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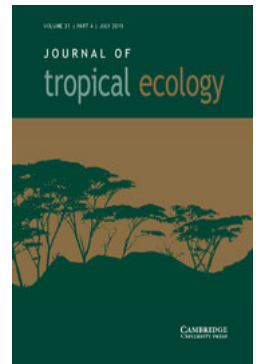
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Stable carbon and oxygen isotopes in tree rings show physiological responses of *Pericopsis elata* to precipitation in the Congo Basin

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Abstract: In equatorial regions, where tree rings are less distinct or even absent, the response of forests to high-frequency climate variability is poorly understood. We measured stable carbon and oxygen isotopes in anatomically distinct, annual growth rings of four *Pericopsis elata* trees from a plantation in the Congo Basin, to assess their sensitivity to recorded changes in precipitation over the last 50 y. Our results suggest that oxygen isotopes have high common signal strength ($EPS = 0.74$), and respond to multi-annual precipitation variability at the regional scale, with low $\delta^{18}O$ values (28–29‰) during wetter conditions (1960–1970). Conversely, $\delta^{13}C$ are mostly related to growth variation, which in a light-demanding species are driven by competition for light. Differences in $\delta^{13}C$ values between fast- and slow-growing trees (c. 2‰), result in low common signal strength ($EPS = 0.37$) and are driven by micro-site conditions rather than by climate. This study highlights the potential for understanding the causes of growth variation in *P. elata* as well as past hydroclimatic changes, in a climatically complex region characterized by a bimodal distribution in precipitation.

Key Words: Africa, Congo, stable isotopes, tree rings, tropical rain forest

INTRODUCTION

The Congo Basin is a key area for the global carbon cycle, hosting the second largest tropical forest after the Amazon (Detwiler & Hall 1988). Yet, the degree to which the Central African forest will cope with future global changes is under debate (Otto *et al.* 2013, Zelazowski *et al.* 2011). Understanding centennial scale growth dynamics of past tropical forests can provide baseline information for assessing future climate change impacts; unfortunately, such data are rare before the instrumental record (Gebrekirstos *et al.* 2014, Rozendaal & Zuidema 2011).

Tree rings can potentially fill this gap in our knowledge. In the tropics, the use of tree rings has been hindered by the lack of annual rings in most tree species, thus limiting their application for dendrochronological studies (Loader *et al.*

2013, Rozendaal & Zuidema 2011). However, tree-ring stable carbon and oxygen isotopes ($\delta^{13}C$, $\delta^{18}O$) in some cases have been shown to reflect tree growth response to climate forcing, even when annual rings are missing or unclear (Evans & Schrag 2004, Poussart *et al.* 2006).

Stable isotopes in tree rings are determined by distinct processes (McCarroll & Loader 2004). Generally, tree physiology controls $\delta^{13}C$, with fractionation occurring during uptake of CO_2 through the stomata (diffusion, c. −4‰) and during CO_2 -fixation (carboxylation, c. −27‰). $\delta^{13}C$ is therefore influenced by changes in the relative importance of diffusional versus biochemical limitations of photosynthesis (Francey & Farquhar 1982). Such changes occur as a result of environmental factors like water availability, light, but also nutrients and competition with neighbouring trees (McCarroll & Loader 2004). In contrast, tree-ring oxygen isotopes are more directly influenced by physical and climatic factors, rather than tree-internal physiological fractionations. Precipitation amount (amount effect, i.e. the depletion

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of heavy isotopes with increasing rainfall), together with altitudinal and continental effects (i.e. Rayleigh fractionation) are the most relevant factors determining $\delta^{18}\text{O}$ in precipitation (equilibrium processes, Dansgaard 1964). This precipitation isotope signal, taken up by the roots, is the major signal incorporated in plants, although further modification occurs in the plant leaves during transpiration, causing an enrichment controlled mainly by relative humidity and relatively constant biochemical enrichment (Roden *et al.* 2000). Stable isotope tree-ring series in the tropics are still rare and a relatively recent approach compared with temperate zones (Barbour 2007, Helle & Schleser 2004, McCarroll & Loader 2004, Schleser *et al.* 1999). Additionally, the attribution of isotopic changes to single environmental factors is often difficult to achieve (Gebrekirstos *et al.* 2014). This is particularly true for regions characterized by a bimodal distribution in precipitation (e.g. Eastern Congo), where the responses of species are controlled by multiple factors and still poorly documented.

In this study, we explore the nature of isotopic variability in tree-ring series from *Pericopsis elata* (Harms) van Meeuwen, a light-demanding species common in moist semi-deciduous forest of Central and Western Africa (Vivien & Faure 2011), and with the advantage of annual growth rings (De Ridder *et al.* 2014). Specifically, we combine stable isotopes, ring-widths and precipitation data to test whether stable isotopes may record climate variability over the last c. 50 y, in an area characterized by a bimodal distribution in precipitation (two wet and two dry seasons). Alternatively, the isotopic composition in *Pericopsis elata* may be mostly driven by local growth conditions (e.g. light availability), thus masking the climate signal. For this study, we focused on two slow- and two fast-growing trees, to account for the relative importance of tree growth for isotopic fractionation.

METHODS

Site

The Yoko reserve (00°21'–00°06'N, 025°13'–025°17'E) is a protected area (Institut Congolais de la Conservation de la Nature, ICCN) located c. 20 km south of Kisangani (Tshopo district, Province Orientale, Democratic Republic of Congo, Figure 1). The area is relatively flat and with a total area of approximately 7000 ha, delimited by the Congo and the Biaro rivers (Figure 1b). It is presently covered by dense and semi-deciduous forest stands (Congolese mixed moist semi-evergreen forest), including light-demanding (*P. elata*, *Milicia excelsa*, *Musanga cecropioides*, *Piptadeniastrum africanum*) and shade-tolerant tree species (*Cynometra* sp., *Gilbertiodendron dewevrei*, and mostly *Scorodophloeus*

zenkeri, see Lomba-Bosombo 2002). Mean temperature in the region is around 25°C with maximum insolation between January–February and a minimum in August (Kisangani meteorological station, 1901–2009). Monthly precipitation (annual mean 1700 mm) shows a bimodal pattern (short and long rainy seasons: April–May and September–November, respectively), associated with the latitudinal migration of the Intertropical Convergence Zone (ITCZ). Relative humidity in the Congo Basin is mainly delivered by westerly winds from the Gulf of Guinea and recycled through the rain forests, before being delivered further east (Williams *et al.* 2012). Continental-scale climate patterns, such as the ENSO or the Indian Ocean Dipole (IOD) can also affect precipitation variability over decades (Farnsworth *et al.* 2011).

