site) were taken. Not all species are represented on all sites (Fig. 6). From each tree a lumped sample covering the last 50 tree rings was taken for $\delta^{13}\text{C}$ analysis to get a mean tree value.

Cellulose was extracted from the wood, the samples were combusted to CO_2 and $\delta^{13}\text{C}$ was mass-spectrometrically measured (Brenninkmeijer, 1983). Ecologically defined humidity indices were determined for TWD, TWH and all sites in Court (Aellen, pers. comm.). The principle of the method is that every plant is assigned a moisture index according to its appearance in different habitats and the plant community as a whole defines the moisture index of the site (Ellenberg, 1974). We can not exclude other factors than moisture conditions to vary systematically between sites (e.g.,

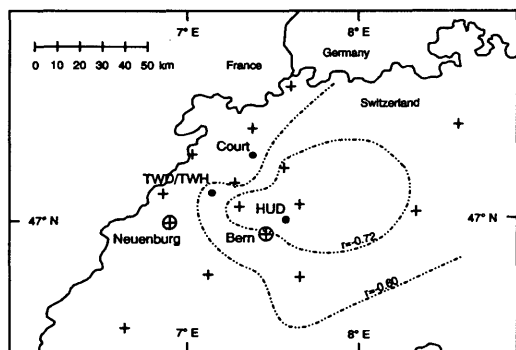


Fig. 1. Map of Switzerland with the tree sites (●) and the precipitation stations (+) that were used for calculations and the weather stations Bern and Neuenburg (⊕). The dashed lines are the isopleths of the correlation coefficient $r = -0.72$ ($p < 0.001$) and $r = -0.60$ ($p < 0.01$) for the correlation of the $\delta^{13}\text{C}$ series "Hub Dry" = HUD with the precipitation amount May + June + July (for first differences).

light, pollution or nutrient status). Yet, the careful selection of sites and trees should minimize this possible interference.

4. Results and discussion

4.1. Tree ring study

The $\delta^{13}\text{C}$ curves of cellulose of individual beech trees are shown in Fig. 2 for the site "Twann Dry" = TWD. There is a good agreement between the four trees in certain periods of the record, for instance from 1947 to 1959, whereas the curves strongly differ in other time periods. To give a statistical measure of the similarity of the $\delta^{13}\text{C}$ curves, we calculated the variance common to all series according a procedure for analysis of variance (Fritts, 1976). We obtain a value of 31 %, i.e., 31 % of the variability of the $\delta^{13}\text{C}$ data can be attributed to a macroclimatic influence. The remaining 69 % is "noise" due to factors which influence the $\delta^{13}\text{C}$ in different trees differently. For the site "TW Humid" = TWH, the $\delta^{13}\text{C}$ curves of the four trees show poor agreement with each other and the common variance is 16 % only (Fig. 3). We therefore find that the common variance of the $\delta^{13}\text{C}$ curves of different trees is higher at the dry site than at the humid site. For comparison it is interesting to note that a similar result on the influence of site conditions has also been found for tree ring width (Schweingruber, 1988). Regarding $\delta^{13}\text{C}$, Leavitt and Long (1984) recommended to use at least four trees to develop time series representative of the whole site, a study

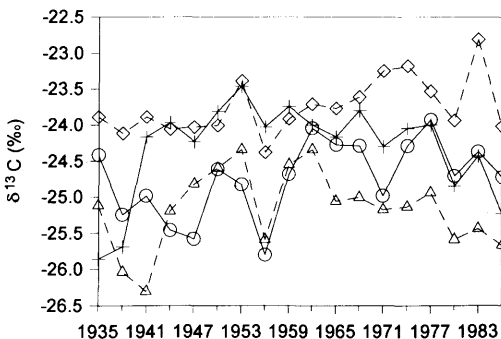


Fig. 2. $\delta^{13}\text{C}$ values of individual trees from the site "Twann Dry" = TWD. Each data point is the result of a sample consisting of 3 successive rings.

