

# Potential of tree-ring analysis in a wet tropical forest: A case study on 22 commercial tree species in Central Africa



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## ABSTRACT

Implementing sustainable forest management requires basic information on growth, ages, reproduction and survival of exploited tree species. This information is generally derived from permanent sample plots where individual trees are monitored. Accurately estimating growth rates and especially tree ages from plots is however challenging, as plots often contain only few individuals of the exploited species and monitoring periods cover only a fraction of the life-span of most trees.

Alternatively, tree-ring analysis is increasingly used to obtain accurate age estimates and growth rates for tropical tree species, especially in regions with seasonally harsh conditions. However, for species from wet tropical forests (>4000 mm year<sup>-1</sup> rainfall) few tree-ring studies exist. Under persistent high levels of rainfall, formation of distinct tree rings is uncertain due to the lack of strong seasonal variation in climate factors. Here we evaluated the potential of applying tree-ring analysis on commercial tree species in a wet tropical forest in Central-Africa. For this purpose we screened the wood anatomy of 22 tree species for the presence of tree-ring structures and, on a subset of five species, we assessed crossdating potential and evaluated the annual character of tree-ring formation by radiocarbon dating.

A total of 14 of the 22 tree species showed distinct tree-ring boundaries. Radiocarbon proved annual tree-ring formation in four of the five tested species. Crossdating between trees was problematic for all species and impeded exactly dating each detected ring and building tree-ring chronologies. We also show that diameter growth rates vary strongly between and among species, with important consequences for the calculation of future timber yields.

Tree-ring analysis can thus be applied on tree species growing in wet tropical forests to obtain growth rates. We argue that tree-ring analysis should actually be applied on more tree species from different areas to obtain accurate, site specific growth data. This data is urgently required to design and improve sustainable forest management practices.

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## 1. Introduction

While constituting the world's second largest tropical forest belt, the West and Central African rain forests are relatively poorly studied. Over 44 million hectares of these forests have been designated for selective logging (Bayol et al., 2012). Sustainable management of these forests is hence essential to ensure a continued supply of timber without affecting their services and functions (e.g., carbon retention). Planning sustainable forest management requires basic ecological information of the exploited species (e.g., age, growth trajectories, regeneration and survival). This information can for instance be used to calculate future timber

yields in selective logging operations (e.g., Rozendaal et al., 2010). Despite the relevance for designing and evaluating forest management, such calculations have only been performed for a limited set of tropical tree species worldwide and are almost absent in Africa (Putz et al., 2012; De Ridder et al., 2013b). This paucity of studies is worrisome seen the importance of and great public attention given to sustainable management of (African) tropical forests.

In tropical forestry research, basic ecological information on exploited tree species – diameter growth rates and ages – is commonly obtained from measurements of trees in Permanent Sample Plots (PSPs). The contribution of PSPs to providing this information on African timber species has, however, remained very limited. PSPs are still scarce in tropical Africa (Verbeeck et al., 2011) and the uneven geographical distribution of PSPs implies that information on commercially important forest areas is missing (Picard et al., 2010). In addition, most PSPs are small, typically one hectare,

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and therefore contain only few individuals of commercial tree species, which typically occur at densities of  $<5$  trees  $\text{ha}^{-1}$  (Poorter et al., 1996; Hall et al., 2003). And finally, the monitoring period of most PSPs spans just a fraction of the ages of trees, often resulting in biased tree-age estimations (Martínez-Ramos and Alvarez-Buylla, 1998) leading to a lack of accurate long-term data on ages and growth of commercial tree species.

An alternative and relatively fast approach to obtain tree ages and growth data is the use of tree-ring analysis (Brienen and Zuidema, 2006a; Schöngart et al., 2006; Rozendaal et al., 2010). Data obtained from tree rings typically consider information on growth across the entire life-span of trees and can thus be used to calculate ages and growth trajectories of logged trees. These data can also be used to calculate ages of trees to reach the legally set logging diameters (minimum cutting diameter, MCD). For forest management, tree-ring analysis can thus be used to supplement data from PSPs. In Africa, tree-ring studies have mostly been performed in dry, sub-tropical areas outside important wood-producing areas (e.g., Dunwiddie and LaMarche, 1980; Till and Guiot, 1990; Gourlay, 1995; Stahle et al., 1999; Tarhule and Hughes, 2002; Wils et al., 2010, 2011). Despite the knowledge that many commercial tree species in tropical Africa form annual rings (Mariaux, 1967; Détienné, 1989), tree-ring analysis has hardly been applied to aid forest management in West and Central Africa (De Ridder et al., 2013b; Gebrekirstos et al., 2014) and never so in wet forests of these regions.

Working with tree rings in tropical wet forests presents specific challenges. Under such persistently wet conditions, growth of trees has suggested to be continuous (Raven et al., 1999) and distinct annual tree rings to be absent (Swaine, 1994; Kurokawa et al., 2003). Although annual tree-rings formation has been proved for species growing in wet tropical forests (Fichtler et al., 2003), the absence of strong growth-limiting environmental factors can result in only weak variation in cambium activity. This weaker cambium activity with increasing precipitation levels may thus lead to less variation in wood anatomy and hence in tree-ring visibility (Moya and Filho, 2009). Lack of a growth-limiting factor that synchronises cambium activity in a given species also leads to varying growth patterns among individual trees, as local growing conditions are likely more influential than climate factors. This reduction of the 'common signal' in tree growth also affects crossdating and hampers chronology building for tree populations growing under very wet conditions (Fritts, 1976). Thus, for tree-ring studies in wet tropical forests, identifying ring boundaries and investigating their annual character is essential prior to obtaining growth data and tree ages.

Here we present results of a tree-ring study on commercial tree species in a wet ( $\sim 4100$  mm rainfall  $\text{year}^{-1}$ ) lowland tropical forest in the Southwest province of Cameroon. We first performed a screening for tree-ring boundaries in the wood of 22 commercial species. We expected to find distinct tree-ring boundaries in several species. The presence of a dry season and the seasonality in phenology (15 of the 22 species have a (brevi-)deciduous character) may induce periodic cambial dormancy, causing the formation of tree-ring boundaries. Next, we performed a more detailed analysis on a subset of five species showing clear tree-ring boundaries. We assessed the crossdating potential of these species and tested the annual character of tree-ring formation by radiocarbon dating. Finally, we described diameter-growth patterns and determined maximum tree ages and ages at minimum cutting diameters for this subset of species.

## 2. Materials and methods

### 2.1. Study area

Samples were collected inside the Forest Management Unit (FMU) 11.001, of Transformation REEF Cameroon (TRC, 2008). This FMU is certified by the Forest Stewardship Council (FSC) and is

located in the Southwest Region of Cameroon, between  $5^{\circ}23'N$ ,  $9^{\circ}09'E$  and  $5^{\circ}23'N$ ,  $9^{\circ}12'E$ , adjacent to Korup National Park (Fig. 1). The vegetation of the region consists of semi-deciduous lowland rainforest ( $\sim 200$  m a.s.l.) of the Guineo-Congolian type (cf. White, 1983), dominated by Leguminosae–Caesalpinioideae. Soils in the area are deep, skeletal (lithosols), with high sand content and a low pH (Gartlan et al., 1986). Due to leaching by the high rainfall, soils are nutrient poor and only a thin organic layer is present (Newbery et al., 1997). Regional climate is equatorial, with an unimodal rainfall distribution and a dry season from December to February (monthly rainfall  $< 60$  mm, cf. Worbes, 1995). Rainfall amounts vary between nearby weather stations: at the Bulu station (40 km to the South of the study area) annual rainfall averaged 5220 mm, whereas at the Mamfé Airport station (40 km to the North) it averaged 2920 mm (Fig. 1). Although total rainfall amounts vary between stations, both stations show an unimodal rainfall distribution. At our site, we expect annual rainfall to be intermediate, and similar to the 4082 mm measured at the Nguti weather station, located 27 km to the East (data not available; Nchanji and Plumptre, 2003). Temperature data was only available for the Mamfé station and shows little variation between months: maximum temperature averaged  $30.2^{\circ}C$  and minimum  $23.7^{\circ}C$ . A climate diagram for the Mamfé station is presented in Fig. 1.

### 2.2. Study species, sample collection and preparation

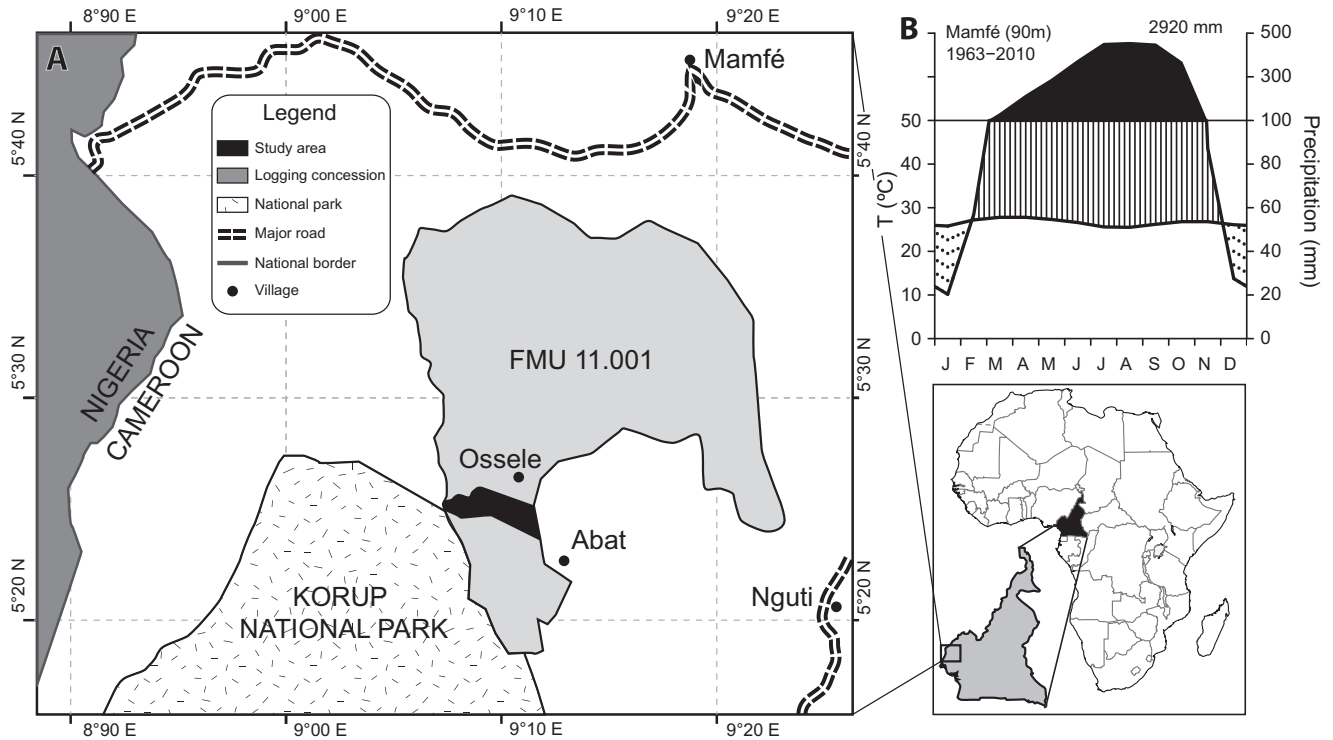
Between June 2010 and May 2012, we collected samples of 601 individuals belonging to 22 tree species (Table 1). Nearly all 22 species belong to the top-35 most logged species in Central Africa (Ruiz-Pérez et al., 2005) and commercial names, guild, distribution and uses are given in Table 1. We collected cross-sectional samples (discs) from 177 felled trees and increment cores from 424 standing trees, in three to four directions, using 5.15 mm increment borers (type Suunto and Haglof). Samples were taken at 1 m stem height or above anomalies or buttresses. Each sampled tree was geo-referenced (Garmin GPS60X) and we measured diameter at breast height (dbh) using a diameter tape.

About 90% of the samples were collected in a stratified random sampling design, inside an unlogged and seemingly undisturbed area of the FMU (TRC, 2008). For this purpose, we installed circular plots of c. 1 hectare at random coordinates inside 16 cells of  $300 \times 300$  m (located in a virtual grid of  $4 \times 4$  cells). Inside these plots, all trees  $>5$  cm dbh of our target species were sampled. The remaining samples were collected non-randomly, from large trees or from individuals of less abundant tree species. These samples were collected to increase the amount of species and the amount of large and presumably old trees in our analysis. For some rare species we collected only a few individuals or only increment cores, as rare species were spared from logging or because there was no commercial demand at the time (Table 2).

To allow inspection of tree-ring structures, all samples were air dried. Discs were polished with increasingly finer sandpaper, from grain 40 up to 1000, and increment cores were either polished or cut using a large sliding microtome (Gärtner and Nievergelt, 2010).

### 2.3. Tree-ring analysis

We investigated the potential for tree-ring analysis of the 22 commercial tree species (henceforth called 'screened species') by assessing the presence of distinct tree-ring boundaries. On a subset of five species, the 'subset species', we performed a detailed analysis to assess their cross-dating potential, test the annual character of tree-ring formation by radiocarbon dating, and assess their general growth patterns. The subset species were selected based on the presence of clear tree-ring structures, tree abundance in the



**Fig. 1.** (A) Map of study site: 2012 cutting block (black) of the Forest Management Unit 11.001 (light grey). Korup National Park (hatched), Nigerian border (dark grey), major villages, and roads are also shown. Inlay shows the location of the study site in Cameroon. (B) Climate diagram for Mamfé Airport weather station (cf. Walter and Lieth, 1960; period 1968–2009) indicating dry season (rainfall < temperature, dotted area) and rainy season (>100 mm month<sup>-1</sup>; black area).

**Table 1**

Characteristics of 22 commercial tree species from a wet tropical forest in Cameroon: commercial name, guild, Minimum Cutting Diameter (MCD) in Cameroon, distribution (W Africa = West Africa, C Africa = Central Africa, CAM = Cameroon, NIG = Nigeria), main applications of wood, and previous studies on the potential of tree-ring analysis.

