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Seasonal variations in the stable oxygen isotope ratio of wood cellulose reveal annual rings of trees in a Central Amazon terra firme forest

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Abstract In Amazonian non-flooded forests with a moderate dry season, many trees do not form anatomically definite annual rings. Alternative indicators of annual rings, such as the oxygen ($\delta^{18}\text{O}_{\text{wc}}$) and carbon stable isotope ratios of wood cellulose ($\delta^{13}\text{C}_{\text{wc}}$), have been proposed; however, their applicability in Amazonian forests remains unclear. We examined seasonal variations in the $\delta^{18}\text{O}_{\text{wc}}$ and $\delta^{13}\text{C}_{\text{wc}}$ of three common species (*Eschweilera coriacea*, *Iryanthera coriacea*, and *Protium hebetatum*) in Manaus, Brazil (Central Amazon). *E. coriacea* was also sampled in two other regions to determine the synchronicity of the isotopic signals among different regions. The annual cyclicity of $\delta^{18}\text{O}_{\text{wc}}$ variation was cross-checked by ^{14}C dating. The $\delta^{18}\text{O}_{\text{wc}}$ showed distinct seasonal variations that matched the amplitude observed in the $\delta^{18}\text{O}$ of precipitation, whereas seasonal $\delta^{13}\text{C}_{\text{wc}}$ variations were less distinct in most cases. The $\delta^{18}\text{O}_{\text{wc}}$ variation patterns were similar within and between some individual trees

in Manaus. However, the $\delta^{18}\text{O}_{\text{wc}}$ patterns of *E. coriacea* differed by region. The ages of some samples estimated from the $\delta^{18}\text{O}_{\text{wc}}$ cycles were offset from the ages estimated by ^{14}C dating. In the case of *E. coriacea*, this phenomenon suggested that missing or wedging rings may occur frequently even in well-grown individuals. Successful cross-dating may be facilitated by establishing $\delta^{18}\text{O}_{\text{wc}}$ master chronologies at both seasonal and inter-annual scales for tree species with distinct annual rings in each region.

Keywords Tropical moist forest · Stable carbon isotope ratio · Radiocarbon dating · Wood anatomy · Tree-ring detection

Introduction

Tropical trees growing in climates with weak seasonality generally do not form anatomically distinct or regular annual rings. Trees in the floodplain forests of the Amazon basin (várzea and igapó) often form annual rings due to seasonal changes in the river water level (Worbes 1997). However, most of the trees growing in non-flooded (terra firme) forests, which cover the Amazon basin extensively, tend to lack distinct annual rings. Our knowledge of forest dynamics in the region, including rates of individual tree growth, mortality, and lifespan, is limited (Chambers et al. 2013), in part due to the absence of annual rings as a convenient dating tool. Such information is critical for understanding many processes related to forest dynamics and carbon cycling and for evaluating the impacts of future climate change on tropical ecosystems (e.g., Clark et al. 2003; Clark 2007; Brien et al. 2010; Vlam et al. 2014).

Instead of using visible annual rings, several recent studies have used alternative indicators that vary seasonally,

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Fig. 1 Mean monthly precipitation and stable oxygen isotope ratio of precipitation ($\delta^{18}\text{O}_{\text{prec}}$) in Manaus, Brazil. The data are the means from 1965 to 1990, provided by the Global Network of Isotopes in Precipitation (IAEA/WMO 2015)

such as stable carbon ($\delta^{13}\text{C}$) and oxygen isotope ratios ($\delta^{18}\text{O}$) of wood (e.g., Leavitt and Long 1991; Evans and Schrag 2004; Poussart et al. 2004; Verheyden et al. 2004a), vessel density and size (Verheyden et al. 2004b, 2005a; Ohashi et al. 2009, 2014), and calcium in wood (Poussart et al. 2006). These indicators show cyclic intra-annual variations, which are attributed to seasonal changes in environmental conditions and/or the physiological status of trees, allowing annual rings to be identified. However, the underlying mechanisms of these cyclic features are not well understood, limiting the applicability of these alternative indicators. The number of the studies in the humid tropics, where monthly precipitation usually exceeds 60 mm throughout the year, remains limited (e.g., Pons and Helle 2011; Ohashi et al. 2014).

According to the Köppen Climate Classification for Brazil (Alvares et al. 2013), the Amazon basin has a tropical monsoon climate (Am) in the eastern part and a tropical rainforest climate (Af) in the western part. In the Central Amazon area surrounding Manaus, the climate is intermediate between Am and Af; there is a moderate dry season during which the monthly precipitation drops to nearly 60 mm for 1 month and <100 mm for 1–3 months (around August; Fig. 1). Such a moderate dry season exists over a large region because of a climatic gradient across the Amazon basin (Davidson et al. 2012). Forests in the area are usually considered tropical moist forests as defined by Holdridge (1947).

In humid areas where distinct seasonality in $\delta^{18}\text{O}$ of precipitation ($\delta^{18}\text{O}_{\text{prec}}$) exists, we would expect the $\delta^{18}\text{O}$ of wood cellulose ($\delta^{18}\text{O}_{\text{wc}}$) to be a better indicator of annual rings than the $\delta^{13}\text{C}$ of wood cellulose ($\delta^{13}\text{C}_{\text{wc}}$) or vessel features. Because $\delta^{18}\text{O}_{\text{wc}}$ reflects both relative humidity and source water signals (Roden et al. 2000; McCarroll and Loader 2004), biological modification of the $\delta^{18}\text{O}$ seasonal

variations would be minimal. In contrast, seasonal variations in $\delta^{13}\text{C}_{\text{wc}}$ and vessel features mainly reflect biological factors. The $\delta^{13}\text{C}_{\text{wc}}$ variation depends on stomatal conductance, photosynthesis rate (Farquhar et al. 1989; McCarroll and Loader 2004), and post-photosynthetic processes, such as use of carbon reserves (Helle and Schleser 2004). The variation in vessel features relies on the biological response to water availability and unidentified internal factors that seem to be related to leaf phenology and phytohormones (Ohashi et al. 2014). In addition, the radial growth of trees in the humid tropics tends to be asynchronous even within the stem circumference of an individual tree, and the growth cycle does not seem to be strictly annual (Ogata et al. 2002; Ohashi et al. 2014). Thus, using an annual-ring indicator that is affected less by biological factors would be the best approach to detect annual rings in the humid tropics.

