



## $\delta^{13}\text{C}$ response surface resolves humidity and temperature signals in trees

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**Abstract**—Stem cellulose of bean plants (*Vicia faba*) grown under controlled conditions exhibits inverse linear carbon–isotope reactions to changes in both relative humidity (RH) and temperature (T), readily mappable as a planar  $\delta^{13}\text{C}$  response surface in RH–T space. The analogous response surface for annual late-wood cellulose  $\delta^{13}\text{C}$  from a field calibration using fir trees (*Abies alba*) in the Black Forest, southern Germany, also supports resolution of independent  $\delta$ -RH and  $\delta$ -T effects. The response of cellulose  $\delta^{13}\text{C}$  to RH and T derived from this new calibration differs markedly from estimates based on univariate linear regression analysis: The sensitivity of  $\delta^{13}\text{C}$  to RH is stronger than that inferred previously (c.  $-0.17\text{‰}/\%$  vs.  $-0.12\text{‰}/\%$ , respectively), whereas the  $\delta$ -T coefficient is weaker and reversed in sign (c.  $-0.15\text{‰}/\text{K}$  vs.  $+0.36\text{‰}/\text{K}$ ). This new perspective on the coupled influence of moisture and temperature changes on tree-ring cellulose  $\delta^{13}\text{C}$  helps to unify divergent observations about carbon–isotope signals in trees, especially the broad range of apparent  $\delta$ -T relations obtained in calibration studies, which are often used as paleoclimate transfer functions. Although this highlights the large potential uncertainties surrounding paleoclimate reconstruction based solely on  $\delta^{13}\text{C}$  data, coupling of the carbon–isotope response–surface approach with equivalent response surfaces for hydrogen or oxygen isotopes may afford new opportunities for investigating the nature of past climate variability and change from tree-ring sequences. Copyright © 2000 Elsevier Science Ltd

### 1. INTRODUCTION

Carbon–isotope labelling of terrestrial C3 plant matter is described consistently by the well known Farquhar et al. (1982) model

$$\delta^{13}\text{C}_{\text{plant}} = \delta^{13}\text{C}_{\text{air}} - \epsilon_a - (\epsilon_b - \epsilon_a)(c_i/c_a) \quad (1)$$

which indicates that the isotopic separation between plant matter ( $\delta^{13}\text{C}_{\text{plant}}$ ) and its carbon source, atmospheric carbon dioxide ( $\delta^{13}\text{C}_{\text{air}}$ ), is a function of  $\epsilon_a$  and  $\epsilon_b$ , respectively the discrimination against  $^{13}\text{CO}_2$  associated with diffusion of  $\text{CO}_2$  into the leaf and subsequent biochemical effects during tissue synthesis, moderated by  $c_i/c_a$ , the ratio of  $\text{CO}_2$  concentrations within the leaf and the ambient atmosphere. Carbon–isotope sensitivity of plants to climatic parameters, the basis for the use of plant matter  $\delta^{13}\text{C}$  as a paleoclimate proxy, is believed to reflect primarily environmental influence on  $c_i/c_a$ , which is usually manifested by strong correlations between  $\delta^{13}\text{C}$  and parameters reflecting moisture and/or temperature variability (Farquhar et al., 1989). ( $\delta^{13}\text{C}$  values express deviations in the  $^{13}\text{C}/^{12}\text{C}$  ratio in a sample, such that  $\delta^{13}\text{C} = 1000[(R_{\text{sample}}/R_{\text{standard}}) - 1]$  ‰, where  $R$  refers to the respective  $^{13}\text{C}/^{12}\text{C}$  ratios in the sample and a given reference standard. Eqn. 1 is independent of the standard used;  $\delta^{13}\text{C}$  values herein are referred to PDB.)

Statistically defined  $\delta^{13}\text{C}$ -climate relations for recent plant cellulose are frequently generated from modern calibration data sets for application as quantitative transfer functions to reconstruct paleoclimate. The strongest univariate relations are generally those between  $\delta^{13}\text{C}$  and relative humidity, temperature,

precipitation amount, or soil moisture status (e.g., see Lipp et al., 1991, 1996b; Schleser et al., 1999; Ramesh et al., 1986; Leavitt, 1993; Feng and Epstein, 1995; Pendall et al., 1999), although apparent  $\delta^{13}\text{C}$ -temperature ( $\delta$ -T) relations are most often applied as transfer functions, because of the desire to infer paleotemperature. One of the limitations on the applicability of univariate statistical transfer functions is the problem of mutual correlation between different significant environmental parameters, which reduces confidence in reconstruction of a single parameter unless correlated parameters are also known to have varied exactly as in the calibration period (Schleser et al., 1999; Pendall et al., 1999). This is a variant of the familiar “no analog” situation in the calibration of paleoenvironmental indicators. Strong mutual correlations between parameters, coupled with relatively small ranges of variability over calibration periods and large isotopic analytical uncertainties, may also compromise the effectiveness of multivariate statistical analysis of calibration data, leading to poorly constrained or ambiguous assessment of the actual isotopic sensitivity to different environmental variables.

