



# Wood anatomy variability under contrasted environmental conditions of common deciduous and evergreen species from central African forests

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## Abstract

**Key message** Wood density profiles revealed significant differences in wood formation along a precipitation gradient in the Congo Basin. The response of trees to climate change varies depending on leaf phenology properties.

**Abstract** Tropical forests face increasing pressures due to climate change and yet, the response of trees to varying climate conditions remains poorly understood. In the present study, we aim to fill some gaps by comparing the leaf phenology and the pith-to-bark wood anatomical variability of 13 common tree species of the Democratic Republic of Congo among three sites presenting contrasted rainfall regimes. We measured pith-to-bark density profiles on which we applied wavelet analyses to extract three descriptors, which we further used as proxies to describe and compare wood anatomical variability. They describe the growth periodicity, regularity and the amplitude of variations of the anatomical patterns. Our results show that evergreen species tend to have significantly higher anatomical variability where rainfall seasonality is more pronounced. Deciduous species, in spite of shedding leaves for longer periods in drier sites, did not show significant differences in their anatomical variability. The analyses of density profiles and phenology records suggest that the seasonality of precipitation influences both leaf phenology and cambial activity. The high intra-site variability in phenology and anatomy suggests that site-related micro-climate conditions also influence cambial activity.

**Keywords** Wood density · Wood anatomy · Leaf phenology · Wavelet analysis · Tropical tree growth · Climate change

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## Introduction

Tropical forests cover about 7% of the terrestrial surface and store about 25% of its carbon (Bonan et al. 2008; Pan et al. 2011). They are key players in the global carbon cycle (Bonan 2008; van der Werf et al. 2009; Pan et al. 2011; Sexton et al. 2016) and provide short- and long-term services to the society. Tropical forests, however, are

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increasingly threatened by anthropogenic pressure (FAO 2016) and global warming (James et al. 2013). Extreme climatic events and the prolonged dry seasons (IPCC 2013) are expected to aggravate tree mortality and to affect tree growth (Allen et al. 2010; Phillips et al. 2010; Greenwood et al. 2017). Although substantial shifts in growth and biomass allocation were observed in the tropical forests (Chave et al. 2008; Lewis et al. 2009; Dong et al. 2012), these processes have yet to be understood in the framework of climate change. A better understanding of the influence of the climate change on forest dynamics is therefore essential to predict the future of tropical forests (Rozendaal and Zuidema 2011; Pucha-Cofrep et al. 2015) and to adapt to potential shifts in forest species composition (Scheffer et al. 2001; Phillips et al. 2010).

The current knowledge on tree sensitivity to climate change is mainly based on experimental studies of leaf-level physiological responses, but the exact influence of climate on the growth of woody biomass remains largely unknown (Zuidema et al. 2013). Moreover, our understanding of the influence of climate seasonality on leaf phenology in the tropics is limited (Moreau 2016). Remote sensing studies, which cover large geographic extents at high temporal resolution, show promising results in research on vegetation responses to seasonal climatic changes (Viennois et al. 2013; Philippon et al. 2016). Yet, persistent artefacts due to acquisition conditions induce errors in the estimations of the vegetation response to climate variability (Morton et al. 2014). Moreover, species-specific monitoring is hampered by the high canopy diversity (Baldeck et al. 2015). Additional field data to support remote sensing data and refine the estimates of forest productivity and carbon storage are thus needed (Babst et al. 2014; Moreau 2016).

It is well known that seasonal variation of environmental conditions such as precipitation or solar irradiance drives leaf shedding (Couralet et al. 2010; Borchert et al. 2015; Moreau 2016), exerting thus an influence on cambial dormancy (Brienen et al. 2016; Nath et al. 2016). Both leaf shedding and cambial dormancy are coupled to climatic seasonal variation at varying degrees, depending on the leaf shedding habit of the species (Borchert 1999) and the intensity of the climatic variations (Worbes 1995). Yet, the level of phenological adaptation to varying climatic conditions and its impact on wood formation are poorly understood (O'Brien 2008; Couralet et al. 2010; Vlam et al. 2014).

Trees respond to changing environmental conditions by adjusting their cambial activity, which depends on the species and/or the age of a tree (Wimmer 2002; Fonti et al. 2010; De Ridder et al. 2013; De Micco et al. 2016) and affects the structure of wood anatomical features (Chave et al. 2009). A considerable amount of information on tree growth conditions can thus be obtained through the analyses

of growth rings and other patterns in the wood tissue (Wiemann 1998; Wimmer 2002; Groenendijk et al. 2014).

Wood anatomy variation is an important source of information on tree adaptation (Gartner 1995; Larson 2012; Beeckman 2016; Tarelkin et al. 2016). Studying intraspecific anatomical and phenological variation across climatic gradients or between contrasting sites therefore constitutes a valuable approach in tree growth research (Carlquist 1988; Villar-Salvador et al. 1997; Wheeler et al. 2007; Fonti et al. 2010).

Previous studies have established a close relationship between anatomical features and wood density (Martinez-Cabrera et al. 2009; Zieminska et al. 2013). Fibres with thicker walls and flattened lumina increase wood density while vessels and parenchyma are negatively correlated to wood density (De Mil et al. 2018). Density variations across a pith-to-bark profile are thus a good indicator of the variations of the fibres' anatomy and the abruptness of change in wood anatomical structure.

Although wood density profiles' variability has been previously used in the study of the influence of the climate on tree growth (Moya and Tomazello Filho 2009), these studies remain descriptive and focus on a limited number of profiles only. On the other hand, wavelet analysis has proven very effective in handling complex, noisy and non-stationary data (Bullmore et al. 2003; Hudson et al. 2011). It has successfully been used in studies of temperature and rainfall shifts (Paluš et al. 2005; Koch and Markovic 2007), changes in vegetation cover (Lu et al. 2007), plant flowering (Hudson et al. 2011) and tree-ring series (Rigozo et al. 2005). However, to the best of our knowledge, wavelet analysis has not yet been applied in wood density studies, although these datasets present characteristics that make them good candidates for this type of analyses.

In this study, we investigated the effect of precipitation seasonality on leaf phenology and wood formation. We combined the recent developments in the field of wood densitometry with signal analysis techniques and compared the variability of wood density profiles of 13 tropical tree species between three sites of the Congo Basin with contrasted precipitation regimes. Pith-to-bark wood density profiles were analysed with wavelet transform (Morlet 1983) and three features summarizing wood formation dynamics were derived. To study leaf phenology, we compiled data from historical databases and compared the synchronicity of phenological events and the lengths of leafless periods of the studied species between two of the three sites. Finally, to study how leaf phenology and wood formation are coupled, we compared the inter-site differences in wood anatomy between trees with different leaf phenologies. We hypothesized that longer and more intense dry seasons lead to increases in the length of leaf shedding periods and to higher variability in wood anatomical features from pith to bark.

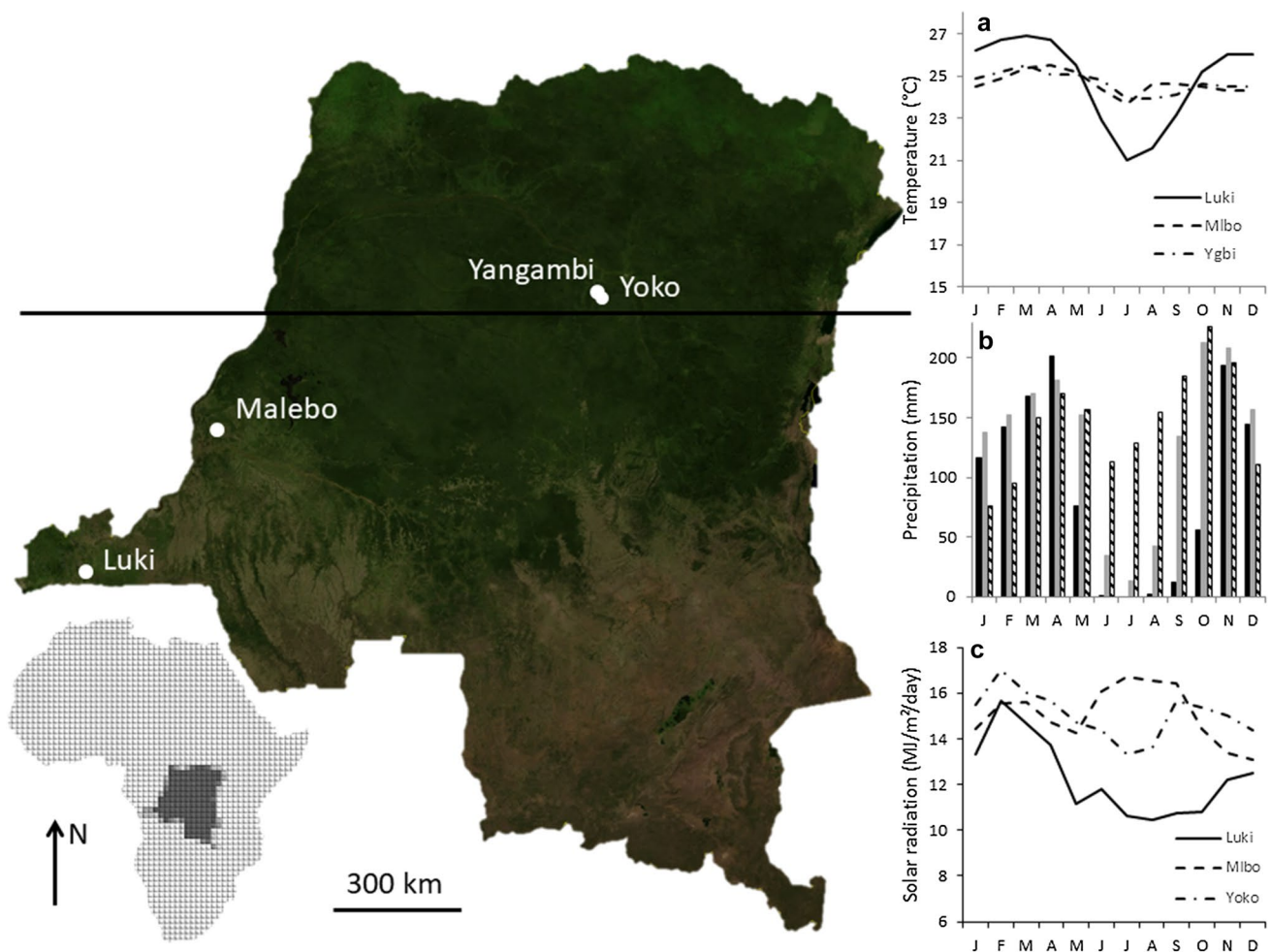
More particularly, we expected to observe more rhythmicity and higher amplitudes in density fluctuations throughout wood density profiles of trees from the driest sites. Furthermore, based on previous findings (Borchert 1999), we also assumed a difference in response between deciduous and evergreen species: more rhythmicity with higher amplitudes of wood density fluctuations in deciduous species.

