LETTERS

Subtropical to boreal convergence of tree-leaf temperatures

Brent R. Helliker[1] & Suzanna L. Richter[2]

The oxygen isotope ratio ($\delta^{18}O$) of cellulose is thought to provide a record of ambient temperature and relative humidity during periods of carbon assimilation[1,2]. Here we introduce a method to resolve tree-canopy leaf temperature with the use of $\delta^{18}O$ of cellulose in 39 tree species. We show a remarkably constant leaf temperature of 21.4 ± 2.2 °C across 50° of latitude, from subtropical to boreal biomes. This means that when carbon assimilation is maximal, the physiological and morphological properties of tree branches serve to raise leaf temperature above air temperature to a much greater extent in more northern latitudes. A main assumption underlying the use of $\delta^{18}O$ to reconstruct climate history is that the temperature and relative humidity of an actively photosynthesizing leaf are the same as those of the surrounding air[3,4]. Our data are contrary to that assumption and show that plant physiological ecology must be considered when reconstructing climate through isotope analysis. Furthermore, our results may explain why climate has only a modest effect on leaf economic traits[5] in general.

The ratio of stable oxygen isotopes ($\delta^{18}O$) in tree-ring cellulose was first used to reconstruct temperatures during tree growth, and a seminal study[6] showed a strong correlation between $\delta^{18}O$ of woody tissue and mean annual temperature (MAT).

Temperature is the main controlling factor for the isotopic composition of precipitation[7], and the $\delta^{18}O$ of precipitation is the primary control on the $\delta^{18}O$ of tree-ring cellulose. Methodological advancements have enabled the measurement of $\delta^{18}O$ in smaller increments of cellulose and have shown that inter-annual and intra-annual variation in tree-ring $\delta^{18}O$ can correlate with episodic or cyclic events, such as tropical cyclones and the El Niño Southern Oscillation, that cause a wholesale change in the $\delta^{18}O$ of precipitation water[8,9].

A secondary control on the $\delta^{18}O$ of tree-ring cellulose is relative humidity through its effects on evaporation. A greater evaporative gradient (lower relative humidity) results in greater loss of the lighter isotope (^{16}O), thereby enriching leaf water in the heavy isotope ^{18}O; this leaf-water isotopic signal is incorporated into sucrose and ultimately into cellulose. Accordingly, several studies have shown that the $\delta^{18}O$ of sucrose, and consequently tree-ring cellulose, records ambient relative humidity[2–4,10,11] and that the recorded humidity signal is more strongly associated with periods of maximal photosynthesis[12,13]. Hence, analysis of the $\delta^{18}O$ of tree-ring cellulose offers the potential to reconstruct the year-to-year history of growth temperature and relative humidity in both living and subfossil trees.

The historical assumption in isotope studies of tree rings has been that leaves in the tree canopy were coupled to the ambient environment, and thus that the temperature and relative humidity experienced by the leaf were equal to those of ambient air. However, it has long been established that leaf temperatures can deviate from ambient temperatures because variation in water loss, convective heat loss, and reflectance can increase or decrease leaf temperatures[14,15]. Leaf temperature affects the evaporative gradient from leaf to air because temperature exponentially affects the saturation vapour pressure of water vapour inside the leaf. Hence, any adaptation that leads to a systematic offset between leaf and ambient temperature can cause leaf relative humidity to be markedly different from ambient relative humidity. The effects of leaf morphology, temperature, and water loss on the enrichment of ^{18}O in leaf water have been well documented at the leaf level in a variety of plants[16–19], but these effects have been largely ignored in tree-ring isotope work.

Whereas the $\delta^{18}O$ analysis of individual tree rings permits the reconstruction of year-to-year changes in weather, we proposed that the analysis of entire, homogenized tree rings provide a multi-year or lifespan-integrated measure of tree responses to average climate. We examined α-cellulose $\delta^{18}O$ values from the wood of 39 deciduous and evergreen tree species across 50° of latitude in North America. These samples came from a larger survey of tree-cellulose $\delta^{18}O$ to determine whether the current understanding of tree-cellulose $\delta^{18}O$ formation could explain the increasing offset between cellulose $\delta^{18}O$ and precipitation $\delta^{18}O$ as the mean annual temperature decreased[20]. Expressing observed cellulose ^{18}O as an ^{18}O enrichment above source water ($\Delta^{18}O_c$) removes the well-established temperature effects on the $\delta^{18}O$ of precipitation (and consequently cellulose $\delta^{18}O$) and highlights the distinct biological effects on cellulose $\delta^{18}O$. We found a highly significant and unexpected correlation with MAT, showing that the observed values of cellulose $\Delta^{18}O$ became more and more enriched in ^{18}O above source water as MAT decreased (filled circles in Fig. 1; $F = 844.7$, $P < 0.0001$).