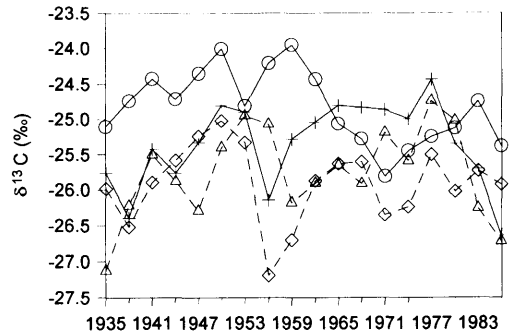


Fig. 3. $\delta^{13}\text{C}$ values of individual trees from the site "Twann humid" = TWH.

carried out in Arizona with pine trees. We also emphasise that for obtaining a representative series, the results from several trees must be averaged. Based on the above findings, we conclude that four trees are a minimum number in temperate-moist climate for beech and may not be enough for sites with humid soil conditions.

In Fig. 4 time series of the mean $\delta^{13}\text{C}$ curves (averages of four trees) are shown for the sites TWD, TWH and "Hub Dry" = HUD. The $\delta^{13}\text{C}$

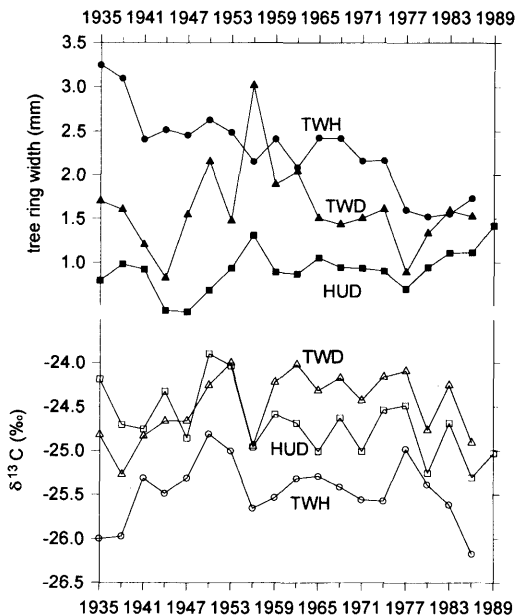


Fig. 4. $\delta^{13}\text{C}$ (below) and ring width values from the sites "Twann Dry" = TWD (Δ), "Twann humid" = TWH (\circ) and "Hub Dry" = HUD (\square). Each of the series represents the mean of four trees.

series from the distant (dry) sites TWD and HUD seem to exhibit closely related variations. Yet the correlation is not significant because of the existence of divergent long-term trends (the significance level is set at $p = 0.05$ in the following if not indicated otherwise). Whereas the HUD series displays a steady decrease with time of 0.12‰ per decade, the $\delta^{13}\text{C}$ values of the TWD series increases for about the first twenty years of the investigated period. No distinct long-term trend is apparent for the TWH site. Thus, in none of the three $\delta^{13}\text{C}$ tree ring series the $\delta^{13}\text{C}$ decrease of about 1‰ in atmospheric CO_2 in the last 50 years (Friedli et al., 1986) is fully reflected. This finding contrasts with several studies showing a distinct decrease (reviewed in Leavitt and Lara, 1994). The depletion of ^{13}C in the atmospheric CO_2 might be masked by an aging trend of the trees in this study. When the $\delta^{13}\text{C}$ tree ring series are detrended by taking first differences of the original $\delta^{13}\text{C}$ values, i.e., differences of consecutive values, a high correlation between the two dry sites results ($r = 0.84$, $p < 0.001$, Fig. 5). The $\delta^{13}\text{C}$ series from

the humid site TWH is less well correlated with the two other sites. When considering first differences a significant correlation results with the nearby dry site TWD ($r = 0.62$, $p < 0.01$), but no significant correlation with the HUD site. Interestingly, one tree from the humid site TWH is well correlated with all trees from the TWD site (Figs. 2, 3). This indicates that (despite the careful tree selection) the trees from a site not necessarily had identical growth conditions.