## Materials and methods

### Study sites

Samples were collected in the Democratic Republic of the Congo (DRC). Three sites, the Yoko Reserve (0.33°N, 25.31°E), the Bolobo forests of Malebo (2.49°S, 16.50°E) and the Man and Biosphere Reserve of Luki (5.39°S 13.4°E), were selected for their contrasting rainfall regimes to compare the differences in wood formation dynamics (Fig. 1).

The Yoko reserve has the highest annual precipitation of ~1780 mm (Cassart et al. 2016) and the least pronounced dry season (Fig. 1b). The Biosphere Reserve of Luki and the forests of Malebo have an average annual precipitation of 1100 mm (Fig. 1b; De Ridder et al. 2013) and 1600 mm (Vancutsem et al. 2006) with an average of three and four dry months, respectively. Relative humidity remains constant throughout the year in Luki, buffering the intensity of the dry season (De Ridder et al. 2013). Moreover, a thick cloud cover decreases the solar radiation during the dry season in Luki (Fig. 1c). The soil types at the study sites are nutrient poor with Xanthic Ferralsol in Yoko (WRB 2014), Ferralic Arenosol in Malebo and Orthic Ferralsol in Luki (FAO 2007). The plant extractable water capacity is the highest in Yoko (8.77–11.65 cm), followed by Luki (6.08–7.11 cm) and Malebo with 4.31–6.08 cm (Dunne and Willmott 2000).



**Fig. 1** Map of the Democratic Republic of Congo showing the geographical location of the three study sites, **a** their monthly average temperature, **b** their monthly precipitation and **c** the average monthly solar radiation. Data: Worldclim2 (Fick and Hijmans 2017)

## Species selection and samples collection

We selected 13 species (Table 1) with abrupt anatomical variations on the pith-to-bark axis. These species are common among the three sites, and cover between 10–20% of the basal area of the forest (Table 1). Seven to thirteen trees per species were sampled at breast height with an increment corer ( $\varnothing = 5.15$  mm, Table 1). Three to four cores were collected per tree, stored in paper straws and then oven dried for 24 h at 103 °C. The cores are now registered and stored in the xylarium of the Royal Museum for Central Africa, Belgium (accession numbers: Tw68460 - Tw68881).

## Wood density and anatomy analysis

### Wood density profiles

The samples were mounted in custom-made cardboard holders and scanned with a resolution of 110  $\mu\text{m}$  using the Nanowood X-ray CT scanner (Dierick et al. 2014), developed at the Ghent University Centre for X-ray Tomography (UGCT; <http://www.ugct.ugent.be>). Top and bottom of the

holders were scanned separately, reconstructed with the Octopus software (Dierick et al. 2004; Vlassenbroeck et al. 2007; licensed by InsideMatters: <http://www.insidematters.eu>) and digitally stitched to obtain a single greyscale volume for each holder. Each single wood core was then extracted from the total greyscale volume and its pith-to-bark density was calculated using air density ( $1.2 \text{ kg m}^{-3}$ ) and a reference material with known density ( $1400 \text{ kg m}^{-3}$ ) and similar elemental composition to wood (De Ridder et al. 2011; Bastin et al. 2015a; De Mil et al. 2016). Structure direction was then manually corrected for ring curvature and radial variations in grain direction (Van den Bulcke et al. 2014), based on which a re-interpolated density profile was calculated (De Mil et al. 2016).

### Wood density profiles as proxies for wood anatomical variation

We used wood density variations as a proxy for the variability of anatomical features between individuals from different study sites. Wood density profiles were detrended to avoid tree size and age-dependent variations (Briffa and Melvin 2011;

**Table 1** Selected species with their leaf shedding behaviour, per-site percentage of the total basal area, number of sampled trees per site, mean diameter and range (in centimetres), number of trees with phe-

nology records per site and the duration of the observations (in years in the twentieth century)

Species	Total basal area (%)			Sampled trees (#)			Min–mean–max diameter (cm)	Trees with phenology records (#)		Observation span (years*)	
	Luki	Mlbo	Yoko	Luki	Mlbo	Yoko		Luki	Ygbi	Luki	Ygbi
<sup>(e)</sup> <i>Anonidium mannii</i> (Oliv.) Engl. & Diels	0.01	0.3	2.8	0	10	10	15–30–46	0	2	–	46–56
<sup>(d)</sup> <i>Canarium schweinfurthii</i> Engl	0.4	0.1	0.3	13	10	10	15–42–65	16	5	47–57	38–52
<sup>(e)</sup> <i>Cola griseiflora</i> De Wild	3.4	1	1.1	10	8	10	11–20–30	0	5	–	38–53
<sup>(d)</sup> <i>Entandrophragma angolense</i> (Welw.) C.DC	0.3	1.7	0.2	10	8	9	19–34–65	6	4	47–57	38–52
<sup>(e)</sup> <i>Gilbertiodendron dewevrei</i> (De Wild.) J. Léonard	0.01	3.3	10.9	10	10	9	17–36–77	0	5	–	38–56
<sup>(e)</sup> <i>Macaranga spinosa</i> (Müll Arg.)	0.03	NA	0.5	9	9	11	15–25–40	1	3	47–57	38–53
<sup>(d)</sup> <i>Milicia excelsa</i> (Welw.) C.C.Berg	0.1	0.9	0.03	9	9	12	32–51–82	31	6	47–57	37–56
<sup>(e)</sup> <i>Ongokea gore</i> (Hua) Pierre	0.1	1.6	0.3	10	8	2	24–41–60	17	3	47–57	38–52
<sup>(e)</sup> <i>Polyalthia suaveolens</i> Engl. & Diels	1.2	4	1.5	10	10	10	20–30–50	50	0	47–57	–
<sup>(e)</sup> <i>Pycnanthus angolensis</i> (Welw.) Warb	0.6	2.9	0.3	10	9	10	23–46–77	27	4	47–57	37–55
<sup>(d)</sup> <i>Ricnodendron heudelotii</i> (Baill.) Pierre ex Heckel	1.4	0.3	0.5	9	9	9	22–52–95	46	3	47–57	43–56
<sup>(e)</sup> <i>Staudtia kamerunensis</i> Warb	2.1	1.2	1.2	10	10	10	13–37–65	46	2	47–57	46–56
<sup>(e)</sup> <i>Tetrorchidium didymostemon</i> (Baill.) Pax & K.Hoffm	0.01	0.02	0.1	9	7	10	14–20–33	7	3	47–57	38–55
Total	9.7	17.3	19.7	119	117	122	–	247	45	–	–

Years\* = years in the twentieth century

(e) = evergreen and (d) = deciduous are leaf phenology data according to the CoForTraits database (Benedet et al. 2015)

Abundance data come from databases used in Kearsley et al. 2013, Bastin et al. 2014 and De Ridder, *comm pers*

Mlbo Malebo, Ygbi Yangambi



Peters et al. 2015) by subtracting a smoothed profile obtained with a moving average of 50 density values. The detrended profiles were analysed with wavelet transform (Morlet 1983) and three descriptors summarizing different aspects of wood formation were derived. These descriptors were then compared between individuals, between species and between sites.

Wavelet analysis allows processing complex signals with varying amplitudes and frequencies (Lau and Weng 1995). It is a powerful tool for the identification of the main periodicities within a signal and the evolution of amplitude, frequency and phase (Farge 1992; Rigozo et al. 2005). The wavelet analysis overcomes the main limitation of the Fourier transform that only identifies the frequencies present in a signal but not their localisation in time (Schaeffli and Zehe 2009). It decomposes the signal into portions of variable length and convolutes them with wavelets generated from an original (mother) wavelet (Farge 1992). The covariance between the two is calculated and the obtained values allow generating a space–frequency representation of the signal (Fig. 2; Schaeffli and Zehe 2009).

With  $D(x)$  the density profile and  $\psi$  the mother wavelet, the continuous wavelet transform (CWT) is expressed as:

$$\text{CWT}(u, s) = \frac{1}{\sqrt{s}} \int D(x) \psi\left(\frac{x-u}{s}\right) dx, \quad (1)$$

where  $u$  and  $s$  represent the space translation and the scaling factor of the mother wavelet, respectively. The scale factor

can be expressed in physical units (centimetres) and measures the width of one density fluctuation.

A Ricker wavelet, also known as Mexican hat (Ricker 1953), was used as the mother wavelet. This wavelet shape has the advantage to enhance local peaks of wood density surrounded by lower density area, with a predefined scale. Several scale factors, each representing the sizes of the wavelets, were tested.