Here we report carbon–isotope data obtained from bean plants (*Vicia faba*) grown under controlled conditions. These results provide new insight into the possible deconvolution of isotope–climate signals in plants growing in nature, as we show through reconsideration of a previously published  $\delta^{13}\text{C}$  calibration data set and dendrochronology for fir (*Abies alba*) from the Black Forest, southern Germany.

### 2. METHODS

*Vicia faba* seedlings were germinated under identical natural conditions. Eighty healthy plants were selected and transferred after about two weeks into four climate chambers (EPOKA facility, GSF-Neuherberg; see Payer et al. 1993) for a 6-week growth period under condi-

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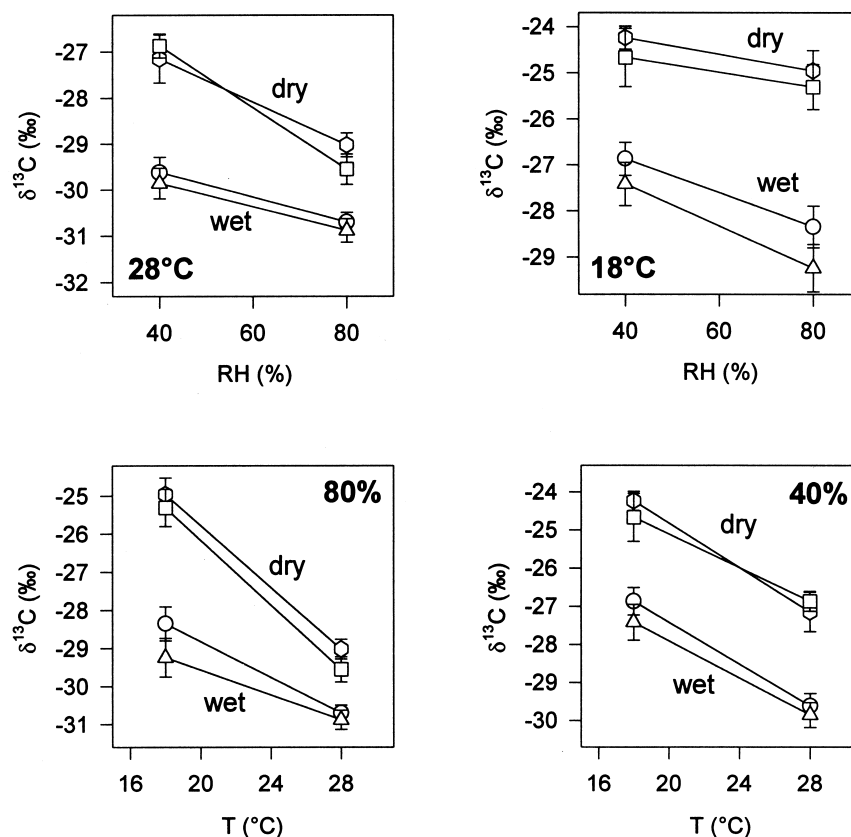


Fig. 1.  $\delta^{13}\text{C}$  values obtained on cellulose from stem ( $\circ$ ,  $\odot$ ) and leaf ( $\Delta$ ,  $\square$ ) cellulose of *Vicia faba* plants in relation to RH and T in four climate chambers. Each data point represents 7 to 10 samples from different plants. Error bars indicate  $1\sigma$ . Flower and root cellulose  $\delta^{13}\text{C}$  (not shown) displayed equivalent relations.

tions of differing, but constant RH and T (40%/18°C; 40%/28°C; 80%/18°C; 80%/28°C). The 20 plants in each chamber were further subdivided, half ("wet treatment") receiving ample daily irrigation to maintain maximum soil moisture levels, whereas the others ("dry treatment") were sparingly irrigated to maintain roughly one half of the saturated soil water content, as determined by weight. All other factors for the four chambers were identical, including the  $\delta^{13}\text{C}$  and concentration of ambient  $\text{CO}_2$  at natural levels, air exchange rate ( $20\times$  per hour), and diurnal light cycle. Selected plant components (stems, leaves, flowers, roots) were harvested at the end of the growth period and the cellulose purified and analyzed using conventional techniques (Sternberg, 1989; Boutton, 1991). Only new plant tissue produced following transfer to the chambers was sampled, to restrict analysis to biomass that had grown under controlled conditions.