The origin of the oxygen atoms in plant cellulose is H_2O ; the oxygen atoms derived from CO_2 are exchanged with those from H_2O by the time cellulose is formed (DeNiro and Epstein 1979). The H_2O is absorbed from roots (source water) and ^{18}O is enriched by transpiration at the leaves (leaf water). The oxygen is then incorporated in sucrose through exchange with carbonyl oxygen during hydration (Sternberg et al. 1986). Furthermore, the oxygen in sucrose partly exchanges with that of xylem water ($\approx$ source water) during cellulose synthesis at the stem cambium. The fraction of exchange during cellulose synthesis is estimated to be about 0.4 for mature trees (Barbour 2007). As a result, the $\delta^{18}\text{O}_{\text{wc}}$ reflects the $\delta^{18}\text{O}$ of both leaf water and source water. In humid areas, where water content in the soil surface is high, we may assume that the source water is essentially rainwater. This assumption is supported by the fact that more than 96 % of fine roots are distributed within the upper 30-cm soil layer in the plateau of a tropical moist forest of the Central Amazon (Noguchi et al. 2014).

In tropical areas, $\delta^{18}\text{O}_{\text{prec}}$ is negatively correlated with the amount of precipitation, a phenomenon known as the “amount effect” (Dansgaard 1964; Rozanski et al. 1993). Due to the gradual removal of moisture as air masses move inland, heavy isotopes are removed preferentially during the condensation process, termed the “continental effect” (Rozanski et al. 1993), and $\delta^{18}\text{O}_{\text{prec}}$ decreases with the distance from the coast. In the Amazon basin, however, the continental effect is rather weak because rainwater is intensively recycled through transpiration and evaporation within the basin (Salati et al. 1979). In addition, the Intertropical Convergence Zone (ITCZ) affects the seasonality of $\delta^{18}\text{O}_{\text{prec}}$ in this region. When the ITCZ crosses the eastern margin of the Amazon basin, moisture from which ^{18}O has been depleted is pushed inland (Matsui et al. 1983; Rozanski et al. 1993). Thus, $\delta^{18}\text{O}_{\text{prec}}$ in the Amazon basin primarily originates from the Atlantic and is locally altered by the amount effect and the position of the ITCZ.

In Manaus, the monthly precipitation and $\delta^{18}\text{O}_{\text{prec}}$ show clear seasonality with a relatively large ($\approx 5\%$) mean amplitude of $\delta^{18}\text{O}_{\text{prec}}$ variation (Fig. 1; IAEA/WMO 2015). The relative humidity is $\sim 90\%$ during the rainy season (generally, December–May) and drops by only 5–10 % during the moderate dry season (which lasts for about 3 months, around August). The reduction in relative humidity causes a reduction in the stomatal conductance of trees (Mooney et al. 1983; Roberts et al. 1990), increasing the $\delta^{18}\text{O}$ of leaf water (Barbour 2007). Thus, the dry season increase in $\delta^{18}\text{O}_{\text{wc}}$ may be amplified by the physiological response of leaves against the water deficit. The growth increment of trees in this area generally decreases or ceases during the moderate dry season, May–September (da Silva et al. 2002). This seasonal growth decline or cessation is another factor affecting the seasonal $\delta^{18}\text{O}_{\text{wc}}$ variation. As the $\delta^{18}\text{O}_{\text{prec}}$ signals do not significantly affect $\delta^{18}\text{O}_{\text{wc}}$ when wood formation is dormant, a discontinuous record of $\delta^{18}\text{O}_{\text{prec}}$ signals in wood cellulose during the dry season can result in a sharper increase in $\delta^{18}\text{O}_{\text{wc}}$. Thus, we hypothesized that the $\delta^{18}\text{O}_{\text{wc}}$ of trees grown in Central Amazon terra firme forests shows distinct annual cycles primarily associated with seasonal $\delta^{18}\text{O}_{\text{prec}}$ variation, potentially amplified by biological responses to the moderate dry season.

The evidence of seasonal variation in $\delta^{18}\text{O}_{\text{wc}}$ has been demonstrated, for example, in ringless trees in a tropical wet forest in Costa Rica (Evans and Schrag 2004) and in seasonally dry forests in Thailand and Indonesia (Pousart et al. 2004; Poussart and Schrag 2005). A similar relationship was also reported for a fast-growing species (*Tachigali myrmecophila*) in Amazonian terra firme forest near Manaus (Ballantyne et al. 2011). However, that study examined only one species over a relatively short time scale (3 years). Further analyses of tree species and locations, including long-lived, dominant tree species growing widely throughout the Amazon, are needed to confirm the potential of using the $\delta^{18}\text{O}_{\text{wc}}$ method throughout the Amazon.

Testing the techniques for detecting annual rings in the Central Amazon is an essential first step to verify the applicability of annual-ring indicators at a larger geographical scale (i.e., throughout Amazonia). In the present study, we addressed the applicability of $\delta^{18}\text{O}_{\text{wc}}$ as an annual-ring indicator in the Central Amazon terra firme forests. First, we investigated radial variations in the $\delta^{18}\text{O}_{\text{wc}}$ of three common species to visualize seasonal cyclicality, if any. To explore the possibility of other annual-ring indicators, we examined radial variations in $\delta^{13}\text{C}_{\text{wc}}$ and occurrences of anatomical growth rings in the same wood samples. Second, we verified whether the $\delta^{18}\text{O}_{\text{wc}}$ cycles reflected annual growth cycles by comparing them with data from radiocarbon (^{14}C) dating. Synchronicity of the isotopic signals was also checked within and between individuals, and between

species and regions. Finally, we discuss the possibilities and limitations of applying the $\delta^{18}\text{O}_{\text{wc}}$ method in the Amazonian tropical moist forest.