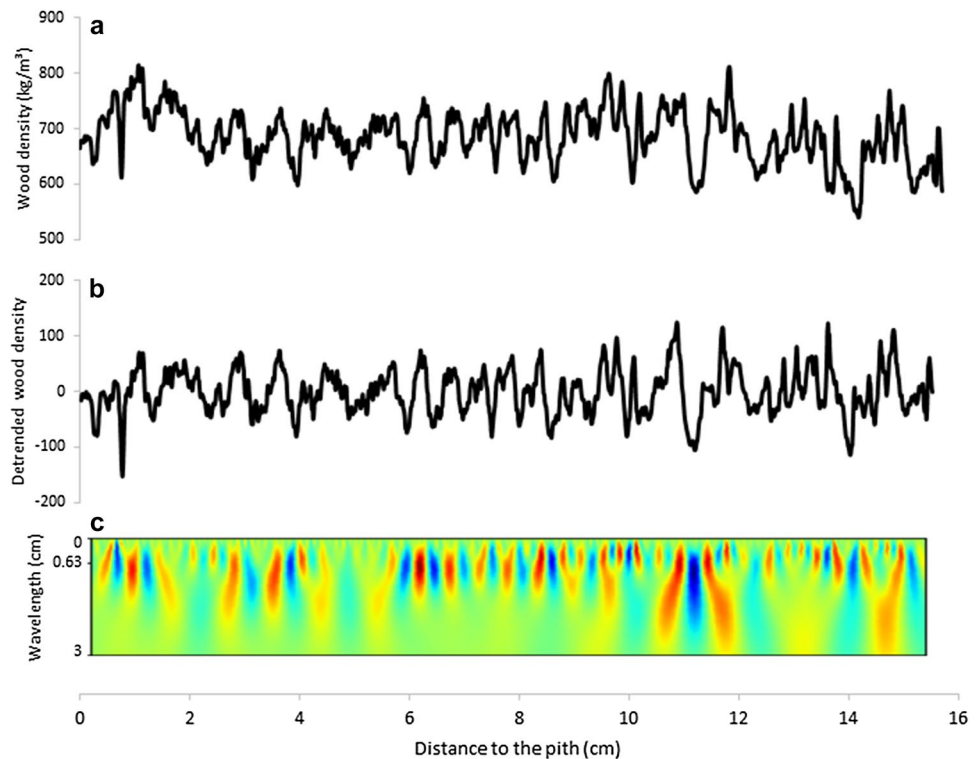
A space–frequency representation of the signal (Fig. 2c) is only qualitative, therefore, three features of the signal, each quantifying a wood formation trend, were calculated:

**The dominant wavelength of wood density fluctuation** Wood density profiles consist of density fluctuations of varying width that are more or less correlated with wavelets generated from a mother wavelet by dilation or compression (Farge 1992). Wavelengths of certain width contribute more to the power spectrum throughout the profile, which enables us calculating the dominant wavelength of density fluctuations in the studied tree. This dominant wavelength reveals the average width of a growth zone in a tree and is represented by the position of the peak in Fig. 3a.

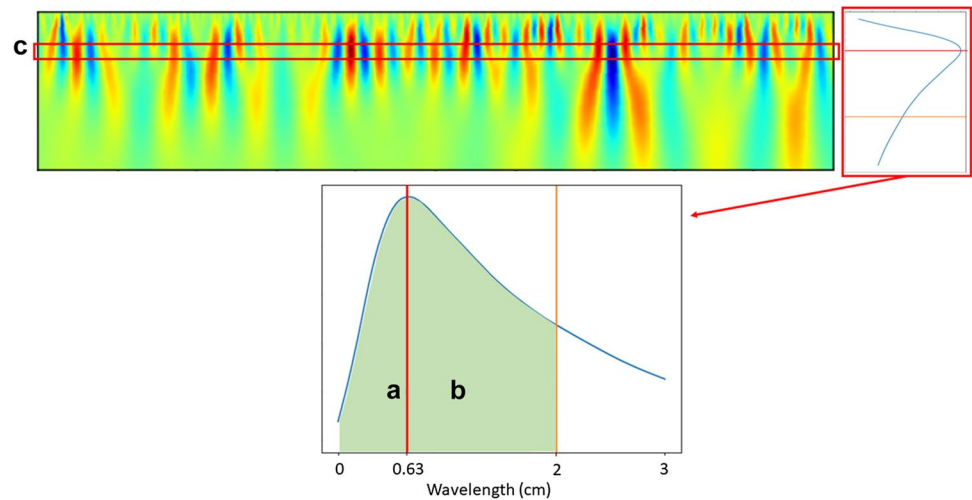
The dominant wavelength was expressed as the scale position of the maximum CWT coefficient values, regardless of the spatial axis:

$$\{x | \forall y : \sum_u \text{CWT}^2(u, y) \leq \sum_u \text{CWT}^2(u, x)\}. \quad (2)$$

**Fig. 2** Superposition of a wood density profile and the correspondent space–frequency representation. In **a** wood density is measured with 3D X-ray tomography with a 110  $\mu\text{m}$  resolution to obtain a pith-to-bark profile. This profile is then detrended in **b** and the result is analysed with a Ricker wavelet of wavelengths varying from 0 to 3 cm to generate a space–frequency representation of the density profile in **c**. Different shades of red/blue indicate a positive/negative correlation between the wavelet and the signal portion while the green background represents no correlation. The intensity of the coloration depends on the amplitude of the variation of the density signal



**Fig. 3** Visual representation of the three growth descriptors derived from the wavelet analysis: **a** the dominant wavelength determining the main periodicity of wood density fluctuation (illustrated by the position of the peak), **b** the frequency distribution determining the regularity of wood formation (illustrated by the area under the curve) and **c** the amplitude of wood density fluctuations (illustrated by the intensity of the red/blue coloration)



**Frequency distribution representing the regularity of wood formation** Related to the first descriptor, the second one estimates the regularity with which wood density fluctuates from pith to bark. Trees forming growth zones of same width need a lower number of different wavelets to characterize their density profile compared to trees with growth zones of varying widths from pith-to-bark. This second descriptor was estimated by calculating the cumulated power of the wavelets with wavelengths from 0 to a threshold value  $th$  (the area under the curve in Fig. 3b):

$$\sum_{s=0}^{th} \sum_u CWT^2(u, s). \quad (3)$$

The threshold value  $th$  was arbitrary set to wavelength of 2 cm as this captured most of the variability of wavelengths in the density profiles (Fig. 2c).

**The amplitude of wood density variation** Besides the rhythmicity of wood density variation, the amplitude is a useful descriptor for comparing the distinctness of growth zones between trees. It can be estimated with the power of the spectrum of the dominant wavelength (Fig. 3c) and can be calculated using the square of weight of the energy of the density signal at the main frequency of the wavelets:

$$\frac{1}{N} \sum_{i=0}^N (d * R(f))^2, \quad (4)$$

where the ‘\*’ operation is a convolution,  $d$  is the wood density profile with  $N$  measures of density and  $R$  is the Ricker function at frequency  $f$ .

## Leaf phenology

We used historical data collected by the former Institut National pour l’Etude Agronomique du Congo belge (INEAC) at both Luki and Yangambi ( $\pm 100$  km to the North-West of Yoko with similar precipitation patterns) to compare leaf phenology between two contrasting climates and to the CoForTraits database (Benedet et al. 2015). Various numbers of trees of each species were observed every 10 days in the period 1947–1957 in Luki (Couralet et al. 2013) and every week in the period 1939–1958 in Yangambi (Table 1, <http://www.cobecore.org>). Yearly observations of each tree were compiled to calculate the mean probability of observing a leafless tree throughout the year for each species. We then calculated the average calendar date of leaf fall, flushing and the temporal aggregation of both events for each species in both sites using circular statistics (Batschelet 1981; Milton 1991; Davies and Ashton 1999). Dates were considered as angles  $\theta_i$  between  $0^\circ$  and  $360^\circ$  and the mean angle  $\bar{\theta}$  was calculated as:

$$\bar{\theta} = \arctan\left(\frac{y}{x}\right) \text{ if } x > 0 \text{ or } \bar{\theta} = 180 + \arctan\left(\frac{y}{x}\right) \text{ if } x < 0 \quad (5)$$

where

$$x = \frac{1}{n} \sum \cos\theta_i \text{ and } y = \frac{1}{n} \sum \sin\theta_i$$

with the number of trees ranging from 1 to  $n$ . The temporal concentration or synchronicity ( $r$ ) allows estimating the

degree of coordination between trees for leaf shedding or flushing:

$$r = \sqrt{(x^2 + y^2)}. \quad (6)$$

Finally, we divided the number of years with observed leaf fall by the total number of years to calculate the probability for a tree of a given species to shed leaves during a year.

### Leaf phenology and wood density variability analysis

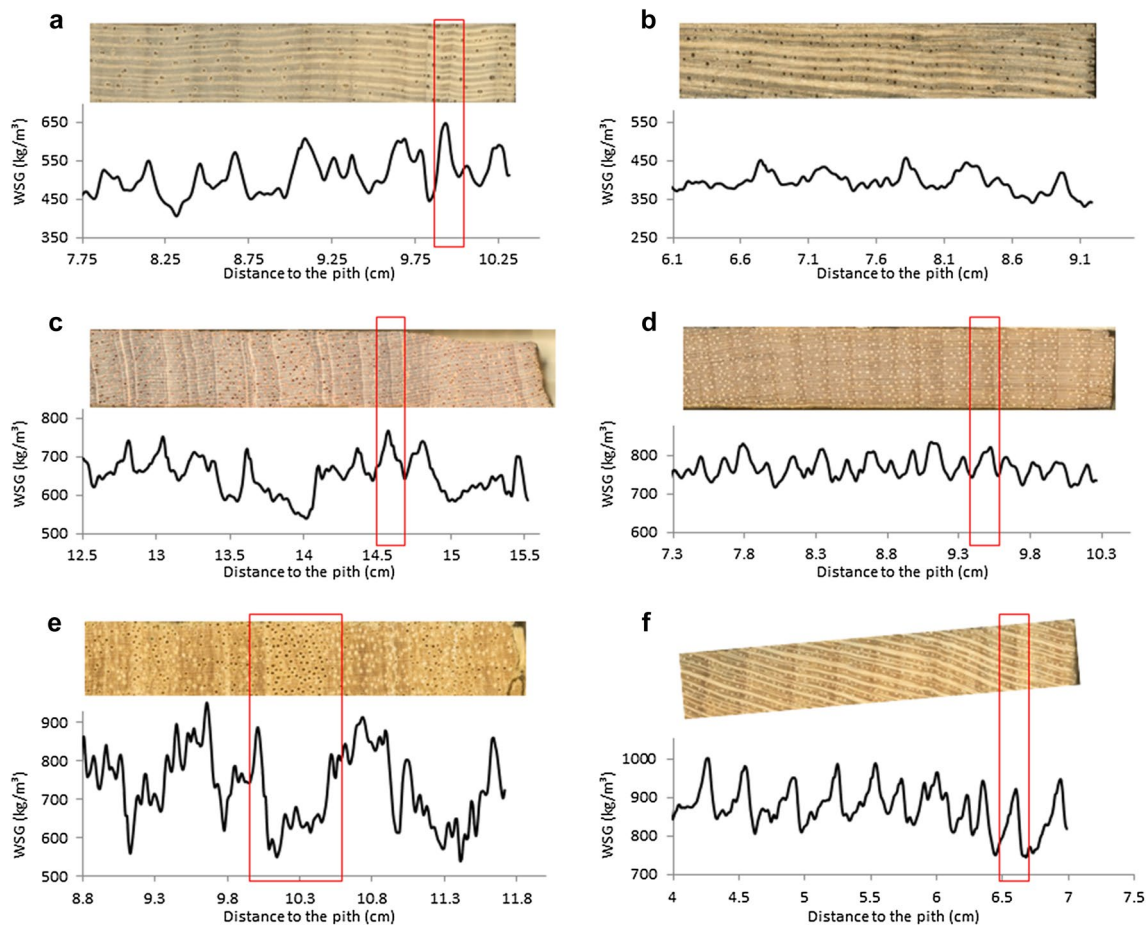
The number of wood cores per tree varying between two and four, wood formation descriptors were averaged at the tree level. The obtained values were then compared between species, sites and leaf phenologies with Kruskal–Wallis and post hoc Dunn tests. The interaction between site and leaf

shedding behaviour was also tested. All analyses were carried out in R 3.3.1 (R Core Team 2016).