### 3. RESULTS AND DISCUSSION

#### 3.1. *Vicia faba*

The data from *Vicia faba* (Fig. 1) clearly show strong isotopic responses to each parameter, with similar  $\delta$ -RH and  $\delta$ -T relations for cellulose from all selected parts, as well as distinct step-wise offsets between the wet and dry irrigation treatments. In each case the plants maintained greater isotopic discrimination under wetter and/or warmer conditions, presumably reflecting higher  $c_i/c_a$  ratio, as depicted by the Farquhar et al. (1982) model, and hence a lower level of environmental stress. Interestingly, even plants having the dry irrigation treatment were apparently not sufficiently moisture-stressed to mask their

isotopic responses to varying RH and T, as observed previously for RH in irrigated and nonirrigated *Tamarix* growing in natural settings in Israel (Lipp et al., 1996b).

Although all plant parts responded similarly, stem cellulose from the bean plants that received the wet treatment can be considered the closest analog for tree-ring cellulose from trees in a moist temperate climatic setting like the Black Forest. Contouring the wet-treatment stem cellulose  $\delta^{13}\text{C}$  data in RH-T space (Fig. 2) reveals that the combined influence of changes in RH and T on  $\delta^{13}\text{C}$  can be readily described as a planar response surface described by:

$$\delta^{13}\text{C} = (-0.032)\text{RH} + (-0.255)\text{T} - 21.1 \quad (2)$$

Comparison of  $\delta^{13}\text{C}$  values calculated using Eqn. 2 with the measured values shown in Figure 2 shows that the independent effects of RH and T on stem cellulose  $\delta^{13}\text{C}$  are essentially linear and additive within the range of conditions spanned by the four climate chambers ( $R^2 = 0.995$ ). Indeed, it is obvious from consideration of Figure 2 that any three points would be sufficient to define a planar response surface containing the fourth point, within the indicated analytical uncertainties. (Interestingly, it is evident from Figure 1 that an analogous response surface could also be defined for the dry-treatment plants, offset to higher  $\delta^{13}\text{C}$  by about 2 to 3‰, although our

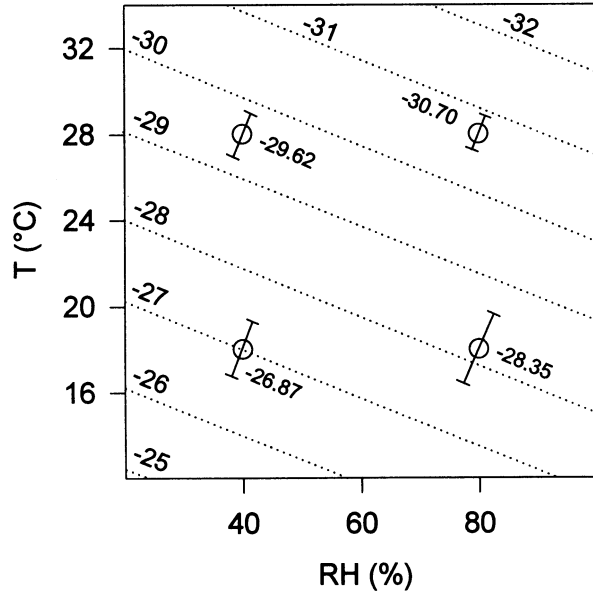


Fig. 2. *Vicia faba* stem cellulose  $\delta^{13}\text{C}$  values plotted in RH-T space. The parallel diagonal lines are  $\delta^{13}\text{C}$  contours, which define an inclined response surface drawn as a best-fit plane to the measured data, described by  $\delta^{13}\text{C} = (-0.032)\text{RH} + (-0.255)\text{T} - 21.1$  (Eqn. 2). The response surface fits within  $1\sigma$  of each data point.

qualitative method of inducing soil moisture stress precludes more rigorous quantitative analysis.)

