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Earth and Planetary Science Letters 218 (2004) 301–316

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Resolving seasonality in tropical trees: multi-decade, high-resolution oxygen and carbon isotope records from Indonesia and Thailand

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Received 16 June 2003; received in revised form 27 October 2003; accepted 4 November 2003

Abstract

Dendrochronological techniques have found limited applications in the tropics because of invisible or indistinct banding in wood. The seasonal cycles of rainfall and relative humidity in these regions, while not sufficient to produce distinct visible rings, may still generate seasonal signals in the oxygen isotopic composition of tree cellulose which can be used for climate reconstruction and chronology. We explore this approach using trees from Indonesia and Thailand, from three different families. Multi-decade $\delta^{18}\text{O}$ records from Javanese cross-dated teak rings and bomb radiocarbon-dated Suar wood lacking visible rings demonstrate the reproducibility of the signal between trees grown at the same locality as well as from wider geographical regions. These results confirm predictions that the trees oxygen isotopic signatures reflect an external climatic forcing. High-resolution $\delta^{18}\text{O}$ records reveal large seasonal cycles: up to 4‰ for Javanese Suar samples and up to 18‰ for a Thai *Podocarpus* sample. We show that the six $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ cycles measured on a *Podocarpus* match the number of growth years for the period spanning the time of wounding and cutting of the wedge section. This result demonstrates that the isotopic cycles found in this tree with indistinct annual rings are indeed seasonal and could be used for chronology. We present evidence that stable isotope chronologies of tropical trees also contain insights in tropical tree physiology and growth dynamics.

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Keywords: oxygen isotopes; carbon isotopes; cellulose; dendrochronology; dendroclimatology

1. Introduction

Patterns of tropical climate variability observed over the past two decades have led some scientists to suggest that the climate of this region is being

affected by anthropogenic climate change [1]. Others have attributed these patterns to natural variability on decadal time scales [2]. Because the tropics appear to play an important role in global climate [3–5], it is critical that we reconstruct patterns of natural variability over the last several centuries.

One approach to reconstruction of natural climate variability involves the generation and statistical analysis of multi-century climate records.

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Unfortunately, only a very small number of locations around the world have instrumental weather records extending back more than a century and most of them are confined to Europe and eastern North America [6]. Proxy records from the tropics, such as those derived from corals, ice cores, varved sediments and speleothems have yielded valuable information about the climate history of the tropical Pacific [7–10] (see fig. 1 of [11]). However, the scarcity of sub-annually resolved climate proxies from tropical locales has impeded assessment of tropical climate evolution over the past few centuries, particularly in terrestrial environments.

Reliable chronologies derived from dendrochronological methods have been few in the tropics. The general absence of anatomically distinct annual growth rings and/or obstacles posed by discontinuous banding and presence of false rings in many tropical tree species make accurate age-modeling difficult [12]. In this paper, we review the theoretical framework and demonstrate an application of tropical isotope dendroclimatology to samples from the forests of Indonesia and Thailand. This strategy exploits the pronounced seasonality of tropical rainfall and humidity, expressed in the oxygen isotopic composition of tree cellulose, to produce seasonally resolved climatic records from tropical woods. In addition, we use carbon isotope data, sample cross-dating, bomb radiocarbon measurements, and known wounding/cutting dates to test the hypothesized stable isotopic chronometer. From these multi-decadal modern records, we discuss the potentials and limitations of this method to yield insights about tropical plant ecophysiology and growth dynamics as well as help close paleo-observational gaps in the forests of southeast Asia.

2. Controls on the stable isotopic composition of tropical wood

The idea of using light stable isotopic signals contained in tree cellulose as recorders of climate was first put forward by Urey [13] when he observed that the $\delta^{13}\text{C}$ of wood varied with environmental air temperature. Three decades later, Epstein et al. [14] suggested that just as the isotopic composition of meteoric water varied with meridional temperature changes, so should the hydrogen isotopic composition of biological systems vary with climate. The idea has since been confirmed in many studies using δD , $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tree cellulose. In this section, we review two models which describe the physical and biochemical pathways taken by the oxygen and carbon isotopes during their incorporation into biomass. Because the trees used for reconstruction were not located close to meteorological stations, we do not have access to sufficient environmental data to quantitatively interpret our data using such models. However, they are useful for understanding how the data we measure can be related to environmental variables.

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2.1. $\delta^{18}\text{O}$ model

Of the three possible sources of oxygen for photosynthetically produced carbohydrates (H_2O , CO_2 and O_2), only the isotopic signature of H_2O is imprinted on the final cellulose product [15–18]. An isotopic mass balance for $\delta^{18}\text{O}$ of tree cellulose is described in Eq. 1 (e.g. [19]), where $\delta^{18}\text{O}_{\text{cx}}$, $\delta^{18}\text{O}_{\text{wx}}$ and $\delta^{18}\text{O}_{\text{wl}}$ correspond to the xylem cellulose, xylem water and leaf water isotopic compositions, respectively, f_o represents the fraction of the carbon-bound oxygen that gets exchanged with medium water (~ 0.42) and ϵ_o is the biochemical fractionation factor ($+27\text{‰}$) [20].

$$\delta^{18}\text{O}_{\text{cx}} = f_o \cdot (\delta^{18}\text{O}_{\text{wx}} + \epsilon_o) + (1 - f_o) \cdot (\delta^{18}\text{O}_{\text{wl}} + \epsilon_o) \quad (1)$$

2.1.1. Effect of source water

At tropical latitudes, Dansgaard [21] observed an inverse relationship between the $\delta^{18}\text{O}_{\text{rain}}$ and the amount of rain (low/high during the wet/dry season, with as much as a 15‰ amplitude). The model described in Eq. 1 implies that such seasonality in the $\delta^{18}\text{O}_{\text{rain}}$ will get recorded in tropical trees which use soil water for their growth [11]. Here, the terms soil water and groundwater refer to the water fractions located above and below the water table, respectively. The amplitude of this signal will be dampened for large trees

(> 10 m) because they tend to rely more heavily on groundwaters which may have residence times long enough to mask the seasonality in the signal [22]. $\delta^{18}\text{O}_{\text{wx}}$ represents a mixture of soil water and groundwater for which the proportions may vary throughout the growing season. Soil water isotopic composition should reflect that of rainfall but could be altered due to evaporative enrichment at the soil surface. There is generally no fractionation associated with water uptake at the roots [23].