In an attempt to explain this observation, we used a physiological model of isotopes in cellulose, starting from the standard assumption that tree-canopy temperature and relative humidity were coupled to ambient environmental conditions (open squares in Fig. 1). A previous cellulose $\delta^{18}O$ model[19] was parameterized by using long-term climate averages (http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_1961_1990_e.html; http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.CPC/.GSOD/.MONTHLY/) and model estimates of $\delta^{18}O$ in precipitation[7] to develop predictions of $\Delta^{18}O_c$. To be conservative in our predictions, we assumed a 15% error in the use of precipitation $\delta^{18}O$ for tree source water and further allowed for a large range of error in the prediction of leaf-water ^{18}O enrichment and the isotopic exchange factors of the cellulose-isotope model (error bars for predictions in Fig. 1; see Methods for details). With leaf temperature set to ambient temperature, the physiological model could not account for the higher enrichment in observed $\Delta^{18}O_c$ at lower MAT even when considering the range of error in the model (the slope was not significantly different from 0; $F = 2.3160$, $P = 0.1327$). The isotopic exchange or fractionation factors associated with cellulose formation show no change with temperature and are relatively constant across species[2,12]. Although there is some evidence that the

[1]Department of Biology, [2]Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, Pennsylvania 19104, USA.

organic-water fractionation factor may change in enriched plant source water[21], this is the reverse of the pattern observed in colder climates. The most parsimonious conclusion from Fig. 1 is therefore that leaf water becomes more enriched than expected as MAT decreases, and this enrichment is recorded in $\Delta^{18}O_c$. The most likely mechanism to cause greater enrichment is that tree-leaf temperature was generally higher than ambient temperature in colder climates; the inverse must be true for leaf relative humidity.

Recognizing that the disagreement between observed and predicted values of $\Delta^{18}O_c$ in Fig. 1 are most probably due to the assumption of equality of leaf and ambient temperatures during photosynthesis, we developed a novel application in which observed tree-cellulose $\delta^{18}O$ can be used to solve for integrated tree-canopy temperature. Tree-leaf temperatures were determined by using the observed cellulose $\Delta^{18}O_c$ data and climate averages and rearranging the same isotope model[19] to solve for the saturated leaf vapour pressure that satisfied observed $\Delta^{18}O_c$. Saturated water vapour pressure has a well-quantified relationship with temperature; a given saturated vapour pressure therefore yields a unique temperature. The mean tree-leaf temperature for all 39 species across 50° of latitude was 21.4 ± 2.2 °C (grey box in Fig. 2a). We found no significant relationship between leaf temperature and MAT or between leaf temperature and growing-season temperature.

These results suggest that most tree photosynthesis occurred when leaf temperatures were about 21 °C, irrespective of latitude and average growing-season temperatures. The $\delta^{18}O$ in a tree ring inherently represents a whole-canopy integration of leaf-level processes that are weighted towards periods of maximal carbon assimilation. This effective homeostasis of leaf temperatures means that there was a significant elevation of leaf temperatures over mean growing-season temperatures in colder climates and, as a corollary, leaf temperatures that were lower than ambient temperatures in hotter, temperate climates (Fig. 2b). In the subtropical sites, tree-leaf temperatures were much closer to ambient temperatures. The relationship of leaf temperature to ambient temperature holds across closely related congeneric species as well as through the larger phylogenetic groupings of angiosperms and gymnosperms.

The logistical constraints on direct, empirical measurements of integrated tree-canopy temperature for an entire growing season mean that there are few data sets in existence with which to compare our results. However, leaf temperature measurements on individual branches of *Abies*, *Picea* and *Pinus* species in subalpine regions of Wyoming, USA, were 5–9 °C above ambient temperatures during periods of maximal photosynthesis[22]. A recent study using infrared thermal imaging of a temperate mixed forest in Switzerland showed that the temperature of dense tree canopies was 4–5 °C higher than ambient temperature[23], and that of less dense canopies was 0.3–2.7 °C higher than ambient temperature. These observations, although indirect, are in agreement with our resolved relationships between ambient and tree-canopy temperatures (Fig. 2b).