The most salient feature of the  $\delta^{13}\text{C}$  response of well watered *Vicia faba* to varying RH and T revealed by Figure 2 is that identical  $\delta^{13}\text{C}$  values could be generated by a linear array of possible RH-T combinations. Alternatively, it is clear that the isotopic sensitivity to a “climate” change defined by a given displacement in RH-T space will be highly dependent on the slope of that trajectory.

### 3.2. *Abies alba*

Previous investigations of Black Forest fir (*Abies alba*) by Lipp et al. (1991) revealed that a stacked  $\delta^{13}\text{C}$  time-series based on annual late-wood cellulose from five trees for the 1959 to 1980 period correlated significantly with varying mean August RH and T recorded during the same period (see Table 1 and Figure 3), yielding the following relations:

$$\delta^{13}\text{C} = (-0.12)\text{RH} - 12.0 \quad (R^2 = 0.668) \quad (3)$$

$$\delta^{13}\text{C} = (+0.36)\text{T} - 26.4 \quad (R^2 = 0.636) \quad (4)$$

Late-wood cellulose  $\delta^{13}\text{C}$  also correlated weakly with mean August precipitation amount. Multiple linear regression of  $\delta^{13}\text{C}$  against both RH and T yielded a moderately significant relation, albeit having excessively high uncertainties in the RH and T coefficients because of the strong mutual correlation between these climate parameters ( $R^2 = 0.674$ ), compounded by the limited ranges of RH, T, and  $\delta^{13}\text{C}$  values within the data set. The apparent  $\delta$ -T relation was subsequently used to generate a speculative paleotemperature record from a composite annual late-wood cellulose  $\delta^{13}\text{C}$  time-series developed from a dendrochronology for Black Forest *Abies alba* spanning AD 1004 to

Table 1. Measured  $\delta^{13}\text{C}$  of annual late-wood *Abies alba* cellulose from the Black Forest, southern Germany (48°33'N; 8°20'E) and mean August RH and T recorded at the nearby Hornsgründe meteorological station for corresponding years of the 1959–1980 period.

$\delta^{13}\text{C}$ of late-wood cellulose (‰ PDB)	Mean August relative humidity RH (%)	Mean August temperature T (°C)
-21.0	76.1	14.9
-21.3	80.9	14.2
-21.3	78.0	13.7
-21.5	83.0	11.6
-21.6	81.0	13.6
-21.8	86.0	10.9
-21.9	83.0	12.8
-21.9	84.0	12.1
-22.0	77.0	13.2
-22.0	86.0	12.9
-22.1	85.0	11.9
-22.2	88.0	10.8
-22.2	83.0	11.2
-22.3	84.0	10.9
-22.4	87.0	11.7
-22.5	85.0	11.7
-22.8	90.0	11.5
-23.1	89.0	10.7
-23.3	90.0	10.0

The  $\delta^{13}\text{C}$  values were normalized to account for the fossil fuel effect on the  $\delta^{13}\text{C}$  of atmospheric  $\text{CO}_2$  (see Lipp et al. (1991) for description of the site and details of sampling and analysis). We discarded data from three years in the original compilation because of unresolvable discrepancies, although these have negligible effect on the prior results of Lipp et al. (1991). The  $\delta^{13}\text{C}$  data represent averages of results from five trees, and have an average uncertainty of about  $\pm 0.5\%$ .

1980. Clearly, the apparent  $\delta$ -RH relation could also have been used to convert the  $\delta^{13}\text{C}$  time-series into a paleohumidity record, although the resulting reconstruction would simply have been identical in detail and opposite in sign, as a consequence of the linear relations between  $\delta^{13}\text{C}$ , RH, and T.

A different perspective on the nature of  $\delta^{13}\text{C}$ -climate relations in the Black Forest fir can be gained through mapping of the  $\delta^{13}\text{C}$  response surface, by analogy to the results of the growth experiments discussed above. Plotting data from the calibration set in RH-T space yields a cluster about a line of slope  $-0.333$ , representing the characteristic average August RH-T variability over the calibration period (Figure 4a). Because of this strong correlation and the small range and high uncertainty of the isotopic data, a variety of planar surfaces could be generated by contouring the corresponding  $\delta^{13}\text{C}$  values, even with the constraints imposed by the apparent  $\delta$ -RH and  $\delta$ -T effects expressed by Eqn. 3 and 4. However, it is evident by inspection that a weak isotopic gradient also exists within the data oblique to the RH-T slope, in the same sense as that observed for *Vicia faba* in the climate chamber experiments. This suggests that the actual  $\delta$ -RH and  $\delta$ -T relations for *Abies alba* must also both have negative coefficients, which further limits the range of possible solutions to the fitting of a response surface. Our best approximation of the  $\delta^{13}\text{C}$  response surface within these constraints is described by