2.1.2. Effect of leaf water enrichment

The model developed by Craig and Gordon [24] describes two isotopic fractionation effects associated with the process of evaporation over an open water surface: an equilibrium effect associated with the phase change from liquid water to vapor (liquid phase gets enriched because the H_2^{18}O molecule has a lower vapor pressure than H_2^{16}O ($\epsilon_e = 9.8\%$ at 20°C [25]) and a kinetic effect caused by the slower diffusion rate of the heavier H_2^{18}O molecule compared to H_2^{16}O . This evaporative enrichment model has been modified by Dongmann and Nürnberg [26] and Flanagan et al. [27] to account for evaporation taking place at the leaf surface (Eq. 2). The extent of leaf water enrichment depends on the equilibrium (α^*) and kinetic fractionation (α_k (air) and α_{kb} (boundary layer)) effects mentioned above, the ratio of the water vapor partial pressures in the atmosphere (e_a), intercellular air space (e_i) and leaf surface (e_s), and the oxygen isotope ratio of water vapor in the air (R_a).

$$R_{\text{wl}} = \alpha^* \left[\alpha_k R_{\text{wx}} \left(\frac{e_i - e_s}{e_i} \right) + \alpha_{\text{kb}} R_{\text{wx}} \left(\frac{e_s - e_a}{e_i} \right) + R_a \left(\frac{e_a}{e_i} \right) \right] \quad (2)$$

As discussed by Flanagan et al. [27] and Barbour et al. [28,29], Eq. 2 predicts a greater leaf water enrichment than is generally observed. This discrepancy results from a Péclet effect, whereby the backward diffusion of H_2^{18}O molecules collecting at the site of evaporation is opposed by the convection of unfractionated water traveling the transpiration stream [28]. The Péclet effect ex-

plains why the discrepancy increases as transpiration rates increase.

Assuming that tree growth spans a period long enough to be affected by the seasonal variations in relative humidity (RH) and that intra-seasonal carbohydrate transfer is negligible, high-resolution measurements of $\delta^{18}\text{O}$ of tropical tree cellulose should reflect the sub-annual pulsing of wet/dry climate of the tropics [11]. In addition, because much of the climate variability that characterizes tropical latitudes occurs over interannual time scales (ENSO, southeast Asian monsoon), these records should be sensitive to these events as they are themselves amplifications of a seasonal-like cycle and should be independent of the occurrence of annual growth rings. Given the variety of tree physiologies, water uptake patterns and root structures found in tropical forests, we expect that relating the precipitation amount and RH to the xylem water and cellulose isotopic composition may in some cases be masked by species-specific effects.

2.2. $\delta^{13}\text{C}$ model

As opposed to the more recent development of oxygen isotope models for plant biomass, the incorporation of carbon isotopes into plants has been studied and modeled for over two decades [30,31]. Eq. 3 summarizes these findings for cellulose produced in C_3 plants. The model illustrates how the carbon isotopic composition of cellulose ($\delta^{13}\text{C}_{\text{cx}}$) is related to that of air ($\delta^{13}\text{C}_a = -7.8\%$ with seasonal variations of $0.4\text{--}0.6\%$ in tropical latitudes [32]), to the fractionation effect related to diffusion of CO_2 through the stomatal pores ($a = 4.4\%$), to isotopic discrimination by the Rubisco enzyme (ribulose biphosphate carboxylase-oxygenase) during carbon fixation ($b = 27\%$) and to the ratio of CO_2 concentrations inside (c_i) and outside (c_a) the leaf. The biochemical fractionation factor (ϵ_b) accounts for post-photosynthetic fractionation effects ($2\text{--}5\%$) [33,34]. Because the c_i/c_a ratio depends on rates of CO_2 fixation (A) as well as stomatal conductance (g_s) (Eq. 4), seasonal variations in $\delta^{13}\text{C}_{\text{cx}}$ will reflect changes in light and moisture availability [35,36] in addition to seasonal changes in $\delta^{13}\text{C}_a$.

$$\delta^{13}\text{C}_{\text{cx}} = \delta^{13}\text{C}_a - a - (b-a)c_i/c_a + \varepsilon_b \quad (3)$$

$$c_i = c_a - A/g_s \quad (4)$$

3. Methods

3.1. Sample descriptions, locations and climatologies

3.1.1. *Tectona grandis*

Two 5 mm wide teak sample cores (SA02A and SA06A) were prepared for isotopic analysis and spanned the period from 1950 to 1990. These samples were collected from a site in Saradan, central-east Java (111°33'E, 7°27'S – 54 km east of the town of Madiun), as shown in Fig. 1a. Precipitation records from Kajoemas (114°20'E, 7°9'S) to the northeast show a large seasonal cycle, which oscillates between a dry season (east monsoon), persisting from May to October and a wet season (west monsoon) (Fig. 1b). Mean annual precipitation is 210 cm/year. As shown by Jacoby and D'Arrigo [37], the intensity of the dry season increases along a west to east gradient on Java (dry season is drier in the east). As both the length of the previous year dry season as well as the amount of precipitation that fell during this period are critical parameters controlling teak growth [37], teak trees from the Saradan site are particularly sensitive to changes in climatic conditions. Several east Java chronologies have in fact shown significant positive correlations with the southern oscillation index (SOI) for the months covering the dry season [38,39].

3.1.2. *Samanea saman*

The Javanese samples Suar1 and Suar3 were collected in a lumber yard on the island of Bali.