Materials and methods

Study sites

Wood samples were collected primarily in the ZF2 experimental forest ($2^{\circ}38'\text{S}$, $60^{\circ}09'\text{W}$, 110 m a.s.l.) of the National Institute for Amazon Research (INPA), characterized by terra firme (non-flooded) forest (Suwa et al. 2013). The collection site is located on the left side of the Negro river basin, about 90 km north of Manaus, Amazonas State, Brazil (Online Resource 1), classified as a tropical rainforest climate according to the Köppen Climate Classification (Alvares et al. 2013). The annual precipitation in Manaus, about 50 km south of ZF2, is 2446 mm (average from 2010 to 2014; Japan Meteorological Agency 2015). Monthly precipitation and the $\delta^{18}\text{O}_{\text{prec}}$ show seasonal variations (Fig. 1, IAEA/WMO 2015). During the moderate dry season, which lasts for about 3 months around August, rainfall is $<100\text{ mm month}^{-1}$.

Wood samples were also collected in two other regions in terra firme forests, Juruá (JU) and Atalaia do Norte (AT) (Online Resource 1), to examine the synchronicity of the $\delta^{18}\text{O}_{\text{wc}}$ signals among different regions. The JU site is located in the Juruá river basin, about 670 km west of ZF2 ($3^{\circ}54'\text{S}$, $66^{\circ}03'\text{W}$, 85 m a.s.l.), and the AT site is located in the Solimões River basin, about 1140 km west of ZF2 ($4^{\circ}17'\text{S}$, $70^{\circ}19'\text{W}$, 110 a.s.l.). These sites also have a tropical rainforest climate. Annual precipitation in Fonte Boa, about 150 km north of JU, is 2688 mm, and that in Benjamin Constant, about 30 km east of AT, is 2470 mm (average from 2010 to 2014; Japan Meteorological Agency 2015). Monthly precipitation at JU and AT usually exceeds 100 mm throughout the year and the dry season is less distinct than in ZF2; however, monthly rainfall drops to nearly 100 mm around August (Online Resource 1). Thus, the seasonal precipitation pattern is relatively similar among the three sites.

Samples

Three common species in terra firme forests were sampled: *Eschweilera coriacea* (family Lecythidaceae; common name Matamatá amarelo), *Iryanthera coriacea* (Myristicaceae; Ucuuba punã), and *Protium hebetatum* (Burseraceae; Breu vermelho). *E. coriacea* and *P. hebetatum* are major component species in terra firme forests; they are often dominant in Amazonia (ter Steege et al. 2013). *E. coriacea* is evergreen, whereas *I. coriacea* and *P.*

Fig. 2 Growth rings of **a** *Eschweilera coriacea*, **b** *Iryanthera coriacea*, and **c** *Protium hebetatum* collected at the ZF2 study site (Manaus). Arrows indicate growth ring boundaries

hebetatum may be evergreen or semi-deciduous (F. Q. Reis, personal communication), but their leaf habits are not well documented at the study site.

All three species have anatomical growth-ring structures (Fig. 2). In *E. coriacea*, growth rings are characterized by apotracheal parenchyma bands and their interval changes. The interval between the bands decreases toward the end of a ring and increases drastically at the beginning of the next ring (Fig. 2a). However, there are many indistinct ring boundaries. In *I. coriacea*, growth-ring boundaries are

defined by clear marginal parenchyma bands that are easy to recognize (Fig. 2b). In *P. hebetatum*, although growth-ring boundaries are indistinct, bands of radially flattened fibers may be observed (Fig. 2c). Similar ring structures with *E. coriacea* and *P. hebetatum* have been reported for *Eschweilera* sp. and *Protium* sp., respectively (Vetter and Botosso 1989).

In the main study site (ZF2), two *E. coriacea* (EC-1, -2) and two *I. coriacea* (IC-1, -2) trees were felled and stem disks were collected at breast height in May 2013. In addition, another *E. coriacea* (EC-3) and one *P. hebetatum* (PH) were sampled in October 2013. These sample trees were located in a single forest with the same structure (<1 km apart). Additional samples of *E. coriacea* were taken from the other two sites (JU and AT) to compare the isotopic signals with those of ZF2. An *E. coriacea* tree was felled and a disk was collected at breast height in July 2013 at JU (EC-JU) and in August 2013 at AT (EC-AT). All individuals reached the canopy in each forest. Their size parameters are shown in Table 1.

Sample preparation

The surfaces of the stem disks were polished roughly with a disk grinder (80 grit) and then finely with a sander (60–200 grit). After ring structures became clear, radii for the isotopic analysis were specified. To verify the synchronicity of the isotopic signals within each individual, two radii were selected for the isotopic analysis in each disk of *E. coriacea* and *I. coriacea* collected in ZF2. The angle between the two radii was initially set to 180° but was adjusted between 120° and 180° to avoid holes due to rot or insect damage. Radial strips with tangential widths of

Table 1 Sample description

Area	Site	Species	Tree no.	DBH (cm)	Height (m)	Sampling date	Radius ID	Number of ¹⁴ C estimates	Sample ID
Manaus	ZF2	<i>Eschweilera coriacea</i>	1	47.7	—	May 2013	A	13	EC-1A
							B	3	EC-1B
			2	38.2	28.0	May 2013	A	9	EC-2A
							B	14	EC-2B
			3	28.0	22.4	October 2013	A	1	EC-3A
							B	0	EC-3B
Manaus	ZF2	<i>Iryanthera coriacea</i>	1	24.8	—	May 2013	A	5	IC-1A
							B	4	IC-1B
			2	30.5	—	May 2013	A	10	IC-2A
							B	3	IC-2B
Manaus	ZF2	<i>Protium hebetatum</i>	1	21.0	20.8	October 2013	A	1	PH
Juruá	JU	<i>E. coriacea</i>	1	20.0	16.1	July 2013	A	0	EC-JU
Atalaia do Norte	AT	<i>E. coriacea</i>	1	24.5	17.0	August 2013	A	0	EC-AT

DBH Diameter at breast height, ID identity

12 mm were sawn from the disks with a band saw. Finally, 1-mm-thick cross-sections were cut with a circular table saw.