Species	Family	Commercial name	Guild <sup>a</sup>	MCD (cm)	Distribution	Main uses wood	Previous tree-ring study?
<i>Azelia bipindensis</i>	Fabaceae (C)	Doussie Rouge	PST	80	(W) + C Africa <sup>a,b</sup>	Furniture, flooring <sup>b,e</sup>	Yes <sup>g</sup>
<i>Azelia pachyloba</i>	Fabaceae (C)	Doussie Blanc	PST	80	(W) + C Africa <sup>a,b</sup>	Furniture, flooring <sup>b,e</sup>	Yes <sup>g</sup>
<i>Bikinia le-testui</i>	Fabaceae (C)	Ekop Mayo	ST	60	C Africa <sup>c</sup>	Plywood, interior <sup>b,f</sup>	No
<i>Brachystegia cynometroides</i>	Fabaceae (C)	Ekop Nom Naga	PST	60	Cameroon <sup>b</sup>	Plywood, interior <sup>b,e</sup>	No
<i>Brachystegia eurycoma</i>	Fabaceae (C)	Ekop Naga	PST	60	CAM + NIG <sup>b</sup>	Plywood, interior <sup>b,e</sup>	No
<i>Canarium schweinfurthii</i>	Burseraceae	Aiele	LLP	60	W + C Africa <sup>a,b</sup>	Plywood, interior <sup>b,e</sup>	Yes <sup>g</sup>
<i>Daniellia ogea</i>	Fabaceae (C)	Faro	ST	60	W + C Africa <sup>a,b</sup>	Plywood <sup>b,e</sup>	No
<i>Didelotia letouzeyi</i>	Fabaceae (C)	Gombé Mamel	ST	60	(W) + C Africa <sup>d</sup>	Furniture, plywood <sup>f,e</sup>	No
<i>Entandrophragma angolense</i>	Meliaceae	Tiama	LLP	80	W + C Africa <sup>a,b</sup>	Veneer, furniture <sup>b,e</sup>	Yes <sup>h</sup>
<i>Entandrophragma candollei</i>	Meliaceae	Kosipo	LLP	90	W + C Africa <sup>a,b</sup>	Veneer, furniture <sup>b,e</sup>	Yes <sup>h</sup>
<i>Entandrophragma utile</i>	Meliaceae	Sipo	LLP	80	W + C Africa <sup>a,b</sup>	Veneer, furniture <sup>b,e</sup>	Yes <sup>h</sup>
<i>Erythrophloeum ivorense</i>	Fabaceae (C)	Tali	LLP	50	W+C Africa <sup>a,b</sup>	Furniture, hydraulic <sup>b,e</sup>	Yes <sup>g,i</sup>
<i>Gilbertiodendron dewevrei</i>	Fabaceae (C)	Limbali	ST	60	(W) + C Africa <sup>b</sup>	Flooring, exterior <sup>b,f</sup>	No
<i>Guarea thompsonii</i>	Meliaceae	Dark bosse	ST	80	(W)+C Africa <sup>b</sup>	Flooring, interior <sup>b</sup>	Yes <sup>g</sup>
<i>Khaya anthoteca</i>	Meliaceae	Acajou d'Afrique	LLP	80	W + C Africa <sup>a,b</sup>	Furniture, veneer <sup>b,e</sup>	Yes <sup>h</sup>
<i>Lophira alata</i>	Ochnaceae	Azobe	LLP	60	W + C Africa <sup>a,b</sup>	Hydraulic, sleepers <sup>b,e</sup>	No
<i>Nauclea diderrichii</i>	Rubiaceae	Bilinga	ST	80	W + C Africa <sup>a,b</sup>	Furniture, sleepers <sup>b,f</sup>	No
<i>Pterocarpus soyauxii</i>	Fabaceae (P)	Padouk rouge	PST	60	W + C Africa <sup>a,b</sup>	Furniture, flooring <sup>b,e</sup>	Yes <sup>g</sup>
<i>Pycnanthus angolensis</i>	Myristicaceae	Ilomba	LLP	60	W + C Africa <sup>a,b</sup>	Plywood, interior <sup>b,e</sup>	No
<i>Rhodognaphalon breviscuspe</i>	Bombacaceae	Kondroti	LLP	60	W+C Africa <sup>a,b</sup>	Plywood, interior <sup>b,e</sup>	No
<i>Staudtia kamerunensis</i>	Myristicaceae	Niove	ST	50	Central Africa <sup>b</sup>	Furniture, flooring <sup>b,e</sup>	Yes <sup>j</sup>
<i>Terminalia ivorensis</i>	Combretaceae	Framire	LLP	60	W Africa <sup>b</sup>	Furniture, plywood <sup>b,e</sup>	Yes <sup>g</sup>

<sup>a</sup> Hawthorne and Jongkind (2006).

<sup>b</sup> PROTA (2012).

<sup>c</sup> Wieringa (1999).

<sup>d</sup> Rietkerk et al. (1996).

<sup>e</sup> CIRAD (2011).

<sup>f</sup> ITTO (1990).

<sup>g</sup> Détienne et al. (1998).

<sup>h</sup> Détienne (1989).

<sup>i</sup> Nzogang (2009).

<sup>j</sup> Worbes et al. (2003).

<sup>\*</sup> Guilds: PST = partially shade tolerant, ST = shade tolerant, LLP = long-lived pioneer.

forest (sample size > 60 individuals), currently being logged in the study area, and the possibility of extracting increment cores, i.e., wood density neither too high nor too low. Four species fulfilled these criteria: *Brachystegia eurycoma* Harms, *Brachystegia cynometroides* Harms, *Daniellia ogea* (Harms) Rolfe ex Holl. and *Terminalia ivorensis* A. Chev. For these species we collected discs and cores of 62–128 individuals per species (Table 2). For a fifth species, *Entandrophragma utile* (Dawe & Sprague) Sprague, which was not very abundant but known to produce very clear tree-rings (Détienne et al., 1998), we also sampled 10 discs.

### 2.3.1. Screening for tree-ring structures

After surface preparation, we evaluated, both macroscopically and under a stereo-microscope (magnification 16–40×, Leica) whether continuous tree rings could be identified around the stem circumference. We classified tree-ring structures and wood anatomical markers for ring boundaries in our species following Coster (1927) and Worbes and Fichtler (2010) in the following four types: (A) variations in wood density, (B) boundaries marked by a marginal parenchyma band, (C) repeated patterns of fibre and parenchyma bands, and (D) variation in vessel distribution and/or size. By following wood-anatomical markers around the circumference of discs, we evaluated their continuity and screened for the occurrence of phenomena that can obscure ring detection. Such phenomena include the presence of wedging rings and intra-annual growth variations. Wedging rings are distinct tree rings that merge (two or more rings join) on certain parts of the stem circumference, induced by local differences in cambial activity. Ring wedging often occurs in slow growing species or on very eccentric stem discs (Wils et al., 2009). Intra-annual growth variations are growth variations that can, in some species, resemble true ring boundaries and therefore lead to ring-misidentification. Characteristics of these intra-annual variations vary between species depending on their specific wood anatomy and may consist of bands of thick-walled fibres (density variations) or be characterised by the presence of (discontinuous) parenchyma bands. For all screened species we systematically identified possible problems and provided categories of the potential for tree-ring analysis using the following categories: high

(++), good (+), possible (+–), low (–) and not possible (––). This potential is based on the presence and distinctness of tree-ring boundaries found in this study, but also in previous tree-ring studies on the same species or congeners (for more details, see Fact sheets in Appendix B).

### 2.3.2. Tree-ring measurements and crossdating potential

We measured ring widths on scanned images of each tree of our subset species using the software WinDendro Regular (version 2009b, Regent Instruments, Canada). For cores, we scanned and measured all cores extracted from individual trees; discs were scanned and rings were measured along four radii. For scanning we used a resolution of 1600–2400 dpi, on a flatbed scanner (Epson Expression 10000XL). To increase tree-ring visibility samples were often wetted and/or scanned with a film of water on the scanner's glass plate. For sample sections with narrow rings, we marked rings under a microscope prior to scanning and on discs we interconnected every 10th to 15th clear ring to facilitate measuring and crossdating.

Crossdating consists of matching patterns of wide and narrow rings between radii measured from the same tree, or between mean ring-width patterns from different trees, to assign a calendar year to each detected ring (Douglass, 1941). We crossdated ring-width series within and among trees, both visually and statistically. Visual crossdating was performed while measuring, by matching ring-width patterns of different radii, and by ensuring that interconnected rings from different radii dated to the same year. Statistical crossdating was performed in WinDendro (version 2009b; Regent Instruments Canada Inc.), using the percentage of parallel run (ppr) between radii, and using the software COFECHA (Holmes, 1983; Grissino-Mayer, 2001). Successful crossdating among ring-width series of the same tree verifies concentric patterns in ring formation. Crossdating of ring-width series of different individuals of the same species becomes possible if radial growth of different individuals is limited or driven by the same external factor (Cook and Kairiukstis, 1990; Worbes, 1995). From these crossdated ring-width series, a site chronology can be calculated that reflects the common variance in growth of the tree

**Table 2**  
Growth-ring characteristics of 22 commercial tree species from a wet tropical forest in Cameroon. Ring boundary codes: (A) wood density variation, (B) marginal parenchyma band, (C) patterns of alternating fibre and parenchyma bands, (D) variations in vessels distribution and/or size, and (–) no ring boundary. Total number of individual trees collected (and number of discs), leaf phenology, difficulties and overall potential are also given. The five selected species for which further analyses were done are in bold.

Species	Tree-ring boundary	# Trees (as discs)	Leaf phenology <sup>a</sup>	Difficulties <sup>b</sup>	Potential
<i>Afzelia bipindensis</i>	B	2 (2)	Deciduous	W	+
<i>Afzelia pachyloba</i>	B	2 (1)	Deciduous	W	+
<i>Bikinia le-testui</i>	B	10 (10)	Evergreen	C + D + S + W	+–
<b><i>Brachystegia cynometroides</i></b>	B	124 (4)	Brevi-Deciduous	D + M + S + W	+–
<b><i>Brachystegia eurycoma</i></b>	B	128 (32)	Brevi-Deciduous	D + M + S + W	+
<i>Canarium schweinfurthii</i>	–/A	5 (3)	Deciduous	n/a	+–
<b><i>Daniellia ogea</i></b>	B	105 (18)	Deciduous	D + S + W	++
<i>Didelotia letouzeyi</i>	–/B	2 (0)	Evergreen	n/a	–
<i>Entandrophragma angolense</i>	B	1 (0)	Deciduous	n/a	++
<i>Entandrophragma candollei</i>	B	1 (0)	Deciduous	n/a	++
<b><i>Entandrophragma utile</i></b>	B	10 (10)	Deciduous	W + S	++
<i>Erythrophleum ivorensis</i>	D	15 (10)	Deciduous	W	+–
<i>Gilbertiodendron dewevrei</i>	B	10 (4)	Evergreen	n/a	+–
<i>Guarea thompsonii</i>	A	1 (1)	Evergreen	n/a	+–
<i>Khaya anthoteca</i>	–	3 (1)	Evergreen	n/a	–
<i>Lophira alata</i>	–	2 (2)	Brevi-Deciduous	n/a	––
<i>Nauclea diderrichii</i>	–	5 (0)	Evergreen	n/a	––
<i>Pterocarpus soyauxii</i>	C + B	5 (1)	Brevi-Deciduous	n/a	+–
<i>Pycnanthus angolensis</i>	–/B	30 (12)	Brevi-Deciduous	n/a	+–
<i>Rhodognaphalon brevicuspe</i>	–/A	5 (1)	Deciduous	n/a	+–
<i>Staudtia kamerunensis</i>	–/B	73 (13)	Evergreen	n/a	+–
<b><i>Terminalia ivorensis</i></b>	A + D	62 (52)	Deciduous	W+S	+

<sup>a</sup> Phenology: deciduous: tree leafless for >4 weeks; brevi-deciduous: tree briefly or only partially leafless; evergreen = trees without leafless periods.

<sup>b</sup> Difficulties: C = coring (wood too hard or to brittle), D = doubtful/vague ring-boundaries, M = rings missed (<sup>14</sup>C analysis), S = periods of slow growth, W = wedging rings, n/a = not assessable.



species. Chronologies are usually calculated as annual averages of standardised ring-widths series. We standardised averaged diameter-growth series for each individual using 15-year cubic splines in COFECHA. Finding correlations between a chronology and annually/seasonally varying climate variables (e.g., precipitation in the rainy season) can be taken as strong evidence that tree-rings are formed annually, in response to these variable. Chronologies can then be used to calibrate the measurements of remaining trees, by synchronising their growth with the chronology and searching for mistakes in ring identification.

To build a chronology for each of the subset species, we first excluded all trees growing in the understorey (<50 cm dbh). Growth of these smaller trees is strongly influenced by competition for light and this competition signal may interfere with the climate-induced variation and thus hamper the detection of common climate-related growth-signals. From these larger trees, we selected the 10 individuals with the clearest tree-ring structures and highest within-tree crossdating as a basis to build the chronologies (i.e., mostly excluding juvenile trees and trees with phases of suppressed growth). We thus searched for the common growth-signal between trees, from a subset of trees assumed to be correctly crossdated and showing the strongest year-to-year variation in growth. We also included individuals for which tree-ring measurements were proven annual by radiocarbon dating (see Section 2.3.3 below).

### 2.3.3. Radiocarbon dating

In the case of weak or absent common growth signals, the annual character of tree-ring formation can be tested by radiocarbon dating, a dating method independent of tree growth (Worbes and Junk, 1989). This method is based on the peak in  $^{14}\text{C}$  in the atmosphere caused by above-ground atomic weapon tests (Nydal and Lovseth, 1981). To verify the annual character of tree-ring formation, we applied the  $^{14}\text{C}$  bomb-peak dating method on our subset species except for *T. ivorensis*. Tree-ring formation for *T. ivorensis* had earlier been proven to be annual (Détienne, 1989) and we assumed rings to be formed annually due to its strong deciduous character in the study area.

Problematic tree-ring structures (e.g., vague or discontinuous rings) are common in the tropical species and may hinder ring identification (Worbes, 2002; Brienen and Zuidema, 2005). It is therefore important to identify whether these structures are actual tree-ring boundaries or structures formed by intra-annual growth variations. To identify these problematic structures, we selected three individuals per species based on the ease of measurements and the clarity of their tree-rings: one individual with 'very clear' rings and good internal crossdating (usually a disc); one individual with 'clear' rings and good internal crossdating but showing some problematic structures; and a third individual showing several problematic structures (i.e., vague rings or anomalous structures; usually cores). With this selection we expected to prove the annual character of ring formation in these species (on the 'very clear' samples), while also being able to verify our definition of tree-ring boundaries and to quantify possible dating errors on the 'normal' and 'problematic' samples.

For each individual, we sampled three to four tree-rings that were pre-dated by ring counting (and crossdating) and spaced eight to ten years apart. From each ring, we collected 35–50 mg of wood to determine radiocarbon age. By analysing samples from different years per individual, it is possible to identify if and where errors in measurements have taken place. If all dates coincide between pre-dated rings and  $^{14}\text{C}$  measurements (margin of error  $\pm 1$  year), rings are formed annually and no measurement errors took place. If a constant discrepancy in measurements is found between all samples in one individual, measurement errors occurred in the wood formed in more recent years (between the most

recent  $^{14}\text{C}$ -dated tree ring and the bark). If a discrepancy is found between samples, measurement errors occurred between the pre-dated rings. By going back to the original wood samples after  $^{14}\text{C}$  dating, it is possible to identify measurement mistakes and verify tree-ring boundary definitions. In the case of discrepancies that cannot be solved, tree-ring formation can still be annual, but measurement errors occur. Including the 'problematic' samples, with less clear rings, allows for an estimation of the frequency of these measurement errors. This estimation is calculated as the probability of ring misidentification by dividing the number of misidentified rings by the period under analysis provides (expressed in errors per 100 years, cf. Soliz-Gamboa et al., 2011).