How does leaf temperature control occur? In warmer climates, leaf temperatures are lowered by evaporative cooling and mechanisms that reduce the absorptance of solar radiation such as decreased leaf angles and reflective leaf hairs[14,15]. These adaptations are counterproductive to warming a leaf in colder environments. One established mechanism for elevating tree-leaf temperatures above ambient temperatures is to increase the number of leaves on a given length of branch, thereby increasing the branch boundary layer and consequently decreasing convective heat loss from individual leaves[22,24]. This mechanism has been shown directly in a few coniferous tree branches[22] and indirectly at the canopy scale, where greater canopy density results in greater elevation of canopy temperature over ambient temperature in both needle-leaved and broad-leaved trees[23].

Trees maintain growth and reproduction over a broad climatic spectrum through an array of physiological and morphological adaptations[22,25], yet the idea that these adaptations converge towards leaf-temperature homeostasis across biomes is new. Early work on plant acclimation to prevailing temperatures focused on the temperature range over which CO_2 assimilation was optimal[25,26]. As a general rule, these photosynthetic temperature optima were found to be lower than or equal to growing-season temperatures in hot climates and higher than the ambient temperatures in cold climates. Our results explain this observation over a broad climatic range and further suggest that the overarching trend is to maintain leaves at an optimal temperature irrespective of mean climate.

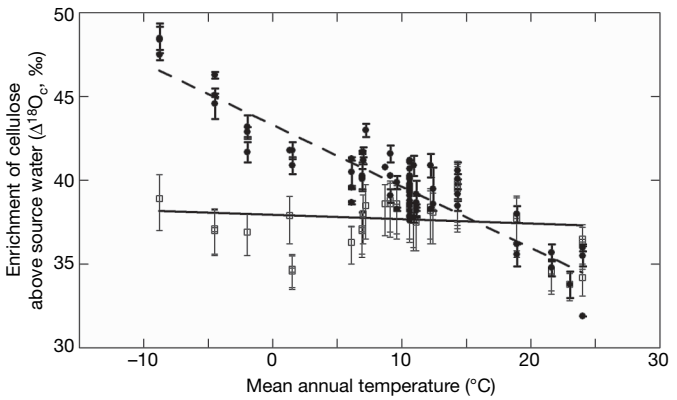

Figure 1 | Plot of predicted and observed cellulose $\Delta^{18}O_c$ against mean annual temperature. For observations of the 39 tree species at 25 sites (filled circles), each point represents a species mean and the error bars indicate the standard deviation for the observations. The predictions (open squares) were based on forcing leaf temperature to equal MAT in the isotope cellulose model[19]. The error bars for the predictions are the upper-end and lower-end predictions using the largest observed ranges in isotopic exchange factors and a ±15% error in plant source water $\delta^{18}O$. Information on species, *n* values, study sites and model estimates can be found in Methods and Supplementary Information.