In our analysis, these thin cross-sections were extracted to purify α -cellulose. Although using whole wood (bulk wood) for isotopic analyses is reportedly acceptable, uncertainties regarding the analysis of whole wood remain (Loader et al. 2003; Ferrio and Voltas 2005; Verheyden et al. 2005b), especially for analysis at intra-annual scales. In addition, a recent advance has allowed the extraction of α -cellulose directly from cross-sectional laths before the subdivision of tree rings (Li et al. 2011; Xu et al. 2011; Kagawa et al. 2015). Therefore, we used α -cellulose for isotope analysis and applied the cross-section method proposed by Kagawa et al. (2015) for the extraction. The chemical protocol was based on the Jayme and Wise method (Green 1963) modified for α -cellulose extraction (Mullane et al. 1988; Loader et al. 1997; Xu et al. 2011).

Stable isotope analysis

To analyze intra-annual variations of $\delta^{18}\text{O}_{\text{wc}}$ and $\delta^{13}\text{C}_{\text{wc}}$, each α -cellulose plate was subdivided with a scalpel under a stereomicroscope. We sliced each subdivision parallel to the curvature of visible ring structure to maximize time-scale resolution by isolating the α -cellulose tissue formed during the same period. The radial interval (resolution) for the subdivision was set to 0.2 mm, which was the minimum thickness that could be achieved by slicing the α -cellulose plate at constant intervals along the curvature. We considered this resolution sufficient for detecting annual cyclicity for canopy-layer trees that had relatively large annual diameter increments. The resolution may be increased by dividing the wood plate (before cellulose extraction) at smaller intervals using a microtome; however, we did not apply a microtome because it was not suitable for slicing sections along curved ring boundaries.

It should be noted that the resolution of 0.2 mm does not match the original sampled wood because of shrinkage during the α -cellulose extraction. Therefore, we calculated the extent of the shrinkage ratio at every radial interval of 1 mm by comparing digitally scanned images before and after the extraction. The resolutions of the isotopic chronologies were then corrected for the radial length of the original wood samples.

Each subdivided sample for isotope analysis weighed 80–200 μg , and the tangential length of the α -cellulose subdivision used for the analysis was ca. 2 mm. Each sample was wrapped with silver foil and dried in a vacuum oven (70 °C) for at least 1 day before isotope analysis.

The outer part (ca. 10–20 mm) of each radial strip was analyzed to determine seasonal variations in isotopic signals. Additional analysis was performed on EC-1A and

EC-2A, which showed clear $\delta^{18}\text{O}_{\text{wc}}$ variations and relatively wide $\delta^{18}\text{O}_{\text{wc}}$ cycle length (i.e., wide $\delta^{18}\text{O}$ ring; see “Results”). The isotopic chronologies of EC-1A and EC-2A were extended back to ca. 1950 AD according to ^{14}C dating. As a result, the radial length analyzed was 99 mm in EC-1A and 66 mm in EC-2A. We measured $\delta^{18}\text{O}_{\text{wc}}$ and $\delta^{13}\text{C}_{\text{wc}}$ of subdivided samples with a high-temperature pyrolysis oven (Hekatech HTO) coupled to an isotope ratio mass spectrometer (Thermo Fisher MAT252) at Forestry and Forest Products Research Institute, Japan. All the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of our samples were presented with respect to the Vienna Standard Mean Ocean Water and Pee Dee belemnite scales, respectively, as in $[\delta^{18}\text{O} \text{ or } \delta^{13}\text{C} (\text{‰})] = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where R is the $^{18}\text{O}/^{16}\text{O}$ or $^{13}\text{C}/^{12}\text{C}$ ratio. Cellulose standards of IAEA-C3 and Merck were used as a reference. The analytical error (1σ) of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ was within 0.2 ‰.

Definition of isotopic rings

We recognized conspicuous cyclic variations of $\delta^{18}\text{O}_{\text{wc}}$ in all sample wood (see “Results”). Each isotopically detected cycle was considered a $\delta^{18}\text{O}$ ring. Determination of the boundary between two cycles (i.e., the beginning of seasonal growth) differs depending on the location and species. For example, in many trees in ZF2 (Manaus), the diameter growth rates decrease in September (da Silva et al. 2002), and the new growing period generally starts in October, when the $\delta^{18}\text{O}_{\text{prec}}$ value starts to decrease in the study area (Fig. 1). Thus, we defined the peaks of $\delta^{18}\text{O}_{\text{wc}}$ variations as the boundaries of $\delta^{18}\text{O}$ rings. Although such a definition may differ in wood samples of other areas (EC-JU, EC-AT), the same definition was applied because seasonal precipitation patterns are similar at all three sites (Online Resource 1). The details of the protocol we used to search the significant peaks in the $\delta^{18}\text{O}$ variations and to determine the $\delta^{18}\text{O}$ ring boundaries are described in Online Resources 2 and 3. The threshold to detect the peaks and boundaries was based on the analytical error (3σ) of two $\delta^{18}\text{O}_{\text{wc}}$ values. The threshold was computed assuming that the analytical error of all $\delta^{18}\text{O}_{\text{wc}}$ values is 0.2 ‰ and according to the law of error propagation (see Online Resource 2).