The strong similarities between the high-frequency $\delta^{13}\text{C}$ variations of the dry sites TWD and HUD, which are 30 km distant from each other, suggest a common cause, most probably climate. On the other hand, we find that this external signal is obscured at the humid site. In the following we will see if this result can be confirmed by direct comparison with climatic data. For the correlation analysis we will take the mean site $\delta^{13}\text{C}$ series of TWD, TWH and HUD (denoted as original $\delta^{13}\text{C}$ values) and first differences of these values. The results of the analysis below are not significantly altered when the data are corrected for the fossil fuel CO_2 input and detrended afterwards. We therefore did not make these corrections in order not to make too many manipulations of the data and because the effect is negligible for the first difference series. Correlation analysis was performed with precipitation amount, temperature and relative humidity. Groups of mean climate data of 1- to 12-month length were calculated for the period from 1934 to 1990. For instance, the series with four months includes the periods from January to April, February to May and so on. The corresponding 3-year-means of these climate data sets were then correlated to the $\delta^{13}\text{C}$ data from TWD, TWH and HUD. The best correlations resulted with mean climate of the months May, June and July, and therefore the main focus of the discussion will be this period.

In Table 1, correlation coefficients and, where these are significant, also regression coefficients are given between $\delta^{13}\text{C}$, meteorological data from Bern and tree ring width for both original values and first differences. The strongest (negative) correlations result when relating differences of precipitation amount to $\delta^{13}\text{C}$ differences for the dry sites TWD and HUD and to a lesser degree also for the humid site TWH. These correlations are also significant, but less distinctly, for original values instead of differences. The slopes

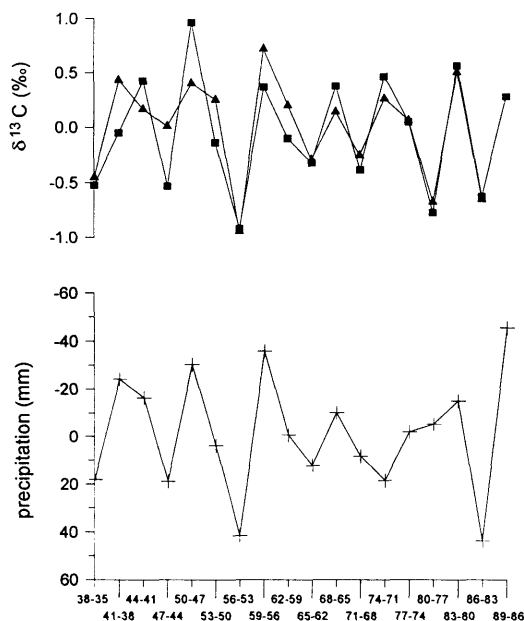


Fig. 5. First differences (differences of consecutive values) of the $\delta^{13}\text{C}$ series from "Twann Dry" = TWD (\blacktriangle) and "Hub Dry" = HUD (\blacksquare) and of the precipitation amount May + June + July in Bern (+). Note the inverse y-axis for the precipitation amount.

Table 1. Correlation coefficients r comparing original values of climatic data from Bern with original $\delta^{13}\text{C}$ data and first differences of climatic data with first differences of $\delta^{13}\text{C}$ data (P = precipitation amount, T = temperature, RH = relative humidity; mean of May, June and July)