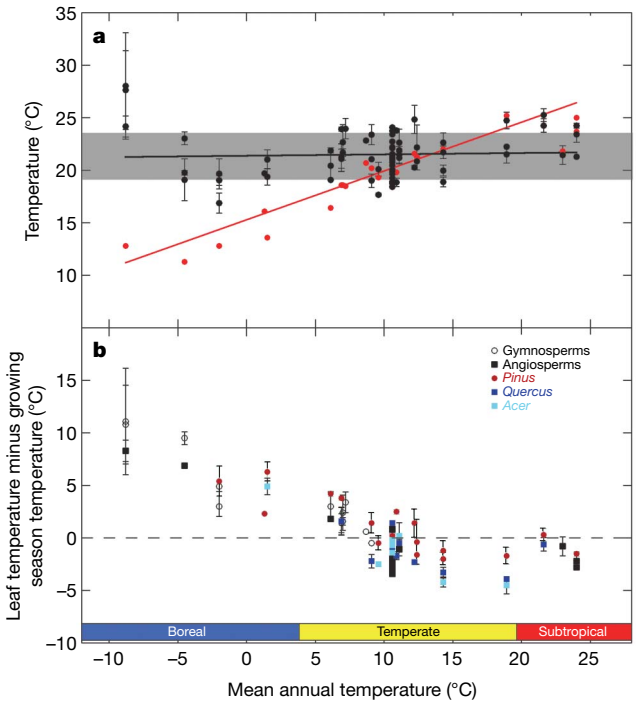

Figure 2 | Resolved tree-canopy temperature versus mean annual temperature. **a**, Leaf temperatures (black) resolved from tree-cellulose $\Delta^{18}O$, and ambient growing-season temperatures (red). The grey box indicates the mean and s.d. of the leaf temperature of all tree species (21.4 ± 2.2 °C). **b**, Plot of integrated tree-leaf temperatures minus ambient growing-season temperatures against mean annual temperature from subtropical to boreal biomes. Error bars indicate s.d.

However, we do not suggest that tree canopies maintain a constant temperature of 21 °C over the course of a day or a season. Rather, we propose that the integrated and apparent homeostatic temperature that our isotope analysis has revealed is more of a long-term target value. Over time, the morphological and physiological characteristics of a tree canopy work to maintain leaf temperatures near that target value within a climatic regime, while the functional plasticity of the photosynthetic apparatus works to maximize carbon uptake in the face of short-term variation in weather. Canopy temperatures can vary drastically in the short term with the vagaries of radiation input caused by clouds, wind speed and the diurnal change in the Sun's angle of incidence. Observed mid-day canopy temperature amplitudes can be as large as 12 °C (ref. 23) and observed temperature-response curves of photosynthesis show a similarly broad range[26]. Within species, photosynthetic temperature optima track changes in ambient temperature with the progression of the growing season. However, there are clear limits, because trees grown at temperatures higher than ambient temperature do indeed show an increase in the photosynthetic temperature optimum above trees grown at ambient conditions, but they also show a much reduced overall growth[27].

The effect of leaf temperature on the difference between leaf and ambient relative humidity has a profound effect on interpretations of $\delta^{18}O$ in plant material. Leaf relative humidity was determined by dividing the saturated vapour pressure at leaf temperature (determined by our isotope analysis) by the ambient vapour pressure from the observed mean climate data. Depending on biome—and even within biomes—the difference between ambient and leaf relative humidity can be significant (Fig. 3). In boreal systems, the differences between leaf and ambient relative humidity were nearly 30%. The broad temperature range encompassed by temperate forested systems makes generalization more difficult, but our data show that ambient relative humidity can be 5–10% above or below leaf relative humidity (Fig. 3). Our analysis shows that reconstructing ambient humidity by using tree-ring $\delta^{18}O$ becomes increasingly dubious as MAT decreases. Caution is therefore advised when interpreting tree-ring $\delta^{18}O$ data from high latitudes for both contemporary samples and samples of relictual wood from high-latitude forests of the past[28]. However, our results proffer a correction for reconstruction, and—perhaps more significantly—the new approach developed here shows that physiological responses to inter-annual temperature variation can be extracted from the $\delta^{18}O$ of tree rings if ambient climatic conditions are known.

Temperature effects on photosynthesis, respiration and water acquisition are primary factors determining tree distribution and will no doubt be of greater concern in the future as global temperatures continue to increase. However, showing specific responses to temperature is a challenging task. Here we have shown that stable-isotope analysis of the α-cellulose in whole-tree cores provides an integration of the responses of both leaf relative humidity and leaf temperature to mean climate. This basic understanding can now be applied to the more rigorous task of analysing inter-annual variation in tree ecophysiological responses to the vagaries of weather as climate has changed over the past century.

The discovery of relatively invariant leaf temperatures has two important ramifications that transcend stable-isotope studies. First, elevated canopy temperature and depressed leaf relative humidity should have a large effect on real and modelled water loss from boreal ecosystems. Second, if the architectural controls of branches on leaf temperature are as widespread as our data suggest, then direct climatic selection on the evolution of leaf traits would be relaxed, whereas the selective force of climate on other plant organs (for example stems and roots) would remain. Our results therefore offer a possible explanation for the unexpected finding[5] that climate is a minor correlate with global leaf economic traits. We propose that climatic constraints on other components of plant function, such as the avoidance of and recovery from xylem cavitation by freezing or the balance between canopy photosynthesis and stem/root respiration, could be more important for tree distribution in colder environments. Finally, the branch morphological characteristics that serve to raise leaf temperatures above ambient temperature in cold environments would inherently limit tree performance and hence distribution in warmer areas and, significantly, in areas where warming is expected to increase.