Radiocarbon estimate of cellulose age

The same α -cellulose plates used for stable isotope analysis were also used for radiocarbon analysis. Growth rings at several positions were cut from the plates. Rather wide rings were selected because at least 1 mg of α -cellulose was required for the analysis. Samples were combusted with CuO in sealed quartz tubes, CO_2 purified and graphite targets prepared for ^{14}C analysis using methods described in Xu et al. (2007). Radiocarbon analyses were

Fig. 3 Radial variations in oxygen ($\delta^{18}\text{O}_{\text{wc}}$; filled circle) and carbon isotope ratios of wood cellulose ($\delta^{13}\text{C}_{\text{wc}}$; open circle), in two radii of three individuals of *E. coriacea* (EC) collected at the ZF2 study site (Manaus): **a, b** EC-1, **c, d** EC-2, and **e, f** EC-3. Dotted lines show annual-ring boundaries estimated from $\delta^{18}\text{O}_{\text{wc}}$. Years written at the top of each figure part are estimates from ^{14}C dating and those at the bottom are estimates from $\delta^{18}\text{O}_{\text{wc}}$. The $\delta^{18}\text{O}$ year is defined to start in October of the previous year and end in September of the current year

performed at the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Facility at the University of California, Irvine, USA. All results were corrected for isotopic fractionation (Stuiver and Polach 1977), with $\delta^{13}\text{C}$ values measured on prepared graphite using the Accelerator mass spectrometer. The precision is about 2–3 ‰ for modern samples based on the long-term reproducibility of secondary standards.

Fraction modern (FM) data were converted to calendar years for wood formation using OxCal [version 4.2 (Bronk Ramsey 2009)] with the calibration curve: Bomb 13 SH3 (Southern Hemisphere mean summer ITCZ) (Hua et al. 2013). Only growth rings with ^{14}C signatures of ≥ 1.0 FM (i.e., the bomb period after 1950 AD) were assigned ages because we needed high accuracy (age error of 1–2 years) to verify the annual cyclicity of $\delta^{18}\text{O}_{\text{wc}}$ variations. Rings with ^{14}C signatures between 0.96 and 1.0 FM are described as “before 1950” in the present study. Results of calendar year are reported using the 95.4 % probability determined from uncertainties in the ^{14}C analysis and the calibration curve (Bronk Ramsey 2009).

Results

Radial variations in $\delta^{18}\text{O}_{\text{wc}}$

Distinct cyclic variations of $\delta^{18}\text{O}_{\text{wc}}$ were observed in all tree species. The mean amplitude of the $\delta^{18}\text{O}_{\text{wc}}$ cycles, defined as the difference between maximum and minimum values in one cycle, was larger (ca. 5–6 ‰) in the *E. coriacea* samples of ZF2 (EC; Fig. 3) and *P. hebetatum* samples (PH; Fig. 5), compared with the *I. coriacea* samples (IC; Fig. 4) (ca. 3–4 ‰).

The radial (seasonal) $\delta^{18}\text{O}_{\text{wc}}$ pattern was similar between the two radii for each of the three EC trees (Fig. 3). The annual mean value of $\delta^{18}\text{O}_{\text{wc}}$ was calculated by pooling all data contained within each $\delta^{18}\text{O}$ ring to compare inter-annual $\delta^{18}\text{O}_{\text{wc}}$ variations between the two radii of a single individual. The comparison showed significant correlations between the two radii in the EC-1 ($p = 0.011$, test by simple correlation coefficient) and EC-3 ($p = 0.018$) trees,

whereas there was no significant correlation in the EC-2 and IC trees.

In order to compare the inter-annual $\delta^{18}\text{O}_{\text{wc}}$ variations between the individuals, the annual mean $\delta^{18}\text{O}_{\text{wc}}$ values of the two radii were averaged for each tree. There was a significant correlation between EC-1 and EC-3 ($p = 0.038$). In addition, the seasonal $\delta^{18}\text{O}_{\text{wc}}$ pattern showed some similarities between the EC trees sampled in Manaus. For example, the minimum $\delta^{18}\text{O}_{\text{wc}}$ value was extremely low in the third cycle from the bark side (e.g., 4–8 mm from the cambium in EC-1A; Fig. 3a) in each EC tree. This remarkable depression was not found in the individuals collected in Juruá (EC-JU) or Atalaia do Norte (EC-AT) (Fig. 6). Although EC-JU and EC-AT also showed seasonal $\delta^{18}\text{O}_{\text{wc}}$ patterns, they differed from those of the EC trees sampled in Manaus.

For the three EC trees in Manaus, the seasonal $\delta^{18}\text{O}_{\text{wc}}$ pattern of the outermost part (e.g., three data points near the cambium) of each radius differed with sampling date. The $\delta^{18}\text{O}_{\text{wc}}$ value decreased steadily in EC-1 (Fig. 3a, b) and EC-2 (Fig. 3c, d), which were felled in May, whereas it increased again in EC-3 (Fig. 3e, f), which was sampled in October. These seasonal $\delta^{18}\text{O}_{\text{wc}}$ patterns corresponded to the seasonal $\delta^{18}\text{O}_{\text{prec}}$ pattern seen in Manaus (Fig. 1).

Radial variations in $\delta^{13}\text{C}_{\text{wc}}$

The cyclic variation in $\delta^{13}\text{C}_{\text{wc}}$ was less distinct than that of $\delta^{18}\text{O}_{\text{wc}}$ for each wood sample. The range of $\delta^{13}\text{C}_{\text{wc}}$ variation within one cycle was usually less than 1 ‰ for the three EC trees from Manaus (Fig. 3). The $\delta^{13}\text{C}_{\text{wc}}$ variation was also small for the EC trees sampled from the other two regions (Fig. 6) and for the other two species (Figs. 4, 5). However, some peaks of $\delta^{13}\text{C}_{\text{wc}}$ coincided with those of $\delta^{18}\text{O}_{\text{wc}}$ in EC (Figs. 3, 7). The $\delta^{13}\text{C}_{\text{wc}}$ value showed a significant correlation with the $\delta^{18}\text{O}_{\text{wc}}$ value in the following wood samples: EC-1A, -1B, EC-2A, -2B, EC-3A ($p < 0.001$), -3B ($p = 0.019$), EC-AT ($p = 0.003$), and IC-2A ($p < 0.001$).