		$\delta^{13}\text{C}$ TWD	$\delta^{13}\text{C}$ TWH	$\delta^{13}\text{C}$ HUD
original values	P	-0.70^{**} ($-0.016^{\circ}/_{\infty}/\text{mm}$)	-0.57^{*} ($-0.014^{\circ}/_{\infty}/\text{mm}$)	-0.53^{*} ($-0.012^{\circ}/_{\infty}/\text{mm}$)
original values	T	0.53^{*} ($0.36^{\circ}/_{\infty}/^{\circ}\text{C}$)	0.31	0.48^{*} ($0.34^{\circ}/_{\infty}/^{\circ}\text{C}$)
original values	RH	0.05	-0.13	-0.42
original values	ring width	-0.09	-0.14	-0.46
differences	P	-0.78^{***} ($-0.016^{\circ}/_{\infty}/\text{mm}$)	-0.57^{*} ($-0.009^{\circ}/_{\infty}/\text{mm}$)	-0.72^{**} ($-0.017^{\circ}/_{\infty}/\text{mm}$)
differences	T	0.60^{**} ($0.34^{\circ}/_{\infty}/^{\circ}\text{C}$)	0.23	0.57^{*} ($0.36^{\circ}/_{\infty}/^{\circ}\text{C}$)
differences	RH	-0.39	-0.23	-0.31
differences	ring width	-0.50^{*} ($-0.37^{\circ}/_{\infty}/\text{mm}$)	-0.34	-0.40

r is indicated for the correlation of tree ring width of the sites TWD, TWH and HUD (mean of the same trees as used for the $\delta^{13}\text{C}$ measurement) with the respective $\delta^{13}\text{C}$ data. Regression coefficients are given in parentheses where significant. Significance levels $p < 0.05^{*}$; $p < 0.01^{**}$; $p < 0.001^{***}$.

of the regression lines are in the range from $-0.009^{\circ}/_{\infty}/\text{mm}$ to $-0.016^{\circ}/_{\infty}/\text{mm}$ (included are all significant slopes for original values and differences for TWD/TWH/HUD). This is somewhat higher than the value of $(-0.004 \pm 0.001)^{\circ}/_{\infty}/\text{mm}$ reported by Lipp et al. (1991) for firs in the Black Forest. Furthermore, positive correlations result with temperature for the two dry sites. Here we find slopes between $0.34^{\circ}/_{\infty}/^{\circ}\text{C}$ and $0.36^{\circ}/_{\infty}/^{\circ}\text{C}$. They are well in the range of recently reported values (Tans and Mook, 1980; Freyer and Belacy, 1983) and agree very well with the results of Stuiver and Braziunas (1987; $0.32^{\circ}/_{\infty}/^{\circ}\text{C}$) and Lipp et al. (1991; $0.33^{\circ}/_{\infty}/^{\circ}\text{C}$). No significant correlation has been found with the relative humidity as could have been expected on the basis of theoretical considerations (see Section 1) and previous studies (Stuiver and Braziunas, 1987; Saurer and Siegenthaler, 1989; Lipp et al., 1991). The relative humidity is a somewhat difficult parameter because long-term variations are of the order of magnitude of the precision of the humidity measurement and may be representative for a small region around the weather station only.

In summary, we find (1) that the total precipitation amount of the months May, June and July most strongly influences the $\delta^{13}\text{C}$ variations, (2) that the first differences of the $\delta^{13}\text{C}$ data, i.e., the short-term isotope variations, contain more climatic information than the long-term trends, and (3) that the $\delta^{13}\text{C}$ data on the dry sites are more strongly influenced by climate than the $\delta^{13}\text{C}$ values on the humid site. Concerning (2) and (3), this