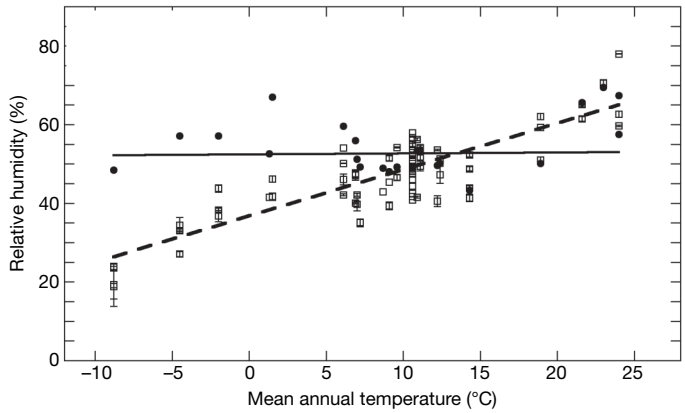

Figure 3 | Comparison of ambient and canopy-based relative humidity. Relative humidity with respect to the leaf (ambient water vapour pressure divided by saturation water vapour pressure at leaf temperature) determined from tree-ring $\Delta^{18}O$ (open squares) and ambient relative humidity (ambient water vapour pressure divided by saturation water vapour pressure at ambient temperature) during the growing season (filled circles). Error bars indicate s.d. of the resolved leaf relative humidity.

METHODS SUMMARY

Sampling and isotope analysis. Tree-ring wood was from a larger meta-analysis[20] of tree cellulose $\delta^{18}O$ (see Table S1 in Supplementary Information and Full Methods). The samples and sites were chosen on the basis of precipitation patterns and climate data availability. The wood was ground, homogenized and α-cellulose was extracted and pyrolysed at 1100 °C. The resulting CO gas was analysed in a Thermo-Finnigan Delta Plus isotope ratio mass spectrometer. All samples were run in triplicate; the standard deviation of the primary referece was 0.23‰. Isotope ratios (δ) were expressed relative to Vienna Standard Mean Ocean Water (VSMOW) by

$$\delta^{18}O = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1{,}000 \quad (1)$$

where R_{sample} is the number isotope ratio of $^{18}O/^{16}O$ and $R_{standard}$ (VSMOW) = 0.0020052.

Isotope discrimination above tree source water was expressed as

$$\Delta = \left(\frac{R_{sample}}{R_{source}} - 1\right) \times 1{,}000 \quad (2)$$

(approximated by $\delta^{18}O_{sample} - \delta^{18}O_{source}$), where R is the molar isotope ratio of either the cellulose or the tree source water.

Model parameterization. To develop predictions for $\Delta^{18}O_c$ we used the average of published observations for the isotope exchange values and used the range of these observations to develop a range of predictions (error bars in Fig. 1; see also Supplementary Table 2). Tree source water was assumed to be equal to precipitation-weighted model outputs[7]. For Fig. 1, leaf temperature was assumed to be equal to ambient temperature and we used observed relative humidity ($= 100 \times e_a/e_i$). Tree-canopy leaf temperature (T_L) was obtained by rearranging the isotope cellulose model to solve for the leaf saturated vapour pressure (e_i). T_L was obtained from e_i by rearranging a standard vapour–pressure–temperature relationship. For all models we used monthly mean temperature and relative humidity, weighted by net primary productivity and growing season length.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

Received 10 March; accepted 28 April 2008.
Published online 11 June 2008.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank A. H. Johnson for discussion of the results; D. Vann and M. Dranoff for help with analysis; and B. Casper, P. Petraitis and D. Brisson for comments on the manuscript. This work was supported by a start-up grant from the University of Pennsylvania and a grant from the A.W. Mellon Foundation.

Author Contributions S.L.R. developed the framework for the sampling scheme and analysed the tree-ring cores. B.R.H. developed the framework for the modelling analysis and wrote the majority of the paper. Both authors discussed the results and commented on the manuscript.