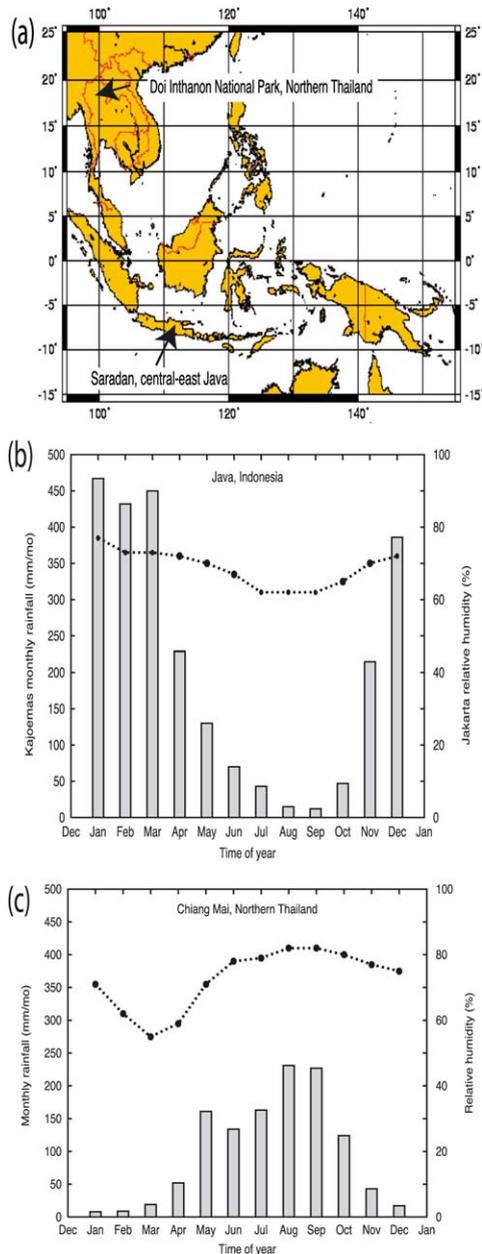


Fig. 1. (a) Sampling locations for Indonesian samples: *T. grandis* (teak) from Saradan, Java (111°33'E, 7°27'S) and *S. saman* (Suar) from Java (unknown exact location) and Thai sample: *P. neriifolius* from Doi Inthanon National Park (DOI), Chiang Mai Province (98°30'E, 18°30'N). (b) Climatic setting of Java, Indonesia showing seasonality in precipitation (bars) and RH (dotted line). Mean annual rainfall in Kajoemas 210 cm/year, 4 months long dry season (with monthly rainfall < 50 cm), monthly minimum RH 62% and maximum RH 77%. (c) Same as (b) but for Chiang Mai, northern Thailand. Mean annual rainfall 100 cm/year, 6 months long dry season, monthly minimum RH 55% and maximum RH 82%. Sample from DOI collected above 1000 m elevation.

Because their exact growth locations on Java are unknown, we construct a spatially averaged seasonal rainfall anomaly index (FMAM, JJAS, ONDJ) (Fig. 5d) based on a calculated 1970–2003 climatology using the Xie and Arkin [40] merged raingauge and satellite data analysis in the region 109–124°E and 11°30'S and 4°30'N. While the radial sections of the samples show a clear boundary between the heartwood and sapwood, they have no well-defined annual rings. These specimens enabled us to test whether the high-resolution oxygen and carbon isotopic records were reproducible between trees of the same species and which did not produce annual rings.

3.1.3. *Podocarpus neriifolius*

A wedge section from a *Podocarpus* collected in the Doi Inthanon National Park (Chiang Mai Province, northern Thailand (98°30'E, 18°30'N – DIN99W Fig. 1a) was prepared for high-resolution isotopic analysis. As described by Kripalani et al. [41], the climate of northern Thailand undergoes two monsoons: a southwest (summer) monsoon, which originates in the Bay of Bengal and Indian Ocean and which brings most of the annual rainfall during the months of May to October and a northeast (winter) monsoon which is characterized by the cool and dry air of the Siberian High during the months of November through February. This monsoonal seasonality is illustrated in Fig. 1c. The section bared a visible scar from coring in October of 1992 and the wedge was cut around the old core wound in February of 1999. This sample offered a unique opportunity to look for an oxygen/carbon isotopic chronometer in a tropical tree with no well-defined growth rings and where the period of growth was independently known.

3.2. High-resolution sampling

High-resolution sampling of the Javanese teak samples (SA02A and SA06A) consisted of manually separating individual rings using a rotary microtome (Spencer Lens Co). The sequentially recovered wood slivers (25 μm) were combined in order to obtain eight equal segments per year

of growth for the period spanning 1950–1990. Because growth rates vary throughout the year, individual sub-annual samples do not represent equal lengths of time [42]. A thin core was cut from the Thai *P. neriifolius* cross-section (DIN99W) which intercepted the site of wounding in October of 1992 and extended to the time of felling of the tree in February of 1999. Banding was discontinuous and therefore unreliable as a sampling guide. Assuming constant annual growth rates throughout the 6 years period, the 20 cm long core was subdivided into 360 μm thick segments in order to recover approximately eight samples per year. The 25 μm thick wood slivers were finely chopped to facilitate the breakdown of the wood during the α -cellulose extraction. For the Suar samples, we used a drill-press with 1 mm outer diameter (o.d.) dentistry drill bits to incrementally recover wood powder from the tree sections.

3.3. Modified α -cellulose extraction

Whole wood is made primarily of cellulose, lignins, waxes, fats, oils and resins. The lignin to cellulose ratio is not constant across a growth ring [43] and can vary from one year to the next [44]. As noted by Kozłowski [45], the cellulose in xylem cells is produced throughout the growing season while the lignin component is often postponed until later in the season. For high-resolution analysis, it is particularly critical that the sample be isotopically homogeneous and that it represents the specific time at which it was produced. For these reasons and because cellulose has a high resistance to chemical and enzymatic degradation, efforts have converged towards using cellulose for oxygen isotopic analysis. We have extracted over 2000 individual wood samples to α -cellulose using a modified Brendel et al. [46] method [11]. The extraction involves soaking the wood samples in a 10:1 mixture of acetic (80%) and nitric (69%) acid at 120°C for 30 min in 1.5 ml polypropylene tubes, followed by a series of rinses using ethanol, deionized water and acetone to remove any breakdown products and facilitate sample dehydration. The samples are then dried in an oven for 30 min at 70°C and further dried in

a vacuum desiccator overnight. The procedure results in very little sample loss and over 100 individual samples (< 1.5 mg) can be extracted in one day. Although tedious, the chemistry is straightforward and can be easily accomplished using minimum laboratory equipment. As reported by Evans and Schrag [11], the external precision of $\delta^{18}\text{O}$ measurements on an in-house wood standard is 0.25‰ ($n=60$), which is comparable to the analytical precision of the mass spectrometer.

3.4. Oxygen and carbon isotopic measurement on continuous flow isotope ratio mass spectrometer (CF-IRMS)

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of α -cellulose samples were measured using a CF-IRMS. The inlet system for the $\delta^{18}\text{O}$ measurements consists of a temperature conversion elemental analyzer (TCEA) connected to a Delta^{plus} XL mass spectrometer via an open split interface (CONFLO II, Finnigan MAT). The system is continuously flushed by high-purity He (99.999%) at about 80 ml/min. The samples (between 80 and 180 μg) are loaded into silver capsules which are manually crimped to exclude air, introduced into the TCEA reactor where they get pyrolyzed at 1450°C , converted into CO and separated from N_2 using a gas chromatograph (GC) column (molecular sieve 5A). Internal precision of the instrument ($\bar{\sigma}$) is routinely less than 0.1‰ . Individual measurements take less than 6 min to analyze and external precision on our Baker cellulose standard varied from one reactor to another ($\bar{\sigma}=0.3\text{‰}$), requiring a reactor change after 250 samples. A Carlo Erba nitrogen analyzer 1500 inlet system was used for the $\delta^{13}\text{C}$ measurements where the cellulose samples (80–180 μg), loaded in tin capsules, are introduced to a combustion reactor temporarily enriched in oxygen and kept at 1020°C . After a flash combustion catalyzed by the tin, the cellulose is oxidized as it passes through chromium oxide and silvered cobaltous cobaltic oxide. The combustion products are subsequently carried by a constant stream of He into a reduction reactor made up of metallic copper kept at 650°C , a magnesium perchlorate water trap and a GC column before the resulting CO_2 enters the mass spectrometer. Individual

measurements take less than 7 min to analyze and external precision ($\bar{\sigma}$) on our Baker cellulose standard averages to less than 0.1‰ , requiring a reactor change after 800 samples.