The fraction modern  $^{14}\text{C}$  ( $F^{14}\text{C}$ ) was determined on the holocellulose portion of the wood samples at the Center for Isotope Research at Groningen University, following their protocol for Accelerator Mass Spectrometry analysis. We used the program CALIBomb (<http://intcal.qub.ac.uk/CALIBomb>) to determine the date of each  $F^{14}\text{C}$  ( $\pm \text{sd}$ ) value using the dataset corresponding to our study region (NH\_Zone 3; Hua et al., 2013). As a given radiocarbon concentration may yield several possible calendar dates, we determined the mostly likely date of each sample based on the dates of the other samples from the same tree, i.e., subsequent samples from bark to center in one tree should have subsequently older ages.

### 2.4. Growth patterns and ages to reach Minimum Cutting Diameters (MCD)

For each of the subset species we calculated annual diameter increments as the average growth of the different radii multiplied by two. Over- or underestimations in growth rates may arise from shrinkage of discs and cores or from measuring tree-ring widths on irregular parts of the stem i.e., in buttresses. Therefore, we applied a correction factor on the diameter increments, accounting for the difference in diameters measured from rings and the diameters measured in the field (cf. Brienen and Zuidema, 2006b). If information on the first formed rings was missing, due to rot in the stem centre or the fact that the pith was not hit when coring, we estimated the distance to the pith assuming a circular growth pattern. To estimate the number of missing years, this distance was divided by the average growth rate of the first five tree rings present in the sample. Furthermore, tree ages presented here are slightly underestimated as ages were calculated from samples obtained at approximately 1 m height. The time to reach this height can vary between fast growing, often light demanding species (e.g., *T. ivorensis*) and slower growing, often shade tolerant species (e.g., *D. ogea*).

The corrected diameter growth rates were used to describe lifetime growth patterns of the subset species. First, we calculated for each species average diameter growth rates (in cm/year) per tree age. This allows for the comparison of patterns in growth rates, i.e., ontogenetic growth patterns between species. We also compared these average growth rates with the rates used in Cameroon for the calculation of future timber yields for these species (cf. MINEF, 2001). Finally, we calculated average cumulative diameters (in cm) per age for each species and used these diameter-age relationships to assess species-specific maximum (for the fastest growing individual), minimum (for the slowest grower), and average ages to reach MCD (as set by Cameroonian legislation for each species).

## 3. Results

### 3.1. Tree-ring structures and distinctness of ring boundaries

Here we discuss briefly the tree-ring structures of the screened species and provide more detailed descriptions for the subset species. In the Supplementary Material (Appendix B) we provide fact sheets for all screened species, with descriptions and images of

tree-ring boundaries, as well as information on applicability for tree-ring analyses. Detailed anatomical descriptions of wood characteristics are also available for most of the screened species in Détienne et al. (1998), Richter and Dallwitz (2000) and on the InsideWood database ([www.insidewood.lib.ncsu.edu](http://www.insidewood.lib.ncsu.edu); Wheeler, 2011).

Of the 22 screened species, 14 formed tree-ring boundaries of which eight species showed a 'good' or 'high' potential for tree-ring analysis (Table 2). All four types of tree-ring structures were observed in the screened species as well as combinations of structures. The most common tree-ring structure was type B (marginal parenchyma bands), as found in most Fabaceae and Meliaceae (Table 2). Two species – *Pycnanthus angolensis* and *Canarium schweinfurthii* – showed relatively clear structures on freshly sawn discs, but structures became unclear or disappeared after drying and polishing. Working with these species might require a different preparation approach (e.g., faster drying to avoid fungus infestations). Some individuals of *Staudtia kamerunensis* and *Gilbertiodendron dewevrei* showed clear anatomical structures. However, these structures were often discontinuous within the individual (disappearing on parts of the circumference), while other individuals completely lacked these structures. *S. kamerunensis* has been suggested to produce annual tree rings in a drier forest (Worbes et al., 2003), but ring formation may not be annual, or could be suppressed, under the high levels of rainfall at our study site.

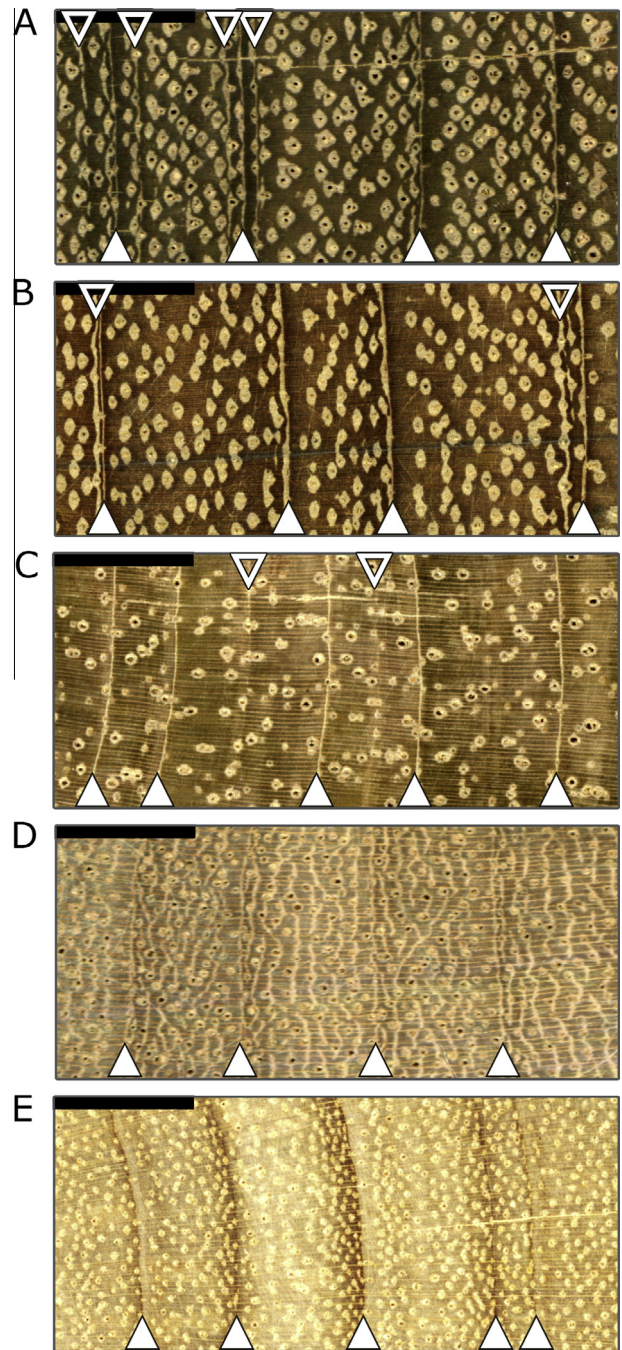
Of the five subset species, *E. utile* showed the most distinct tree-ring boundaries (Fig. 2), consisting of parenchyma bands (growth zone type B), sometimes combined with repeated patterns of fibre and parenchyma bands (type C). Some individuals showed large differences in growth rates between radii (e.g., in trees with asymmetric centres, or with buttresses). In the shorter radii, clarity of ring boundaries decreased and many wedging rings occurred, often hindering ring identification.

*T. ivorensis* also showed very clear tree-ring boundaries that consisted of wood density variations (marked by thick-walled fibres; type A), and variations in vessels distribution and/or size (type D). Juvenile individuals were often fast growing ( $>1 \text{ cm year}^{-1}$ ) and showed the most distinct rings. Growth rates decreased with increasing diameter and rings became very narrow at large diameters. These narrow rings were more difficult to distinguish and measure.

Tree-ring boundaries of *D. ogea* were also clear and consisted of thin (2–3 cells wide) parenchyma bands with sometimes variation in vessel distribution. However, parenchyma bands were sometimes vague or disappeared on certain parts of stem. Vague bands that disappeared along the circumference of the disc or in one of the radii were considered to be intra-annual growth variations, and thus, no true ring boundaries.

For the two *Brachystegia* species, tree-ring boundaries consisted of a thin parenchyma bands with lens-shaped vessels attached to it (closed triangles, Fig. 2). Both *Brachystegia* species also showed interconnected, eye-shaped vessels without the thin parenchyma band (open triangles, Fig. 2). These interconnected vessels often occurred slightly before or after a tree-ring boundary and were often discontinuous on parts of the circumference of the stem. Due to their discontinuous character, we considered these structures to be intra-annual growth variations.

For all our subset species, identifying tree-ring boundaries and ring wedging was easier on discs, where individual rings could be followed, than on cores and also easier for species with parenchyma bands than for *T. ivorensis*, where ring boundaries are marked by thick-walled fibres. Furthermore, tree-ring boundary distinctiveness decreased in more narrow rings: i.e., towards the centre of trees (for the *Brachystegia*'s, *D. ogea* and *E. utile*) and towards the bark (for *T. ivorensis*), or during periods of growth sup-



**Fig. 2.** Tree-ring boundaries of five tree species from a wet tropical forest in Cameroon: A. *Brachystegia cynometroides*, B. *Brachystegia eurycoma*, C. *Daniellia ogea*, D. *Entandrophragma utile*, and E. *Terminalia ivorensis*. Growth direction from left to right; black bar = 5 mm scale, filled white triangles = annual tree-ring boundaries, open white triangles = intra-annual growth variations.

pression. During these slow growing phases, wedging rings were also more common.

### 3.2. Crossdating potential

We first crossdated radii within trees and then among trees (on both single radii and on averages of radii per tree). Good internal crossdating was found for two species: 77% of *D. ogea* trees and 61% of *B. eurycoma* showed high levels of internal crossdating (i.e., a combination of well-matching long-term growth patterns and high ppr values; Table 3). The high levels of within-trees crossdating for these species, facilitated identifying intra-annual



growth variations. However, on cores it was not always possible to ensure whether these anomalous structures were discontinuous over the entire circumference.

For the other species internal crossdating was less successful. Despite the clarity in tree-ring boundaries, all *E. utile* trees showed medium internal crossdating levels, i.e., matching growth patterns but low ppr rates. Growth rates often showed a low degree of synchronous year-to-year variation (complacent rings, cf. Stokes and Smiley, 1996) and crossdating was often only possible using the interconnected rings on discs, especially in trees with buttresses or asymmetric centres. For *T. ivorensis*, high levels of internal crossdating were found in only 34% of trees, while 52% showed 'medium' levels of crossdating. Juvenile individuals often exhibited complacent and wide rings ( $>1 \text{ cm year}^{-1}$ ), but ring-width decreased with age, resulting in very narrow tree rings in large, old trees. Larger *T. ivorensis* individuals also showed more buttresses. Rings were usually very clear in radii following buttresses, but wedging rings occurred in the slow growing parts between buttresses. The wide and complacent rings in juvenile wood and the slow growth with wedging rings in adult wood, often hampered crossdating between radii. Again, crossdating was often only possible using the interconnected rings on discs, or by matching the strong ontogenetic growth trends in radii. The lowest levels of crossdating were found in *B. cynometroides*: only 40% of the trees showed high within-tree crossdating levels, whereas for 37% crossdating levels were low (poorly matching growth patterns and low ppr). As most samples for *B. cynometroides* consisted of cores, it was not possible – as in disc – to interconnect rings to solve crossdating problems.

Crossdating among trees, i.e., finding a common growth signal, proved difficult for all species (Fig. 3). The only species showing some degree of synchronicity in growth was *E. utile*. Two individuals, for which tree-ring formation was proven annual by radiocarbon dating (see Section 3.2. below), showed synchronous growth patterns between ca. 1974 and 1992 (Fig. 3, black lines). Remarkably, these trees showed a low-frequency synchronicity in growth ( $\sim 5\text{--}10$  years) but no synchronicity in annual growth variation (Fig. 3). *B. eurycoma*, *D. ogea*, and *T. ivorensis* individuals showed no synchronicity in growth at all and we did not search for common growth patterns in *B. cynometroides* due to the uncertainties in measurement and low internal crossdating. Without a common growth signal, it was impossible to crossdate samples and ascertain dating of our rings was absolute. We were therefore not able to build chronologies for any of the species.

### 3.3. Radiocarbon dating

The  $^{14}\text{C}$  bomb-peak dating yielded variable results for the four tested species (Fig. 4). In *E. utile*, pre-dated ring measurements

matched radiocarbon ages in all cases and within the 1-year margin of error of radiocarbon dating. This confirms annual ring formation for this species and shows that it also produces reliable annual tree rings under very wet conditions. Close matches between tree-ring and  $^{14}\text{C}$  dates were also found for most measurements in *D. ogea*, again confirming annual tree-ring formation. However, in the *D. ogea* tree with problematic rings, a discrepancy of two years was found (points above the diagonal; Fig. 4), indicating that some of the marked structured were not true ring-boundaries.

In most measurements for *B. eurycoma* we also found close matches between the tree-ring dates and radiocarbon dates. We did, however, also find discrepancies for *B. eurycoma*, with a maximum error of seven years (rings missed). These discrepancies were present in the tree with 'difficult' rings (measurements were shifted 3–5 years) and for the tree with 'very clear' rings. In the latter, discrepancies were present in the inner-most rings, i.e., the juvenile wood), in a difficult part of the disc with slow growth. Except for these rings in juvenile wood, the division into ring clarity was thus reflected in the radiocarbon dating results.

Discrepancies between tree-ring dating and  $^{14}\text{C}$  dating were found for all three individuals of *B. cynometroides*. In this species, rings were missed during measurements (points below the diagonal line; Fig. 4) and the maximum measurement error was 10 years (rings missed). The division into ring clarity classes was not reflected in the radiocarbon dating results for *B. cynometroides*: rings were missed in all three individuals, but surprisingly dating was most accurate in the individuals considered to have problematic rings.

We also calculated the probability of ring misidentification, to quantify the frequency of measurement errors (errors per 100 years, cf. Soliz-Gamboa et al., 2011). This probability was highest for *B. cynometroides*:  $-12.3\%$  (i.e., there is a chance of missing a ring every  $\sim 8$  years). For *B. eurycoma* the mean misidentification probability was  $-3.1\%$ , and for *D. ogea*  $+1.9\%$  (Table 3). Results of the radiocarbon dating and detailed figures per dated tree are given in the Supplementary Materials (Appendix A).