Appearance of anatomical rings

Nearly all the wood samples had more anatomically visible rings than were calculated using $\delta^{18}\text{O}$ rings and fewer anatomically visible rings than were indicated by the number of years as determined by ^{14}C dating. One exception was EC-1A, which had more visible rings than were indicated by ^{14}C dating. In PH, although rings were difficult to recognize (Fig. 2c), they co-occurred with the $\delta^{18}\text{O}$ rings and were consistent with ^{14}C dating (Fig. 5). In some samples (e.g., EC-1B; Fig. 3b), the anatomical ring boundary appeared to be located slightly ahead of the $\delta^{18}\text{O}$ ring boundary.

Fig. 4 Radial variations in $\delta^{18}\text{O}_{\text{wc}}$ (filled circle) and $\delta^{13}\text{C}_{\text{wc}}$ (open circle), in two radii of two individuals of *I. coriacea* (IC) collected at the ZF2 study site (Manaus): **a**, **b** IC-1 and **c**, **d** IC-2. Dotted lines show annual-ring boundaries estimated from $\delta^{18}\text{O}_{\text{wc}}$. Years written at the top of each figure part are estimates from ^{14}C dating and those at the bottom are estimates from $\delta^{18}\text{O}_{\text{wc}}$. The $\delta^{18}\text{O}$ year is defined to start in October of the previous year and end in September of the current year. BP Before 1950; for other abbreviations, see Fig. 3

Radiocarbon-based ages of cellulose C

All calendar years of growth estimated from ^{14}C measurements showed increasing age with inward radial distance from the cambium, and there were no chronological discrepancies (Figs. 3, 4, 5, 7; Online Resource 4). The formation year estimated by counting the number of $\delta^{18}\text{O}$ rings ($\delta^{18}\text{O}$ year) matched reasonably well (≤ 2 years) with the year estimated from ^{14}C dating (^{14}C year) in the outermost parts (10–20 mm from the cambium) of the EC

Fig. 5 Radial variations in $\delta^{18}\text{O}_{\text{wc}}$ (filled circle) and $\delta^{13}\text{C}_{\text{wc}}$ (open circle), in a radius of *P. hebetatum* (PH) collected at the ZF2 study site (Manaus). Dotted lines show annual-cycle boundaries estimated from $\delta^{18}\text{O}_{\text{wc}}$. The year written at the top of each figure part is an estimate from ^{14}C dating and that at the bottom is an estimate from $\delta^{18}\text{O}_{\text{wc}}$. The $\delta^{18}\text{O}$ year is defined to start in October of the previous year and end in September of the current year. White arrows show anatomical growth-ring boundaries. For other abbreviations, see Fig. 3

Fig. 6 Radial variations in $\delta^{18}\text{O}_{\text{wc}}$ (filled circle) and $\delta^{13}\text{C}_{\text{wc}}$ (open circle), in a radius of *E. coriacea* sampled in **a** Juruá (EC-JU) and **b** Atalaia do Norte (EC-AT). Dotted lines show annual-ring boundaries estimated from $\delta^{18}\text{O}_{\text{wc}}$. For other abbreviations, see Fig. 3

and PH trees (Figs. 3, 5). However, the $\delta^{18}\text{O}$ years did not correspond well to the ^{14}C years in the IC trees (Fig. 4). Observed consistency between $\delta^{18}\text{O}$ year and ^{14}C year broke down for longer $\delta^{18}\text{O}$ chronologies measured for the two EC trees (EC-1A and EC-2A) (Fig. 7); the $\delta^{18}\text{O}$ years generally estimated younger ages than the ^{14}C years. In EC-1, the discrepancy between $\delta^{18}\text{O}$ year and ^{14}C year was

relatively small (≤ 5 years) until ~ 85 mm from the cambium, but it increased to more than 10 years inward of that point (Fig. 7a). In EC-2, the discrepancy was much larger at almost the same position (about 30 years in EC-2, vs. about 4 years in EC-1, 50 mm from the cambium) (Fig. 7b).

Discussion

Annual cyclicality of $\delta^{18}\text{O}_{\text{wc}}$

The consistency between the seasonal patterns of $\delta^{18}\text{O}_{\text{prec}}$ and $\delta^{18}\text{O}_{\text{wc}}$ in the EC samples supports our hypothesis that the $\delta^{18}\text{O}_{\text{wc}}$ of the trees reflects $\delta^{18}\text{O}_{\text{prec}}$. The concurrent increase in $\delta^{18}\text{O}_{\text{wc}}$ and $\delta^{13}\text{C}_{\text{wc}}$ values in some individuals implies that the seasonal $\delta^{18}\text{O}_{\text{wc}}$ pattern can also reflect physiological responses to water deficit (e.g., reduction in stomatal conductance) in some cases. The agreement between $\delta^{18}\text{O}$ year and ^{14}C year found in some EC and PH samples indicates that a single cycle of $\delta^{18}\text{O}_{\text{wc}}$ variation generally represents annual radial growth for these species. However, the discrepancies between $\delta^{18}\text{O}$ year and ^{14}C year found in the inner wood of EC-1A, EC-2A, and IC suggest a failure in the interpretation of $\delta^{18}\text{O}$ cycles or in the ^{14}C dating.

The ^{14}C years estimated here did not show any chronological conflicts and increased with inner distance along the radius. The highest ^{14}C signatures that we detected matched the levels observed in atmospheric $^{14}\text{CO}_2$ for the mid-1960s (the so-called bomb peak). These facts suggest that our samples did not experience any noticeable contamination. In addition, ^{14}C dating using the Southern Hemisphere ^{14}C bomb curve has been shown to agree well with dendrochronological dates (Andreu-Hayles et al. 2015). As the ^{14}C dating in the present study is limited within the bomb curve period, which yields an age error of 1–2 years, in the following discussion we assume that the ^{14}C year is a reliable index of time series.