3.5. Radiocarbon measurements on AMS

The Suar isotopic age model is constrained by bomb radiocarbon measurements made on 3 mg samples of α -cellulose. Prepared samples were combusted at 900°C in evacuated quartz tubes using 2 g of a 1:3 mixture of copper:copper oxide. The resulting CO_2 was cryogenically separated in a vacuum line and sent for analysis to the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory. We converted the $\Delta^{14}\text{C}$ data ($\pm 4.5\text{‰}$) to age estimates using an exponential decay curve fitted to atmospheric and tree ring $\Delta^{14}\text{C}$ measurements [47].

4. Results

4.1. Indonesian trees with rings: *T. grandis*

The two 40 year long high-resolution $\delta^{18}\text{O}$ records generated from the Saradan teak cores show large sub-annual isotopic variations (up to 7.0‰ for SA02A in 1974, 1983 and 1989 (Fig. 2) and up to 4.8‰ for SA06A in 1960, 1969 and 1982 (Fig. 3)). The age model is defined by the onset and termination of teak growth in Indonesia from October to May [48]. This roughly coincides with the rainy season. Although the average annual $\delta^{18}\text{O}$ values (26.2‰ for SA02A and 25.8‰ for SA06A) are not statistically different ($P=0.123$), the $\delta^{18}\text{O}$ seasonal amplitude for SA02A (3.8‰) is significantly greater than for SA06A (2.8‰) ($P=0.0006$). In addition, the seasonal $\delta^{18}\text{O}$ variations are on average between two and three times greater than those measured in the $\delta^{13}\text{C}$ records. Although the high-resolution $\delta^{18}\text{O}$ data are noisy, typical seasonal patterns are observed. These include a maximum early on in the growing season, followed by a gradual decrease and often a sharp increase towards the end of the ring. As for the $\delta^{13}\text{C}$ cycles, they are

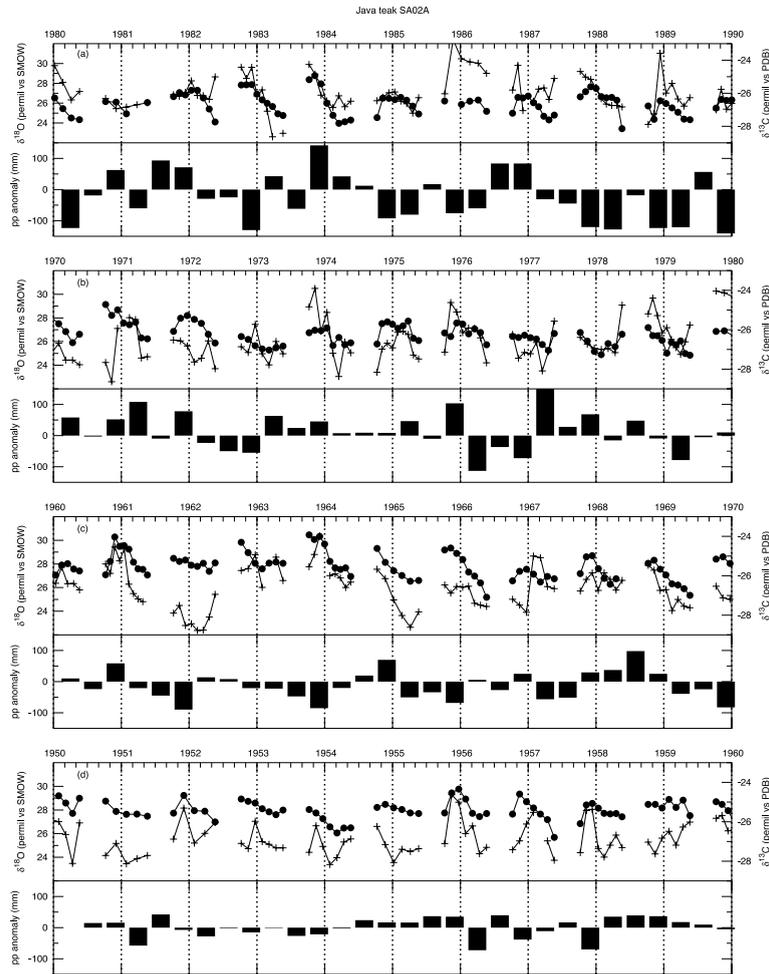


Fig. 2. Comparison of the $\delta^{18}\text{O}$ (crosses) with $\delta^{13}\text{C}$ (filled circles) records for the teak SA02A. Sub-annual samples within individual rings represent equivalent growth increments but may not reflect equivalent time increments as growth rates are likely to vary throughout the year. The age model is based on the fact that most of the teak growth in Indonesia occurs during the rainy season, from October to May [48]. Seasonal precipitation anomalies (FMAM, JJAS, ONDJ) centered on the region 111°E and 7°S [64].

often much better defined than their oxygen counterpart and typically begin with a brief increase in the carbon isotopic values during the early part of the growth season followed by an average decrease of about 1‰ during the remainder of the growth season (but can be as much as 3‰ (1984-SA02A)) (Figs. 2 and 3). A comparison between the SA02A and SA06A annually averaged $\delta^{18}\text{O}$ shows a correlation ($r=0.40$, $P=0.005$) over the length of the record and is improved to $r=0.69$ ($P<0.0001$) over the period of 1950–1980 (Fig. 4a). Maxima (minima) annual mean $\delta^{18}\text{O}$ values

were 29.8 (23.4)‰ for SA02A in 1986 (1962) and 27.6 (23.8)‰ for SA06A in 1980 (1983). There is no significant correlation between the two annually averaged $\delta^{13}\text{C}$ records (Fig. 4b).