Trees of *Pericopsis elata* have been planted in 1953 and 1954 in the reserve (00°19'35.2''N, 25°15'29.7''E), with a distance between trees of c. 5 m. A few *Terminalia superba* Engl. & Diels trees were planted close to the *Pericopsis elata*, and some other species (such as *Elaeis guineensis* Jacq. palms, *Piptadeniastrum africanum* (Hook.f.) Brenan and *Petersianthus macrocarpus* (P. Beauv.) Liben) established spontaneously between the planted trees. In 2010, the distance between trees was c. 9 m. Although a more complete description of the forest stands and micro-site conditions were not available in this remote area at the time of sampling, edaphic conditions were relatively homogeneous in the plantation, and competition for light is the main determinant of tree growth in this light-demanding species. For our study, we randomly selected from the plantation trees with regular stems and without scars.

Ecology of *Pericopsis elata*

Among the long-living, light-demanding tree species, *P. elata* is an ecologically versatile species, coping with both dry and waterlogged conditions (Bourland *et al.* 2012). It can be found in small (1 ha) aggregates, reproducing with anemochoric dispersal. Because of decades of exploitation for its highly valuable timber, it is included in the CITES list of protected species. To establish, *Pericopsis elata* requires forest-gap disturbances (Hawthorne 1995); its distribution in Central Africa was favoured by moderate human impact before the colonial period (Brncic *et al.* 2007). Generally its growing season is determined by seasonal precipitation distributions (from March–April to November, Appendix 1), and wood formation is only interrupted for a few months during the driest season (December–March).

Tree-ring widths and stable isotopes ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) analysis

We collected stem discs from two slow- (discs 1 and 2) and two fast-growing trees (discs 3 and 4, Figure 2a),

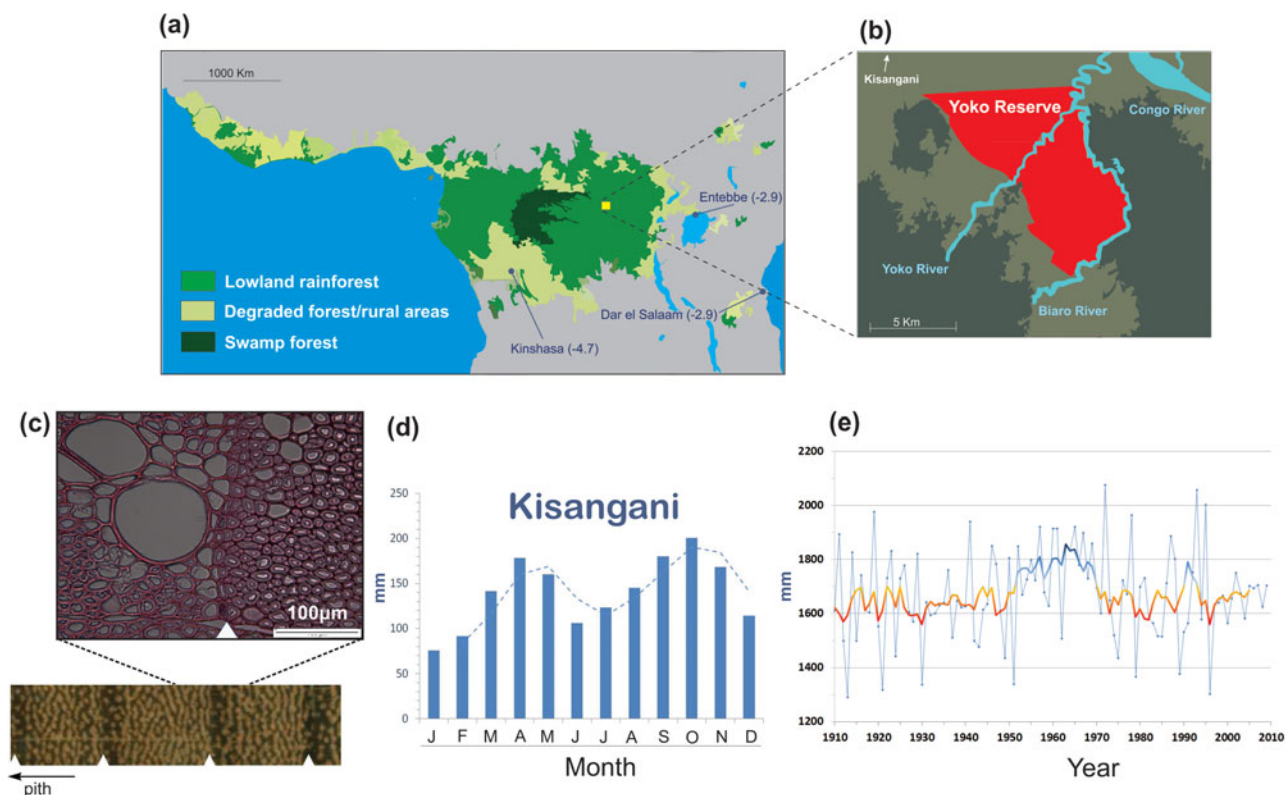


Figure 1. Map of the study site, with MODIS derived distribution of central African rain forest (a) (modified after Mayaux *et al.* 2013); values in brackets indicate long-term average $\delta^{18}\text{O}$, weighted by amount of precipitation at selected GNIP stations (Rozanski *et al.* 1996). The location of the Yoko reserve (b) (modified after Lomba-Bosombo 2002). The microscopic view of a *Pericopsis elata* tree ring (c), showing the anatomically distinct ring border, separating early (dark fibres) and late seasons (light fibres with parenchyma) (c). Monthly rainfall changes, showing the bimodal distribution of precipitation (d). Changes in total precipitation near Kisangani over the last century (van Oldenborgh & Burgers 2005); the thick line represents the 5-y moving average (e).

in the Yoko reserve during 2009–2010. Discs were cut at approximately 30 cm above soil level and tree-ring widths were measured on four rays for each disc, following standard procedures (De Ridder *et al.* 2013a). We measured each ring considering the wood anatomical patterns specific to *P. elata*: a dark layer of fibres and no vessels, followed by a lighter layer with parenchyma produced later in the season (Figure 1c). An anatomically distinct growth-ring border is visible, and is also supported by information from cambial wounding experiments. For each disc, we used one measured ray (i.e. with no missing years, where possible), instead of the average tree-ring series. Cross-dating between trees (Douglas 1941) was not successful due to different growth history of trees (Figure 2a).