## Results

### Wood anatomy, wood density and wavelet analysis

The relationship between wood anatomy and wood density (Fig. 4, Supporting information Fig. S1) shows that wood density is mostly driven by the fibres' anatomy. Zones of flattened fibres with thickened cell walls are translated into density peaks on the pith-to-bark profiles. Growth rings defined by flattened fibres and/or thickened walls can clearly be located on a density profile (Fig. 4a, d, f). The effects of parenchyma and vessels on wood density are less pronounced and it is difficult to locate a variation of these tissues with the help of a density profile. Profiles with the



**Fig. 4** Illustration of the relationship between wood-specific gravity (WSG) and wood anatomy. Representation of the last 3 cm under bark of transversal surfaces of **a** *A. mannii* from Malebo, **b** *A. mannii* from Yoko, **c** *E. angolense* from Malebo, **d** *S. kamerunensis* from Luki, **e** *O. gore* from Malebo and **f** *P. suaveolens* from Luki. WSG

peaks correspond to darker zones defined by flattened fibres and/or thickened fibre walls (red rectangles in **a**, **c**, **d** and **f**). The red rectangle in **e** points to a WSG decrease driven by an increase in vessel density. In **a**, **c**, **d** and **f**, the observed patterns are similar to growth ring boundaries (see Tarelkin et al 2016)

most abrupt density fluctuations show the lowest peak positions values. An irregular rhythmicity in density fluctuations results in wider frequency distributions (and thus greater values). Finally, density profiles with the most frequent and pronounced density fluctuations have the highest values of power spectrum.

Although conspecific trees from different sites are anatomically alike, some details do vary among sites (e.g. Fig. 4a, b). In general, trees growing in Luki and Malebo exhibit more pronounced variations in fibre diameter or wall thickness along the pith-to-bark profile. More examples for all species are given in the Supporting Information Fig. S1. Anatomical differences between Luki, Malebo and Yoko per species are summarized in Table 2. The vast majority of differences occurs mainly at the level of fibres' with only one species showing differences in vessel density variation and no significant parenchyma density variation observed.

## Leaf phenology

Phenology records for all species (Fig. 5) are concordant with the CoForTraits database (Table 3). In Luki, trees show more synchronicity and longer periods of leaf shedding than

in Yangambi (Table 3). However, the probability to observe a leafless tree of a deciduous species during the dry season is similar in Luki and Yangambi (Fig. 5a). The evergreen species, with the exception of *Tetrorchidium didymostemon*, show weak differences between sites and the probability of leaflessness is low in both sites (Fig. 5b). Although some trees of evergreen species show long leafless periods in Luki (*Pycnanthus angolensis* – 115 days, *Ongokea gore* – 50 days), the number of years with leafless events is very low (<20%) compared to the observations of deciduous species (>80%, Table 3).

## Leaf phenology and texture variability

Results of the Kruskal–Wallis/Dunn's comparison tests show that leaf phenology influences the main periodicity of wood formation (dominant wavelength), while both the site and leaf phenology influence the tree growth regularity (frequency distribution) and the amplitude of anatomical variation (Table 4). Deciduous species exhibit density fluctuations with higher amplitudes and narrower widths. Dunn's pairwise comparisons of tree growth descriptors between sites (Table 4) and Fig. 6a reveal that the amplitude

**Table 2** Summary of the intra-species differences of anatomical features between sites

Species	Luki-Malebo	Malebo-Yoko	Luki-Yoko
<i>Anonidium mannii</i>	/	Variations are much more gradual in Yoko samples	/
<i>Canarium schweinfurthii</i>	Variation in fibre diameter is more abrupt in Luki	Variation in fibre diameter is more abrupt in Yoko	Variation in fibre diameter is more abrupt in Luki
<i>Cola griseiflora</i>	(–)	Space between adjacent parenchyma bands varies more in Malebo	Space between adjacent parenchyma bands varies more in Luki
<i>Entandrophragma angolense</i>	Fibre wall thickening is more abrupt in Luki	(–)	Fibre wall thickening is more abrupt in Luki
<i>Gilbertiodendron dewevrei</i>	Fibre wall thickening is more abrupt in Luki	(–)	Fibre wall thickening is more abrupt in Luki
<i>Macaranga spinosa</i>	(–)	Variation in fibre diameter is more abrupt in Malebo	Variation in fibre diameter is more abrupt depending on individuals
<i>Milicia excelsa</i>	Fibre wall thickening is more abrupt in Luki	(–)	Fibre wall thickening is more abrupt in Luki
<i>Ongokea gore</i>	Higher vessel density variation in Malebo	/	/
<i>Polyalthia suaveolens</i>	Fibre wall thickening is more abrupt in Luki	Fibre wall thickening is more abrupt in Malebo	Fibre wall thickening is more abrupt in Luki
<i>Pycnanthus angolensis</i>	Variation in fibre diameter is more abrupt in Malebo	Variation in fibre diameter is more abrupt in Malebo	Variation in fibre diameter is more abrupt in Luki
<i>Ricinodendron heudelotii</i>	Variation in fibre diameter is more abrupt in Malebo	(–)	Variation in fibre diameter is more abrupt in Yoko
<i>Staudtia kamerunensis</i>	Variation in fibre diameter is more abrupt in Luki	Variation in fibre diameter is more abrupt in Malebo	Variation in fibre diameter is more abrupt in Luki
<i>Tetrorchidium didymostemon</i>	Variation in fibre diameter is more abrupt in Luki	Variation in fibre diameter is more abrupt in Malebo	Variation in fibre diameter is more abrupt in Luki

/ = there were no trees in one of the studied sites

(–) = no notable difference was observed between the trees from the studied sites



of density fluctuations is higher in Luki than in less seasonally dry sites such as Malebo and Yoko. Additionally, tree growth rhythmicity is significantly more regular in Luki and Malebo than in Yoko (Fig. 6b). No significant influence of precipitation seasonality was found for growth periodicity (Fig. 6c). Contrasts in cambium activity regularity and anatomical variation are consequently more apparent in drier conditions and for deciduous species.

Site and phenology effects also interact to influence the amplitude of density fluctuations, which is significantly lower in evergreen species from Yoko than in the two other sites, while deciduous species are not different between sites. The wood formation of evergreen species seems more sensitive to shifts in precipitation patterns than that of deciduous trees.

## Discussion

Our study takes place in the framework of the research on the influence of climate change on tree growth. We explored intra- and inter-species differences in leaf phenology and wood anatomy along a precipitation gradient crossing the critical precipitation threshold of 50 mm per month (Worbes 2010; Fichtler and Worbes 2012). Previous studies combined wood density and wood anatomy data and established a strong link between both (Zanne et al. 2010; Zieminska et al. 2013). In our study, we show for the first time, for a large selection of African tropical tree species, that micro-CT density profiles synthesize various aspects of wood growth (i.e. cambial activity rhythmicity, growth-ring distinctness). Moreover, the metrics derived from the wavelet analysis allow to easily compare wood anatomical and growth dynamics within and between plant functional types (i.e. species, phenologies, etc.). Yet, due to the integrative nature of the wood density it remains difficult to disentangle the relative contribution of different anatomical features for the observed variability of wood density.

### Wood anatomy and growth regularity

The deciduous species showed a higher variability in their anatomical structure and more consistent interannual growth patterns, as indicated by the higher amplitudes and the more constant frequencies of density fluctuations. Various studies have explored the link between deciduousness, cambial activity (O'Brien et al. 2008; Brienen et al. 2016) and growth-ring distinctness (Lisi et al. 2008; Nath et al. 2016). Deciduous trees are more likely to form distinct growth rings with abruptly varying anatomical features in response to stress, although several evergreen species forming distinct growth rings have been reported too (Carlquist 1988; Callado et al. 2001; Marcati et al. 2006) and are present in