4.2. Indonesian trees with no rings: *S. saman*

Results from the high-resolution sampling of Suar1 and Suar3 reveal large $\delta^{18}\text{O}$ variations (up to 4‰) (Fig. 5a). A series of samples were analyzed for their radiocarbon content in an attempt to frame the period for which the variations were

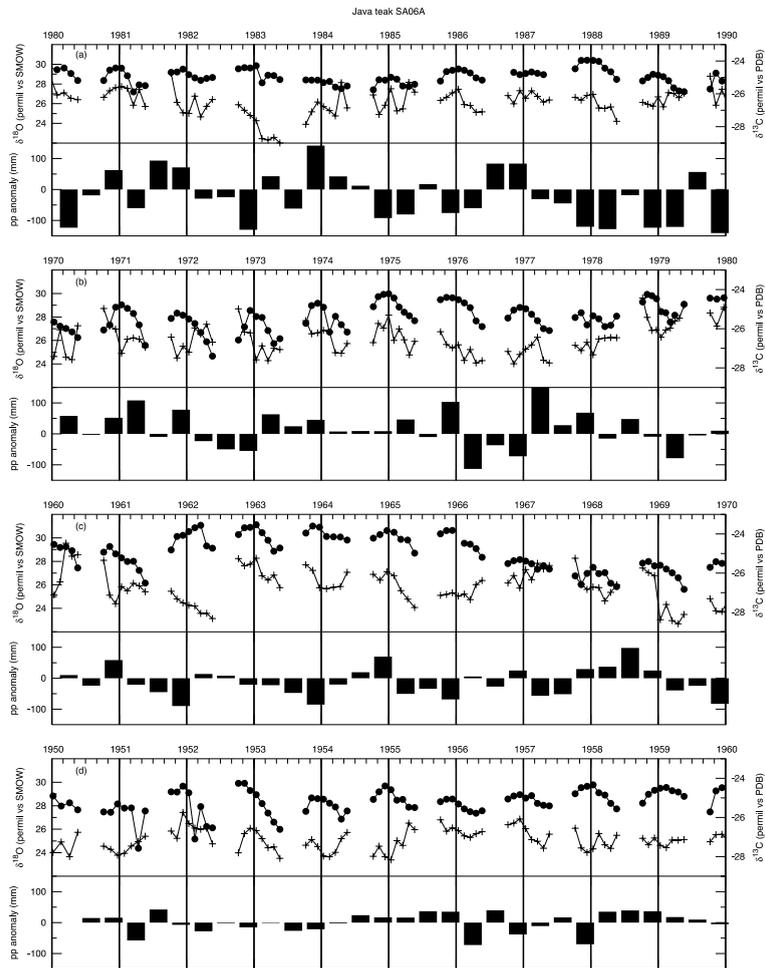


Fig. 3. Comparison of the $\delta^{18}\text{O}$ (crosses) with $\delta^{13}\text{C}$ (filled circles) records for the teak SA06A. Sub-annual samples within individual rings represent equivalent growth increments but may not reflect equivalent time increments as growth rates are likely to vary throughout the year. The age model is based on the fact that most of the teak growth in Indonesia occurs during the rainy season, from October to May [48]. Seasonal precipitation anomalies (FMAM, JJAS, ONDJ) centered on the region 111°E and 7°S [64].

observed and determine whether they were seasonal. The age model shown in Fig. 5 spans the period from 1978 to 1998 and is based on two radiocarbon age end points for each record. As the number of observed oxygen isotopic cycles corresponds closely to the number of years for this period, a seasonal time scale is assigned to these variations based on the assumptions that growth occurs throughout the year and that the isotopic peaks and troughs are synchronous between the two trees as they correspond to times of minima and maxima in seasonal RHs. The

$\delta^{18}\text{O}$ correlation between the two trees, which may not have grown in the same forest, has an $r = 0.68$ ($P < 0.0001$). Especially for the period of 1989–1998, the two trees recorded strikingly similar $\delta^{18}\text{O}$ amplitudes. The $\delta^{18}\text{O}$ records, framed within the radiocarbon age model, can also be used to infer variations in growth rates, as individual samples represented equivalent radial increments (Fig. 5c). In contrast to the oxygen signal, the changes in carbon isotopic composition do not exhibit consistent seasonal-like behavior (Fig. 5b).

4.3. Thai tree with no well-defined rings: *P. neriifolius*

Results from the *Podocarpus* sample (Fig. 6a) show large fluctuations in both the oxygen (up to 18‰) and carbon isotopic ratios (up to 4‰). The results are plotted using an age model based on the seasonal changes in RH. Maxima and minima $\delta^{18}\text{O}$ were assigned an age corresponding to

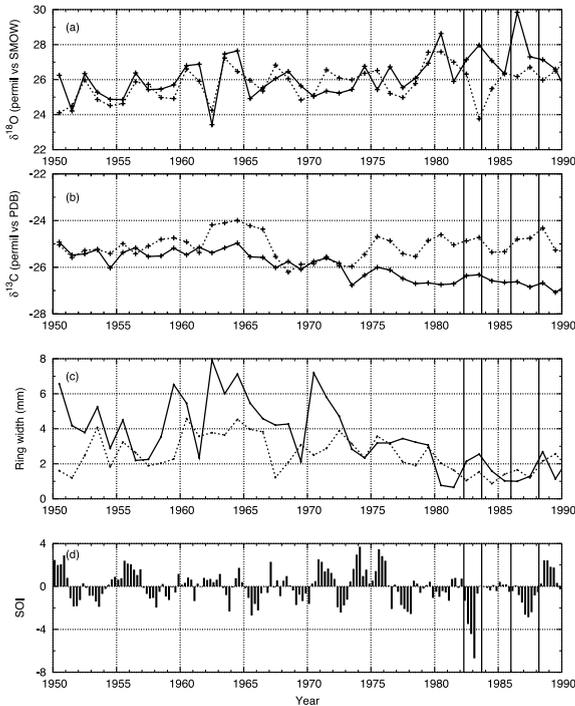


Fig. 4. (a) Comparison of the $\delta^{18}\text{O}$ records of SA02A (solid) and SA06A (dashed) with correlation coefficients $r(1950\text{--}1990)=0.40$ ($P=0.005$) and $r(1950\text{--}1980)=0.69$ ($P<0.0001$). Based on the age and growth rates of the two trees, we observe that the younger SA02A tree appears more sensitive to large El Niño events than SA06A as it probably relies more heavily on seasonal recharges in soil water from rainfall. (b) Same as in (a) but for the $\delta^{13}\text{C}$ records. (c) Ring width comparison between SA02A (dashed) and SA06A (solid) with correlation $r=0.54$ ($P=0.0002$) over the period from 1950 to 1990. For the first 30 years of the record, SA02A has faster growth rates than SA06A as it is much younger (growth curve not removed). A decline in the growth rates of both trees (although more drastic for SA02A) is apparent after the mid-1970s. (d) Seasonally averaged SOI (standardized Tahiti – standardized Darwin) [65]. Low (high) values indicate El Niño (La Niña) events. Vertical solid lines bracket the 1982–1983 and 1986–1987 El Niño events.