$$\delta^{13}\text{C} = (-0.17)\text{RH} + (-0.15)\text{T} - 6.0 \quad (5)$$

which expresses the average  $\delta^{13}\text{C}$  response of *Abies alba*

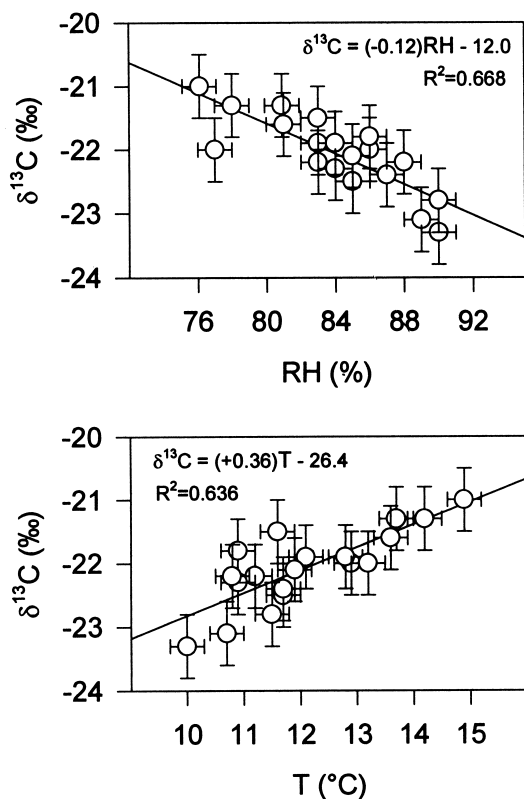


Fig. 3.  $\delta^{13}\text{C}$  values of Black Forest *Abies alba* late-wood cellulose plotted versus mean August RH and T. Data are from Table 1.

late-wood cellulose associated with any trajectory in this RH-T space ( $R^2 = 0.560$ ; see Fig. 5). This relation can be further generalized to express the isotopic response independent of the absolute  $\delta^{13}\text{C}$  values in the calibration data by

$$\Delta^{13}\text{C} = (-0.17)\Delta\text{RH} + (-0.15)\Delta\text{T} \quad (6)$$

which should thus be a good representation of the response surface of *Abies alba* for trees at any site, regardless of the relation between average August RH and T, assuming that these two climate parameters are the primary controls on late-wood cellulose  $\delta^{13}\text{C}$ . It is obvious from consideration of Eqn. 5 and 6 that the small range of isotopic variation within the calibration data set is partly a reflection of the opposing effects of RH and T on  $\delta^{13}\text{C}$ , and that more definitive characterization of the response surface would be possible if these parameters were less strongly correlated, as in the climate chamber experiments.

#### 4. IMPLICATIONS AND CONCLUSIONS

Graphical depiction of the *Abies alba* carbon-isotope response surface clearly shows how strikingly divergent apparent  $\delta\text{-RH}$  and  $\delta\text{-T}$  relations could be obtained from calibration studies of the same tree species growing under different climatic regimes, because the apparent effects will depend on the average RH-T variability during any particular interval. This offers a ready explanation for the broad range of apparent isotope-climate relations reported for various species globally,