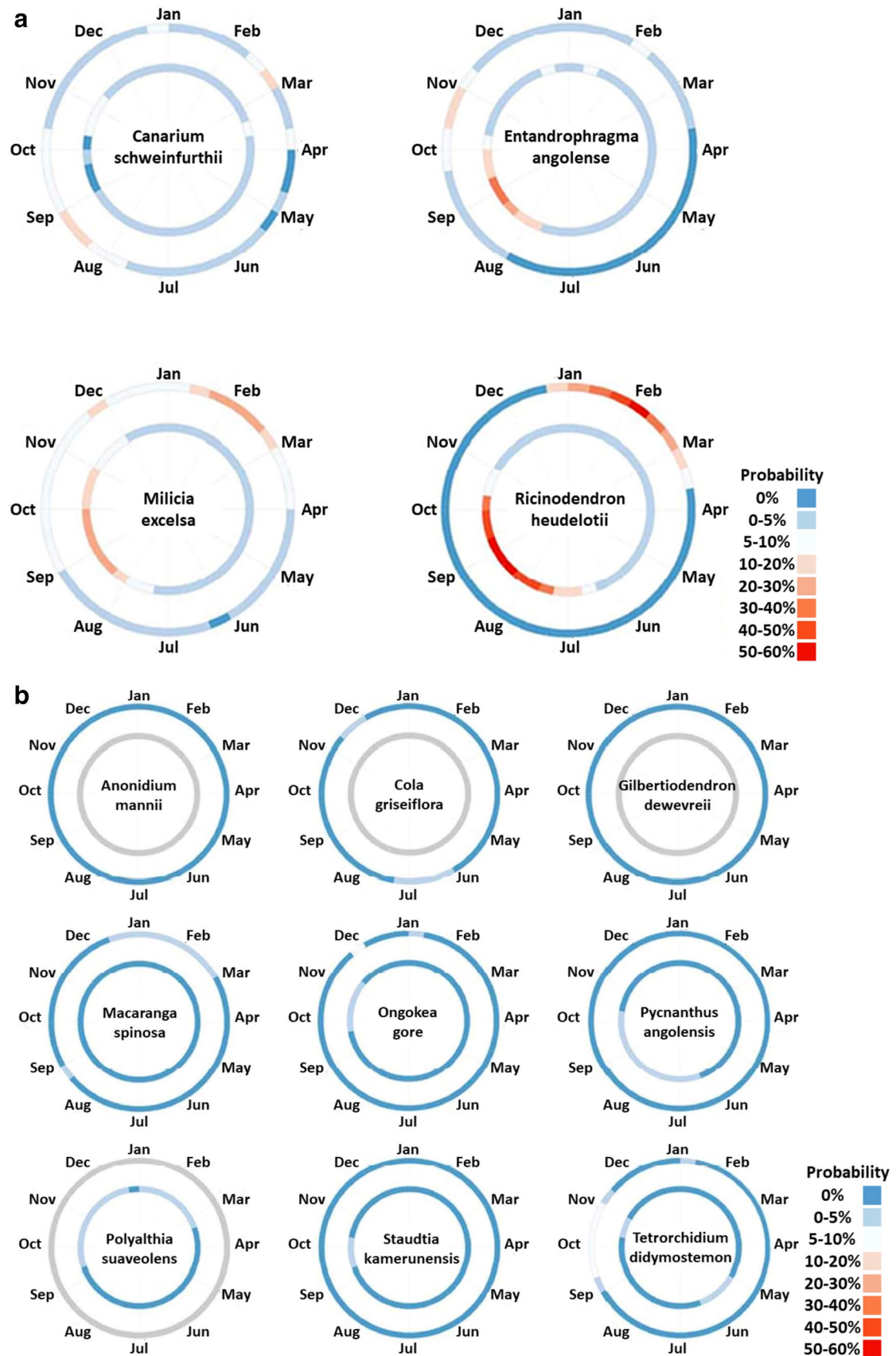
our study (e.g. *S. kamerunensis*, *P. suaveolens* which are among the most common species in Central Africa; Bastin et al. 2015b). Moreover, O'Brien et al. (2008) found a negative correlation between leaflessness and diameter growth patterns. Trees shedding leaves once a year are thus likely to show more regular patterns of wood density fluctuation.

Our results indicated a higher inter-site variability of anatomical features from pith to bark for evergreen species than for leaf-shedding species, with higher variability in the drier sites (Luki, Malebo) compared to the wettest (Yoko). It suggests that even though evergreen species do not generally form distinct growth rings, they still modulate their cambial activity according to environmental conditions (Borchert 1999; O'Brien et al. 2008), and that wood anatomy reveals more subtle responses to climate than leaf phenology. The longest dry seasons in Luki and Malebo, coupled to the lowest plant extractable water capacities of the soils, may cause a periodical water stress that impacts diameter growth and increases variability in anatomical features as it was shown in other tropical regions (Alvim 1964; Borchert 1999; Lisi et al. 2008). Our results hereby corroborate previous research along a precipitation gradient in Costa Rica which showed that *Gmelina arborea* trees growing in sites with less precipitation had the highest density variability due to more distinct growth rings (Moya and Tomazello Filho 2009).

Moreover, trees from drier sites also showed more regular growth patterns (the frequency of wood density fluctuations remains constant throughout the entire core). The lack of strong seasonal growth limiting factors not only reduces the variability in wood anatomy but also affects the interannual regularity of tree growth. Leaf shedding is also less regular and synchronized in Yoko, indicating that tree growth patterns vary from year to year and between individuals. Deciduousness is associated with several tree functions, such as carbon sequestration, reproductive events (Singh and Kushwaha 2016) and lack of its synchronicity could be linked to the interannual irregularity of growth (O'Brien et al. 2008).

### Wood anatomy and leaf phenology

Leaf phenology differs significantly between Luki and Yangambi. Trees shed their leaves by the end of the respective dry seasons in both sites. These results corroborate previous studies that link leaf shedding to seasonal droughts (Borchert 1999; Couralet et al. 2013; Brienen et al. 2016; Nath et al. 2016). The leaf phenology patterns detected in Luki and Yangambi differed by the intensity and the length of leaf shedding. All deciduous species shed leaves for a longer period in Luki and were more synchronous in shedding. These differences may be explained by the longer and more intense dry season in Luki leading to an increased leaf shedding to reduce evapotranspiration (Borchert 1999).



**Fig. 5** Leaf shedding behaviour of **a** deciduous and **b** evergreen species in Luki (inner circle) and Yangambi (outer circle). The red–blue coloration gradient represents the probability to observe a leafless tree of the studied species during the corresponding period of the year. Missing observations are represented in grey

Moreover, several authors reported an insolation-decrease-driven leaf shedding in tropical forests (Biudes et al. 2015; Borchert et al. 2015; Moreau 2016). Luki is the southernmost site with the shortest photoperiod during the dry season of June–September. The decrease in day length and a thick cloud cover during the dry season in Luki negatively affects the light quantity (duration  $\times$  intensity) and might intensify leaf shedding. There is a continuous spectrum of varying leaf-shedding patterns between deciduous and evergreen species in the tropics (Singh and Kushwaha 2016) and some evergreen species experience deciduousness in certain conditions. While leaf shedding was observed for evergreen species, it only concerned very small numbers of trees that are probably not representative of the leaf shedding behaviour of the entire population.

A strong intra-species intra-site variation in leaf phenology was observed. Couralet et al. (2013) reported that, in average, the proportion of leafless trees rarely exceeded 50% per species in Luki, even for the deciduous ones. Moreover, leaf phenology events were asynchronous throughout the years in Luki (Couralet et al. 2013; De Mil et al. unpublished) and other regions (Borchert et al. 2015). The lack of synchronicity in leaf shedding and flushing complicates any generalization about environmental drivers of leaf phenology (Viennois et al. 2013) and proves that site-dependent micro-environmental variations strongly influence leaf phenology and tree growth (De Frenne and Verheyen 2016; Singh and Kushwaha 2016). Furthermore, this hampers cross-dating of tree rings, which complicates further the studies of the relationship between tree growth and the environment. Due to the historical nature of the phenology data used in this study, it is difficult to characterize site-dependent micro-environmental conditions of tree growth. Yet, the large temporal span and the number of trees described in these databases represent a rare and valuable source of information within forest ecology and a unique opportunity to assess the variation of leaf-shedding in the last 70 years.

The predicted shifts of precipitation regimes due to climate change (James et al. 2013) will influence tree growth and it is critical to assess its impact on tropical forests. Our results suggest a higher sensitivity to growth conditions of evergreen species. They showed the highest anatomy variability in sites with the most pronounced seasonality, indicating that evergreen tree growth might be more affected by changing environmental conditions. Further exploration of tree species plasticity in cambial regulation and ultimately carbon allocation should provide more information on

the effects of climate change on tropical forests. Ongoing research by De Mil and colleagues (unpublished) showed encouraging results in estimating past cambial activity and leaf phenology based on intra-annual wood anatomy. Periodic cambial wounding proved its efficiency in tree growth studies (Mariaux and Bossanyi 2016) and could help linking different climatic events to wood anatomy. The integration of these techniques with a more thorough description of micro-environmental growth conditions and long-term climate records should provide useful insights in tree growth–climate change relationship.

## Methodological considerations

Fonti et al. (2010) stressed the importance of studying wood anatomical variability in tree growth research. However, the authors warned about the risks of analysing too few anatomical features which might lead to obscured or reduced ecological information. Fast CT scanning of wood cores and wavelet analysis are powerful tools for analysing density profiles and wood anatomical variation of a large number of samples. The development of metrics quantifying different aspects of wood density variability also reduces the subjectivity of visual assessments while limiting the required labour cost. Our methodology, therefore sidesteps in part the issue of historically labour-intensive methodologies that hamper the efforts of the scientific community of acquiring ecologically significant number of samples (Brodribb 2017).

Furthermore, our study showed that wavelet analysis has the potential to reveal wood formation dynamics and resource allocation changes over the years and to provide effective tools for studying the climate impact on tree growth.

While it is tempting to link the fluctuation patterns of xylem features to climate records, our dataset contains limitations currently hampering that approach. Since trees' annual growth rates are not constant, a transposition of a density profile to a time grid necessitates an adapted approach (Verheyden 2004). The anchor-point method fixes annual reference points on a timeline (Paillard et al. 1996), allowing thus to superimpose the density profiles over the climate data. This method was successfully applied by Verheyden et al. (2005) who linked vessel variation profiles to climate data with a Fourier transformation. However, the annual nature of the observed rings in our sample set and the seasonality of their formation are still to be confirmed. Although the observed mean ring widths in our sample set (0.4–1 cm) are within the range of annual diameter increments reported in the literature (Lisi et al. 2008; O'Brien et al. 2008), additional studies are needed to confirm that rings are annual and to determine during which moment of the year they are formed. These studies, while feasible, are complicated by the influence of site-dependent

**Table 3** Summary of the leaf shedding behaviour in Luki and Yangambi: mean length of the leafless period for each species in both sites, inter-tree synchronicity of leaf fall and flushing and the proportion of years with observed leaf shedding averaged on the species level

Species	Length of leafless period (days)		Synchronicity ( $r$ )		Proportion of leafless years	
	Luki	Yangambi	Luki	Yangambi	Luki	Yangambi
<sup>(e)</sup> <i>Anonidium mannii</i>	NA	0	NA	/	NA	0 (2)
<sup>(e)</sup> <i>Cola griseiflora</i>	NA	22.56	NA	0.44	NA	0.06 (5)
<sup>(d)</sup> <i>Canarium schweinfurthii</i>	13.30	7.98	0.31	0.15	0.31 (16)	0.65 (5)
<sup>(d)</sup> <i>Entandrophragma angolense</i>	34.79	13.13	0.71	0.55	0.55 (6)	0.52 (4)
<sup>(e)</sup> <i>Gilbertiodendron dewevrei</i>	NA	0	NA	/	NA	0 (5)
<sup>(d)</sup> <i>Milicia excelsa</i>	46.93	33.91	0.62	0.39	0.59 (31)	0.83 (6)
<sup>(e)</sup> <i>Macaranga spinosa</i>	0	10.05	/	0.59	0 (1)	0.11 (3)
<sup>(e)</sup> <i>Ongokea gore</i>	50	7.5	1	0.95	0.01 (17)	0.06 (3)
<sup>(e)</sup> <i>Pycnanthus angolensis</i>	115	0	1	/	0.01 (27)	0 (4)
<sup>(e)</sup> <i>Polyalthia suaveolens</i>	29.26	NA	0.83	NA	0.02 (50)	NA
<sup>(d)</sup> <i>Ricinodendron heudelotii</i>	79.93	32.13	0.81	0.95	0.64 (46)	0.84 (3)
<sup>(e)</sup> <i>Staudtia kamerunensis</i>	30	0	1	/	0 (46)	0 (2)
<sup>(e)</sup> <i>Tetrorchidium didymostemon</i>	40	33.75	0.26	0.71	0.03 (7)	0.07 (3)