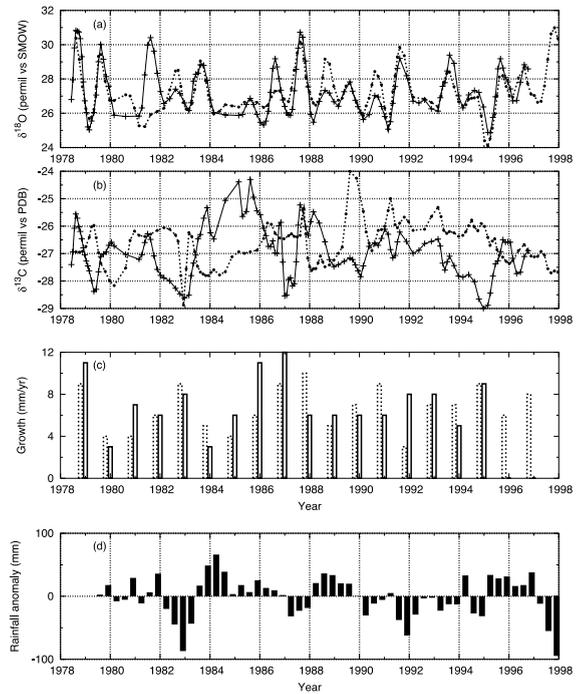


Fig. 5. (a) $\delta^{18}\text{O}$ comparison between Suar1 (dashed) and Suar3 (solid). The amplitudes of the oxygen isotopic variations are remarkably similar suggesting that the trees are recording an environmental forcing that was common to both ($r=0.68$, $P<0.0001$). The chronology of the ringless trees is based on estimated radiocarbon age model (see text for details). (b) Same as in (a) but for $\delta^{13}\text{C}$. (c) Growth rate estimates for Suar1 (dashed) and Suar3 (solid) obtained using the measured radiocarbon ages. (d) Seasonal precipitation anomalies (FMAM, JJAS, ONDJ) for the region 109–124°E and 11°30'S and 4°30'N [40].

the timing of minimum (March) and maximum (August) RH respectively (data from Computer Section, Climatology Division and Meteorological Department, Thailand). The ages of the remaining data points were linearly interpolated between the tie points. The associated $\delta^{13}\text{C}$ measurements were assigned the $\delta^{18}\text{O}$ age scale. The six well-defined $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ cycles match the number of growth years for the period spanning the time of wounding and cutting of the wedge section. The amplitudes of the isotopic seasonal cycles exhibit large fluctuations from one year to the next. Timing and amount of growth are estimated in Fig. 6b using both the age model developed above and the fact that all subsamples were collected over the same distance (360 μm increments). As

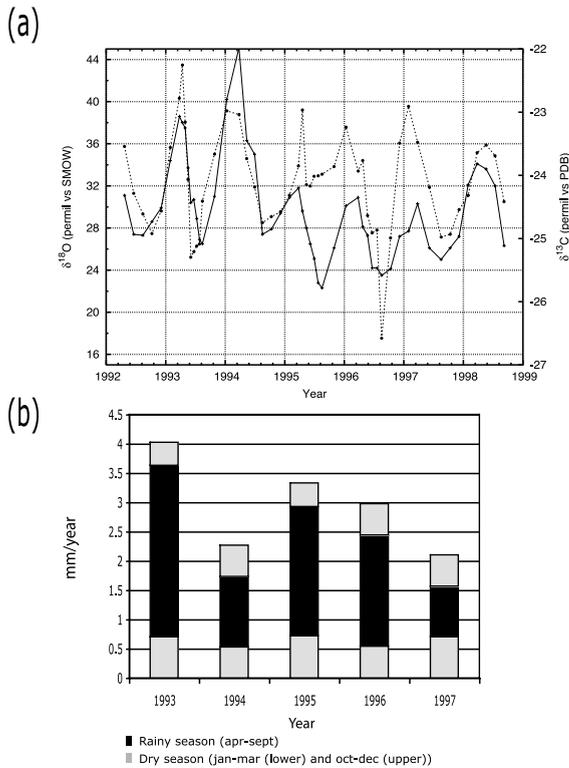


Fig. 6. (a) High-resolution $\delta^{18}\text{O}$ (solid) and $\delta^{13}\text{C}$ (dashed) records of the *P. neriifolius* DIN99W from the Doi Inthanon National Park, northern Thailand. Data are fit to an age model based on the time of wounding (10/92) and time of cutting (02/99) of the wedge section as well as seasonal changes in RH (see text for details). The number of well-defined isotopic cycles corresponds to the number of years elapsed between wounding and cutting of the sample. The data illustrate how high-resolution isotopic records may be used as independent chronometers of tropical climate history. (b) Growth rate estimates based on isotopic age model shown in (a).

is apparent in Fig. 6b, most of the growth (although not all) occurs during the wet season and large interannual variations exist.

5. Discussion

5.1. Indonesian trees with rings: *T. grandis*

Teaks are ring porous to semi-ring porous deciduous trees of the *Verbenaceae* family. They are in-

digenous to much of southeast Asia. The teak growth cycle involves making large quantities of vessel elements at the onset of the growing season, followed by production of thick-walled fibers once their plumbing system is secured. This style of growth results in well-defined annual growth rings. The dendroclimatic potential of this species has been considered in several studies and a number of chronologies from Java now extend as far back as AD 1514 [37,49,50]. The high-resolution $\delta^{18}\text{O}$ measurements of the two teak cores did not result in well-defined seasonal cycles whereas the accompanying $\delta^{13}\text{C}$ did. Because late season photosynthates produced in teak trees can be stored and utilized at the beginning of the next season of growth [37], carbohydrate transfer can distort the isotopic signal recorded in the early part of the growing season. The magnitude of this effect should vary according to changing growth dynamics, rendering the interpretation of sub-annual $\delta^{18}\text{O}$ records difficult. The more distinctly defined $\delta^{13}\text{C}$ sub-annual signal confirms the expectation that carbohydrate transfer should have less of an imprint on the carbon isotopic signature because $\delta^{13}\text{C}$ seasonal variations are two to three times smaller than those measured for the oxygen isotopes. Seasonal variations in $\delta^{13}\text{C}$ can be explained in light of the isotopic model developed in Eqs. 3 and 4. At the onset of the growth season during leaf out, rates of CO_2 fixation (A) will be low, c_i high and the Rubisco discrimination effect high; this will result in low $\delta^{13}\text{C}$ values. As A increases during the growth season, c_i will decrease, causing the $\delta^{13}\text{C}$ to increase to a seasonal maximum followed by a decrease as the tree approaches senescence and c_i increases again. Consistent with this model, years with highest $\delta^{13}\text{C}$ values in both samples also corresponded to years with the widest growth rings.