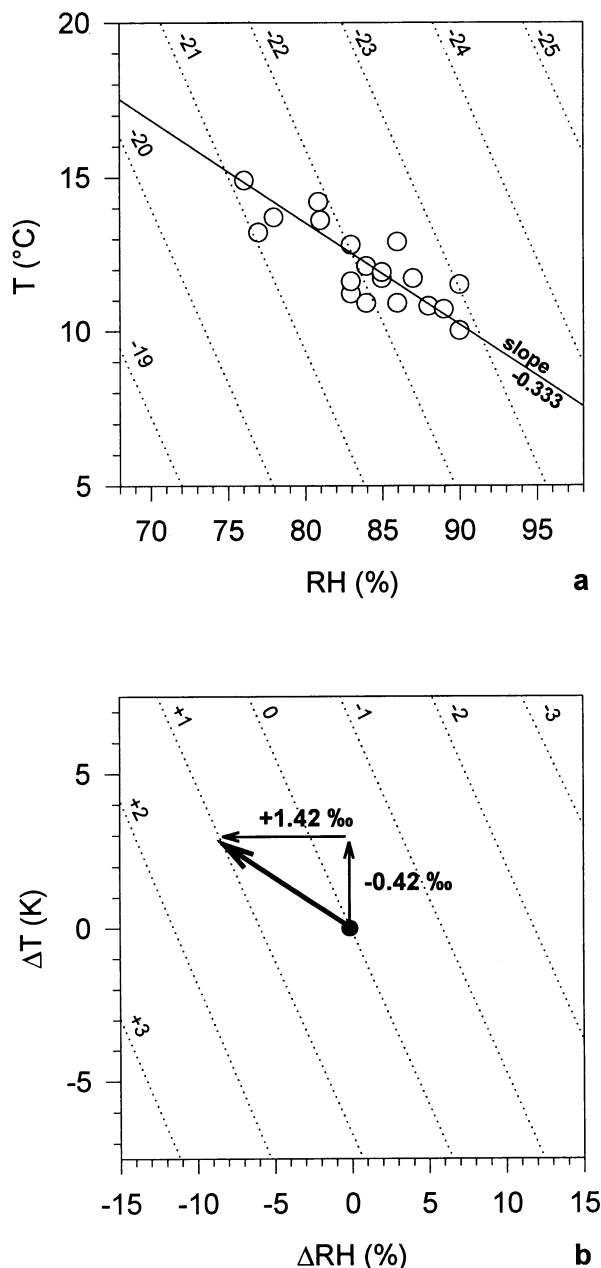


Fig. 4. (a), Data points from the Black Forest *Abies alba* calibration set plotted in RH-T space. The dotted lines are the  $\delta^{13}\text{C}$  contours of a best-fit inclined plane constrained by the apparent  $\delta\text{-RH}$  and  $\delta\text{-T}$  effects along the line of slope  $-0.333$ , which corresponds to the average sense of interannual RH-T variation during the calibration period. The  $\delta^{13}\text{C}$  response surface is described by Eqn. 5:  $\delta^{13}\text{C} = (-0.17)\text{RH} + (-0.15)\text{T} - 6.0$ . (b), Carbon-isotope response surface for Black Forest *Abies alba* expressed in terms of  $\Delta^{13}\text{C}$  response in  $\Delta\text{RH}-\Delta\text{T}$  space. The heavy arrow from the origin represents a trajectory producing a  $+1\text{‰}$   $\Delta^{13}\text{C}$  signal through coupled changes in RH and T along a slope of  $-0.333$ . The orthogonal vectors resolve the trajectory into two components, showing that a T-dependent depletion of  $-0.42\text{‰}$  is offset by an RH-dependent enrichment of  $+1.42\text{‰}$  to yield the observed  $+1\text{‰}$  response.

as recently reviewed by Schleser et al. (1999). Apparent  $\delta\text{-RH}$  and  $\delta\text{-T}$  relations for *Abies alba*, for example, could have

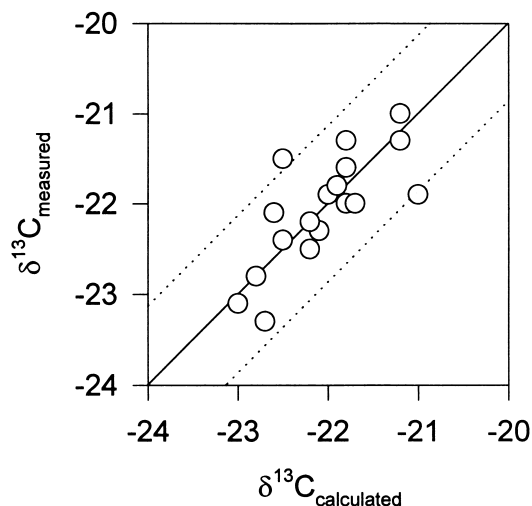


Fig. 5. Comparison of measured  $\delta^{13}\text{C}$  values for late-wood cellulose of Black Forest *Abies alba* with values calculated using the equation for the response surface (Eqn. 5). The dashed lines represent the 95% prediction interval.

various magnitudes and either positive or negative signs (though not simultaneously positive), depending on the nature of average climate variability during a calibration period. Maximum  $\delta^{13}\text{C}$ -climate sensitivity would obviously occur for coupled RH-T changes having trajectories perpendicular to the contours of the response surface, yielding coupled apparent relations according to this calibration as strong as about  $-0.21\text{‰}/\%$  and  $-1\text{‰}/\text{K}$ . In contrast, sensitivity would progressively weaken and ultimately disappear as climate trajectories approached the slope of the isotopic contours, owing to the counteractive effects of RH and T on  $\delta^{13}\text{C}$ .