### 3.4. Growth patterns and ages at MCD

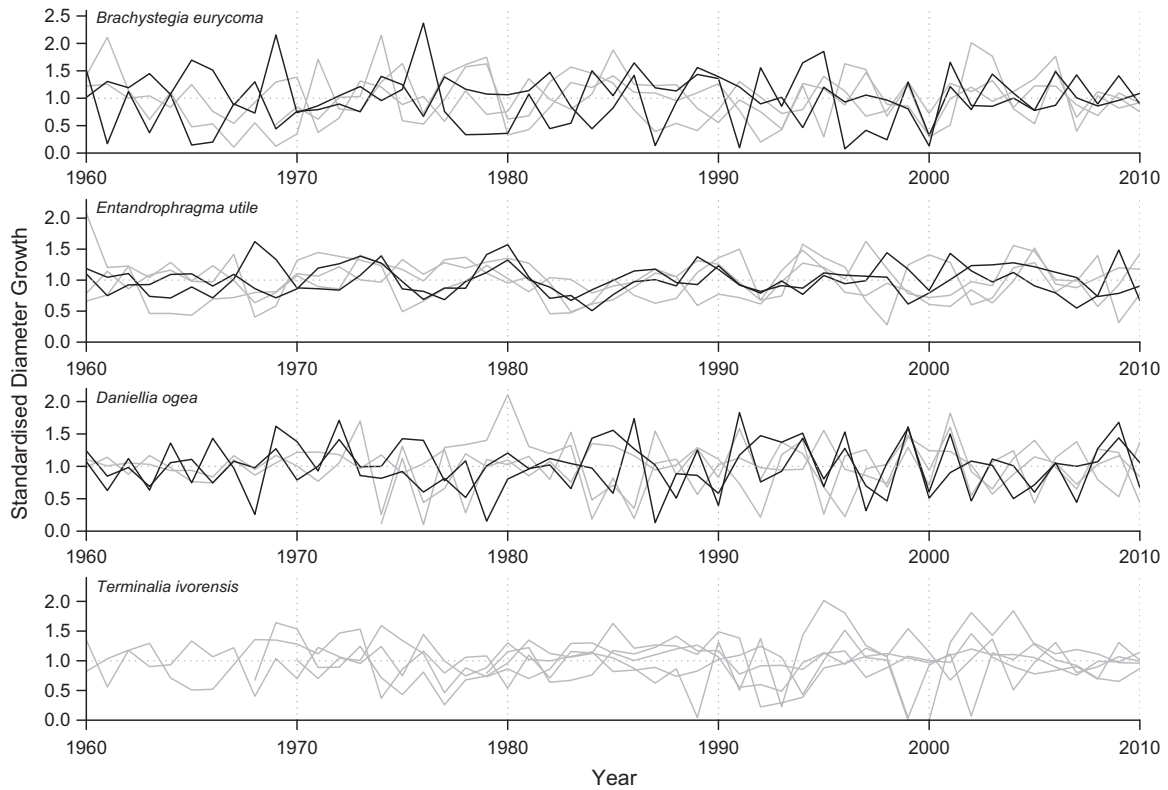
The five subset species showed large differences in ages, growth rates and lifetime growth trajectories. *D. ogea* and *E. utile* had the longest lifespans ( $>275$  years old), while the other three species reached maximum ages of 180–200 years (Table 3). Average growth rates ( $\pm$ standard deviations) ranged between  $0.43 \pm 0.35 \text{ cm year}^{-1}$  for *D. ogea* and  $0.96 \pm 0.71 \text{ cm year}^{-1}$  for *T. ivorensis* (Table 3). Lifetime growth patterns also varied between species, with *B. cynometroides* showing rather constant growth rates over time, while *B. eurycoma*, *E. utile*, and *D. ogea* presented low juvenile growth rates

**Table 3**

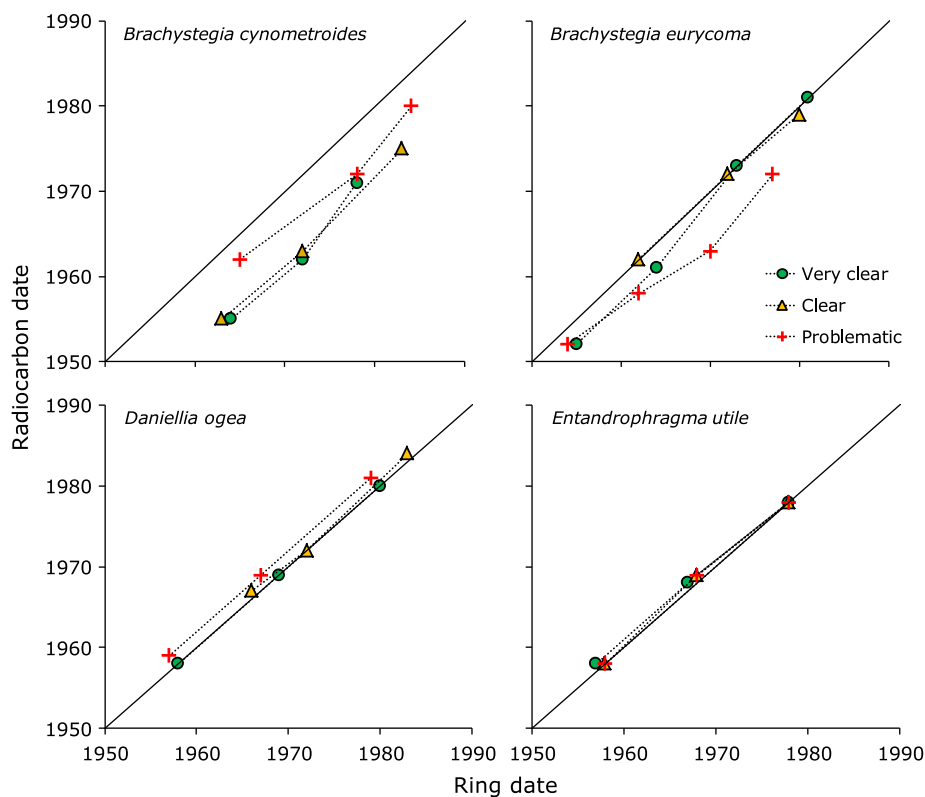
Growth and age characteristics of five selected commercial tree species from a wet tropical forest in Cameroon. Number of trees collected, number of trees cored (3–4 cores per tree) and discs. Diameter growth and age at Minimum Cutting Diameter (MCD) refers to the population average. Crossdating level: high (well-matching growth patterns and high ppr), medium (matching growth patterns, intermediate ppr), and low (poorly matching growth patterns and low ppr). Percentage of ring misidentification (RMI): based on radiocarbon dating, is the average amount of misidentified rings divided by the period of measurement (cf. Soliz-Gamboa et al., 2011). Positive values indicate that anatomical structures were erroneously identified as tree-ring boundaries; negative values indicate that rings were missed.

Species	# Trees	Cores/ discs	Diameter growth (cm/year, $\pm$ SD)	Age at MCD (year, range)	Crossdating level (high/medium/low)	RMI (in%)
<i>Brachystegia cynometroides</i>	124	120/4	$0.45 \pm 0.29$	126 (58–154)	40%/23%/37%	$-12.3$
<i>Brachystegia eurycoma</i>	128	96/32	$0.56 \pm 0.48$	100 (48–135)	61%/33%/6%	$-3.1$
<i>Daniellia ogea</i>	105	87/18	$0.43 \pm 0.35$	148 (77–214)	77%/23%/0%	1.9
<i>Entandrophragma utile</i>	10	0/10	$0.72 \pm 0.40$	126 (79–203) <sup>a</sup>	0%/100%/0%	$<1$
<i>Terminalia ivorensis</i>	62	10/52	$0.96 \pm 0.71$	45 (21–91)	34%/52%/14%	n.a.

<sup>a</sup> MCD = 60 cm, except for *E. utile* = 80 cm.



**Fig. 3.** Standardised (residual) diameter growth rates of five individuals with clear rings for *Brachystegia eurycoma*, *Daniellia ogea*, *Entandrophragma utile*, and *Terminalia ivorensis* in a wet tropical forest in Cameroon. Black lines represent individual trees correctly dated using radiocarbon dating (not applied on *T. ivorensis*); grey lines represent other individuals showing clear rings (i.e., no doubtful structures and good internal crossdating). Standardization performed with a 15-year cubic spline.



**Fig. 4.** Comparison of dates from tree-ring measurements and  $^{14}\text{C}$  bomb-peak derived dates for four species in a wet tropical forest in Cameroon. Rings are formed annually when symbols are on the diagonal  $Y = X$  line. Connected symbols represent measurements on the same individual. Three categories of tree-ring clarity were distinguished: *very clear* – tree-ring boundaries were very clear with good internal crossdating; *clear* – some doubtful structures but good internal crossdating; *problematic* – tree showing typical problems for the species (e.g., vague or discontinuous rings). Detailed results provided in [Supplementary Materials Appendix A](#).



that increased at intermediate ages, decreasing again slightly for older trees. *T. ivorensis* trees exhibited an ontogenetic growth pattern typical for light-demanding species, with high growth rates ( $>1 \text{ cm year}^{-1}$ ) for juvenile trees that strongly decreased with age (Fig. 5). The presented growth rates of *B. cynometroides* likely overestimate actual growth rates because of the high frequency of rings missed.

Growth rates also varied strongly within species, inducing large variation in ages to reach MCD (Fig. 6). For instance, *T. ivorensis* trees reached MCD on average after 45 years, but ages varied more than fourfold, ranging from 21 to 91 years. In the slowest growing species, *D. ogea*, MCD was reached after 148 years on average, but this ranged from 77 to 214 years (for all species, see Table 3).

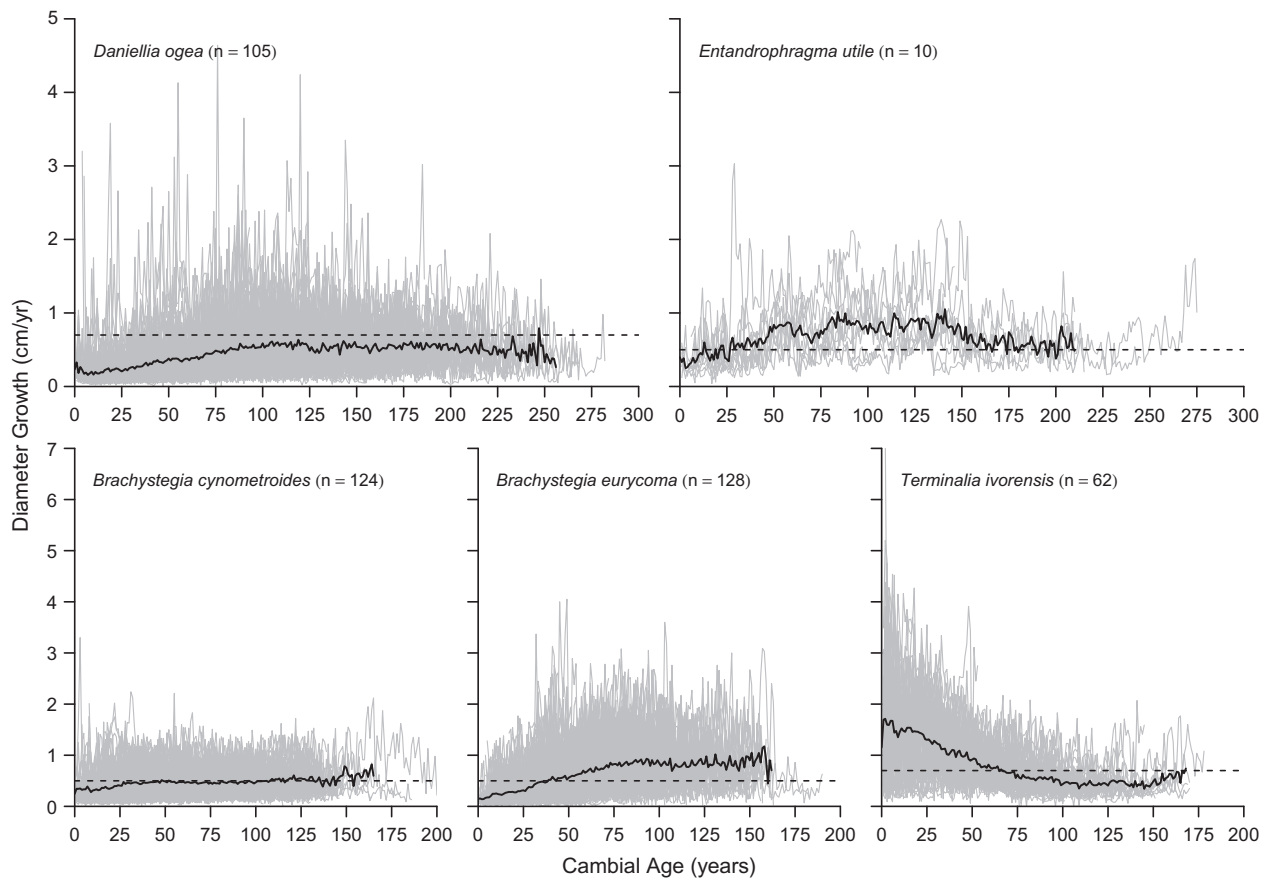
#### 4. Discussion

We evaluated the potential to apply tree-ring analysis in a wet Central-African lowland tropical forest. Even under wet tropical conditions, 14 of the 22 tree species produced visible tree-ring boundaries. The annual character of tree-ring formation was proven using radiocarbon dating for three species, while a fourth species showed rings were frequently missed. Although clear and annually formed rings were present in four species, we were unable to build chronologies. Growth rates varied strongly between and within species, implying that different species reach MCDs at different ages and that ages also vary strongly within species.

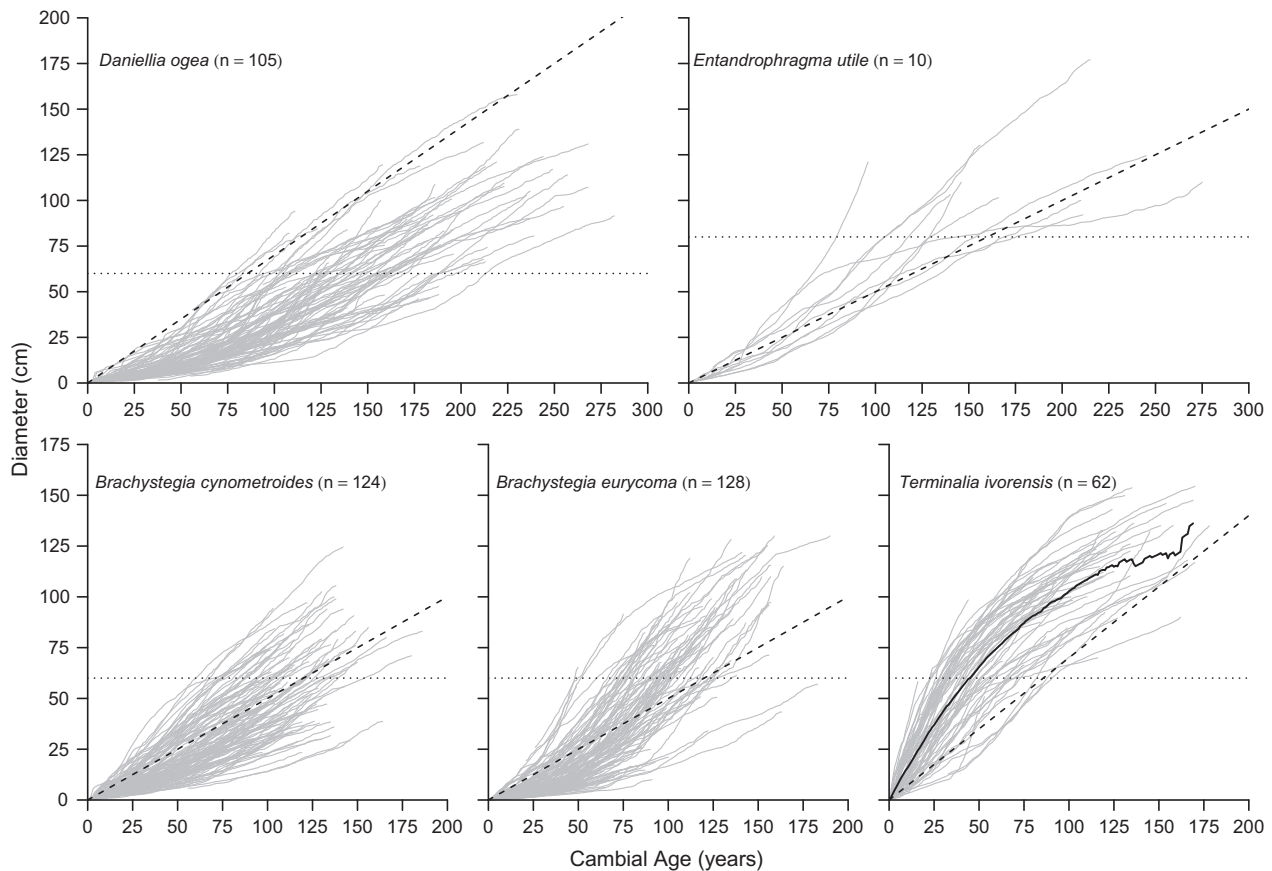
##### 4.1. Tree-ring boundaries and annual ring formation in wet tropical forests