To define each $\delta^{18}\text{O}_{\text{wc}}$ annual cycle, at least two data points (minimum and maximum values) are necessary. In this study, the sampling interval of 0.2 mm required a minimum width of 0.4 mm radial growth year $^{-1}$ for detection. Mean annual radial growth rates, calculated as the ratio of sample length to ^{14}C year, were the largest in EC (0.8–3.0 mm year $^{-1}$), followed by PH (0.4 mm year $^{-1}$) and IC (0.1–0.7 mm year $^{-1}$). Thus, the relatively large deviation between the $\delta^{18}\text{O}$ years and the ^{14}C years in IC may be attributed to insufficient sampling resolution to define $\delta^{18}\text{O}$ years in this species. A lack of spatial sampling resolution may also result in the smaller $\delta^{18}\text{O}_{\text{wc}}$ amplitude in IC compared with EC and PH. In future studies, samples of very slow-growing species must be subdivided at a higher resolution with a rotary microtome, or relatively fast-growing

Fig. 7 Radial variations in $\delta^{18}\text{O}_{\text{wc}}$ (filled circle) and $\delta^{13}\text{C}_{\text{wc}}$ (open circle), in radii of two individuals of *E. coriacea* collected at the ZF2 study site (Manaus): **a** EC-1 and **b** EC-2. Dotted lines show annual-ring boundaries estimated from $\delta^{18}\text{O}_{\text{wc}}$. Years written at the top of

each figure part are estimates from ^{14}C dating and those at the bottom are estimates from $\delta^{18}\text{O}_{\text{wc}}$. The $\delta^{18}\text{O}$ year is defined to start in October of the previous year and end in September of the current year. For abbreviations, see Figs. 3 and 4

species should be selected for the purpose of tree-ring analysis.

Apart from these methodological issues, the discrepancies between $\delta^{18}\text{O}$ year and ^{14}C year might also be explained by features of the sampled wood itself, which sometimes contained cessations of wood formation for a whole growing season (missing ring) or in certain radii (wedging ring). The occurrence of missing or wedging rings was indicated by the fact that ^{14}C year was often greater than or equal to $\delta^{18}\text{O}$ year. For example, in EC-2B (Fig. 3d), since the outermost $\delta^{18}\text{O}$ ring was formed in 2013, the ring estimated as 2009 ± 2 by ^{14}C dating should have formed in 2010. Likewise, the adjacent $\delta^{18}\text{O}$ ring should be dated 2009, but it was estimated to be formed in 2005.5 ± 1.5 . Apparently, one or two rings may be missing at this point in EC-2B. Similarly, larger discrepancies found for the longer $\delta^{18}\text{O}$ chronology in EC-2A were unlikely to be caused by insufficient resolution of analysis, because the radial variations in $\delta^{18}\text{O}_{\text{wc}}$ of the sample tree were rather smooth and continuous (see Fig. 7b; 25–45 mm from cambium), and also because narrower $\delta^{18}\text{O}$ rings were detected in the inner parts of both EC-2A and EC-1A. Consequently, the frequent occurrence of missing or wedging rings may have caused the large discrepancies between $\delta^{18}\text{O}$ year and ^{14}C year in these two trees. This implication is supported by the dendrometer study in the same site (da Silva et al. 2002) showing that some commercial species, including *E. coriacea*, presented an annual increment equal to zero.

The ages of tropical trees determined by ^{14}C dating often differ from those determined by other methods, such as counting anatomically visible rings or performing indirect estimations using periodic annual increment (Martinez-Ramos and Alvarez-Buylla 1998; Worbes and Junk 1999). For example, some tropical trees have been estimated by ^{14}C dating to be over 1000 years old, including those in Amazonian terra firme forests (Chambers et al. 1998) and in tropical rainforests of Southeast Asia (Kurokawa et al. 2003). The ^{14}C estimates are much older than the maximum age, ca. 500 years, that has been estimated (in other tree species) from ring counting or other indirect estimations (Worbes and Junk 1999).

One explanation for these observations is that missing or wedging rings are common in tropical forests. If such rings only occur occasionally in a tree, they may be detected by cross-dating with ring-width chronology (Worbes 1999) or $\delta^{18}\text{O}$ chronology (Anchukaitis et al. 2008). However, if they occur frequently, cross-dating with ^{14}C years may be the most reliable way to detect them (Pearson et al. 2011). Anchukaitis et al. (2008) found some missing rings in a sample of *Ocotea tenera* in a tropical montane cloud forest in Costa Rica and suggested that the missing years were not clearly associated with any climatic cause. On the other hand, tree-ring dating and ^{14}C dating reportedly matched well, for example, in several species in an old-growth tropical rainforest in Costa Rica (Fichtler et al. 2003) and in *Pseudolmedia rigida* in a basimontane seasonal humid forest in Bolivia (Andreu-Hayles et al. 2015). The factors

that cause missing or wedging rings in the tropics are still unclear. The frequent occurrence of missing rings implied in this study explains the discrepancy between ^{14}C dating and visible rings and aids our understanding of the growth characteristics of Amazonian trees.

Within-tree and inter-tree $\delta^{18}\text{O}_{\text{wc}}$ variations

The similarities in seasonal $\delta^{18}\text{O}_{\text{wc}}$ patterns between the two radii of each EC tree and in the inter-annual $\delta^{18}\text{O}_{\text{wc}}$ variations between EC-1 and EC-3 suggest that $\delta^{18}\text{O}_{\text{wc}}$ ring analysis has an advantage over anatomical ring analysis. Furthermore, some remarkable events, such as the extremely low $\delta^{18}\text{O}_{\text{wc}}$ value that was seen commonly in the third cycle from the bark side, can be used for cross-dating among individuals. However, the $\delta^{18}\text{O}_{\text{wc}}$ similarity is not always found even within an individual tree, as seen in the outermost $\delta^{18}\text{O}_{\text{wc}}$ rings of EC-3A and EC-3B (Fig. 3e, f). In a study of several other species in other areas, $\delta^{18}\text{O}_{\text{wc}}$ circumferential variability within a tree was ca. 0.5–2 ‰ (Leavitt 2010). In addition, the occurrence of missing or wedging rings can be the critical factor causing the low synchronicity of $\delta^{18}\text{O}_{\text{wc}}$ variation within and between individuals. Thus, performing the $\delta^{18}\text{O}_{\text{wc}}$ analysis on two or more radii is necessary to detect the occurrence of wedging rings and obtain representative $\delta^{18}\text{O}_{\text{wc}}$ values for each individual.