Species-dependent effects are also likely to influence the  $\delta^{13}\text{C}$  response surface, as suggested by the apparent  $\delta$ -RH and  $\delta$ -T relations obtained from similar calibration data for late-wood cellulose of spruce (*Picea abies*), from another site in southern Germany (Schußbach, located about 170 km northeast of the Black Forest site; see Lipp et al., 1996a). The apparent effects for Schußbach spruce ( $-0.05\text{‰}/\%$  and  $+0.23\text{‰}/\text{K}$ ) cannot be accommodated on any possible approximation of the response surface for Black Forest fir, although a reasonable *Picea abies* response surface can be readily defined.

It is clear from consideration of Figure 4 that *Abies alba* is not a straightforward isotopic monitor for climates having a similar style of variability to that of the calibration period in the Black Forest, characterized by a steep inverse relation between shifting RH and T. In addition to damping of the overall  $\delta$ -T sensitivity, for example, even modest shifts of several percent in RH can have a large impact on changes in T inferred from the apparent  $\delta$ -T relation, including possibly reversing the sign. This contributes to high uncertainties, especially for significantly differing climates of the past, because of the likelihood that the relation between fluctuations in RH and T also differed from that of the calibration period. As a result, accurate assessment of the real uncertainty surrounding a paleotemperature estimate based on a univariate  $\delta$ -T calibration would require precise constraints on the probable paleohumidity, and vice

versa. (Analogous uncertainties would prevail, of course, in the interpretation of  $\delta^{13}\text{C}$  dendrochronologies for climates having positively correlated RH-T variability, owing to mutual reinforcement of the  $\delta$ -RH and  $\delta$ -T responses.)

On the other hand, it may be possible to exploit this aspect of  $\delta^{13}\text{C}$ -climate relations in *Abies alba* as a sensitive indicator of changes in the moisture-temperature relation at a site, which is likely to be an important feature of many climate signals. Possible evidence for this exists in the long-term Black Forest *Abies alba*  $\delta^{13}\text{C}$  dendrochronology (Figure 6a), which shows episodes of pronounced interannual variability during the late Medieval Warm Period, suggesting that subsequent Little Ice Age cooling may have been associated with a steepening of the average interannual RH-T trajectory, leading to damping of the isotopic response. The declining trend in average  $\delta^{13}\text{C}$  values during the onset of the LIA was probably a response to simultaneously increasing RH and decreasing T, which can be visualized as a progressive displacement in the average location of the interannual RH-T trajectory in RH-T space.

$\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values of tree-ring cellulose are also sensitive to moisture and temperature, primarily through RH-dependent evaporative enrichment of leaf waters and the isotopic composition of local meteoric water (Burk and Stuiver, 1981; Yapp and Epstein, 1982; Ramesh et al., 1986; Edwards and Fritz, 1986; White et al., 1993), which is commonly correlated strongly with temperature (Rozanski et al., 1993). The climatic sensitivity of both isotopes can be expressed as response surfaces (Edwards and Fritz, 1986) analogous to that for  $\delta^{13}\text{C}$ , suggesting that potential may exist to develop quantitative indices of changing moisture-temperature relations in the past by coupling  $\delta^{13}\text{C}$  with  $\delta^2\text{H}$  or  $\delta^{18}\text{O}$  from the same ring sequences. In counterpoint to  $\delta^{13}\text{C}$ , the contours of  $\delta^2\text{H}$  or  $\delta^{18}\text{O}$  have positive slopes in RH-T space (assuming a significant meteoric water  $\delta$ -T relation exists) and therefore the sign of isotopic responses will not be strongly sensitive to changes in the slope of inverse RH-T fluctuations. Coupling of the response of either of these isotopes with  $\delta^{13}\text{C}$  should thus provide a sensitive proxy for changes in this aspect of climate variability. The Black Forest *Abies alba* dendrochronology again provides support for this hypothesis, based on systematic variability between shifts in  $\delta^{13}\text{C}$  and  $\delta^2\text{H}$  at different time scales (Figure 6). For example, the MWP-LIA transition is marked by a shift from negatively to positively correlated  $\delta^{13}\text{C}$ - $\delta^2\text{H}$  variability at century scale, consistent with steepening of the interannual RH-T trajectory, as speculated above. The same general shift is also apparent at decadal scale, punctuated by periodic century-scale oscillations. Marked variability at decadal scale is evident, as well, possibly indicative of moisture-temperature variability in response to phenomena like the North Atlantic Oscillation (e.g., see Hurrell, 1995; Appenzeller et al., 1998).