We found no significant correlation between the two annually averaged $\delta^{13}\text{C}$ records (Fig. 4b). The 40 year average annual $\delta^{13}\text{C}$ for SA02A (-26.0‰) was significantly lighter than for SA06A (-25.0‰) ($P < 0.0001$). As previously shown by Francey and Farquhar [51], large $\delta^{13}\text{C}$ variations ($1\text{--}4\text{‰}$) around the circumference of a tree as well as amongst neighboring trees, can occur due to differing levels of irradiance, nu-

trients, growth rates and water stress. Therefore, it is no surprise that such differences should be present between SA02A and SA06A during this period. Despite these differences, during the El Niño years of 1957–1958, 1963–1964, 1969–1970 and 1982–1983, both samples show relative $\delta^{13}\text{C}$ enrichments, consistent with the isotopic model. However, neither samples captured the 1976–1978 event and showed high $\delta^{13}\text{C}$ values in 1975–1976 (La Niña), 1979–1980 (SA06A only).

While the sub-annual $\delta^{18}\text{O}$ records are noisy, annual averages are reproducible between the two teaks. This suggests an external forcing, most likely climatic, as the two cores originate from two separate trees which grew in the vicinity of each other. The Jakarta weather station is 600 km away from the sampling site and is the only $\delta^{18}\text{O}$ record available for this region. The record is incomplete (data not shown) and year-to-year comparison with the tree records is not feasible as large regional variations are likely to exist. However, the amplitude of $\delta^{18}\text{O}$ variations (seasonal to interannual; 4–10‰) is similar to what one would predict from the isotopic model.

Based on the age and growth history of the teak samples, we can venture a potential explanation for the connection between climate, teak physiology and water relations as well as attempt to explain the apparent decrease in correlation between the $\delta^{18}\text{O}$ records after the mid-1970s. Although the exact age of the teak trees is unknown, we know that SA02A is at least 80 years younger than SA06A (visual estimate based on ring boundary alignments alongside the cores). In addition, comparison of the ring widths of the two samples ($r=0.54$, $P=0.0002$) substantiates the idea that SA02A is still a juvenile tree, as the growth rates are at times more than double those of SA06A (Fig. 4c).

Although root growth depends on many environmental factors such as soil texture and structure, roots generally grow toward soil with higher water content. All else being equal, a mature deeply-rooted tree capable of accessing groundwater when soil water is low, will be more tolerant of drought than a younger shallow-rooted tree [52]. A negative correlation ($r=-0.41$, $P=0.005$) between ring width and annually averaged $\delta^{18}\text{O}$ of

SA02A suggests that optimal growth conditions (large ring width) for a tree dependent on soil water uptake, require abundant rainfall (low $\delta^{18}\text{O}_{\text{rain}}$) previous to, as well as during the wet season. This is not apparent in the older SA06A ($r=0.04$).

Although SA06A's isotopic signature follows closely that of SA02A during the period from 1950 to the mid-1970s, the $\delta^{18}\text{O}$ records suggest that following an increase in intensity and frequency of El Niño events after the mid-1970s [53], SA06A may have exploited deeper water supplies and as a result, its $\delta^{18}\text{O}$ was not as sensitive as that of SA02A at recording the large 1982–1983 and 1986–1987 events (Fig. 4a,d). Several lines of evidence support this idea. First, the light $\delta^{18}\text{O}$ signature of the tree, particularly during the 1982–1983 El Niño, may reflect the use of isotopically depleted groundwaters, as they are often recharged by high elevation light $\delta^{18}\text{O}$ rainfall (altitude Rayleigh distillation effect). Second, the fact that SA06A generally exhibits smaller seasonal $\delta^{18}\text{O}$ variations than SA02A results mainly from its lighter yearly $\delta^{18}\text{O}$ maximum since their average yearly $\delta^{18}\text{O}$ minima are not significantly different. As $\delta^{18}\text{O}$ maxima often occur during the early part of the growing season, prior to maximum rainfall, light values may reflect the preference for the older tree to use its deeper root system for water uptake until sufficient precipitation can supply its shallower roots. Further evidence that both trees may have been water stressed is apparent in the heavy $\delta^{13}\text{C}$ values during the two El Niño events as well as the decline in ring widths (more dramatic for SA02A), apparent from the mid-1970s onwards (Fig. 4b). However, the ring widths corresponding to the specific years of 1982–1983 and 1986–1987 did not record the two large El Niño events, as would be seen through the occurrence of thinner rings.

The negative correlation between the $\delta^{18}\text{O}$ of SA02A and the SOI ($r=-0.33$, $P=0.02$) suggests that when the SOI is low (El Niño event), the $\delta^{18}\text{O}$ of SA02A cellulose increases in response to decreases in rainfall amount and/or RHs. This potential relationship is supported during the El Niño years 1963–1964, 1972–1973 and 1977–1978 (Fig. 4a).

5.2. Indonesian trees with no rings: *S. saman*

Suar (or Rain) trees are fast growing, deciduous species native to South America and belong to the *Fabaceae* family. They were dispersed in the tropics at least 100 years ago. Contrary to the teaks, which have well-defined annual growth rings, Suar trees have no visible rings to assist in age model development. The use of bomb radiocarbon for dating tropical trees involves a number of uncertainties [54–57] including decreases in radiocarbon content relative to the atmosphere due to soil respiration, internal carbohydrate transfer, species-specific effects as well as changes in the length and timing of growing season. The remarkable agreement found between the $\delta^{18}\text{O}$ records of Suar1 and Suar3 suggests that such effects are minor and that the chronologies are robust. The close agreement between the number of isotopic cycles and the estimated radiocarbon ages also provides support for the oxygen isotopic age model. Reproducibility of the amplitude of the $\delta^{18}\text{O}$ between the two records suggests that the trees are recording climatic information which extends beyond their immediate environment. As the exact sample locations are not known, we use a regional precipitation anomaly index to investigate the potential for a first-order climate connection (Fig. 5d). We observe that the low rainfall years of 1983, 1987, 1991 and 1997 (also El Niño years) correspond to enriched $\delta^{18}\text{O}$ values in the tree records, as the isotopic model would predict. Because local precipitation patterns likely affect the tree isotopic records, comparison with a regional index is not ideal and may explain some of the disagreements observed between the records. The poor performance of the $\delta^{13}\text{C}$ records at capturing seasonality may be a reflection of physiological species-specific effects and/or other local environmental influences. A comparison of growth rate estimates shows that, with the exception of 1979, the years 1983, 1987 and 1995 correspond to years when both trees had some of their highest growth rates as well as years when El Niño events were taking place. It is conceivable that Suar trees are not as water stressed as some other species during such events. This is also sug-

gested by the small and irregular sub-annual $\delta^{13}\text{C}$ signals.