We measured stable isotopes ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) on each tree and ring separately, without pooling samples for maximizing sample size (as sometimes done for temperate species, Saurer *et al.* 1995). This implied a lower number of measured samples, but allowed accounting for differences in the isotopic signal due to varying growth patterns (Figure 2a). For isotope analysis, we manually split each

selected ray with a scalpel obtaining *c.* 50 samples per disc, with each sample representing 1 y of tree growth. Alpha cellulose was extracted using standard methods from 1 mg of ground wood material prior to stable isotope analysis (Boettger *et al.* 2007). We excluded the innermost rings because photosynthesis rates may be different in the first years of growth and the influence of soil-respired CO_2 higher (Fichtler *et al.* 2010). In total, we considered 47 rings for disc 1 (1962–2008), 51 for disc 2 (1960–2010), 53 for disc 3 (1958–2010) and 51 for disc 4 (1960–2010, Table 1). For data analyses, we considered the common period between discs (1962–2008).

To determine carbon isotopic ratios, samples were combusted to carbon dioxide at 1025°C using an elemental analyser (EA-1110; Carlo Erba Thermoquest, Milan, Italy), and the isotope ratios measured with a Delta S isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). Oxygen isotopic ratios were determined after pyrolysis to CO at 1420°C using a Pyro cube (Elementar, Hanau, Germany) connected in continuous flow mode to a Delta Plus XP (Thermo Finnigan, Bremen, Germany).

Table 1. *Pericopsis elata* tree-ring series used in this study. Trees were sampled in 2008 and 2010 in an even-aged plantation (1953–1954) located in the Yoko reserve (Eastern Congo). Age interval considered for stable isotope series did not include the first years of growth. Discs 2–4 were harvested at the beginning of the growing season, resulting in a not fully formed ring in year 2010.

Disc	Museum code	Year of plantation	Gbh (cm)	Tree height (m)	Sampling date	Age interval considered for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ analyses	No. of rings analysed
1	Tw60900a	1954	97	20–22	11 August 2008	1962–2008	47
2	Tw622010a	1954	125.9	NA	24 May 2010	1960–2010	51
3	Tw62209a	1953	150.6	25–28	25 May 2010	1958–2010	53
4	Tw62212a	1953	178.8	NA	24 May 2010	1960–2010	51

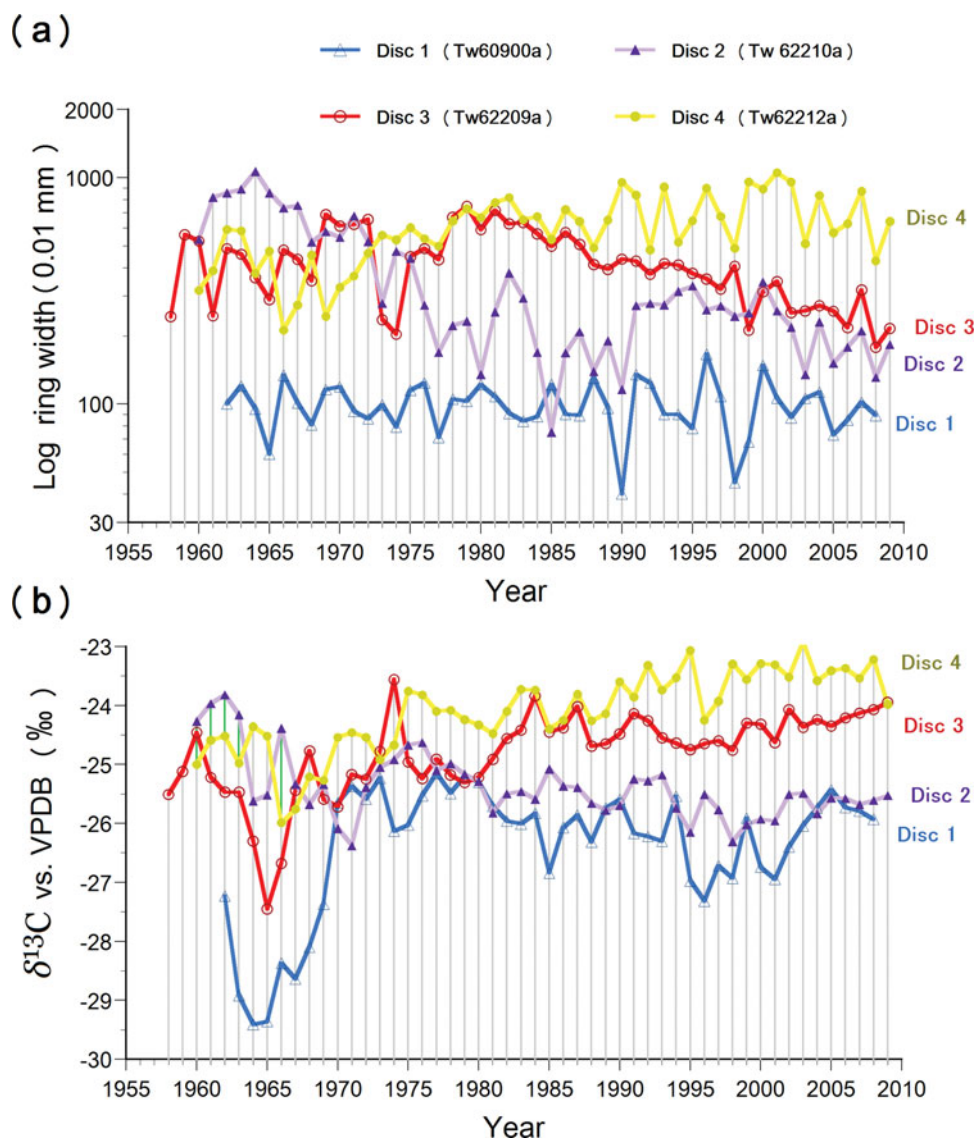


Figure 2. *Pericopsis elata* tree-ring widths showing slow- (discs 1 and 2) and fast-growing trees (discs 3 and 4); values are on a log scale to highlight variation in low $\delta^{13}\text{C}$ (a). $\delta^{13}\text{C}$ series on alpha-cellulose expressed relative to the Vienna Pee Dee belemnite VPDB; $\delta^{13}\text{C}$ values were corrected by adding the difference between preindustrial and present $\delta^{13}\text{C}$, to account for the increase in carbon dioxide from fossil fuels since 1950 (b).

Carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopic ratios are expressed relative to the Vienna Pee Dee belemnite VPDB ($\delta^{13}\text{C}$, Coplen 1995), and Vienna Standard Mean Ocean Water VSMOW ($\delta^{18}\text{O}$), respectively (details in Saurer & Siegwolf 2004). The overall precision was 0.1‰ for carbon and 0.2‰ for oxygen. For $\delta^{13}\text{C}$, we accounted for the global increase in carbon dioxide from fossil fuels since 1950 (Epstein *et al.* 1990), which reduced the ^{13}C content in the atmosphere (McCarroll *et al.* 2010). We therefore corrected all $\delta^{13}\text{C}$ values by adding the difference between pre-industrial and present $\delta^{13}\text{C}$, for each year.

Data analysis

Instrumental climate data in the tropics are generally sparse and discontinuous; we therefore compared different precipitation datasets from instrumental records, including areas close to the sampling site (Kisangani, 20 km distant), or in the region (Yangambi, 100 km distant). Since most of these data are too fragmentary, or do not entirely cover our series (1958–2009), we only considered the interpolated (between 0 and 1°N and 24° and 25°E) precipitation time-series from 1908 to 2009, at local-to-regional scale (Royal Netherlands Meteorological Institute KNMI, van Oldenborgh & Burgers 2005, and NCAS British Atmospheric Data Centre). Temperature has generally little influence on growth conditions of tropical species, at least in this area (De Ridder *et al.* 2013b), and indeed our stable isotope series are only weakly correlated with temperature (Appendix 1). The KNMI data show a period of higher annual precipitation in the 1960s, followed by a drying trend (Figure 1e). When decomposing the time series, the distribution of seasonal precipitation during the two halves of the rainy season (short and long wet seasons) is also variable over the decadal time-scale (Appendix 1). We therefore compared our isotopic data, with changes in monthly and seasonal precipitation over the last 50 y (Appendices 2 and 3). All time-series are presented with raw data (with exception for the $\delta^{13}\text{C}$ corrected for fossil-fuel emissions). No standardization was applied to avoid losing any low-frequency signal (Robertson *et al.* 1997).

For carbon and oxygen isotopes, we calculated the expressed population signal EPS (Briffa & Jones 1990) to assess the common signal strength of different trees. We used the averaged oxygen isotopes values (but not $\delta^{13}\text{C}$ series, because of lower inter-series correlations), to check whether oxygen isotopes in our series are related to precipitation data. The averaged $\delta^{18}\text{O}$ values are reported with confidence intervals calculated with a Student's-*t* distribution. Additionally, we calculated the coefficient of variation CV (a normalized measure of dispersion), RBAR (a measure of common variance) and standard deviation statistics (Frank *et al.* 2007, Kress *et al.* 2010).

We also considered GNIP stations (Global Network of Isotopes in Precipitation) located in the west and the east of the Congo Basin (Figure 1a), to assess the isotopic signature of different source of air masses on precipitation (Araguas-Araguas *et al.* 2000). We only used the weighted mean as reported in Rozanski *et al.* (1996), because GNIP series are often discontinuous and do not allow a full comparison with our $\delta^{18}\text{O}$ series. Also, the closest station with continuous data (Entebbe, Uganda, Figure 1a), shows an isotopic signature which is mostly biased by moisture derived from evaporated water from Lake Victoria (Rozanski *et al.* 1996), and therefore not considered in this study.

RESULTS

Ring-width series and stable isotopes

The analysed stem discs showed large differences in ring-width patterns (Figure 2a), reflecting the different growth dynamic of trees growing in monospecific plantations. Disc 1 showed relatively constant narrow rings, suggesting less favourable conditions for tree growth, likely caused by the presence of a nearby growing *Terminalia superba* tree. Disc 1 also showed series of narrower rings, with minimum values in 1965, 1990 and 1998 (Figure 2a). Discs 2 and 3 exhibited highly variable ring-widths, with narrower rings after 1971 (disc 2) and 1980 (disc 3, Figure 2a). Disc 4 was still dominant at the time of sampling, and under more open conditions and light availability; ring widths showed a constant growth pattern, with favourable conditions for tree growth after 1977 (Figure 2a).

The common signal strength was different between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ series, with Expressed Population Signal (EPS) much lower for $\delta^{13}\text{C}$ (= 0.37) than for $\delta^{18}\text{O}$ (= 0.74). Fast-growing trees (discs 3 and 4) were less depleted (i.e. higher $\delta^{13}\text{C}$ values) than slow-growing trees (i.e. disc 1, Figure 2b). For instance, between 1975 and 2010, discs 3 and 4 showed 2‰ higher values on average than discs 1 and 2 (c. −24‰ vs −26‰, Figure 2b). Disc 2, with high variability in tree-ring widths, had lower $\delta^{13}\text{C}$ values when tree growth decreased (after 1971, Figure 2). We also observed more variability in $\delta^{13}\text{C}$ during the period with highest total precipitation (1958–1970, Figure 1e), with disc 1 (slow-growing tree) reaching values as low as −29‰.

Correlations between oxygen and carbon, and between ring widths and stable isotopes, were significant only in a few discs and depended on their growth rates (Table 2). For instance, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were significantly correlated ($r = 0.53$, $P < 0.01$) only in disc 1, i.e. the tree with the slowest growth rates. Ring-widths and $\delta^{13}\text{C}$ were significantly correlated only in disc 4 ($r = 0.54$, $P < 0.01$),

Table 2. Pearson's product-moment correlation between ring widths and stable isotopes in *Pericopsis elata*, measured on four discs from the Yoko reserve (Eastern Congo). Positive correlations exist between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in disc 1 and between $\delta^{13}\text{C}$ and tree growth in disc 4; asterisk (*) indicates significance level at $P < 0.01$. Correlations are calculated over the common interval 1962–2008.