This study is one of the very few tree-ring studies performed in wet tropical forests ( $>3000 \text{ mm year}^{-1}$ ; Zuidema et al., 2012) and the first one conducted in wet African forests. Even under these wet conditions, tree-ring structures were formed in 14 of the 22 commercial tree species. Overall, most tree species forming tree-ring boundaries were (brevi)deciduous, whereas evergreen species (e.g., *K. anthoteca*, *D. letouzeyi*) and species with a very short leafless period (e.g., *L. alata*, *P. angolensis*) mostly showed no or vague tree-ring boundaries. In about 36% of the screened species (8 out of 22), the potential for tree ring analysis is good or high (+ or ++, Table 2). This proportion is in accordance with studies from dry (Tarhule and Hughes, 2002; Brienen et al., 2009) and humid forests (Beltrán Gutiérrez and Valencia Ramos, 2013), suggesting that the potential of tree-ring analysis for wet forest is similar to that of drier environments. Anatomical wood descriptions exist for most of the 22 tree species (Richter and Dallwitz, 2000) and annuality of ring formation had been studied for several of them, albeit in drier sites (Détienne and Mariaux, 1977; Détienne et al., 1998; Worbes et al., 2003). For 10 of the screened species this is the first time the potential for tree-ring analysis is evaluated (Table 1) and for three species – *B. eurycoma*, *D. ogea* and *B. cynometroides* – this is the first time the annual nature of ring formation is evaluated.

Radiocarbon dating confirmed annuality of tree-ring formation but also showed measurement mistakes or occasional absence of (distinguishable) tree-ring boundaries occurred (Fig. 4). This



**Fig. 5.** Diameter growth rates vs. cambial age of five tree species from a wet tropical forest in Cameroon. Each grey line represents diameter growth values of an individual tree; black lines show average growth rates if  $>5$  samples were available. Dashed lines show the growth rates for each species in Cameroon used for timber yield calculations (cf. MINEF, 1999).



**Fig. 6.** Lifetime growth trajectories for five tree species in a wet tropical forest in Cameroon. Each grey line represents the lifetime growth trajectory of an individual tree; black lines show the average growth pattern if >5 samples were available; dashed horizontal lines indicate minimum cutting diameters (MCD) and diagonal lines show the growth rates for each species in Cameroon used for timber yield calculations (cf. MINEF, 1999).

independent dating allows for correcting tree-ring boundary markings on samples. However, in both *Brachystegia* species, we were unable to locate all rings missed. Growth rates for these species are thus somewhat overestimated, especially for *B. cynometroides* (Table 3). The typical slow growth rates of this species, combined with the low rates of internal crossdating further hampered detection of mistakes and probably increased ring misidentification. On the other hand, points within individuals were mostly parallel to the  $x = y$  line in Fig. 3, indicating that the number of rings between (radiocarbon dated) samples within a tree was estimated quite accurately. Although ring misidentification is thus common, we believe that ring measurements in *B. cynometroides* can still provide valuable basic information on the growth rates of this species. It is important to work with discs instead of cores to reduce measurement errors. Alternatively, a correction factor to account for ring misidentifications could be applied (e.g., by decreasing growth rates of *B. cynometroides* with 12.6%), but establishing a reliable correction factor would require (costly) radiocarbon analyses on many more individuals.

In *D. ogea*, intra-annual growth variations were present and not always identified. Identifying these structures was often difficult, especially on cores or during periods of slow growth (e.g., juvenile rings). Growth rates could thus be slightly underestimated (as indicated by the radiocarbon dating), however we expect the high levels of internal crossdating to have limited the amount of misidentified rings.

For all subset species we found problems common to tropical dendrochronology: small, wedging or vague rings and intra-annual structures resembling tree-ring boundaries. These problems have been

reported in several studies and have led previous researchers to recommend to perform ring measurements on discs rather than cores (Worbes, 2002; Brienen and Zuidema, 2005), which we reiterate here.

#### 4.2. Chronology building and asynchronous growth under wet conditions

Despite the high levels of internal crossdating and the proven annual ring formation for several species, we were unable to cross-date measurements among trees. Chronologies of *E. utile* have been successfully built in drier forest areas (Nzogang, 2009). However, in this study, crossdating among individuals was weak and we only observed synchronicity at 5–10 year cycles for individuals standing close to each other. Growth variation might thus be driven by other factors: local factors (e.g., soil depth, water table), internal cycles (e.g., reproduction) or canopy dynamics (Fritts and Swetnam, 1989).

The strong ontogenetic growth trend in *T. ivorensis* and the difficult identification of rings near the bark made crossdating in this species harder. Difficulties to build chronologies using a few discs of young (~30 years) trees were also reported for the congener *T. superba* (Couralet, 2010), but chronologies have been built recently for that species (De Ridder et al., 2013a). In the Congolese Mayombe forest, *T. superba* produced clear rings and growth correlated to local precipitation, whereas in the wetter forests in Ivory Coast, ring clarity was lower and growth showed no correlations to local climatic variables (De Ridder et al., 2013a). A similar decrease in ring clarity with increasing precipitation was also reported for *Gmelina arborea* in Costa Rica (Moya and Filho, 2009).

*T. ivorensis* is most commonly found in dryer forests (1250–3000 mm; PROTA, 2012) and may thus be growing on the wetter edge of its distribution in our study site. Precipitation thus may not limit growth, thwarting the common growth signal (Cook and Kairiukstis, 1990). The combination of complacent rings, irregular growth and lower ring clarity may thus have hampered detecting common growth signals.

Despite the many discs and the good internal crossdating of *D. ogea* and *B. eurycoma*, we were unable to crossdate measurements among individuals. Growth was not even synchronous between trees growing near one another: two fast growing *B. eurycoma* individuals (Be169 and Be170) of similar size (~60 cm diameter), showing very clear rings, high levels of internal crossdating and growing ~30 m apart did not show synchronous growth patterns. Chronologies have been built for congeners from drier forests (*D. oliveri*, Schöngart et al., 2006) or savannah (*B. spiciformis*, Trouet et al., 2006), suggesting – again – that the high amounts of rainfall in our study site reduce the synchronicity in growth.

Are there other factors that could explain this apparent lack in a common growth signal? We believe that not only the high levels of rainfall, for some species the wetter edge of their distribution could obscure the common growth-signal (cf. Cook and Kairiukstis, 1990), but also (observed) asynchronous leaf-fall. During the dry season, individuals of *B. eurycoma*, *B. cynometroides*, *D. ogea*, and *T. ivorensis*, growing near each other could be simultaneously in different stages of leaf change (i.e., with old leaves, without leaves and with new leaves). This could cause cambial activity – and thus growth – to be asynchronous between trees, especially at the beginning of the growing season.

Building chronologies for tree species in the wet tropics is thus challenging, even if those species possess clear rings that are formed annually. The cycles of (inter)annual cambial activity and wood formation are poorly understood, while forming the basis for tree-ring studies. Filling this knowledge gap requires a more intensive evaluation (than we have done) of tree-ring formation. This evaluation should go further than descriptions of tree-ring boundaries (cf. Alves and Angyalossy-Alfonso, 2000; Richter and Dallwitz, 2000; Beltrán Gutiérrez and Valencia Ramos, 2013) and should include periodic dendrometric measurements, like summarized for South American woody species by (Callado et al., 2013). This can be done either by periodic cambial wounding (e.g., Mariaux, 1967; Trouet et al., 2012; Tolera et al., 2013) or successive micro-sampling for evaluations of cambium activity throughout a given period (cf. Amobi, 1973; Krepkowski et al., 2011; Volland-Voigt et al., 2011). This would be especially insightful when combined with phenological observations (i.e., leaf flushing, fruiting; e.g., Borchert, 1999) and high-resolution meteorological data. Further techniques that show promising results for tropical tree-ring studies should also be explored. For instance, X-ray densitometry can be applied to aid in recognizing tree-ring boundaries (Worbes, 1995) and the analysis of stable isotope ratios (e.g., carbon and oxygen) has shown promising results in tropical species as a proxy to reconstruct climate (cf. Brienen et al., 2012).

#### 4.3. Application for forest management studies

Tree-ring analysis can be applied in wet tropical forests to obtain local and species-specific growth data and tree ages that can be used to plan and evaluate forest management. In Cameroon, management decisions (e.g., MCD and logging intensities) are based on timber yield calculations using the software TIAMA (MINEF, 1999). These calculations are done using legally set average growth rates for each species, established by the Ministry of Forestry and Wildlife in Cameroon. We argue that three potential problems arise when using set growth rates to calculate future timber yields: (1) set rates may be incorrect (i.e., too high or too

low), potentially leading to incorrect regulations on logging intensity or length of cutting cycle; (2) ontogenetic growth patterns are ignored when using a single life-time average growth rate for a given species; and (3) persistent differences in growth between individuals are ignored if one species-average value is used.

First, we found discrepancies between the set growth rates and the actual (measured) values for the subset species. The legally set rates in Cameroon for these species are: 0.5 cm year<sup>-1</sup> for *B. eurycoma*, *B. cynometroides*, and *E. utile* and 0.7 cm year<sup>-1</sup> for *T. ivorensis* and *D. ogea* (MINEF, 2001). *B. eurycoma*, *B. cynometroides* and *E. utile* showed similar growth rates to the set rates. On the other hand, *D. ogea* showed rates that were 39% lower than the set rates and *T. ivorensis* 47% higher. These discrepancies between legally set and actual growth rates may lead species to be under- or overexploited. If growth rates used in yield simulations are higher than actual rates, future timber yields for a species will be overestimated. This may lead to the species being exploited at higher intensities than it is able to regrow. The discrepancies found here highlight the importance of measuring accurate growth rates for each managed species. Preferably, these rates should be measured locally, as rates vary within species for trees growing in different areas (Therrell et al., 2007). Growth rates found here were, however, comparable with those reported for the same species at other sites (cf. Nzogang, 2009), for congeneric species (Worbes et al., 2003; Schöngart et al., 2006; Trouet et al., 2006; De Ridder et al., 2013b) and for other tropical wet forest tree species (e.g., Fichtler et al., 2003; Brienen and Zuidema, 2006a).

Second, ignoring the ontogenetic growth trend found for many species may also lead to incorrect management decisions. For instance in a light-demanding species as *T. ivorensis*, growth rates decrease strongly with age. Until an age of ca. 65 years, the average growth rate for *T. ivorensis* trees is higher than the set rates (Fig. 5). At this age though, most trees have already reached the MCD (Fig. 6). Growth in young years is thus relatively more important for wood production than at higher ages. This is the opposite for more shade tolerant species as *B. cynometroides* and *D. ogea*, that show increasing growth rates with age.

And finally, the fan-shaped growth trajectories found here (Fig. 6) indicate that persistent differences in growth rates are present in our species. These differences strongly influence size-age variations within a species (Bullock et al., 2004) and may lead to underestimations of estimated future timber yields (Brienen and Zuidema, 2007). Calculation of timber yields should thus include this variation and not be calculated using only average growth rates. Growth data presented here contain this variation and can thus be used to produce more accurate and species-specific estimations of future timber yields.

#### 4.4. Outlook and recommendations

Here we show for the first time the potential for tree-ring studies in an African wet tropical forest. Annual ring formation in wet tropical forests has been shown before (Dünisch et al., 2003; Fichtler et al., 2003), but studies in (non-flooded) wet tropical forests are an exception (Zuidema et al., 2012). Although possible, there are some limitations and difficulties of working with tree-rings in such wet climates. Not finding a common growth-signal (i.e., not being able to build chronologies) implies that annuality has to be proven using (expensive) radiocarbon dating analyses. Furthermore, the lack of a chronology also limits the options for quality checking as ring measurements cannot be compared across samples, potentially reducing accuracy. It is therefore essential to assess cycles of wood formation (see Section 4.2) in combination with (traditional) tree-ring analysis.

We reiterate the importance of working with discs instead of cores, especially when studying wet forest species. Working with

discs allows for a higher accuracy in tree-ring identification and we argue that obtaining discs directly at sawmills would greatly facilitate fieldwork. On the other hand, working solely with discs also limits sample collection to trees above the MCD and to (the small group of) commercial species. Increment cores can be used to expand sampling to smaller trees or to species not being logged and successful tropical tree-ring studies exist based (almost) solely on increment cores (e.g., Schöngart et al., 2006) or on a combination of discs and cores (e.g., De Ridder et al., 2013a,b). Therefore, we recommend working with discs as the basis to identify (problems in) ring-boundaries and using cores to expand sample sizes and species.

Obtaining discs at the sawmills facilitates fieldwork, without reducing the applicability of the measured tree-ring data. Many of the meta-data relevant for tree-ring analysis and necessary to calculate future timber yields (e.g., tree location, densities per hectare, dbh, bole height, etc.) can nowadays be obtained from logging inventories. Although these data may be less accurate than actual measurements in the field (e.g., tree locations are usually roughly estimated), time gained probably outweighs possible losses in accuracy. Furthermore, trees being logged are usually above MCD, thus representing a subset of successful, surviving trees. Growth rates of these (successful) trees may be more representative for the growth of trees to be logged in the future and thus provide more accurate yield estimations (Rozendaal et al., 2010). We also recommend working with sample sizes >35–50 (large) trees per species, as done in this study, to obtain accurate growth rates and quantification of persistent growth differences. Setting up national or regional (multi-country) tree-ring laboratories should be encouraged, to measure growth rates for more species, locally and in different forest areas per country or region.

Finally, from a forest management perspective in (Central) Africa, we recommend focusing tree-ring analysis on the 15 most exploited tree species. These species comprise ~92.5% of the total volume logged in tropical Africa (Ruiz-Pérez et al., 2005) and most of these species (12 out of 15) produce tree-ring boundaries (Richter and Dallwitz, 2000). Four of these species were included in this study (*C. schweinfurthii*, *E. utile*, *E. ivorensis*, and *P. soyauxii*). We also express the importance of reporting and publishing both the successful studies (i.e., species with annual rings, chronologies and climate-growth correlations) and the failures (i.e., no annual rings, no chronologies). Publications are probably biased to the successes, whereas knowledge on which species do not form rings is equally important.