confirms the result from the beginning of this section where we compared the $\delta^{13}\text{C}$ series from the 3 sites with each other. With the aim of paleoclimatic reconstruction in mind it is disturbing that the long-term $\delta^{13}\text{C}$ trends are less well correlated to climate than the short-term variations (as was also found by Freyer and Belacy (1983) and Leavitt and Long (1988)). A possible explanation are aging trends (i.e., genetically determined, species dependent $\delta^{13}\text{C}$ shifts in time which also could occur in a constant environment). Lipp et al. (1991), for instance, found increasing $\delta^{13}\text{C}$ trends over the whole life span of numerous fir trees from the last millennium. Such trends can tentatively be corrected for (assuming a linear increase) but nevertheless are not well understood. Besides, aging trends are also a serious problem in climatic reconstructions based on tree ring width variations (Schweingruber, 1988). Concerning (1), it is important to note that the period of the strongest influence of the carbon isotope composition corresponds to the growing season. This by itself (beyond the statistical significance) adds much to the credibility of the results of the correlation analyses. An interesting difference is apparent here to the correlation of $\delta^{13}\text{C}$ in late wood with climate of August reported by Lipp et al. (1991). The early wood is also influenced by previous year carbohydrates and may therefore disturb the climate-isotope relationship when using the whole tree rings. In our study we did not separate early and late wood (mainly because a visual distinction is difficult for beech) which may explain why we find

the best correlation with an earlier period of the growing season.

Tree ring width data were analysed in an analogous way as $\delta^{13}\text{C}$ data in order to allow a direct comparison. In Fig. 4, 3-year-means of tree ring width of the same trees as used for $\delta^{13}\text{C}$ measurement are shown for the three sites under study. The curves of the dry sites TWD and HUD are significantly correlated to each other ($r = 0.49$, $p < 0.05$). This correlation is somewhat improved by taking first differences ($r = 0.59$, $p < 0.05$), but it is not as good as the corresponding correlation between first differences of $\delta^{13}\text{C}$ data ($r = 0.84$, $p < 0.001$). The ring width curve of the humid site TWH is not significantly correlated to either of the two other sites (neither for original values nor for first differences), whereas the $\delta^{13}\text{C}$ difference series of TWH and the nearby dry site TWD are significantly correlated ($r = 0.62$, $p < 0.01$). We conclude that $\delta^{13}\text{C}$ variations at different sites show more similarities than ring width variations (when the same number of trees is analysed). Tree ring width data were for one site (and for differences only) weakly correlated with $\delta^{13}\text{C}$ (see Table 1). Such a negative correlation would be understandable in terms of warm and dry years causing narrow rings and high $\delta^{13}\text{C}$ values. A more significant correlation might be found between $\delta^{13}\text{C}$ and tree ring area rather than width (Stuiver et al., 1984). The climatic significance of ring width variations for beech for the sites TWD and TWH was thoroughly evaluated on a larger data set of 2x12 trees (Z'Graggen, 1992). It was found that mainly spring precipitation influences ring width. Yet the amount of explained variance by climate variables in a multiple regression analysis is rather small, especially on the humid site ($r^2 = 0.26$ for TWH, $r^2 = 0.41$ for TWD; Z'Graggen, 1992). One explanation for this stressed by Z'Graggen (1992) is the influence of short-term damaging events, like, e.g., frost after the onset of bud sprouting, which are not accounted for in an analysis with monthly temperature means.

4.2. A closer look at climatic implications

In this section we first (in (a)) estimate the geographical extent of validity of the above derived climate-isotope relations. Such considerations are useful with a view to the reconstruction of climate variables. Second (in (b)), we look more closely at the intercorrelation of the climate

variables. For instance, when the temperature is relatively high in summer, the precipitation amount and the relative humidity will in general be relatively low in the temperate-moist climate of Switzerland. Therefore, multiple regression analysis should give further insights into the causes of the carbon isotope variations.

(a) The $\delta^{13}\text{C}$ difference series from TWD and HUD were correlated with precipitation data from 15 precipitation stations situated in the Swiss Central Plateau and Jura (Fig. 1). With these calculations it was possible to calculate the area in which the $\delta^{13}\text{C}$ data are related to the precipitation data at a significance level of $p < 0.001$ ($r = -0.72$) and $p < 0.01$ ($r = -0.60$). The result for the HUD site is shown in Fig. 1. In an area of 3000 km² the climate-isotope relation is significant at $p < 0.001$ and in most of the eastern part of the Central Plateau (at least 7200 km²) the relation is significant at $p < 0.01$. The corresponding areas for the TWD site are similar in magnitude but are more extended in the direction north-west to south-east.