Disc	Growth rate	$\delta^{18}\text{O}$ vs $\delta^{13}\text{C}$	$\delta^{13}\text{C}$ vs avgGrowth	$\delta^{18}\text{O}$ vs avgGrowth
1	Slow	0.53*	−0.10	−0.12
2	Slow	−0.25	0.30	−0.58
3	Fast	0.29	−0.30	−0.05
4	Fast	0.31	0.54*	0.28

a fast-growing tree (Figure 2a), $\delta^{18}\text{O}$ and ring widths were instead weakly correlated for all discs (Table 2).

$\delta^{18}\text{O}$ and precipitation data 1958–2009

Considering the high common signal strength for $\delta^{18}\text{O}$, we averaged $\delta^{18}\text{O}$ series (Figure 3a) to allow comparison with the available 50 y of instrumentally recorded changes in precipitation (Appendix 1). At multi-annual scale, trends in $\delta^{18}\text{O}$ followed changes in total precipitation (but not in temperature, Appendix 1). In general, low $\delta^{18}\text{O}$ values occurred during 1960–1970, i.e. the period with higher precipitation (and to a lesser extent, during 1990–1995, Figure 3b–d). This period was followed by increasing $\delta^{18}\text{O}$ values and a declining precipitation trend (i.e. after 1970, Figure 3d). We found, however, low correlations between $\delta^{18}\text{O}$ series and annual or seasonal precipitation (Appendix 2 and 3). In particular, the weakened $\delta^{18}\text{O}$ signal strength after 1980 (see increased C.I. in Figure 3b), was due to changing growth rates in disc 2, particularly after 1988 (Figure 2a), overall weakening the correlation between total precipitation and our $\delta^{18}\text{O}$ series. Low signal strength in $\delta^{18}\text{O}$ was also particularly marked for years 1965, 1984 and 1992–1994 (high STDEV and CVar in Figure 3c), and reflected by lower mean inter-series correlation (e.g. low RBAR between 1992–1995). By considering 5-y average values, the correlation between total precipitation and $\delta^{18}\text{O}$ series (all discs) was significant ($r = -0.7$, $P < 0.01$).

DISCUSSION

Physiological and climatic controls over tree-ring $\delta^{13}\text{C}$

The $\delta^{13}\text{C}$ signal in tree-rings is usually interpreted as the interplay between stomatal conductance (influenced by atmospheric humidity and soil moisture) and photosynthesis (influenced by light and nutrients availability), determining the total amount of intracellular CO_2 in

the leaf, and therefore the carbon isotope discrimination (McCarroll & Pawellek 2001). For instance, high $\delta^{13}\text{C}$ values may result from increased photosynthesis or stomatal closure, depending on the relative importance of moisture for tree growth in the considered region. In Kenya, Gebrekirstos *et al.* (2009) found that moisture stress results in high $\delta^{13}\text{C}$ in different *Acacia* species from semi-arid areas of East Africa. The (inverse) relationship between precipitation and $\delta^{13}\text{C}$ in tree rings has also been used for regional-scale river flow reconstructions (Wils *et al.* 2010). In the Congo Basin instead, where moisture stress is a less limiting factor, we expect stomatal conductance to play a minor role for $\delta^{13}\text{C}$ fractionation, compared with photosynthesis. We tested this by comparing our $\delta^{13}\text{C}$ series with precipitation data and ring-width measurements, which can be used as indicators of photosynthetic rates (Worbes *et al.* 2003).

Our data show a marked inter-tree variability in absolute $\delta^{13}\text{C}$ values (Figure 2). Fast-growing trees tend to have around 2‰ higher values on average than slow-growing trees. Such differences in absolute $\delta^{13}\text{C}$ have also been observed for subtropical forest species growing under different growth conditions, with lower $\delta^{13}\text{C}$ values in shade conditions (West *et al.* 2001). Indeed, shading is a limiting factor for tree growth, especially for long-lived, light-demanding species such as *P. elata* (Bourland *et al.* 2013). Instead, water stress is not controlling growth variation between trees, as stomatal closure would result in higher $\delta^{13}\text{C}$, rather than low $\delta^{13}\text{C}$ values as in our data (i.e. in the slow-growing discs 1 and 2, Figure 2). In agreement with the carbon fractionation theory (McCarroll & Pawellek 2001) our data therefore suggest that variation in $\delta^{13}\text{C}$ is driven by individual growth histories of each tree, which at our site is mainly determined by variation in light availability. For instance, Disc 1 grew under reduced light conditions, due to a nearby *Terminalia superba* tree. The weak correlation between $\delta^{13}\text{C}$ and ring widths on the yearly basis (Table 2) is possibly due to the relative importance of photosynthesis and stomatal conductance, which may be different during wet (e.g. 1950–1970) and dry periods (e.g. after 1970, Figure 3d), thus indicating an unstable climate-isotope relationship (Reynolds-Henne *et al.* 2007). In our data, photosynthetic rates are reflected in the $\delta^{13}\text{C}$ variability in one tree only (disc 4, fast-growing), as suggested by the correlation with ring widths ($r = 0.54$, $P < 0.01$).

In the slow-growing disc 1, $\delta^{13}\text{C}$ variability is instead more controlled by precipitation, as shown by $\delta^{13}\text{C}$ values before 1970 (as low as −29‰, Figure 2b). Indeed, low $\delta^{13}\text{C}$ values in slow-growing trees may result from the additive effect of low light availability (low photosynthetic rate), and wetter conditions (high stomatal conductance). A further mechanism explaining such low $\delta^{13}\text{C}$ values could be related to CO_2 from soil respiration (containing