(e)=evergreen and (d)=deciduous are phenology data according to the CoForTraits database (Benedet et al. 2015)

NA data not available

/ = no leaf shedding during the observation period

The numbers between brackets in the last two columns are the total number of trees in the database

micro-environmental conditions and the subsequent challenges in cross-dating of the tree rings. Moreover, a higher temporal resolution is needed to account for differences in intra-annual growth rates (De Ridder et al. 2004) and study the effects of seasonal variations of climate. We advocate

**Table 4** Summary of the comparison of the density profile descriptors between the studied sites and leaf phenology.  $P$  values are calculated with the Kruskal–Wallis test

Grouping factor	Growth descriptor	Mean (SD)	$p$ value
Site	Dominant wavelength	L: 0.67 (0.13) M: 0.66 (0.1) Y: 0.67 (0.08)	0.3
	Frequency distribution	L: 3.79 (1.44) M: 4.01 (1.34) Y: 4.47 (1.9)	<0.05
	Amplitude of fluctuation	L: 13,791 (7326) M: 11,446 (6056) Y: 9948 (6824)	<0.001
Phenology	Dominant wavelength	D: 0.69 (0.08) E: 0.65 (0.11)	<0.001
	Frequency distribution	D: 3.75 (1.82) E: 4.27 (1.47)	<0.001
	Amplitude of fluctuation	D: 12,814 (6075) E: 11,158 (7255)	<0.01

The dominant wavelength is expressed in cm while the two other descriptors are unitless. The lowest values of frequency distribution indicate the most constant frequency of wood density fluctuation throughout the profile

L Luki, M Malebo, Y Yoko, D Deciduous, E Evergreen

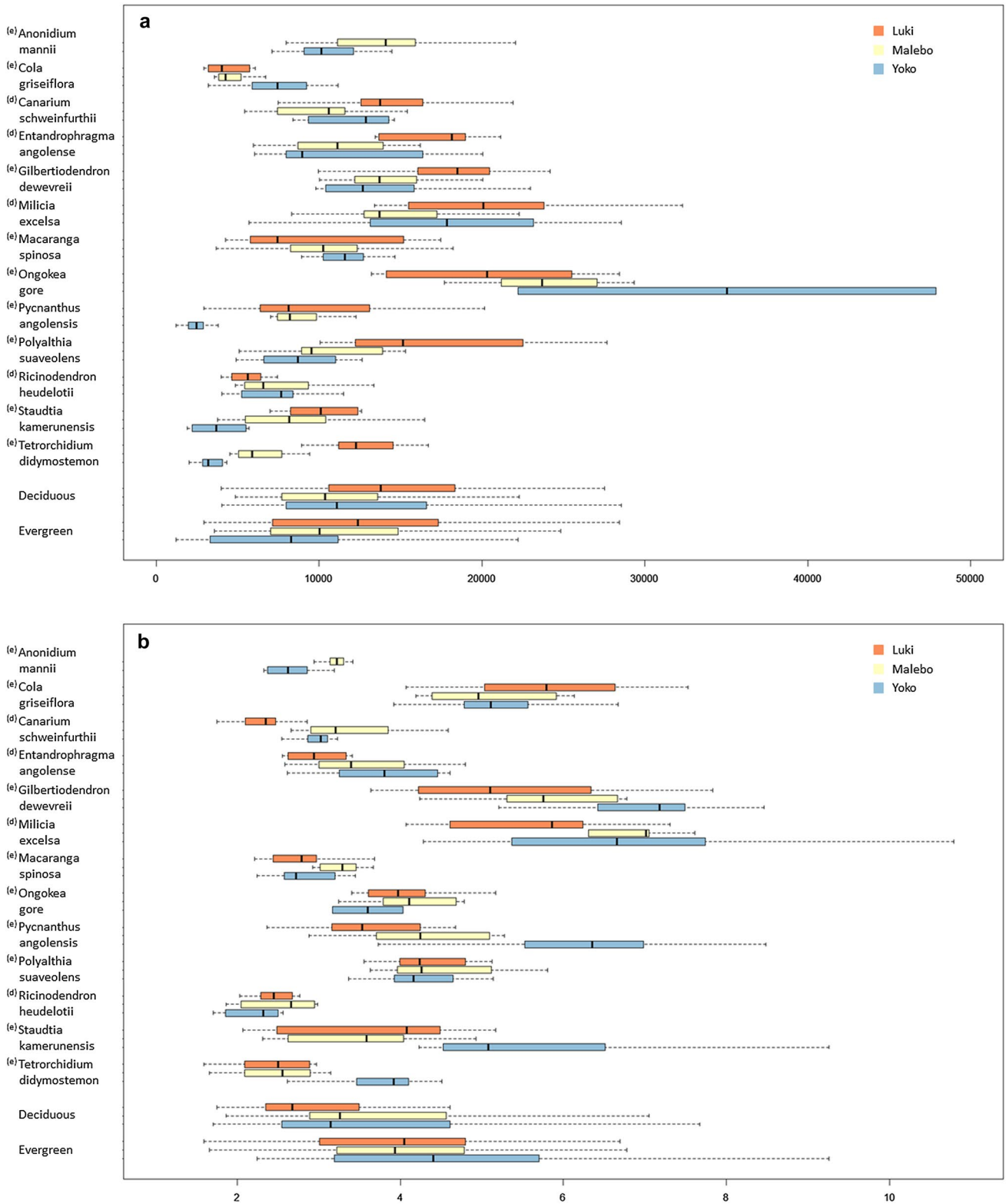
in favour of monitoring cambial activity and leaf phenology with sub-annual resolution (with dendrometers, cambial wounding, micro-coring; see De Mil 2017), which will help linking data such as wood density profiles to climate records and studying the influence of climate on tree growth.

Monitoring leaf phenology with standardized and automated methods will also help updating the databases used in this study. Although it would take a long time to reach the time spans of previous observations (10–20 years), automation can increase the number of monitored trees, which could help addressing the issues of representativity or site-depending micro-environmental conditions. Moreover, the current data are 60 to 80 years old and were gathered in a climatic context different from the current one (IPCC 2013). Comparing past and present leaf phenologies would unravel a lot of information on trees adaptation to the recent climate change.

## Conclusions

In this study we investigated the relationship between precipitation seasonality, leaf phenology and pith-to-bark variability of wood anatomy. We showed that anatomical features vary more abruptly, more regularly and that trees shed their leaves for longer periods under environmental conditions with distinct seasonality. Leaf shedding differed among species and growth habit. While deciduous species shed leaves more in the driest site, they did not show significant





**Fig. 6** Intersite differences of the values of **a** amplitude of density fluctuations, **b** frequency distribution and **c** the dominant wavelength of the pith-to-bark wood density variations, calculated with, respectively, Eq. 4, Eq. 3 and Eq. 2. Each single value represents the average

at the tree level of the values of each density profile. Species leaf phenology is indicated by (e)=evergreen species and (d)=deciduous species. The lowest categories (Deciduous and Evergreen) are a collection of all the trees of all the species belonging to the said category

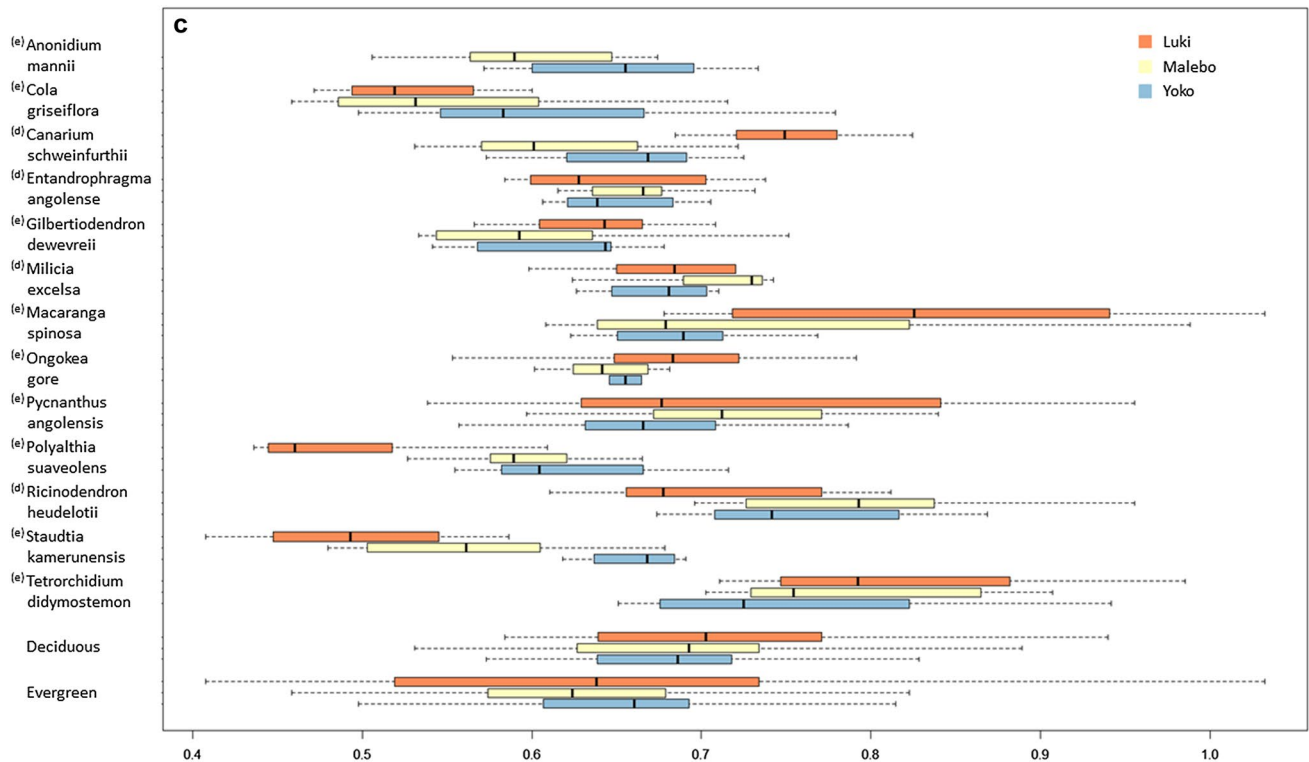


Fig. 6 (continued)

differences in wood structure between sites. On the other hand, evergreen species showed a higher variation in wood anatomy across sites, indicating a higher sensitivity to varying climatic conditions. Although several general trends of inter-site and inter-species growth differences could have been shown, our study also highlighted the large intra-site and intra-species variability, hampering our ability to cross-date samples between them and stressing thus the importance of describing the micro-environmental conditions in further studies. To address these challenges, we advocate in favour of the development of standardized methods to monitor leaf phenology and study wood anatomy variations of large numbers of samples with sub-annual temporal resolutions. By proposing new methods for studying tree growth with wood density profiles, our study opens interesting perspectives in the study of tropical forests and on carbon stock variations.