(b) To better understand the combined influence of different climate variables on the carbon isotope composition, we carried out multiple regression analyses. This was done for first differences of mean May/June/July precipitation (ΔP), temperature (ΔT) and relative humidity (ΔRH) for the two weather stations Bern and Neuenburg, correlating these data sets to differences of the TWD and HUD $\delta^{13}\text{C}$ series according to the following equation:

$$\Delta\delta = a + b \Delta P + c \Delta T + d \Delta \text{RH}. \quad (2)$$

Because of the intercorrelation of the climate variables a principal component analysis should yield more reliable results than a straightforward multiple regression analysis and is performed in the following according to Fritts (1976). In a principal component analysis, the 3-dimensional normalised (mean = 0, $\sigma = 1$, index n) climate data set is transformed into a new set of 3 orthogonal variables, say climate modes, whereby the first climate mode explains most of the climate variance. Multiple regression analysis with the $\delta^{13}\text{C}$ data is then made taking the 3 (uncorrelated) climate modes as variables instead of ΔP , ΔT and ΔRH . If there are one or more significant coef-

ficients a, b, c, d , these are transformed back and expressed in terms of the original climate data.

We found that the first climate mode is very similar for Bern and Neuenburg and explains 76.7% and 78.4% of climate variability respectively. The weight of precipitation, temperature and relative humidity in this mode is of similar magnitude, whereas the sign for temperature is opposite to the sign for precipitation and relative humidity. Thus, in a period where, e.g., the temperature is relatively high and the precipitation amount and the relative humidity are relatively low, climate can be readily described by the first climate mode.

Multiple regression analysis with the climate modes showed that only the first climate mode is significantly related to $\delta^{13}\text{C}$. After transforming back the respective coefficients, the following two equations expressed in original climate variables (still normalised, index n) are found:

$$\begin{aligned} {}^n\Delta\delta_{\text{TWD}} &= -0.15 {}^n\Delta P + 0.16 {}^n\Delta T - 0.16 {}^n\Delta\text{RH}, \\ r &= 0.83, \quad \text{climate data from Neuenburg;} \end{aligned} \quad (3)$$

$$\begin{aligned} {}^n\Delta\delta_{\text{HUD}} &= -0.11 {}^n\Delta P + 0.12 {}^n\Delta T - 0.13 {}^n\Delta\text{RH} \\ r &= 0.61, \quad \text{climate data from Bern} \end{aligned} \quad (4)$$

The two main results are:

(i) The coefficients are similar for both $\delta^{13}\text{C}$ series and for both weather stations (eqs. (3) and (4)).

(ii) The relative strength of the influences of ΔP , ΔT and ΔRH on $\Delta\delta$ is directly given by the coefficients because eqs. (3) and (4) are expressed in normalised data. The effects of the 3 climate variables on $\delta^{13}\text{C}$ are apparently all of the same order of magnitude, whereby the effects of precipitation and of relative humidity are negative and the effect of temperature is positive (this statement is equivalent to saying that $\delta^{13}\text{C}$ is mainly determined by the first climate mode). It is therefore not possible from the statistical analysis to establish one isolated primary climate parameter which determines the $\delta^{13}\text{C}$.

To calculate the multiple regression equation for non-normalised data we combined climate data from Neuenburg and Bern and the $\delta^{13}\text{C}$ data from TWD and HUD. This should yield the best estimate for the climate-isotope-relationship.

$$\begin{aligned} \Delta\delta &= -0.006^\circ/\text{mm } \Delta P + 0.16^\circ/\text{°C } \Delta T \\ &\quad - 0.051^\circ/\text{°}\% \Delta\text{RH} - 0.014^\circ/\text{°}\%. \end{aligned} \quad (5)$$

The multiple correlation coefficient is 0.72. The coefficients in (5) seem to be rather different compared to the coefficients of the simple regression equations given in Table 1. The explanation is that only the first climate mode (warm/dry and cold/humid) was considered with the above procedure (because the other modes were not significantly related to $\delta^{13}\text{C}$). We therefore removed, as an example, "wet and warm components" which obscure the simple regressions.