There is a great potential to use tree-ring analysis, even in wet tropical forests, to provide essential ecological data that can be used for forest management. Tree-ring analysis obviously only provides growth rates of surviving trees. Combining growth rates from rings with survival and regeneration data from PSP in the same forests would allow for realistic simulations of population growth (cf. Couralet et al., 2005). This would be especially interesting when combined with (long-term) monitoring studies on the effects of logging and silvicultural treatments on the development of exploited forests (cf. Peña-Claros et al., 2008; Gourlet-Fleury et al., 2013). Such an analysis would allow for a more accurate evaluation of the consequences of forest exploitation. We hope that this study (and the supplemented fact sheets) may form the beginning of a better information basis for sustainable forest management in (Central) Africa.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.03.037>.

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## Supplementary Material

### Appendix A – Radiocarbon dating

**Table S1:** Ring dates and radiocarbon ( $^{14}\text{C}$ ) dates for four tree species from a wet tropical forest in Cameroon. For each of the species 3-4 samples were analysed. Ring dates were determined by counting rings back in time from the bark. Radiocarbon dates were determined with the program CALIBomb (<http://intcal.qub.ac.uk/CALIBomb>), using the fraction of  $^{14}\text{C}$  ( $\pm\text{sd}$ ) in the wood (measured by Accelerator Mass Spectrometry on holocellulose) using the NH\_Zone3 (Hua & Barbetti 2013). Positive differences indicates that ring dates were overestimated (i.e. false rings) and negative differences indicate and underestimation of the date (i.e. missing rings). Percentages of rings missed was calculated as the amount of rings missed per measurement and the period over which these rings were missed (average percentages calculated over all measurements per species). \*For *E. utile* amount of rings missed was within the measurement accuracy of radiocarbon dating and percentages were not calculated.

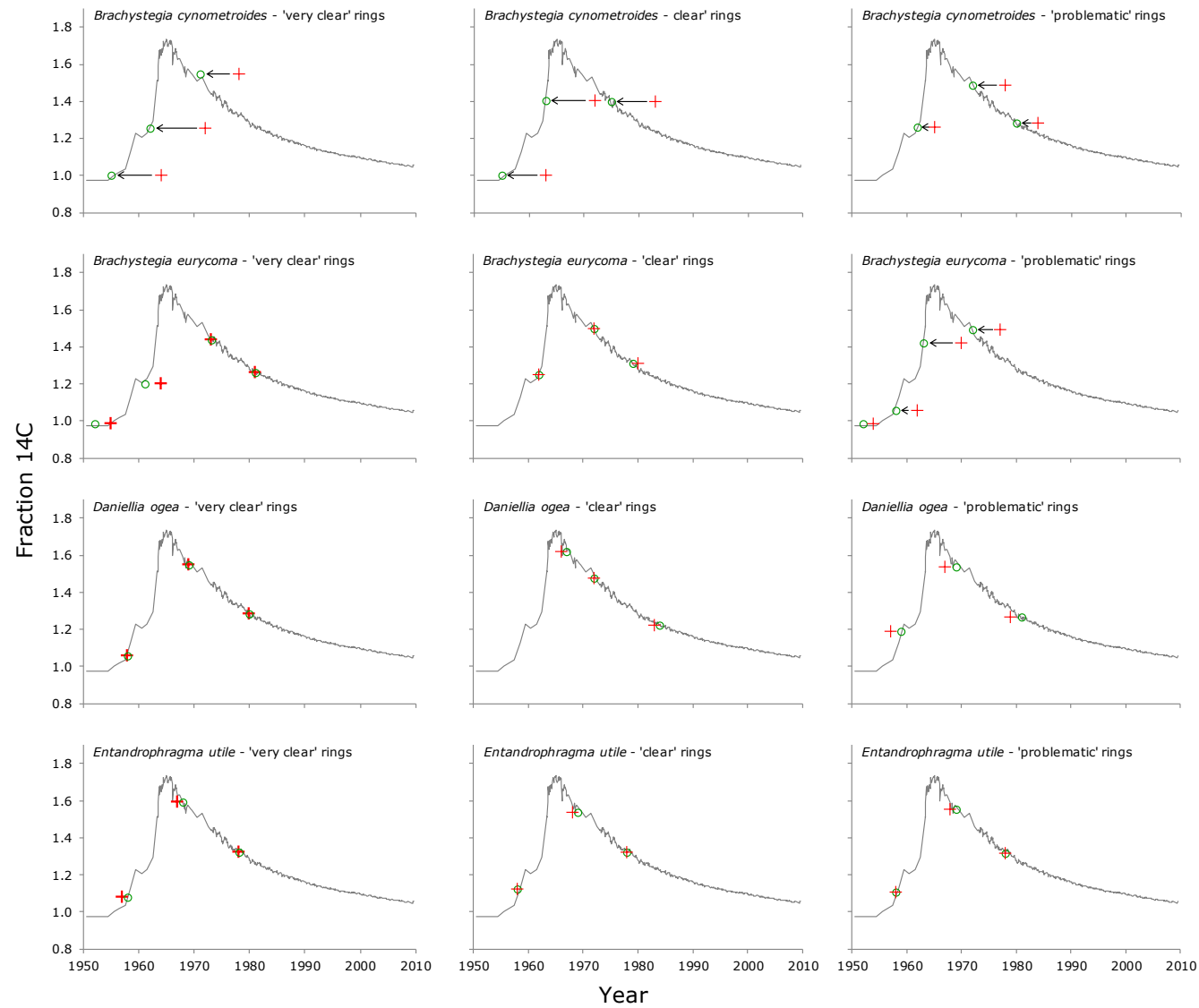
Species	Ring clarity	Tree-ring date	Radiocarbon date	$^{14}\text{C}$ fraction (in %)	Sigma $^{14}\text{C}$ fraction	Amount missed rings	Period over missed rings	Amount/Period missed rings	Average missed rings (in%)
<i>Brachystegia cynometroides</i>	Very clear	1964	1955	100.22	0.37	1	8	12.5%	
<i>Brachystegia cynometroides</i>	Very clear	1972	1962	125.46	0.46	-3	6	-50.0%	
<i>Brachystegia cynometroides</i>	Very clear	1978	1971	154.66	0.56	-7	33	-21.2%	
<i>Brachystegia cynometroides</i>	Clear	1963	1955	100.35	0.38	1	9	11.1%	
<i>Brachystegia cynometroides</i>	Clear	1972	1963	140.55	0.48	-1	11	-9.1%	
<i>Brachystegia cynometroides</i>	Clear	1983	1975	139.73	0.47	-8	28	-28.6%	
<i>Brachystegia cynometroides</i>	Problematic	1965	1962	126.22	0.45	3	13	23.1%	
<i>Brachystegia cynometroides</i>	Problematic	1978	1972	148.54	0.53	-2	6	-33.3%	
<i>Brachystegia cynometroides</i>	Problematic	1984	1980	128.43	0.46	-4	27	-14.8%	<b>-12.3%</b>
<i>Brachystegia eurycoma</i>	Very clear	1955	1952	98.38	0.33	0	9	0.0%	
<i>Brachystegia eurycoma</i>	Very clear	1964	1961	120.20	0.39	-3	9	-33.3%	
<i>Brachystegia eurycoma</i>	Very clear	1973	1973	143.56	0.47	0	8	0.0%	
<i>Brachystegia eurycoma</i>	Very clear	1981	1981	125.88	0.43	0	30	0.0%	
<i>Brachystegia eurycoma</i>	Clear	1962	1962	124.83	0.42	0	10	0.0%	
<i>Brachystegia eurycoma</i>	Clear	1972	1972	149.60	0.47	1	8	12.5%	
<i>Brachystegia eurycoma</i>	Clear	1980	1979	131.07	0.42	-1	31	-3.8%	
<i>Brachystegia eurycoma</i>	Problematic	1954	1952	98.40	0.34	2	8	-3.5%	
<i>Brachystegia eurycoma</i>	Problematic	1962	1958	105.83	0.36	3	8	37.5%	
<i>Brachystegia eurycoma</i>	Problematic	1970	1963	141.99	0.47	-2	7	-28.6%	
<i>Brachystegia eurycoma</i>	Problematic	1977	1972	149.49	0.48	-5	34	-14.7%	<b>-3.1%</b>

**Table S1 (continued)**

<b>Species</b>	<b>Ring clarity</b>	<b>Tree-ring date</b>	<b>Radiocarbon date</b>	<b><sup>14</sup>C fraction (in %)</b>	<b>Sigma <sup>14</sup>C fraction</b>	<b>Amount missed rings</b>	<b>Period over missed rings</b>	<b>Amount/Period missed rings</b>	<b>Average missed rings (in%)</b>
<i>Daniellia ogea</i>	Very clear	1958	1958	105.91	0.39	0	11	0.0%	
<i>Daniellia ogea</i>	Very clear	1969	1969	154.89	0.52	0	11	0.0%	
<i>Daniellia ogea</i>	Very clear	1980	1980	128.61	0.45	0	31	0.0%	
<i>Daniellia ogea</i>	Clear	1966	1967	162.02	0.51	1	6	16.7%	
<i>Daniellia ogea</i>	Clear	1972	1972	147.83	0.49	-1	11	-9.1%	
<i>Daniellia ogea</i>	Clear	1983	1984	122.26	0.42	1	28	3.6%	
<i>Daniellia ogea</i>	Problematic	1957	1959	118.83	0.41	0	10	0.0%	
<i>Daniellia ogea</i>	Problematic	1967	1969	153.51	0.50	0	12	0.0%	
<i>Daniellia ogea</i>	Problematic	1979	1981	126.86	0.44	2	32	6.3%	<b>1.9%</b>
<i>Entandrophragma utile</i>	Very clear	1957	1958	107.94	0.40	0	10	*	
<i>Entandrophragma utile</i>	Very clear	1967	1968	159.29	0.55	1	11	*	
<i>Entandrophragma utile</i>	Very clear	1978	1978	132.17	0.47	0	33	*	
<i>Entandrophragma utile</i>	Clear	1958	1958	112.44	0.41	-1	10	*	
<i>Entandrophragma utile</i>	Clear	1968	1969	153.86	0.55	1	10	*	
<i>Entandrophragma utile</i>	Clear	1978	1978	132.10	0.47	0	33	*	
<i>Entandrophragma utile</i>	Problematic	1958	1958	110.48	0.41	0	20	*	
<i>Entandrophragma utile</i>	Problematic	1978	1978	131.60	0.47	-1	-10	*	
<i>Entandrophragma utile</i>	Problematic	1968	1969	155.44	0.52	1	43	*	*



Figure S1:  $^{14}\text{C}$  fraction in wood of pre-dated rings (*red crosses*) and the corresponding radiocarbon dates (*green circles*) for four species from a wet tropical forest in Cameroon. When pre-dated rings and radiocarbon dates correspond, ring dating was correct. Discrepancies (indicated by *arrows*) indicate measurement mistakes. *Grey lines* are the reconstructed northern hemisphere zone 3 radiocarbon values (NH\_Zone3, cf. Hua & Barbetti 2013)



**References:**

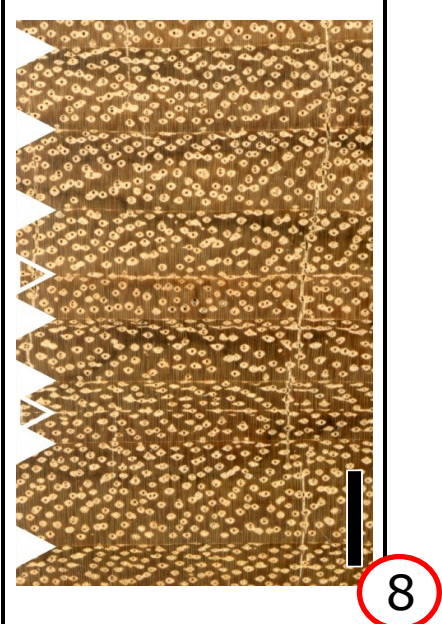
Hua, Q., Barbetti, M., Rakowski, A.Z., 2013. Atmospheric radiocarbon for the period 1950-2010. Radiocarbon 55, 2059-2072.

## Supplementary material

### Appendix B – Fact sheets

Each fact sheet comprises of:

1. Species name [COMMERCIAL NAME]
2. Indicative potential for tree-ring analysis:
  - ring analysis has high potential (++)
  - ring analysis has good potential (+)
  - ring analysis might be possible (+-)
  - ring analysis has low potential (-)
  - ring analysis not possible (--)
3. The tree-ring boundaries found in this study
4. Problems encountered in this study or mentioned in the literature
5. The possibility of sampling with increment cores
  - i.e. wood neither too tough or too brittle to be cored
6. Potential and applications to apply tree-ring analysis on this species
  - Based on findings of this study and on literature
  - Also includes the tree densities for the study area (based on own observations and from inventory of 3200 ha (TRC 2011-2012)
7. A description of the ring boundary as given in the InsideWood database
8. Scale bar = ~ 5mm

1	<b><i>Afzelia bipindensis</i> [DOUSSIE ROUGE]</b>	2 +	
3	<b>Ring boundary:</b> <ul style="list-style-type: none"><li>- (B) Marginal parenchyma band</li><li>- (A) Density variations (<i>sometimes</i>)</li></ul>		
4	<b>Problems:</b> <ul style="list-style-type: none"><li>- Wedging rings, especially in periods of slow growth</li><li>- Sometimes vague ring boundaries on certain portions of the disc</li><li>- False/discontinuous ring boundaries (<i>open triangles</i>) distinguishable from true rings (no thin continuous parenchyma line)</li></ul>		
5	<b>Sampling with increment cores:</b> <ul style="list-style-type: none"><li>- Yes, wood toughness intermediate</li></ul>		
6	<b>Potential and applications</b> <ul style="list-style-type: none"><li>- Good potential to obtain growth data.</li><li>- Climate-growth relations found for congeners growing in drier forests (<i>Afzelia africana</i>; Schongart et al. 2006). Might thus have potential for climatic reconstruction.</li></ul>		
7	<b>Boundary description (IAWA hardwood codes):</b> <ul style="list-style-type: none"><li>- (1) growth ring boundaries distinct</li></ul>		
			8

### ***Afzelia bipindensis* Harms [DOUSSIE ROUGE]**

+

#### **Ring boundary:**

- (B) Marginal parenchyma band
- (A) Density variations (*sometimes*)

#### **Problems:**

- Wedging rings, especially in periods of slow growth
- Sometimes vague ring boundaries on certain portions of the disc
- Discontinuous ring boundaries lacking parenchyma bands (*open triangles*), needs to be evaluated