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**Author contributions** YT, KH, JVB, JFB, HB and CC planned and designed the research. YT, JDB and KH collected data. YT, SH and OD performed experiments. YT, KH, JB, JFB and CC analysed and interpreted data. YT and KH wrote the manuscript. All the co-authors revised the manuscript.

### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

### References

- Allen C, Macalady A, Chenchouni H, Bachelet D, McDowell N, Venetier M, Kitzberger T, Rigling A, Breshers D, Hogg E et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag* 259:660–684
- Alvim P (1964) Tree growth periodicity in tropical climates. In: Zimmerman M (ed) *The formation of wood in forest trees*. Academic Press, New York, pp 479–495
- Babst F, Bouriaud O, Papale D, Gielen B, Janssens I, Nikinmaa E, Ibrom A, Wu J, Bernhofer C, Köstner B et al (2014)

- Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites. *New Phytol* 201:1289–1303
- Baldeck C, Asner G, Martin R, Anderson C, Knapp D, Kellner J, Wright S (2015) Operational tree species mapping in a diverse tropical forest with airborne imaging spectroscopy. *PLOS ONE* 10:e0118403
- Bastin JF, Fayolle A, Tarelkin Y, Van den Bulcke J, de Haulleville T, Mortier F, Beeckman H, Van Acker J, Serckx A, Bogaert J, De Cannière C (2015a) Wood specific gravity variations and biomass of central african tree species: the simple choice of the outer wood. *Plos One* 10:e0142146
- Bastin JF, Barbier N, Réjou-Méchain M, Fayolle A, Gourlet-Fleury S, Maniatis D, de Haulleville T et al (2015b) Seeing Central African forests through their largest trees. *Sci Rep* 5:13156
- Batschelet E (1981) *Circular statistics in biology*. Academic Press, London
- Beeckman H (2016) Wood anatomy and trait-based ecology. *IAWA Journal* 37:127–151
- Benedet F, Doucet J, Fayolle A, Gourlet-Fleury S, Vincke D. Cofortraits, African plant traits information database. version 1.0. [http://coforchange.cirad.fr/african\\_plant\\_trait](http://coforchange.cirad.fr/african_plant_trait) [accessed 28 September 2016]
- Biudes M, Vourlitis G, Machado N, de Arruda P, Neves G, de Almeida Lobo F, Neale C, de Souza Nogueira J (2015) Patterns of energy exchange for tropical ecosystems across a climate gradient in Mato Grosso, Brazil. *Agric For Meteorol* 202:112–124
- Bonan G (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449
- Borchert R (1999) Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. *IAWA J* 20:239–247
- Borchert R, Calle Z, Strahler A, Baertschi A, Magill R, Broadhead J, Kamau J, Njoroge J, Muthuri C (2015) Insolation and photoperiodic control of tree development near the equator. *New Phytol* 205:7–13
- Brienen R, Schöngart J, Zuidema P (2016) Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees. In: *Tropical Tree Physiology*. Springer International Publishing, 439–461
- Briffa K, Melvin T (2011) A closer look at regional curve standardization of tree-ring records: justification of the need, a warning of some pitfalls, and suggested improvements in its application. In: *Dendroclimatology*. Springer Netherlands, 113–145
- Brodribb T (2017) Progressing from ‘functional’ to mechanistic traits. *New Phytol* 215:9–11
- Bullmore E, Fadili J, Breakspear M, Salvador R, Suckling J, Brammer M (2003) Wavelets and statistical analysis of functional magnetic resonance images of the human brain. *Stat Methods Med Res* 12(5):375–399
- Callado C, Barros C, Costa C, da Silva Neto S, Scarano F (2001) Anatomical features of growth rings in flood-prone trees of the Atlantic rain forest in Rio De Janeiro, Brazil. *IAWA J* 22:29–42
- Carlquist S (1988) *Comparative wood anatomy*. Springer, Berlin
- Cassart B, Angbonga Basia A, Titeux H, Andivia E, Ponette Q (2016) Contrasting patterns of carbon sequestration between Gilbertiodendron dewevrei monodominant forests and Scorodophloeus zenkeri mixed forests in the Central Congo basin. *Plant Soil* 414:309–326
- Chave J, Condit R, Muller-Landau H, Thomas S, Ashton P, Bunyavejehewin S, Co L, Dattaraja H, Davies S, Esufali S et al (2008) Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biol* 6:e45
- Chave J, Coomes D, Jansen S, Lewis S, Swenson N, Zanne A (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366
- Couralet C, Sterck F, Sass-Klaassen U, Van Acker J, Beeckman H (2010) Species-specific growth responses to climate variations in understory trees of a central african rain forest. *Biotropica* 42:503–511
- Couralet C, Van den Bulcke J, Ngoma L, Van Acker J, Beeckman H (2013) Phenology in functional groups of central African rainforest trees. *J Trop For Sci*, 361–374
- Davies S, Ashton P (1999) Phenology and fecundity in 11 sympatric pioneer species of macaranga (Euphorbiaceae) in borneo. *Am J Bot* 86:1786–1795
- De Mil T (2017) Intra-annual to multi-decadal xylem traits in a tropical moist semi-deciduous forest of Central Africa. Ghent University. Faculty of Bioscience Engineering, Ghent
- De Mil T, Tarelkin Y, Hahn S, Hubau W, Deklerck V, Debeir O, Van den Bulcke J (2018) Wood density profiles and their corresponding tissue fractions in tropical angiosperm trees. *Forests* 9(12):763
- De Frenne P, Verheyen K (2016) Weather stations lack forest data. *Science* 351:234–234
- De Ridder F, Schoukens J, Pintelon R, Gillikin DP, André L, Baeyens W, de Brauwere A, Dehairs F (2004) Decoding non-linear growth rates in biogenic environmental archives. *Geochem Geophys Geosyst* 5:Q12015. <https://doi.org/10.1029/2004GC000771>
- De Ridder M, Van den Bulcke J, Vansteenkiste D, Van Loo D, Dierick M, Masschaele B, De Witte Y, Mannes D, Lehmann E, Beeckman H et al (2011) High-resolution proxies for wood density variations in Terminalia superba. *Ann Bot* 107:293–302
- De Ridder M, Trouet V, Van den Bulcke J, Hubau W, Van Acker J, Beeckman H (2013) A tree-ring based comparison of Terminalia superba climate–growth relationships in West and Central Africa. *Trees* 27:1225–1238
- De Mil T, Vannoppen A, Beeckman H, Van Acker J, Van den Bulcke J (2016) A field-to-desktop toolchain for X-ray CT densitometry enables tree ring analysis. *Ann Bot* 117:1187–1196
- De Micco V, Campelo F, Cherubini P, Battipaglia G, Bräuning A, Grabner M, De Luis M (2016) Intra-annual density fluctuations in tree rings: how, when, where, and why? *IAWA Journal* 37:232–259
- Dierick M, Masschaele B, Hoorebeke L (2004) Octopus, a fast and user-friendly tomographic reconstruction package developed in LabView®. *Meas Sci Technol* 15:1366–1370
- Dierick M, Van Loo D, Masschaele B, Van den Bulcke J, Van Acker J, Cnudde V, Van Hoorebeke L (2014) Recent micro-CT scanner developments at UGCT. *Nucl Instrum Methods Phys Res Sect B* 324:35–40
- Dong S, Davies S, Ashton P, Bunyavejehewin S, Supardi M, Kassim A, Tan S, Moorcroft P (2012) Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. *Proceedings of the Royal Society B: Biological Sciences* 279: 3923–3931
- Dunne K, Willmott C (2000) Global Distribution of Plant-Extractable Water Capacity of Soil (Dunne). ORNL DAAC, Oak Ridge, Tennessee, USA. <https://doi.org/10.3334/ORNLDAAAC/545>. Accessed 15 Mar 2017
- FAO (2007) Digital soil map of the world. FAO, Rome
- FAO (2016) State of the World’s forests. FAO, Rome
- Farge M (1992) Wavelet transforms and their applications to turbulence. *Ann Rev Fluid Mech* 24(1):395–458
- Fichtler E, Worbes M (2012) Wood anatomical variables in tropical trees and their relation to site conditions and individual tree morphology. *Iawa Journal* 33(2):119–140
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37(12):4302–4315
- Fonti P, Von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H, Eckstein D (2010) Studying global change through