5.3. Thai tree with no well-defined rings: *P. neriifolius*

P. neriifolius, of the *Podocarpaceae* family, is a long-lived and widespread tropical evergreen tree which grows at 1000–1400 m elevation. The presence of discontinuous or convergent rings renders cross-dating of this species difficult and has limited its use in dendrochronological studies [58]. Using the independent means of dating derived from the time of wounding and cutting of the wedge section, we can validate the claim that well-defined seasonal variations in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were being recorded during growth of this tree. This result illustrates that the species is an excellent candidate for isotope dendrochronology. Several circumstances could have given rise to the unusually large amplitudes observed in the $\delta^{18}\text{O}$ record of the Thai sample. In contrast to the teak and Suar trees (above), which were both deciduous, the *P. neriifolius* is an evergreen species and was probably capable of growing throughout the year assuming that water supplies were not limited. A continuous growth pattern may, in turn, ensure that the full seasonal $\delta^{18}\text{O}$ cycle gets recorded by the tree. In addition, the fact that the tree was growing on a steep mountain slope may have increased its sensitivity to climate, as is often observed in tree ring studies [59]. Unfortunately, there is very little environmental data available from this site to compare with the isotopic model described in Section 2 [19]. Comparison with instrumental records of precipitation is difficult due to the high spatial variability apparent from the sparsely distributed stations. Nonetheless, the trend of increasing $\delta^{18}\text{O}$ seasonal minima for the period of 1995–1998 is consistent with a decreasing trend of wet season rainfall (data not shown). The creation of longer isotopic tree records from Thailand is underway and will enable us to further investigate the potentials of this method for generating proxy rainfall estimates. With the exception of the years 1993 and 1994, the measured range in amplitude of the $\delta^{18}\text{O}$ seasonal cycle (6–8.5‰) is very similar to the observed annual var-

iations in the $\delta^{18}\text{O}$ precipitation values from Bangkok (6–9.5‰) [60]. We cannot exclude the possibility that the anomalous 12 and 18‰ cycles measured on the *Podocarpus* samples for the years 1993 and 1994 respectively reflect a combination of environmental and physiological effects, perhaps as a consequence of the wounding in 1992.

The large interannual variations in the cellulose $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ and in the estimated growth rates suggest that this tree was sensitive to its environment and that the development of multi-decadal isotopic records from this species could yield valuable information about the paleoclimatic history of the region. The assumption that changes in RH are synchronous with changes in cellulose $\delta^{18}\text{O}$ is likely correct but should be tested independently using dendrometer bands.

5.4. Tropical isotope dendroclimatology limitations and future applications

Construction of multi-century paleo-rainfall proxies from high-resolution isotopic measurements in tropical trees will require that a number of limitations be addressed. In order to recover the details of the seasonal cycle, a minimum of four to six samples are needed per year of growth. Although the amount of wood necessary for isotopic analysis is small (<2 mg), the total yearly growth places a limit on the number of individual subsamples that can be retrieved consistently. In addition, independent means of dating at least one position of the sample is necessary (radiocarbon, knowledge of felling or wounding date) and may sometimes be unavailable. Specific anatomical features such as wedging and missing rings may not be easily identified. In some instances, however, the technique may be of use to dendrochronological studies for which the nature of a ring (true or false ring) is questioned, as has successfully been done using carbon isotopes [61]. Tropical forests are hosts of incredible diversity and the list of potential species is extensive. In addition, old trees in the tropics are becoming a rarity and, when left standing, are often subject to fungal attacks and degradation, which render their trunks hollow [62].

Earlier studies of high-resolution $\delta^{18}\text{O}$ of cellu-

lose from mid-latitude trees with rings demonstrated, over the period of a few years, a relationship between the seasonal isotopic variations and environmental conditions [36,63]. Using recent advances in continuous flow mass spectrometry and α -cellulose extraction [11], we have shown that the generation of replicated 40 year long sub-annual isotopic records is possible. Dendrochronologists have been studying tree rings for more than 100 years and have developed a set of rules to follow in the selection of specimens that are most appropriate for climate reconstruction. Although many of these selection criteria are likely to overlap with those used for tropical isotope dendroclimatology, we have yet to uncover the specific set of rules required to best select trees for isotopic climate reconstruction. Our technique allows us to quickly evaluate whether a particular species is successful at recording seasonal-like isotopic signals and hence assists in the derivation of these new selection rules.

Comparison of modern $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sub-annual time series with the observational record reveals the potential for this proxy to record unusual climatic events. Isotopic records derived from Indonesian and Thai forests, along with records from South America [11] suggest that this approach may be successfully applied in much of the tropics and extended to investigations beyond the observational record, making use of fossil samples recovered from these regions. In addition to climatic investigations, the recovery of sub-annual isotopic records from trees will likely yield valuable insights about tree physiology and growth dynamics relevant to tropical forest environments.

6. Conclusion

The potential of tropical isotope dendroclimatology for producing new proxy records of climatic and ecological variability has been explored using samples from Indonesia and Thailand. Analysis of two annually averaged $\delta^{18}\text{O}$ records from Javanese teaks grown in the same locality demonstrates the reproducibility of their isotopic signatures and suggests a common climatic influ-

ence between 1950 and 1980. The $\delta^{18}\text{O}$ records also suggest that the sensitivity of the two trees to large El Niño events was dependent on tree age and associated differences in tree physiology. High-resolution $\delta^{18}\text{O}$ records from two Javanese Suar trees grown in different locations and lacking visible rings reveal large and reproducible seasonal cycles (up to 4‰), particularly for the 1989–1998 period. At least some El Niño events coincided with enriched $\delta^{18}\text{O}$ values (1983, 1987, 1991 and 1997). Results from the Thai *Podocarpus* sample reveal large variations in the $\delta^{18}\text{O}$ (up to 18‰) and in the $\delta^{13}\text{C}$ (up to 4‰). The six isotopic cycles measured matched the number of growth years (as defined by time of wounding and cutting of wedge section) and provided strong evidence that the recorded cycles are seasonal and could be used for chronology. Given the high biodiversity of tropical forests, our findings demonstrate the potential for the generation of multi-century climate records from long-lived tropical trees. However, such records will require a more complete understanding of the suitability of a range of species and their habitats.

Acknowledgements

The authors would like to thank Missy Holbrook and Adam Maloof for their useful suggestions, Brendan Buckley and Rosanne D'Arrigo for kindly providing the wood samples, Ethan Goddard and Greg Eiseheid for technical assistance and Tom Guilderson for the radiocarbon measurements. This research was supported by NSERC and the Teresa Heinz Scholarship for Environmental Research to P.F.P. and NSF grants OCE-9733688 and ATM-0214328 to D.P.S. and NSF grant ESH-0214130 to M.N.E. The manuscript has benefited from the constructive criticism of two anonymous reviewers.
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