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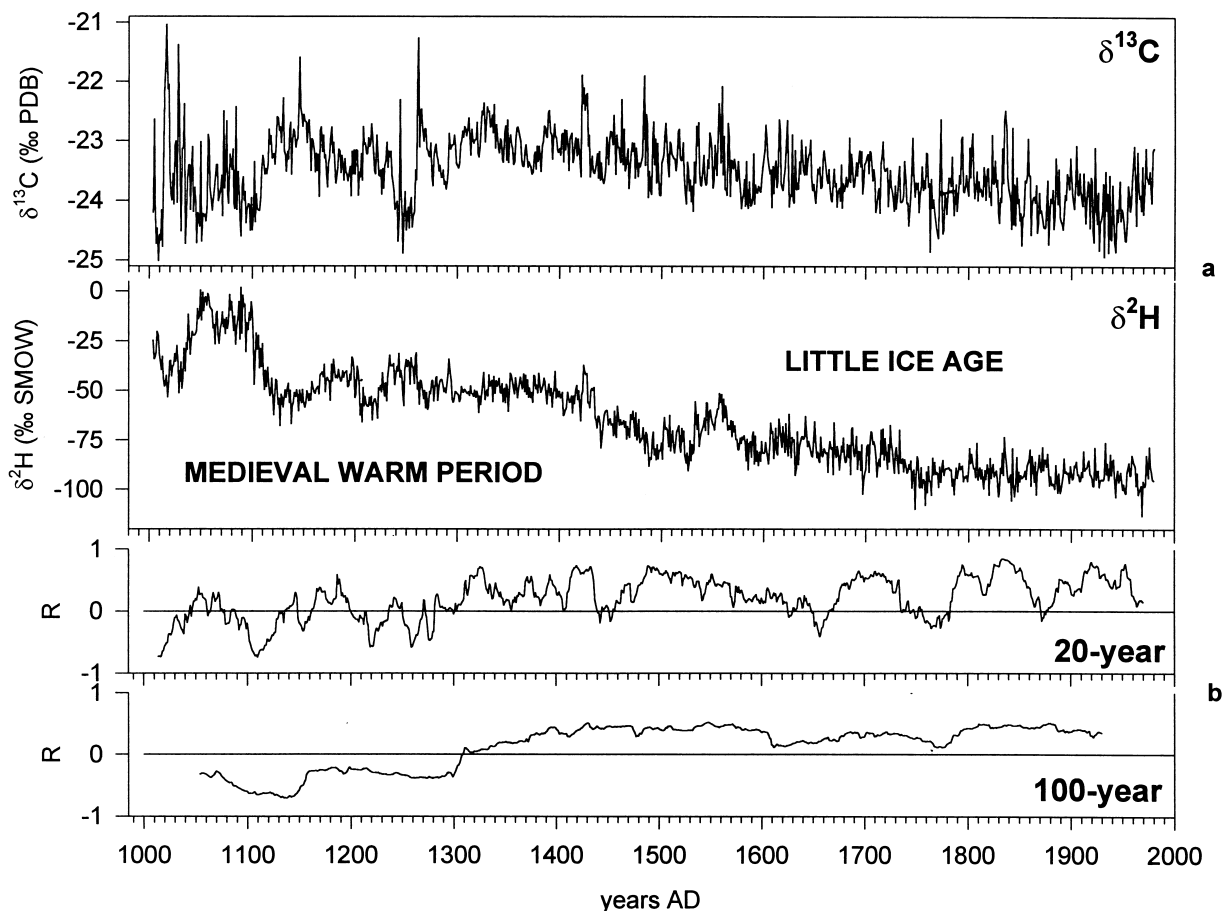


Fig. 6. (a),  $\delta^{13}\text{C}$  and  $\delta^2\text{H}$  time series from the Black Forest *Abies alba* AD 1004 to 1980 dendrochronology. Preparation of the  $\delta^2\text{H}$  series (not previously published) is based on the same samples of nitrated cellulose, as described by Lipp et al. (1991). (b), Running means of the correlation coefficients between annual late-wood cellulose  $\delta^{13}\text{C}$  and  $\delta^2\text{H}$  values using 20- and 100-yr moving windows, showing systematic changes in  $\delta^{13}\text{C}$ - $\delta^2\text{H}$  variability at different time scales, possibly related to shifts in the average slope of RH-T variability.

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