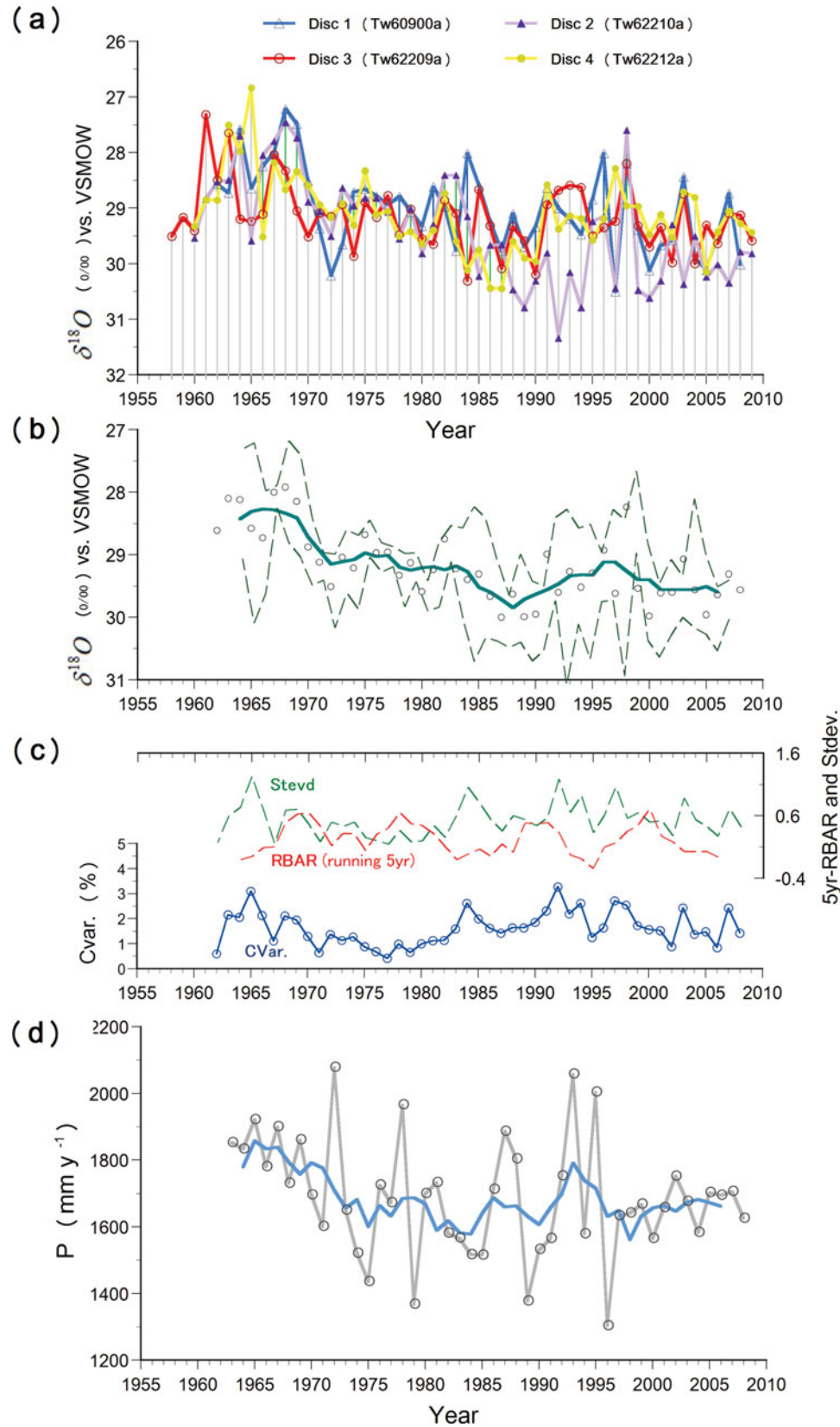


Figure 3. $\delta^{18}\text{O}$ measured on four stem discs from *Pericopsis elata*, relative to the Vienna Standard Mean Ocean Water VSMOW. Raw $\delta^{18}\text{O}$ series on alpha-cellulose (a); note the inverted Y axis to allow comparison with precipitation variability. Averaged $\delta^{18}\text{O}$ series (b); solid line represents the 5-y running mean and dashed lines the 90% CI of the four averaged series. Standard deviation (SD), 5-y running mean correlation coefficient (RBAR) and coefficient of variation (CV) (c). Total precipitation variability over the last 50 y; the blue line represents the 5-y running average (d).

less ^{13}C), during early stages of growth in a more closed canopy (isotope juvenile effect, Fichtler *et al.* 2010). Early-stage effects are instead less marked (or absent) in the other trees.

Taken together, such variable responses of carbon fractionation to photosynthesis and stomatal conductance in trees of different growth histories may explain why overall $\delta^{13}\text{C}$, tree-ring width and precipitation series are weakly related in our series (Appendix 2 and 3). Indeed, multiple controls over $\delta^{13}\text{C}$ fractionation such as nutrient availability (Kyereh *et al.* 1999, Veenendaal *et al.* 1996), root development (Ampofo 1972), solar irradiance and forest openness (e.g. grazing, fire, logging), are difficult to disentangle at this step. Notwithstanding these uncertainties, our data suggest that variation in $\delta^{13}\text{C}$ in *Pericopsis elata* is driven by light availability, rather than water stress.

Relationship between tree-ring $\delta^{18}\text{O}$ and precipitation

Factors controlling $\delta^{18}\text{O}$ in tree rings mostly depend on precipitation sources and physiological processes, including transpiration (McCarroll & Loader 2004). Rayleigh fractionation should result in ^{18}O depletion (i.e. low $\delta^{18}\text{O}$) in precipitation at our site, relative to values recorded closer to the ocean source (c. -2% to -3% , Figure 1a; Araguas-Araguas *et al.* 2000). The isotope ratio of precipitation is also influenced by transpiration processes resulting in recirculation of moisture, a mechanism less subject to ^{18}O depletion than land-evaporated water (Gat & Matsui 1991). Transpiration processes are still relatively less well documented in the Congo Basin than for the Amazon (Gat & Matsui 1991). This isotopic signature (i.e. high $\delta^{18}\text{O}$ values) is also visible in GNIP stations outside of the Congo basin (Levin *et al.* 2009), highlighting the relative importance of the Congo rain forest as a source of moisture for neighbouring regions.