#### **Sampling with increment cores:**

- Yes, wood toughness intermediate

#### **Potential and applications**

- Good potential to obtain growth data. Needs proof on the annual character of ring formation.
- Climate-growth relations found for congeners growing in drier forests (*Afzelia africana*; Schongart et al. 2006). Might thus have potential for climatic reconstruction.
- Ring boundaries considered annual and clear (Détienne et al. 1998)
- Rare in the study area:  $\sim 0.002$  trees.ha<sup>-1</sup> (> 80 dbh)

#### **Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct



### ***Afzelia pachyloba* Harms [DOUSSIE BLANC]**

+

#### **Ring boundary:**

- (B) Marginal parenchyma band
- (A) Density variations (*sometimes*)

#### **Problems:**

- Wedging rings, especially in periods of slow growth
- Sometimes vague ring boundaries on certain portions of the disc
- Discontinuous ring boundaries lacking parenchyma bands (*open triangles*), needs to be evaluated

#### **Sampling with increment cores:**

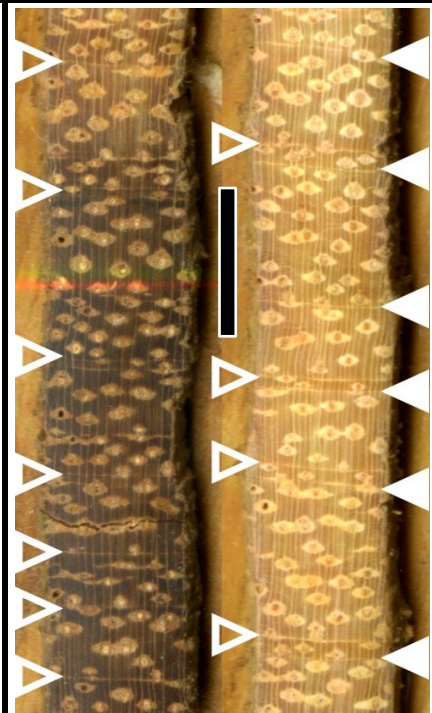
- Yes, wood toughness intermediate

#### **Potential and applications**

- Good potential to obtain growth data. Needs proof on the annual character of ring formation.
- Climate-growth relations found for congeners growing in drier forests (*Afzelia africana*; Schongart et al. 2006). Might thus have potential for climatic reconstruction.
- Ring boundaries considered annual and clear (Détienne et al. 1998)
- Rare in the study area:  $\sim 0.01$  trees.ha<sup>-1</sup> (> 80 dbh)

#### **Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct



***Bikinia le-testui* (Pellegr.) Wieringa [EKOP MAYO]**

+/-

**Ring boundary:**

- (B) Marginal parenchyma band
- (A) Density variations (*sometimes*)

**Problems:**

- Wedging rings, especially in periods of slow growth
- Discontinuous ring boundaries / parenchyma (*open triangles*)
- Rings can be very narrow in juvenile wood.

**Sampling with increment cores:**

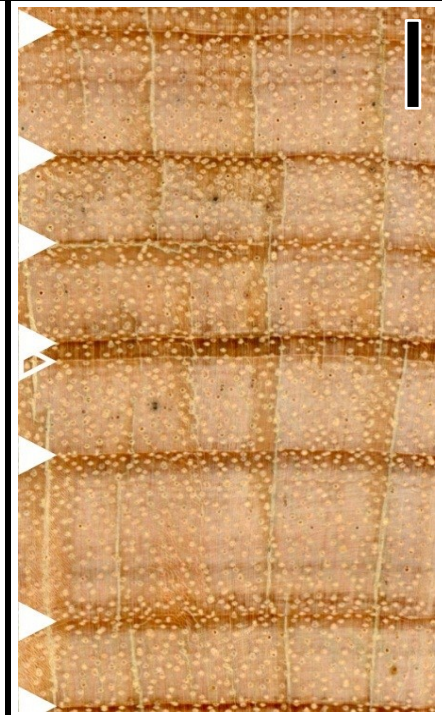
- No, wood very tough (fibrous)

**Potential and applications**

- Crossdates well internally.
- Annuality needs to be proven
- Trees can have buttresses (up to ~2.0m height)
- Useful to obtain growth data.
- Work with discs. Coring is difficult and presence of wedging rings.
- Clustered distribution, rare: ~0.16 trees.ha<sup>-1</sup> (>60cm dbh)

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



***Brachystegia cynometroides* Harms [EKOP NOM NAGA]**

+/-

**Ring boundary:**

- (B) Marginal parenchyma band (*closed triangles*)

**Problems:**

- Wedging rings, especially in periods of slow growth
- Discontinuous boundaries / intra-annual growth variations present. Often near tree-ring boundaries (*open triangles*)
- Rings can be very narrow (in juvenile wood).

**Sampling with increment cores:**

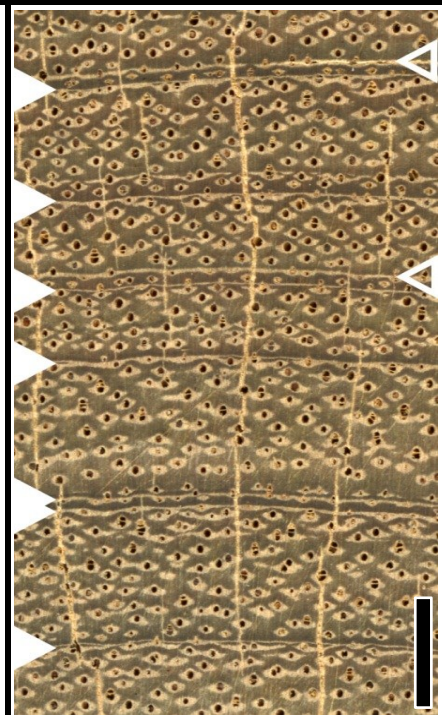
- Yes, wood intermediate toughness

**Potential and applications**

- Useful to obtain growth data (but measurement mistakes occur).
- Ideally work with discs, due to false and wedging rings.
- Clustered distribution, locally abundant: ~7 trees.ha<sup>-1</sup> (>5cm dbh)

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent





***Brachystegia eurycoma* Harms [EKOP NAGA]**

+

**Ring boundary:**

- (B) Marginal parenchyma band
- (A) Density variations (*sometimes*)

**Problems:**

- Wedging rings, especially in periods of slow growth
- Discontinuous boundaries / intra-annual growth variations present. Often near tree-ring boundaries (*open triangles*)
- Rings can be very narrow (in juvenile wood).

**Sampling with increment cores:**

- Yes, wood intermediate toughness

**Potential and applications**

- Crossdates well internally. No buttresses.
- Useful to obtain good quality growth data.
- Ideally work with discs, due to discontinuous and wedging rings
- Clustered distribution, locally abundant:  $\sim 8 \text{ trees.ha}^{-1}$  ( $> 5 \text{ cm dbh}$ )

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



***Canarium schweinfurthii* Engl. [AIELE]**

+/-

**Ring boundary:**

- No ring boundaries
- (A) Density variations

**Problems:**

- Wedging rings, especially in periods of slow growth
- Rings are vague, little difference late vs. early wood
- Presents discontinuous structures (*open triangles*)
- Juvenile wood with unclear/vague structures

**Sampling with increment cores:**

- Yes, wood is soft

**Potential and applications**

- Strong deciduous character => rings possibly annual
- Potential to obtain growth data (important spp).
- Work with discs, due to vague rings
- However, no ring boundaries cf. Detienne et al. (1998)
- Requires pinning / cambial wounding experiments to determine annual character of ring structures
- Rare in the study area:  $\sim 0.02 \text{ trees.ha}^{-1}$  ( $> 60 \text{ dbh}$ )

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent



***Daniellia ogea* (Harms) Rolfe ex Holl. [FARO]**

++

**Ring boundary:**

- (B) Marginal parenchyma band
- (A) Density variations (*sometimes*)

**Problems:**

- Wedging rings, especially in periods of slow growth
- Rings can be vague and presents discontinuous structures resembling true rings (more often in juvenile wood)
- Slow growth of juvenile trees, tree ages may be underestimated

**Sampling with increment cores:**

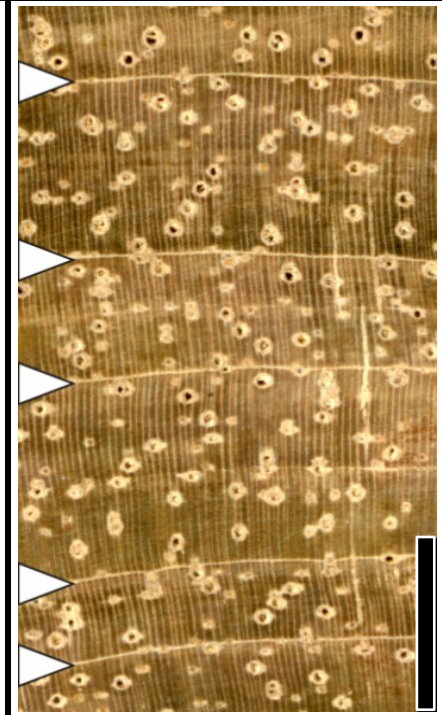
- Yes, wood intermediate toughness

**Potential and applications**

- Crossdates well internally. No buttresses
- Good potential to obtain high quality growth data.
- Climate-growth relations found for congeners growing in drier forests (*D. oliveri*; Schongart et al. 2006).
- Ideally work with discs, due to discontinuous and wedging rings.
- Clustered distribution, rare:  $\sim 0.05$  trees.ha<sup>-1</sup> (>60cm dbh)

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



***Didelotia letouzeyi* Pellegr. [GOMBÉ MAMEL]**

-

**Ring boundary:**

- No ring boundaries
- (B) Parenchyma bands (*sometimes, closed triangles*)
- (A) Density variations (*sometimes, open triangles*)

**Problems:**

- Sometimes shows very thin parenchyma bands and some density variations are present. Also large parts without any visible structures (*right image*)

**Sampling with increment cores:**

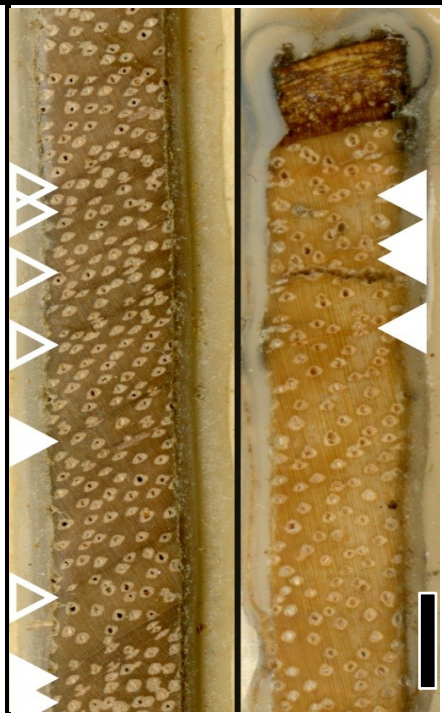
- Yes, wood intermediate toughness

**Potential and applications**

- Presence of some ring boundaries. May form rings during drier years
- Perhaps rings in drier forests
- Ideally work with discs
- Requires pinning / cambial wounding experiments
- Rare:  $\sim 0.04$  trees.ha<sup>-1</sup> (>60cm dbh)

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent





***Entandrophragma angolense* (Welw.) C.D.C. [TIAMA]**

++

**Ring boundary:**

- (B) Marginal parenchyma band
- (C) Alternating fibre and parenchyma bands (*sometimes*)
- (A) Density variations (*sometimes*)

**Problems:**

- Wedging rings
- Rings may be narrow or unclear (*open triangles*)
- Rings less clear than in other *Entandrophragma* spp (Détienne et al. 1998)

**Sampling with increment cores:**

- Yes, wood intermediate toughness

**Potential and applications**

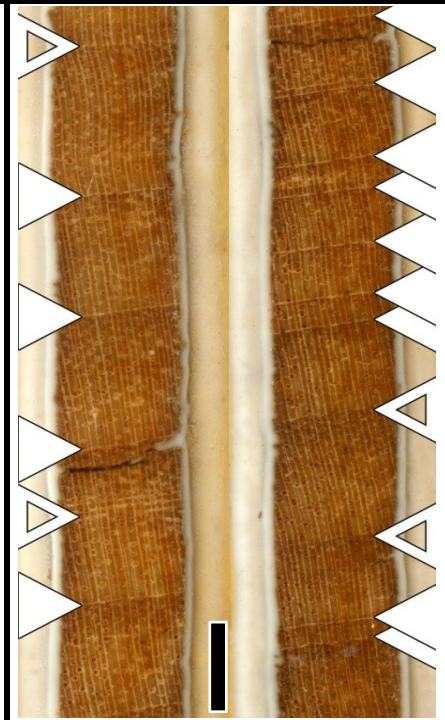
- Widespread species with high commercial value
- Good potential to obtain growth data
- Climate-growth relations found for congeners growing in drier forests (Nzongang 2009)

(Nzongang 2009)

- Rare in the study area:  $\sim 0.004$  trees.ha<sup>-1</sup> (> 80 dbh)
- Ideally work with discs, due to buttresses

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



***Entandrophragma candollei* Harms [KOSIPO]**

++

**Ring boundary:**

- (B) Marginal parenchyma band
- (C) Alternating fibre and parenchyma bands (*sometimes*)
- (A) Density variations (*sometimes*)

**Problems:**

- Wedging rings
- Rings may be narrow or unclear (*open triangles*)
- Slow grower

**Sampling with increment cores:**

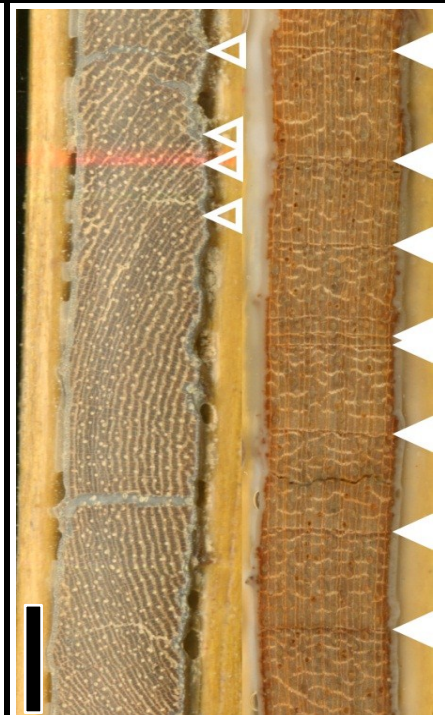
- Yes, wood intermediate toughness

**Potential and applications**

- Good potential to obtain growth data
- Has wedging rings but no false rings (cf. Détienne et al. 1998)
- Slow growth / shade tolerant => ages may be underestimated
- Climate-growth analysis possible in drier forests (Nzongang 2009)
- Rare in the study area:  $\sim 0.003$  trees.ha<sup>-1</sup> (> 80 dbh)
- Ideally work with discs, due to slow growth rates

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent



***Entandrophragma utile* (Dawe & Sprague) Sprague [SIPO]**

++

**Ring boundary:**

- (B) Marginal parenchyma band
- (C) Alternating fibre and parenchyma bands (*sometimes*)
- (A) Density variations (*sometimes*)

**Problems:**

- Wedging rings, especially in areas between buttresses
- Weak crossdating between radii (in this study)
- Sometimes vague ring boundaries on certain portions of the disc
- Slow growth of juvenile trees, age may be underestimated

**Sampling with increment cores:**

- Yes, wood intermediate toughness

**Potential and applications**

- Good potential to obtain growth data (important sp.)
- Climate-growth relations found in drier forests (Nzongang 2009)
- Rare in the study area:  $\sim 0.009$  trees.ha<sup>-1</sup> (> 80 dbh)
- Ideally work with discs, due to weak (internal) crossdating.