Summarising Subsections 4.1 and 4.2, we find that a combination of climatic factors determines the $\delta^{13}\text{C}$ in tree rings. Periods with warm + dry or cold + humid conditions during May, June and July most strongly influence $\delta^{13}\text{C}$. Correlations with individual climatic parameters can therefore give only a limited insight into the climate-isotope relationship. Concerning reconstructions it might be more interesting to get information about one individual climatic parameter. We conclude from the 1-dimensional regression analysis (Table 1) that for this purpose $\delta^{13}\text{C}$ yields most information about the precipitation amount.

4.3. Site influence study and palaeoclimatic significance of $\delta^{13}\text{C}$ values

For this study, we selected sites which differ greatly in moisture conditions and determined mean $\delta^{13}\text{C}$ values covering the last fifty years (1939–1989) of beech, pine and spruce trees (6 trees per species and per site). By measuring the last 50 tree rings, we assume to get a value representative for each tree and thus a mean site $\delta^{13}\text{C}$ value for each species by taking the average of all tree $\delta^{13}\text{C}$ values. In Fig. 6, the mean site $\delta^{13}\text{C}$ values for beech, pine and spruce are shown as a function of the moisture index of the site. Also indicated are the values for beech at the sites "Twann Dry" = TWD and "Twann Humid" = TWH. First, it is obvious that the $\delta^{13}\text{C}$ values are markedly different for the three species, the two conifer species having higher values than beech. According to the discrimination model, eq. (1), this might be due to differences of the water-use efficiency (Farquhar et al., 1982), probably genetically determined. Secondly, a strong moisture dependence of the $\delta^{13}\text{C}$ values is apparent for all

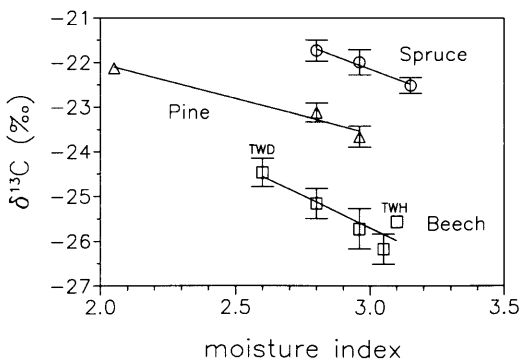


Fig. 6. Mean site $\delta^{13}C$ values for beech (*Fagus silvatica*, \square , $n = 6$), spruce (*Picea abies*, \circ , $n = 6$) and pine (*Pinus silvestris*, \triangle , $n = 6$) with standard error of the mean (not indicated where smaller than symbol size) versus the moisture index of the sites. All sites are near Court, Swiss Jura (Fig. 1). Indicated are also the corresponding values for the beech trees from the sites "Twann Dry" = TWD and "Twann Humid" = TWH. The solid lines are the regression lines.

tree species ($p < 0.01$ for beech and pine, $p < 0.05$ for spruce): The drier the site conditions are the more positive tree $\delta^{13}C$ values are found. This is in agreement with eq. (1) with the (likely) assumption that trees on a dry site have to economise water by closing their stomata. This is also consistent with the result described in Subsections 4.1 and 4.2 namely the inverse correlation of temporal variations of precipitation amount and tree ring $\delta^{13}C$. Further we find that the slopes of the regression lines for three tree species analysed agree within the error limits, i.e., a similar moisture dependence as for the deciduous tree beech seems to be valid for the conifers pine and spruce.