Superimposed on these large-scale, spatial patterns are temporal changes in $\delta^{18}\text{O}$ of source precipitation (Levin *et al.* 2009). These changes should be reflected in the variation of tree-ring oxygen isotopes, assuming source water to be the dominant factor (Saurer *et al.* 1997), albeit modified by leaf water enrichment and biochemical fractionations (Roden *et al.* 2000). In our data, the forcing by regional variation in moisture balance is reflected by the strong signal coherency in $\delta^{18}\text{O}$ of tree rings. This value ($\text{EPS} = 0.74$) is slightly lower than that conventionally accepted for reaching the theoretical population chronology (0.85, Wigley *et al.* 1984), but still suggests a common signal in $\delta^{18}\text{O}$ (in contrast to $\delta^{13}\text{C}$). In general, the similarity between total precipitation and $\delta^{18}\text{O}$ trends (Figure 3b–d) shows that regional precipitation has influence over $\delta^{18}\text{O}$, at

least at the decadal scale. This anti-phase (i.e. low $\delta^{18}\text{O}$ values with high precipitation) is also more marked during periods of wetter conditions, such as 1950–1970 (Figure 1e). The Congo Basin and neighbouring areas (Sahel, Horn of Africa) experienced anomalously wetter conditions between 1950 and 1970, a trend out of phase with higher subtropical latitudes (Nicholson 2000), also visible in the westernmost part of the Congo Basin (Samba & Nganga 2012). It was followed by a reduction in precipitation during the 1970s and 1980s (mostly June–September precipitation, Williams *et al.* 2012). These decadal scale changes in precipitation are well reflected by our $\delta^{18}\text{O}$ series (Figure 3b–d). This decreasing trend in precipitation has been attributed to warming of the South Atlantic and Indian Oceans (Hagos & Cook 2008, Williams *et al.* 2012), although the relative sea surface temperature forcing (ENSO oscillations) on decadal scale precipitation variability is still relatively unclear (Camberlin *et al.* 2009, Nicholson 2000).

The observed relationship between $\delta^{18}\text{O}$ and total precipitation recorded in the instrumental record is in agreement with the theoretical fractionation mechanism related to precipitation intensity, or amount effect, and with the leaf isotope enrichment theory (Roden *et al.* 2000), suggesting higher enrichment under dry conditions (or less enrichment under humid conditions). Such local effects of changes in relative humidity can also be related to atmospheric circulation changes, and are therefore not easy to separate.

In general, the decadal changes in precipitation are mirrored by trends in $\delta^{18}\text{O}$, but the relationship between precipitation and $\delta^{18}\text{O}$ is much weaker on the annual basis (Appendix 2 and 3). Partly, this could be related to the quality of the meteorological data, or data not being fully representative for the study site. In their record from the Amazon, Brien *et al.* (2012) explained low $\delta^{18}\text{O}$ -precipitation correlation scores with additional depletion resulting from air mass movement over the continent (Rayleigh distillation). If precipitation variability exerts a major control over $\delta^{18}\text{O}$ fractionations over decades, other factors, such as local conditions for tree growth (e.g. disc 2 in Figure 2a), soil water evaporation and leaf water enrichment (Roden *et al.* 2000), can be dominant at the annual scale, weakening the correlation between precipitation and $\delta^{18}\text{O}$.

Potential and limitations of stable isotope analyses in *Pericopsis elata* tree rings

Factors controlling variation in tree-ring isotope ratios at low altitudes in the tropics are still poorly understood, and few tree-ring stable isotope series exist for tropical Africa, due to site remoteness and challenges in tree-ring dating. In this respect, our study contributes

to ongoing research in the tropics, by focusing on a widespread light-demanding species, and on a key region for palaeoclimatological studies (Russell & Johnson 2005, Verschuren *et al.* 2009). Species-specific responses to high-frequency climate variability can also complement information about long-term responses of plant communities in tropical Africa (Brncic *et al.* 2007, Colombaroli *et al.* 2014, Oslisly *et al.* 2013).

Our tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ series generally agree with expected mechanisms for isotope fractionation (McCarroll & Loader 2004), but with some important differences. First, our results highlight the different sensitivity of stable carbon and oxygen isotopes to climatic factors in the light-demanding *P. elata*. $\delta^{13}\text{C}$ absolute values seem to reflect local differences in growth factors, which in light-demanding species are controlled by competition for light (and to a lesser extent, by water stress). $\delta^{18}\text{O}$ trends are instead controlled by precipitation over the multi-annual scale (Figure 3), with enriched $\delta^{18}\text{O}$ values reflecting both large-scale atmospheric circulation changes, and humidity-driven enrichment by the leaves of the specific species. Secondly, the use of four trees for stable isotope studies in tree rings is often justified to represent a site isotope signal (Leavitt & Long 1984). However, this seems not to be sufficient for carbon isotopes series in *P. elata*, given the rather variable response of individual trees (Figure 2a). A larger sample size may be used to strengthen the link between $\delta^{13}\text{C}$ and specific growth patterns (Figure 2), allowing estimation of local growth rates in *P. elata* and, indirectly, its productivity over time (Mbow *et al.* 2013), or for reconstructing patch-scale dynamics (Gebrekirstos *et al.* 2014). Also, once applied to a pool of species with different traits (e.g. pioneer vs shade-tolerant), $\delta^{13}\text{C}$ series may allow differentiating the degree of shade tolerance, and thus classify functional types of species with poorly understood ecology (Werner & Maguas 2010). Oxygen isotopes instead show a stronger signal coherency than carbon in our trees (Figure 3). A higher EPS for $\delta^{18}\text{O}$ series could be achieved by including more trees with only constant growth rates (e.g. for discs 1, 3 and 4 in Figure 2). The sensitivity of $\delta^{18}\text{O}$ to precipitation changes indicates the potential in *P. elata* tree rings for precipitation reconstructions before the historical record. Stable isotopes from tree-rings are available from Western (van der Sleen *et al.* 2015) and Eastern Africa (Gebrekirstos *et al.* 2009), but are very scarce (if not absent) in this area, which is characterized by a complex bimodal precipitation distribution (Figure 1d). Climate reconstructions from the Congo Basin, one of three major convective regions on the planet, are urgently needed to improve our understanding about synoptic climate systems delivering rainfall to the African rain forest, as also highlighted by disagreements in the existing model projections of future Congo rainfall (IPCC 2013).