- investigation of the plastic responses of xylem anatomy in tree rings. *New Phytol* 185:42–53
- Gartner B (1995) *Plant stems: physiology and functional morphology*. Academic Press
- Greenwood S, Ruiz-Benito P, Martínez-Vilalta J, Lloret F, Kitzberger T, Allen C, Fensham R, Laughlin D, Kattge J, Bönisch G et al (2017) Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecol Lett* 20:539–553
- Groenendijk P, Sass-Klaassen U, Bongers F, Zuidema P (2014) Potential of tree-ring analysis in a wet tropical forest: a case study on 22 commercial tree species in Central Africa. *For Ecol Manag* 323:65–78
- Haralick R, Shanmugam K, Dinstein I (1973) Textural features for image classification. *IEEE Trans Syst Man Cybern SMC-3*:610–621
- Hudson I, Keatley M, Kang I (2011) Wavelet characterization of eucalypt flowering and the influence of climate. *Environ Ecol Stat* 18(3):513–533
- IPCC (2013) Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK et al (eds), *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge: Cambridge University Press
- James R, Washington R, Rowell D (2013) Implications of global warming for the climate of African rainforests. *Philos Trans R Soc B: Biol Sci* 368:20120298–20120298
- Kearsley E, de Haulleville T, Hufkens K, Kidimbu A, Toirambe B, Baert G, Huygens D, Kebede Y, Defourny P, Bogaert J et al (2013) Conventional tree height–diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. *Nat Commun* 4:2269
- Koch M, Marković D (2007) Evidences for climate change in Germany over the 20th century from the stochastic analysis of hydro-meteorological time-series. In *MODSIM 2007 International Congress on Modelling and Simulation*, Christchurch, New Zealand
- Larson PR (2012) *The vascular cambium: development and structure*. Springer Science & Business Media
- Lau K, Weng H (1995) Climate signal detection using wavelet transform: how to make a time series sing. *Bull Am Meteorol Soc* 76(12):2391–2402
- Lewis S, Lloyd J, Sitch S, Mitchard E, Laurance W (2009) Changing ecology of tropical forests: evidence and drivers. *Annual review of ecology. Evolut Syst* 40:529–549
- Lisi C, Roig F, Voigt A, Maria V, Tomazello Fo M, Ferreira-Fedele L, Botosso P (2008) Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in Southeast Brazil. *IAWA J* 29:189–207
- Lu X, Liu R, Liu J, Liang S (2007) Removal of noise by wavelet method to generate high quality temporal data of terrestrial MODIS products. *Photogr Eng Rem Sens* 73(10):1129–1139
- Marcatti C, Oliveira J, Machado S (2006) Growth rings in cerrado woody species: occurrence and anatomical markers. *Biota Neotropica* 6
- Mariaux A, Bossanyi I (2016) Nature and periodicity of growth rings in African timber: can they be used to determine the age of trees? *Bois et Forêts des Tropiques* 327:51–76
- Martínez-Cabrera H, Jones C, Espino S, Schenk H (2009) Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. *Am J Bot* 96(8):1388–1398
- Milton K (1991) Leaf change and fruit production in six neotropical moraceae species. *The Journal of Ecology* 79:1–26
- Moreau I (2016) *Evidencing land cover dynamics and tropical forest seasonality: the benefit of 13 years of daily global observation (SPOT-VEGETATION)*. PhD thesis, Université Catholique de Louvain, Belgium
- Morlet J (1983) Sampling theory and wave propagation. *Issues in Acoustic signal/Image processing and recognition*, 1: 233–261
- Morton D, Nagol J, Carabajal C, Rosette J, Palace M, Cook B, Vermote E, Harding D, North P (2014) Amazon forests maintain consistent canopy structure and greenness during the dry season. *Nature* 506:221–224
- Moura Y, Galvão L, dos Santos J, Roberts D, Breunig F (2012) Use of MISR/Terra data to study intra- and inter-annual EVI variations in the dry season of tropical forest. *Remote Sens Environ* 127:260–270
- Moya R, Tomazello Filho M (2009) Wood density variation and tree ring demarcation in *Gmelina arborea* trees using X-ray densitometry. *Cerne* 15(1):92–100
- Nath C, Munoz F, Péliissier R, Burslem D, Muthusankar G (2016) Growth rings in tropical trees: role of functional traits, environment, and phylogeny. *Trees* 30:2153–2175
- O'Brien J, Oberbauer S, Clark D, Clark D (2008) Phenology and stem diameter increment seasonality in a costa rican wet tropical forest. *Biotropica* 40:151–159
- Paillard D, Labeyrie L, Yiou P (1996) Macintosh program performs time series analysis. *Eos, Transactions, American Geophysical Union* 77: 379
- Paluš M, Novotná D, Tichavský P (2005) Shifts of seasons at the European mid-latitudes: Natural fluctuations correlated with the North Atlantic oscillation. *Geophys Res Lett.* <https://doi.org/10.1029/2005GL022838>
- Pan Y, Birdsey R, Fang J, Houghton R, Kauppi P, Kurz W, Phillips O, Shvidenko A, Lewis S, Canadell J et al (2011) A Large and Persistent Carbon sink in the world's forests. *Science* 333:988–993
- Peel M, Finlayson B, McMahon T (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrol Earth Syst Sci Dis* 4:439–473
- Peters RL, Groenendijk P, Vlam M, Zuidema PA (2015) Detecting long-term growth trends using tree rings: a critical evaluation of methods. *Global change biology* 21(5):2040–2054
- Philippon N, de Lapparent B, Gond V, Sèze G, Martiny N, Camberlin P, Cornu G, Morel B, Moron V, Bigot S et al (2016) Analysis of the diurnal cycles for a better understanding of the mean annual cycle of forests greenness in Central Africa. *Agric For Meteorol* 223:81–94
- Phillips O, van der Heijden G, Lewis S, López-González G, Aragão L, Lloyd J, Malhi Y, Monteagudo A, Almeida S, Dávila E et al (2010) Drought-mortality relationships for tropical forests. *New Phytol* 187:631–646
- Poorter L, McDonald I, Alarcón A, Fichtler E, Licona J, Peña-Claros M, Sterck F, Villegas Z, Sass-Klaassen U (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol* 185:481–492
- Pucha-Cofrep D, Peters T, Bräuning A (2015) Wet season precipitation during the past century reconstructed from tree-rings of a tropical dry forest in Southern Ecuador. *Global Planet Change* 133:65–78
- R Core Team (2016) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Ricker N (1953) Wavelet contraction, wavelet expansion, and the control of seismic resolution. *Geophysics* 18(4):769–792
- Rigozo N, Nordeman D, Echer E, Vieira L, Echer M, Prestes A (2005) Tree-ring width wavelet and spectral analysis of solar variability and climatic effects on a Chilean cypress during the last two and a half millennia. *Climate of the Past Discussions* 1(1):121–135
- Rozendaal D, Zuidema P (2011) Dendroecology in the tropics: a review. *Trees* 25:3–16
- Schaeffli B, Zehe E (2009) Hydrological model performance and parameter estimation in the wavelet-domain. *Hydrol Earth Syst Sci* 13(10): 1921



- Scheffer M, Carpenter S, Foley J, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596
- Sexton J, Noojipady P, Song X, Feng M, Song D, Kim D, Anand A, Huang C, Channan S, Pimm S et al (2016) Conservation policy and the measurement of forests. *Nature Climate Change* 6(2):192–196
- Singh K, Kushwaha C (2016) Deciduousness in tropical trees and its potential as indicator of climate change: a review. *Ecological indicators* 69:699–706
- Tarelkin Y, Delvaux C, De Ridder M, El Berkani T, De Cannière C, Beeckman H (2016) Growth-ring distinctness based on IAWA's definition: variability and consequences for trait analysis. *IAWA Journal* 37:275–294
- Van den Bulcke J, Wernersson E, Dierick M, Van Loo D, Masschaele B, Brabant L, Boone M, Van Hoorebeke L, Haneca K, Brun A et al (2014) 3D tree-ring analysis using helical X-ray tomography. *Dendrochronologia* 32:39–46
- van der Werf G, Morton D, DeFries R, Olivier J, Kasibhatla P, Jackson R, Collatz G, Randerson J (2009) CO<sub>2</sub> emissions from forest loss. *Nat Geosci* 2:737–738
- Vancutsem C, Pekel J, Kibambe L, Blaes X, de Waseige C, Defourny F (2006) République démocratique du Congo - occupation du sol. Carte Géographique. Presses Universitaire de Louvain. Bruxelles, Belgique
- Verheyden A (2004) *Rhizophora mucronata* wood as a proxy for changes in environmental conditions, a study on the wood anatomy, stable isotope chemistry and inorganic composition of a Kenyan mangrove species. PhD Thesis. Brussels, Belgium: Vrije Universiteit Brussel
- Verheyden A, De Ridder F, Schmitz N, Beeckman H, Koedam N (2005) High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. *New Phytol* 167(2):425–435
- Viennois G, Barbier N, Fabre I, Couteron P (2013) Multiresolution quantification of deciduousness in West-Central African forests. *Biogeosciences* 10:6957–6967
- Villar-Salvador P, Castro-Díez P, Pérez-Rantomé C, Montserrat-Martí G (1997) Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. *Trees* 12:90–96
- Vlam M, Baker P, Bunyavejchewin S, Zuidema P (2014) Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. *Oecologia* 174:1449–1461
- Vlassenbroeck J, Dierick M, Masschaele B, Cnudde V, Van Hoorebeke L, Jacobs P (2007) Software tools for quantification of X-ray microtomography at the UGCT. Nuclear instruments and methods in physics research section a: accelerators, spectrometers. Detectors Associated Equipment 580:442–445
- Wheeler E, Baas P, Rodgers S (2007) Variations in dicot wood anatomy: a global analysis based on the insidewood database. *IAWA Journal* 28:229–258
- Wiemann M, Wheeler E, Manchester S, Portier K (1998) Dicotyledonous wood anatomical characters as predictors of climate. *Palaeogeogr Palaeoclimatol Palaeoecol* 139:83–100
- Wimmer R (2002) Wood anatomical features in tree-rings as indicators of environmental change. *Dendrochronologia* 20:21–36
- Worbes M (1995) How to measure growth dynamics in tropical trees a review. *IAWA J* 16:337–351
- Worbes M (2010) Wood anatomy and tree-ring structure and their importance for tropical dendrochronology. In: *Amazonian Floodplain Forests*. Springer Netherlands, 329–346
- WRB (World reference base for soil resources) (2014) International soil classification system for naming soils and creating legends for soil maps. *World Soil Reports*, (106). FAO. Rome
- Zanne A, Westoby M, Falster D, Ackerly D, Loarie S, Arnold S, Coomes D (2010) Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Am J Bot* 97:207–215
- Ziemska K, Butler D, Gleason S, Wright I, Westoby M (2013) Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB PLANTS* 5:plt046–plt046
- Zuidema P, Baker P, Groenendijk P, Schippers P, van der Sleen P, Vlam M, Sterck F (2013) Tropical forests and global change: filling knowledge gaps. *Trends Plant Sci* 18:413–419

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