Brienen et al. (2012) reported that “inter-annual” variations in $\delta^{18}\text{O}_{\text{wc}}$ of *Cedrela odorata* trees sampled in northern Bolivia were correlated strongly with those of $\delta^{18}\text{O}_{\text{prec}}$ measured at considerably distant sites (>1000 km) in the Amazon, including Manaus. In the case of *E. coriacea*, however, the seasonal $\delta^{18}\text{O}_{\text{wc}}$ patterns of the trees in Manaus were not similar to those in the other two study areas (EC–JU, EC–AT; Fig. 6). The extremely low $\delta^{18}\text{O}_{\text{wc}}$ value in the third cycle from the bark side in the EC trees in Manaus was not found in the EC–JU and EC–AT trees. Assuming that the third cycle is not missing in EC–JU and EC–AT, this fact suggests that the seasonal patterns of both $\delta^{18}\text{O}_{\text{wc}}$ and $\delta^{18}\text{O}_{\text{prec}}$ depend primarily on the amount effect, which varies regionally. This dependency of $\delta^{18}\text{O}_{\text{wc}}$ was also suggested by Ballantyne et al. (2011), who reported a significant correlation between seasonal fluctuation in $\delta^{18}\text{O}_{\text{wc}}$ and monthly precipitation for one tree species (*T. myrmecophila*) growing in the same area as our study site (ZF2). Their findings support the expectation that seasonal $\delta^{18}\text{O}_{\text{wc}}$ patterns may differ among regions, even if the inter-annual patterns are similar.

Efficacy of each annual-ring indicator

The $\delta^{13}\text{C}$ pattern was not a robust annual-ring indicator in Manaus and other regions of the Amazon with a moderate dry season. The small range in the $\delta^{13}\text{C}_{\text{wc}}$ cyclic variation

found for all examined species indicates that these trees do not experience serious drought stress or may not change their photosynthetic rate to a large extent throughout the year in the study regions. Much larger seasonal $\delta^{13}\text{C}_{\text{wc}}$ variations were reported for trees growing in seasonally dry forests in the tropics of Southeast Asia (Poussart et al. 2004; Poussart and Schrag 2005; Ohashi et al. 2009). However, the distinct $\delta^{13}\text{C}_{\text{wc}}$ peaks that coincided fairly well with the $\delta^{18}\text{O}$ ring boundary in EC trees (e.g., Fig. 7) can provide useful supplementary information in the analysis of the $\delta^{18}\text{O}_{\text{wc}}$ pattern for annual-ring detection.

Anatomical growth rings could be formed annually in some cases. Although the ring boundaries of PH (radially flattened fibers) are difficult to recognize (see Fig. 2c, d), the consistency with $\delta^{18}\text{O}$ ring and ^{14}C dating suggests that a band of the flattened fibers may be used as an annual-ring indicator. On the other hand, the anatomical rings of EC were mostly unreliable as an annual-ring indicator, as there were many circumferentially discontinuous or indistinct rings. The fact that the anatomical ring count was smaller than the ^{14}C year count in most samples indicates that the ring is not necessarily formed every year. The exception was EC-1, a tree that may have grown faster than the other sampled trees and hence formed a greater number of rings (i.e., false rings) than the number of ^{14}C years. In addition, some ring boundaries seemed to have formed at the beginning of the moderate dry season, because many boundaries appeared with the sharp increase in $\delta^{18}\text{O}_{\text{wc}}$ variations. Similarly, the $\delta^{18}\text{O}_{\text{wc}}$ analysis suggested that the ring boundary formed at the end of the peak of the wet season for one species of deciduous dipterocarp tree in Thailand (Poussart et al. 2005). Even in our limited study of three species, it was unclear how ring boundary formation was associated with the stable isotopic ring patterns. Anatomical wood structure is the easiest and least expensive indicator of annual rings, and thus it is necessary to discover the linkage between visible rings and $\delta^{18}\text{O}_{\text{wc}}$.

We conclude that $\delta^{18}\text{O}_{\text{wc}}$ is a promising indicator of annual rings for several tree species in Manaus. Comparisons between three different regions indicate that the method using a cyclic $\delta^{18}\text{O}_{\text{wc}}$ pattern may be applied to the terra firme forest throughout the Amazon. To confirm this possibility, however, further investigations are necessary. First, linkages between the seasonal $\delta^{18}\text{O}_{\text{wc}}$ pattern and the local amount and $\delta^{18}\text{O}$ content of precipitation should be investigated in various regions. Second, missing or wedging rings, which appeared to be common even in well-grown dominant trees, should be verified more carefully by cross-checking their numbers with ^{14}C dating. Finally, establishing a reliable cross-dating tool (i.e., longer master chronologies of $\delta^{18}\text{O}_{\text{wc}}$ at both seasonal and inter-annual scales for tree species with distinct annual rings in each region) is needed to advance tropical dendrochronology in the Amazon.

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Author contribution statement S. O., F. M. D., A. K., T. K., S. E. T., M. I., and N. H. designed the experiment. S. O. and F. M. D. conducted the fieldwork. S. O. and A. K. performed wood anatomical and stable isotope analyses, and S. E. T. and X. X. performed radio-carbon analysis. S. O., F. M. D., A. K., and T. K. wrote the manuscript; other authors provided editorial advice.

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