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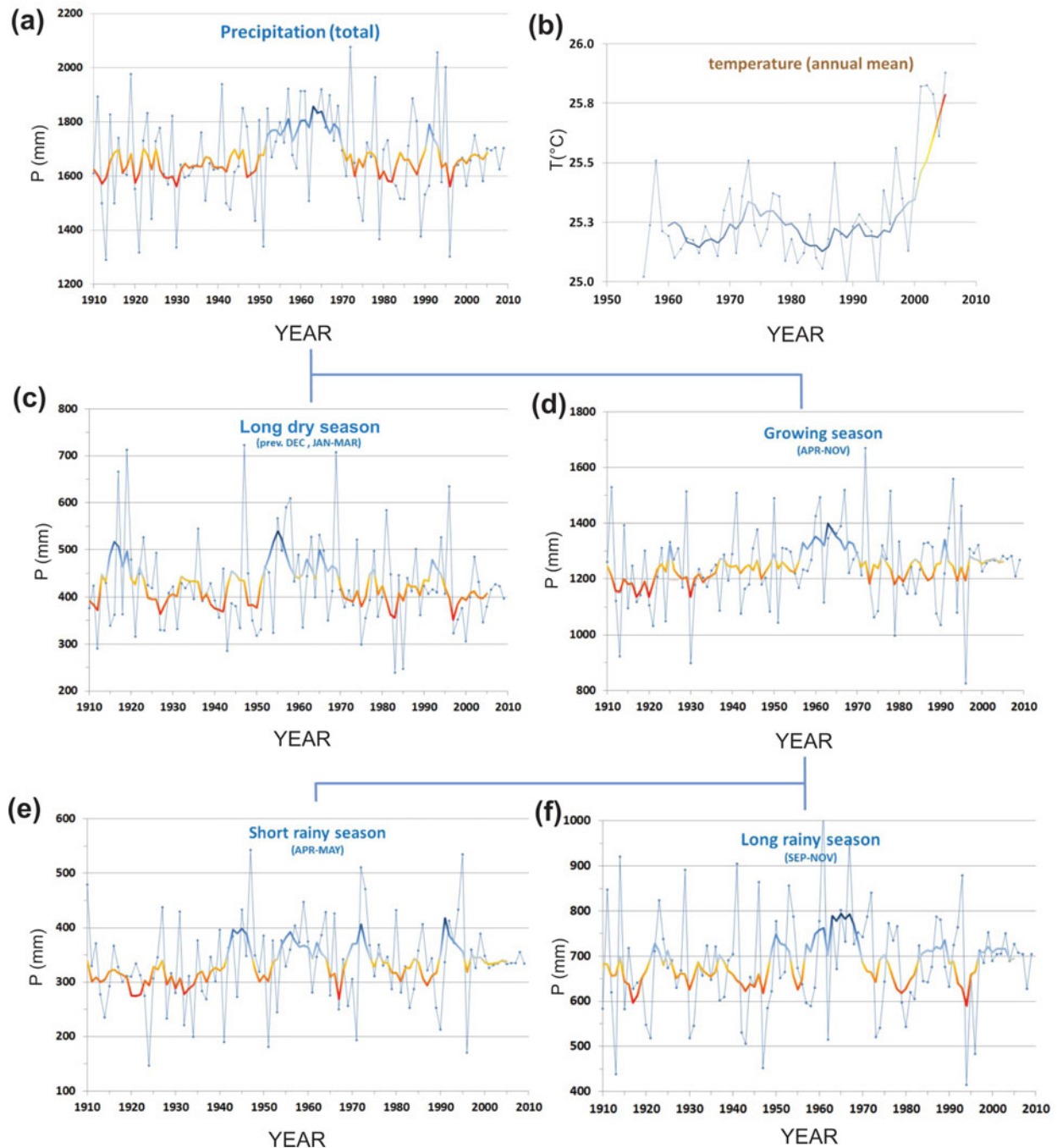
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Appendix 1. Temperature and precipitation time series (a–b, Kisangani area), showing the relative contribution of seasonal precipitation (c–f) to total annual rainfall (a). The bimodal pattern in precipitation (long and short rainy seasons) is mostly associated with the latitudinal migration of the ITCZ (see main text). Precipitation data are from the NCAS British Atmospheric Data Centre, accessed with the KNMI climate explorer (van Oldenborgh & Burgers 2005). Temperature data are from Kahindo Muhongya (2011).

Appendix 2. Pearson's product-moment correlation values showing a weak linear relationship on the annual basis between stable isotopes ($\delta^{18}\text{O}$ and corrected $\delta^{13}\text{C}$) measured on *Pericopsis elata*, and monthly precipitation in Eastern Congo (Kisangani area).

Disc	Stable isotope	January (mm)	February (mm)	March (mm)	April (mm)	May (mm)	June (mm)	July (mm)	August (mm)	September (mm)	October (mm)	November (mm)	December (mm)
1	Carbon	-0.03	0.08	0.00	0.11	-0.14	0.09	-0.20	0.07	-0.06	0.24	0.31	0.29
	Oxygen	-0.04	-0.09	0.10	-0.02	-0.05	0.15	-0.23	0.05	-0.04	0.02	-0.02	0.12
2	Carbon	0.21	-0.15	-0.02	0.17	0.18	-0.10	0.16	0.05	0.15	-0.09	0.06	0.14
	Oxygen	-0.14	-0.01	-0.10	-0.03	0.00	0.08	-0.15	0.01	-0.12	-0.10	0.16	0.12
3	Carbon	-0.09	0.04	0.03	0.02	-0.18	0.19	-0.20	-0.27	-0.02	0.11	0.24	0.10
	Oxygen	-0.17	-0.08	0.05	-0.07	-0.07	-0.08	0.01	-0.09	-0.01	-0.02	0.02	-0.03
4	Carbon	-0.21	0.11	-0.22	-0.08	-0.07	0.04	-0.33	-0.30	0.11	0.00	0.20	0.03
	Oxygen	-0.19	-0.03	0.13	-0.07	-0.10	0.15	0.03	-0.07	0.04	0.19	0.19	-0.01

Appendix 3. Pearson's product-moment correlation considering the seasonal distribution of precipitation in Eastern Congo (Kisangani area), with the growing season for *Pericopsis elata* between April and November.

Disc	Stable isotope	Long dry season (December–March)	Short dry season (June–July)	Short rainy season (April–May)	Long rainy season (August–November)	Growing season (April–November)
1	Carbon	-0.10	-0.03	-0.08	0.12	0.04
	Oxygen	0.08	-0.10	-0.22	0.18	-0.02
2	Carbon	0.04	0.10	-0.20	0.17	0.09
	Oxygen	-0.01	0.12	-0.10	0.10	0.08
3	Carbon	0.05	0.08	-0.21	0.24	0.13
	Oxygen	0.02	0.07	-0.17	0.29	0.19
4	Carbon	0.17	0.08	-0.10	0.11	0.08
	Oxygen	0.19	-0.04	0.03	0.13	0.11