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



***Erythrophleum ivorense* A.Chev. [TALI]**

+/-

**Ring boundary:**

- (A) Density variations (*closed triangles*)
- (B) Marginal parenchyma band (*sometimes*)

**Problems:**

- Wedging rings, especially in periods of slow growth and between buttresses
- Ring boundaries can be vague (*open triangles*) on certain portions of the disc

**Sampling with increment cores:**

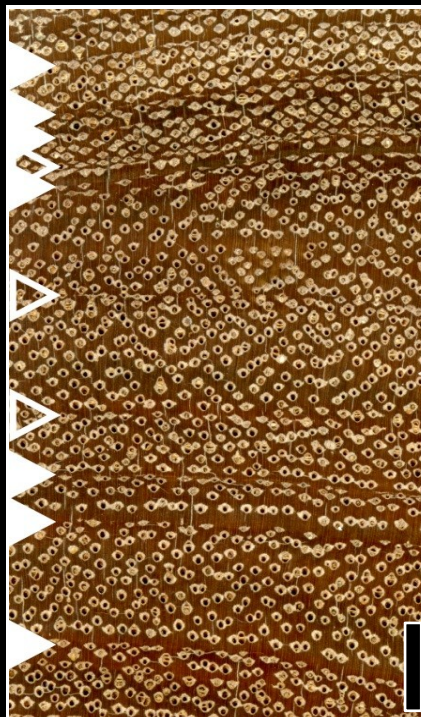
- No, wood tough

**Potential and applications**

- Good potential to obtain growth data (important species)
- Climate-growth relations found in drier forests (Nzongang 2009)
- Might thus have potential for climatic reconstruction.
- Common in the study area:  $\sim 0.3$  trees.ha<sup>-1</sup> (>70 dbh)
- Ideally work with discs, due to wedging rings in buttresses

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent





***Gilbertiodendron dewevrei* (De Wild.) J.Léonard [LIMBALI]**

+/-

**Ring boundary:**

- (B) Marginal parenchyma bands (*closed triangles*)

**Problems:**

- Rings can be vague, discontinuous parenchyma bands (*open triangles*)
- Wedging and more vague rings in juvenile wood

**Sampling with increment cores:**

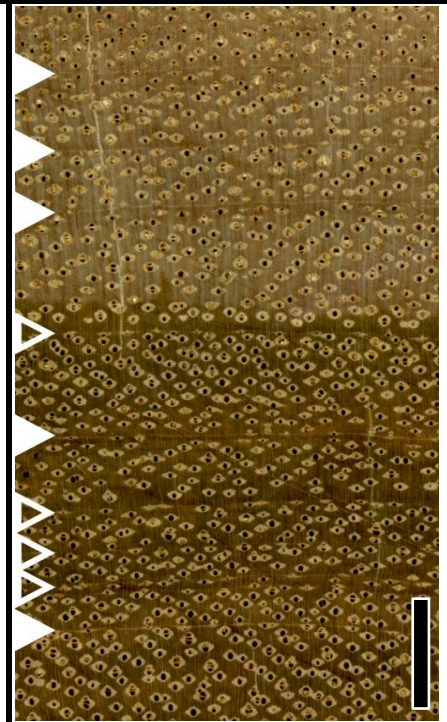
- No, wood very tough (fibrous)

**Potential and applications**

- Potential to obtain growth data
- Widespread in Africa
- Gregarious species: forms monodominant stands
- Locally very abundant: ~80 trees.ha<sup>-1</sup> (>5cm dbh)

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct



***Guarea thompsonii* Sprague & Hutch. [DARK BOSSÉ / BOSSÉ FONSSÉ]**

+/-

**Ring boundary:**

- (A) Density variations (*closed triangles*)
- (B) Marginal parenchyma band (*sometimes*)

**Problems:**

- Slow growth
- Vague or discontinuous ring boundaries on portions of the disc (*open triangles*)

**Sampling with increment cores:**

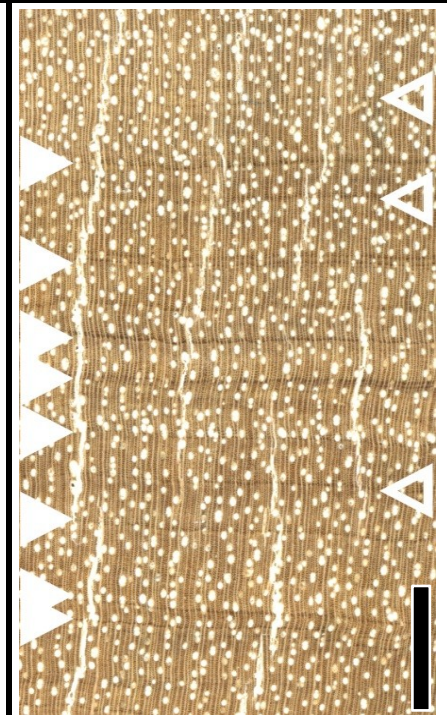
- Yes, wood toughness intermediate

**Potential and applications**

- Congener suggested to produce annual rings (*G. cedrata*; Détienne et al. 1998)
- Important commercial species
- Potential to obtain growth data but requires thorough evaluation of annuality ring formation (pinning / cambial wounding)
- Rare in the study area: ~0.003 trees.ha<sup>-1</sup> (> 80 dbh)

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



***Khaya anthoteca* C. DC. [ACAJOU DE BASSAM]**

-

**Ring boundary:**

- No ring boundaries
- (A) Density variations (*open triangles*)

**Problems:**

- Some density variations present, but unclear (difficult to distinguish)

**Sampling with increment cores:**

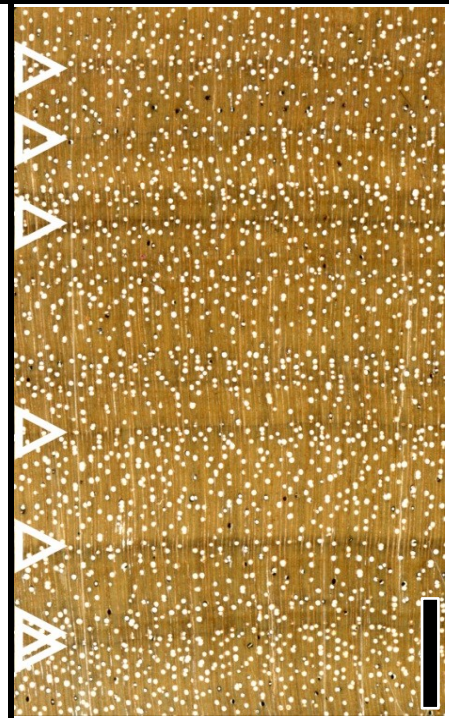
- Yes, wood toughness intermediate

**Potential and applications**

- From cambial marking experiment: ring analysis not possible (Détienne et al. 1998)
- Evergreen species: might have continuous growth in wet tropical forests. It however, shows density variations.
- Commercially important species, interesting to apply screening and cambial wounding (in drier forests) to assess ring formation.
- Rare in the study area:  $\sim 0.04$  trees.ha<sup>-1</sup> (> 80 dbh)

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent



***Lophira alata* Banks ex P.Gaertn. [AZOBE]**

--

**Ring boundary:**

- No ring boundaries

**Problems:**

- Shows broad wavy bands of parenchyma in a homogeneous structure only occasionally showing some patterns of density variation

**Sampling with increment cores:**

- No, wood is too tough

**Potential and applications**

- Tree ring analysis is not possible with standard techniques.
- Relatively common in the study area:  $\sim 0.65$  trees.ha<sup>-1</sup> (> 80 dbh)

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent





***Nauclea diderrichii* Merr. [BILINGA]**

--

**Ring boundary:**

- No ring boundaries

**Problems:**

- Wood diffuse-porous without apparent growth-ring patterns

**Sampling with increment cores:**

- Yes, but wood is tough

**Potential and applications**

- Tree ring analysis is not possible with standard techniques.
- Rare in the study area:  $\sim 0.01$  trees.ha<sup>-1</sup> (> 80 dbh)

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent



***Pterocarpus soyauxii* Taub. [PADOUK ROUGE]**

+/-

**Ring boundary:**

- (C) Alternating fibre and parenchyma bands (*sometimes*)
- (B) Marginal parenchyma band

**Problems:**

- Rings are not very clear and working with cores is not possible
- Wedging rings occur in juvenile wood and between buttresses

**Sampling with increment cores:**

- Yes, wood is tough but corable

**Potential and applications**

- May be used for estimation of growth rates
- Annual rings and climate-growth relations found for congeners growing in drier forests (*P. angolensis*; Fichtler et al. 2004).
- Deciduous character might not be annual, therefore, ring formation should be studied together with phenological observations.
- Commercially important species, interesting to apply screening and cambial wounding to assess ring formation
- Rare in the study area:  $\sim 0.14$  trees.ha<sup>-1</sup> (> 70 dbh)

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent



***Pycnanthus angolensis* (Welw.) Warb. [ILOMBA]**

+/-

**Ring boundary:**

- No ring boundaries
- (A) Density variations (*sometimes*)

**Problems:**

- Structures clear on certain parts of the disc (*closed triangles*)
- Sometimes vague structures on portions of disc (*open triangles*)
- Large parts (>6cm) radii without ring structures (*top of the image*) and (clear) structures disappear

**Sampling with increment cores:**

- Yes, but wood is rather brittle and breaks easily

**Potential and applications**

- On freshly sawn discs ring structures can be seen (*below*)
- Deciduous species, perhaps annual rings (in drier forests)
- Rare in the study area:  $\sim 0.3$  trees.ha<sup>-1</sup> (> 60 dbh)

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent



***Rhodognaphalon brevicuspe* (Sprague) Roberty [KONDROTI]**

+/-

**Ring boundary:**

- No ring boundaries
- (A) Density variations (*sometimes*)

**Problems:**

- Ring boundaries can be vague on certain portions of the disc

**Sampling with increment cores:**

- Yes, but wood is rather brittle and breaks easily

**Potential and applications**

- Rings very similar to other Bombacaceae (e.g. *Ceiba pentandra*), similarly, rings are probably annual but working with discs is required to be able to distinguish rings and problems (Worbes et al. 2003).

- Rare in the study area:  $\sim 0.07$  trees.ha<sup>-1</sup> (> 60 dbh)

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent

No image available



***Staudtia kamerunensis* Warb. [NIOVÉ]**

+/-

**Ring boundary:**

- (B) Marginal parenchyma band

**Problems:**

- Parenchyma bands very thin (*closed triangles*)
- Ring boundaries disappear on certain parts of discs (*open triangles*)
- Slow grower (1 to 4 mm yr<sup>-1</sup>, PROTA 2012)
- Large sections of radii (>4 cm) without ring structures

**Sampling with increment cores:**

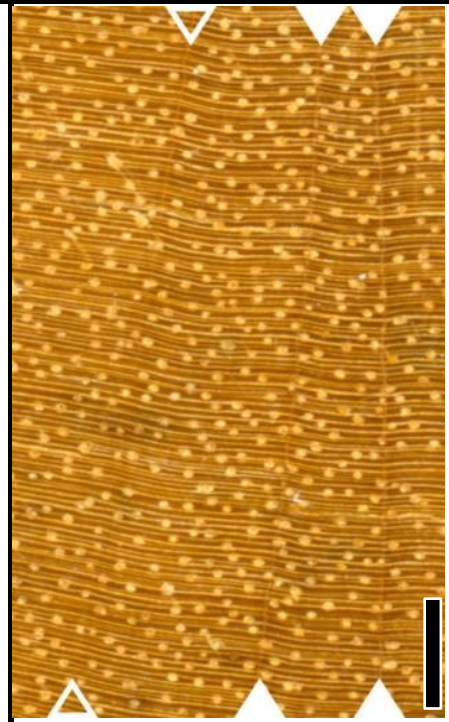
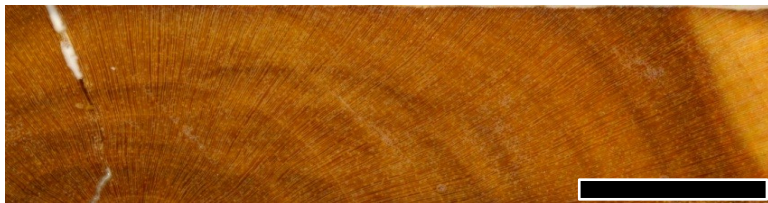
- Yes, wood tough but corable

**Potential and applications**

- Rings not formed annually, maybe only in dry years
- Suggested to form annual rings in drier forest (Worbes et al. 2003) but annuality was not tested
- Important commercial species
- Abundant in study area: ~12 trees.ha<sup>-1</sup> (>5 cm dbh)

**Boundary description (IAWA hardwood codes):**

- (2) growth ring boundaries indistinct or absent



***Terminalia ivorensis* A.Chev. [FRAMIRÉ]**

+

**Ring boundary:**

- (A) Density variations (*sometimes*)
- (D) variations in vessels distribution and/or size

**Problems:**

- Wedging rings, especially on large trees (between buttresses)
- Ring boundaries vague on outer parts of disc

**Sampling with increment cores:**

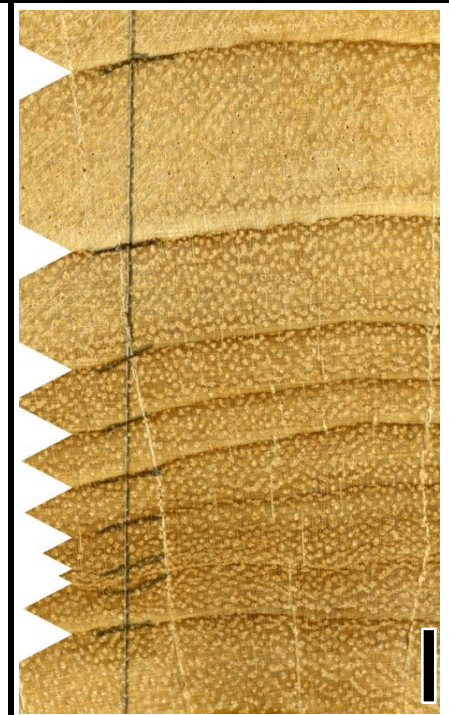
- Yes, wood toughness intermediate

**Potential and applications**

- Good potential to obtain growth data.
- Climate-growth relations found for congeners growing in drier forests (*T. superba*; de Ridder et al. 2013). Might thus have potential for climatic reconstruction (in drier forests).
- Rare in the study area: ~0.2 trees.ha<sup>-1</sup> (> 60 dbh) but common around villages and in secondary forests

**Boundary description (IAWA hardwood codes):**

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



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