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METHODS

Tree species and isotope analysis. Tree-ring wood was obtained from 39 species at 25 sites (see Supplementary Table 1) in eastern North America and the Caribbean. The samples and sites were pulled from a larger meta-analysis[20] of tree-cellulose $\delta^{18}O$ based on nearly equal distribution of summer and winter precipitation to satisfy our assumption that, over the lifetime of a tree, the precipitation-amount-weighted mean of $\delta^{18}O$ was equal to water available for plant uptake ($\delta^{18}O_s$). All sample sites were chosen by the availability of class A climate data from nearby weather stations at similar altitudes. The cores were ground, homogenized and α-cellulose was extracted from a 0.2–0.3-g subsample with a 90:10 mixture of acetic acid (80%; v/v) and nitric acid (69%; v/v) at 120 °C for 2 h. Samples were then washed in ethanol and subsequent ethanol–acetone washes[29]. Additionally, the samples were rinsed with 10% and then 17% NaOH to remove hemicelluloses[27]. Samples were weighed into silver capsules and pyrolysed at 1,100 °C in a Costech Elemental Analyser. The CO gas evolved flowed online into a Thermo-Finnigan Delta Plus isotope ratio mass spectrometer. All samples were run in triplicate. Daily precision of the instrument ranged from 0.06 to 0.35‰, and the standard deviation for reference standards was 0.23‰ ($n = 83$). Isotope ratios (δ) were expressed relative to Vienna Standard Mean Ocean Water (VSMOW) by

$$\delta^{18}O = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1{,}000 \quad (1)$$

where R is the molar isotope ratio of $^{18}O/^{16}O$ and $R_{standard}$ (VSMOW) = 0.0020052.

Isotope discrimination above local precipitation water (the assumed tree source water) was expressed as

$$\Delta = \left(\frac{R_{sample}}{R_{source}} - 1\right) \times 1{,}000 \quad (2)$$

(approximated by $\delta^{18}O_{sample} - \delta^{18}O_{source}$), where R is the molar isotope ratio of either the cellulose or tree source water.

Theory. A previous cellulose $\delta^{18}O$ model[19] was used to predict $\Delta^{18}O_c$ (see Fig. 1):

$$\Delta^{18}O_c = \Delta^{18}O_{lw}(1 - p_{ex}p_x) + \varepsilon_c \quad (3)$$

where $\Delta^{18}O_{lw}$ is the $\delta^{18}O$ of leaf water (relative to plant source water) in which the sucrose substrates for cellulose are synthesized, ε_c is the equilibrium fractionation factor between organically bound oxygen and synthesis water, p_{ex} is the number of organically bound oxygen atoms in leaf-formed sucrose that exchange with xylem water on cellulose formation during tree-ring synthesis (range 0 to 1) and p_x is the proportional deviation of the isotope ratio of xylem water from plant source water (range 0 to 1).

The isotope ratio of water in which the sucrose substrates for cellulose are synthesized ($\Delta^{18}O_{lw}$) is a balance of enriched water at the evaporative site ($\Delta^{18}O_{es}$) and unenriched vein water in the leaf. This balance can be described by a Péclet effect ($\wp = LE/CD$) that accounts for the opposing fluxes of evaporative, convective flux through the leaf (E) across a given path length (L) as opposed to the diffusion of water away from the evaporative sites (CD, where C is the molar density of water and D is the diffusivity of $H_2{}^{18}O$ in water):

$$\Delta^{18}O_{lw} = [\Delta^{18}O_{es}(1 - e^{-\wp})]/\wp \quad (4)$$

The description of ^{18}O enrichment in leaf water at the evaporative site within a leaf can be described by

$$\Delta^{18}O_{es} = \varepsilon^* + \varepsilon^k\left(\Delta^{18}O_v - \varepsilon^k\right)\frac{e_a}{e_i} \quad (5)$$

(refs 30, 31), where $\Delta^{18}O_v$ is the atmospheric water vapour $\delta^{18}O$ relative to source water and ε^k and ε^* are the kinetic and temperature-dependent equilibrium fractionation factors for water (vapour) diffusion and evaporation. The evaporative gradient of water loss from the leaf to the atmosphere is represented by e_a/e_i, which is the ambient vapour pressure divided by the saturation vapour pressure at leaf temperature.