We discuss now the potential application of our results for palaeoclimate reconstruction. We consider it useful to make a distinction regarding the climatic significance between (i) mean tree $\delta^{13}C$ values (i.e., one sample covering essentially all tree rings, as discussed above) and (ii) short-term $\delta^{13}C$ variations (as discussed in Subsection 4.1). Accordingly, two types of questions differing in the desired time resolution can be addressed to: (i) One would like to investigate, as a hypothetical example, whether the period from 5000BP to 4000BP was drier than the period from 4000 BP to 3000 BP in Greece (as was inferred from lake-level changes, Harrison et al., 1993) and (ii) one would like to reconstruct short-term variations of the

precipitation amount in these periods, for instance determine the frequency of drought events (to simplify the discussion we talk about the difference between dry and humid conditions when actually the difference between dry/warm and humid/cold is most important for the $\delta^{13}C$, see Subsection 4.2).

(i) The mean $\delta^{13}C$ value of a tree is the result of the combined influence of climate and local site conditions. A tree growing in a humid period on a dry site may exhibit the same mean $\delta^{13}C$ value as a tree growing in a dry period on a humid site. Thus, it is difficult to interpret the $\delta^{13}C$ value of an arbitrarily found tree in terms of climate. Yet, strong climate changes influence the site conditions: More sites can be expected to be dry in a dry period than in humid period. According to the results of this section, the mean $\delta^{13}C$ values of trees which lived in a relatively dry period should be more positive than the $\delta^{13}C$ values of trees which lived in a more humid period, if, of course, one does not mix different species. Therefore, the mean $\delta^{13}C$ value of a number of trees from a certain period is probably related to the climatic (humidity) conditions of this period. A prerequisite is that several trees from the same species are available to yield a reliable mean. This approach is intended to yield information about long-term climatic changes. A comparison with independent methods (historical data, pollen and sediment records) is necessary.

(ii) As shown in the preceding sections, the short-term $\delta^{13}C$ variations are related to climate mainly on dry sites. Yet, when dealing with fossil wood for reconstruction purposes, one usually has no information about site conditions and therefore does not know if the established climate-isotope relationship holds for the investigated tree. The above results show that the mean $\delta^{13}C$ value of a tree indicates the local moisture conditions of the site where it was growing. This means that only trees with relatively high mean $\delta^{13}C$ values, thus stemming from a dry site, should be used to reconstruct short-term climate variations. For instance for beech trees, the mean value of the well suited TWD site is -24.5‰ , of the humid TWH site it is -25.5‰ (see Fig. 6). The limit below which beech trees should not be used can therefore tentatively be estimated from Fig. 6 to be about -25‰ .

Existing data about the relationship between

site conditions and mean $\delta^{13}\text{C}$ values of the trees growing there are scarce. In our opinion, however, they are essential to determine the reliability of climatic reconstructions using $\delta^{13}\text{C}$ in tree rings. To extend this investigation one could, for instance, compare sites with similar humidity conditions but with variable summer temperature.

5. Conclusions

We find that in a time period when warm and dry conditions prevail during May, June and July, relatively high $\delta^{13}\text{C}$ values will be produced in the cellulose of tree rings of beech trees compared to a time period with cold and wet conditions. If the reconstruction of individual climatic parameters is desired it is the precipitation amount which will probably yield the most reliable results. Site conditions are of great significance for the climate-

isotope relationship: (i) less climatic information is stored in tree ring $\delta^{13}\text{C}$ on a humid site than on a dry site and (ii) the mean tree $\delta^{13}\text{C}$ value depends on the humidity condition of the site for beech as well as for the conifers spruce and pine. We conclude that $\delta^{13}\text{C}$ analyses of tree rings are a promising tool for climate reconstructions provided the influence of site conditions is taken into account.

6. Acknowledgements

Thanks are due to K. Aellen and S. Z'Graggen for helpful discussions and for assistance in sampling. Comments of Chr. Körner helped to improve the manuscript. We much appreciate the careful isotope measurements by M. Töngi. This work was supported by the Swiss National Science Foundation.

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