To solve for tree-canopy leaf temperature (T_L) from the observed cellulose $\Delta^{18}O_c$, equations (4) and (5) were inserted into equation (3), which was rearranged to solve for e_i:

$$e_i = \frac{\left(\Delta^{18}O_v - \varepsilon^k\right)e_a}{\left(\frac{\left(\Delta^{18}O_c - \varepsilon_c\right)\wp}{(1 - p_{ex}p_x)(1 - e^{-\wp})}\right) - \varepsilon^* - \varepsilon^k} \quad (6)$$

T_L was obtained from e_i by rearranging a standard vapour–pressure–temperature relationship[32]:

$$T_L = \frac{240.97\left(\ln\frac{e_i}{0.61365}\right)}{17.502 - \left(\ln\frac{e_i}{0.61365}\right)} \quad (7)$$

Model parameterization. To develop predictions for $\Delta^{18}O_c$ (open squares in Fig. 1) we used the average of published observations for the parameters in equations (1)–(3) and used the range of these observations to develop the largest possible range of predictions (error bars in Fig. 1; see also Supplementary Table 1). The oxygen isotope ratio of observed and predicted cellulose ($\Delta^{18}O_c$) were presented relative to tree source water to highlight tree-specific isotopic enrichment above a common source water at a given site. Tree source water was assumed to be equal to the precipitation-weighted model outputs in ref. 7. These model outputs are based on observations from the Global Network of Isotopes in Precipitation (http://isohis.iaea.org) and have been shown to correspond well to the observed $\delta^{18}O$ in tree source water over a variety of sites[21]. To develop a range for source water inputs, we assumed a ±15% error in this source water value. We used $p_{ex}p_x = 0.4$ and $\varepsilon_C = 27$‰ (refs 2, 12, 33) and varied $p_{ex}p_x$ from 0.38 to 0.42, the range observed for trees in both tightly controlled greenhouse conditions and natural field conditions. The average atmospheric water vapour $\delta^{18}O$ relative to source water ($\Delta^{18}O_v$) was determined by assuming equilibrium with amount-weighted precipitation inputs ($\delta^{18}O_s$) at the mean growing-season temperature. As temperature varies seasonally, the equilibrium fractionation between precipitation water and water vapour will change, therefore the value of $\Delta^{18}O_v$ important to leaf water enrichment should correspond to growing-season temperatures. To determine the Péclet number ($\wp$) for each species we had to determine a value for transpiration E and the effective path length for diffusion L. We solved for E using $E = g\,(e_i - e_a)/P$, where g is stomatal conductance to water vapour and P is atmospheric pressure. The value of g was obtained from global estimates by biome and within a biome by gymnosperm versus angiosperm[34], weather-station relative humidity was used to determine e_i and e_a, and P was determined by sample site altitude. Observed values of L have ranged from 0.004 to 0.240 mm. However, studies that have determined L from sucrose $\delta^{18}O$, and not just the offset of observed bulk leaf water from predictions of equation (3), have found L to be consistently smaller than the high end of this range. We used a value for L of 0.015 m and a range of 0.004–0.05 m. For our predictions in Fig. 1, we assumed that leaf temperature equalled ambient temperature and e_a/e_i could be obtained from observed relative humidity ($= 100 \times e_a/e_i$). We used growing season values of monthly mean temperature and relative humidity from the weather-station data, weighted by monthly net primary productivity, to drive the models. For a particular site the growing season length was determined by estimates of growing degree days[35]. It should be noted that predicted cellulose and leaf temperature values vary little if only the monthly means of July and August are used for growing-season temperature at each site. In summary, the error bars for the predictions in Fig. 1 are the upper-end and lower-end predictions using the following ranges: $p_{ex}p_x = 0.38$–0.42 and $L = 0.004$–0.05 mm, given a ±15% error in $\delta^{18}O$ in plant source water.

We first solved for e_i (and subsequently T_L) by using growing-season air temperature as the initial determinant of ε^*—the only temperature-controlled variable on the right-hand-side of equation (6). The initial calculation of T_L was then used to determine ε^* for the second iterative determination of e_i and T_L. Four iterations were performed to arrive at the final T_L. On average, T_L differed by 0.3 °C from the final value after the second iteration and by 0.03 °C after the third iteration. It should be noted that changes in e_i would force changes in plant transpiration (E) because we used a constant canopy conductance to water vapour. Such a change in E could force a change in the Péclet number, $\wp$. However, we maintained a constant $\wp$ to solve for canopy leaf temperature because updating E and $\wp$ at every iterative step for every species and site was computationally difficult. We did, however, perform this exercise with a few select species and found no significant difference between solved values of T_L.

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