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Wood Density Variations of Tropical Trees Differing in Shade-Tolerance and Leaf Phenology of the Congo Basin

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Abstract- Wood density (WD) is not only a key element in tropical forest ecology to estimate tree biomass but also an indicator of timber quality, and it integrates many aspects of tree mechanical properties and functioning. Notably, contrasting patterns of radial variation of WD have been demonstrated and are related to regeneration guilds (light-demanding vs. shade-bearing) but haven't been demonstrated to be related to leaf phenology (deciduous vs. evergreen). With the destructive method and the "archimed" principle, we investigated the WD radial variation of nine timber tree species harvested in the eastern region of Cameroon. The result showed that WD differed significantly among these nine species ($P > 0.05$). Their average WD was 0.70 ± 0.05 ; 0.79 ± 0.14 ; 0.69 ± 0.05 ; 0.55 ± 0.03 ; 0.81 ± 0.03 ; 0.63 ± 0.08 ; 0.65 ± 0.08 ; 0.64 ± 0.05 ; 0.44 ± 0.07 g.cm³ for *Azela bipendensis*, *Cylicodiscus gabunensis*, *Entandrophragma cylindricum*, *Entandrophragma utile*, *Erythrophloeum suaveolens*, *Mansonia altissima*, *Milicia excelsa*, *Pterocarpus soyauxii* and *Triplochiton scleroxylon*. Variation in WD from bark-to-pith enabled three distinct patterns: type 1 in which WD increases (*A. bipendensis*); type 2 in which WD decreases (*C. gabunensis*, *E. cylindricum*, *E. utile*, *E. suaveolens*, *M. excelsa* and *P. soyauxii*); and type 3 in which WD values are substantially equal (*M. altissima* and *T. scleroxylon*). All nine timber tree species were deciduous. At the level of light requirement succession, the pioneer species were *E. suaveolens*, *M. excelsa*, *T. scleroxylon* and the other one was non-pioneer light demander species: *C. gabunensis*, *A. bipendensis*, *E. cylindricum*, *P. soyauxii*, *M. altissima* and *E. utile*. In addition, we found that WD in this study compared to the DRYAD global repository may strongly differ depending on

the species (up to 133% for *T. scleroxylon* and less than 96% for *A. bipendensis*). Therefore, when estimating forest biomass in specific sites, we recommend that future studies on WD include the analysis of the effect of vertical variation with long-term phenological data and anatomical analysis in the same species and use a large sampling size, including individuals of both the same and different species.

Keywords: wood density, radial variation, tropical forest, shade tolerance, leaf phenology, congo basin.

1. INTRODUCTION

Reduction of tropical forest areas has a great impact on the amount of carbon dioxide stored in the atmosphere (Houghton 1985) because the forest is a great essential source of the world producing oxygen (O₂) and storing carbon dioxide (CO₂). Importantly, CO₂ is an influential gas leading to climate change. Estimating the aboveground biomass (AGB) content is necessary for considering the total carbon content stored in the forest ecosystem (Ketterings et al. 2001; Chave et al., 2004). This AGB is generally estimated by using allometric equations, the variables involved in such equations are the diameter at breast height, total height, and wood density (WD) or more conventionally the wood-specific gravity (WSG). Chave et al. (2005; 2014) showed that this calculation is used in the majority of studies involving allometric models. WD is one of the most important variables in forest and wood science as it is crucial for understanding tree structures and functions, and is relevant for timber properties and the energy content of the material. WD is calculated by dividing the oven-dry mass of a sample by the mass of a volume of water equal to the volume of the sample at a particular moisture content (ASTM 2011). According to Panshin & de Zeeuw 1980; Chave et al. 2009, it is a major predictor of wood's mechanical properties and is also a trait distinguished by chemical and anatomical traits (Lachenbruch & McCulloh 2014). A key source of information on tree adaptation is the variety in wood anatomy (Beeckman 2016; Tarelkin et al. 2016).

The anatomical structure of wood, which includes the features of the vessels and fibres, can be used to describe the density fluctuations inside a tree (Roque & Filho 2007). In hardwood species, the ratio or

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quantity of various cell types and their spatial patterns determine this WD variation. These cell types include axial parenchyma, vessels, fibres, and rays (Panshin & de Zeeuw 1970). De Mil et al. (2018) shown that whereas vessels and parenchyma are adversely connected to the WD of the tree growth rate during ontogeny, fibres with thicker walls and flattened lumina increase WD. DRYAD is a global repository from which the average WD values at the species or genus level have been derived (Zanne et al. 2009). Using these repositories (Zanne et al. 2009; Chave et al. 2009) could result in an overestimation of WD for the species community of roughly 16 %. (Ramananantoandro et al. 2015). Also according to these archives, tropical WD (for light- to heavy-wood) range from 0.1 to 1.5 g.cm⁻³ (Zanne et al. 2009; Chave et al. 2009). In the tropical regions of the planet, this variety has been well preserved (Détienne & Chanson, 1996; Turner, 2001). Nonetheless, the majority of species have values that are quite near to the mean (Détienne & Chanson 1996). It was demonstrated by Chave et al. (2006) and Maniatis et al. (2011) that species differences in WD were bigger than those between them. With differences between shade-tolerant and light-demanding species (Chave et al. 2009; King et al. 2005). Light-demanding species are thought to require investment in denser wood to survive in a mature forest when there is greater competition for light since they are so sensitive to light exposure (Nock et al. 2009; Wiemann & Williamson 1988). In general, the fast growth of light-demanding species in the early stages is often associated with the production of softwood with low density (Woodcock & Shier 2002; Nock et al. 2009), in contrast with shade-tolerant species produced denser wood and grow very slowly (Woodcock & Shier 2002). Thought to offer a competitive edge, this relationship between density and growth can actually shorten a tree's lifespan (Wiemann & Williamson 1988). Greater resistance to physical harm and dangerous infections is induced by high values of WD (Putz et al. 1983; King et al. 2006; Chao et al. 2008). Together with a tree's vertical profile (Henry et al. 2010; Wassenberg et al. 2014) and radial profile, WD can also reveal changes inside the tree (Henry et al. 2010; Plourde et al. 2015; Osazuwa-Peters et al. 2014; Lehnebach et al. 2018). Within specific trees, WD can also vary radially from pith to bark (Wiemann & Williamson 1988; 1989; Henry et al. 2010; Hietz et al. 2013). These density variations across a pith-to-bark profile are thus a good indicator of the variations of the fibres' anatomy and the abruptness of the change in wood anatomical structure.

The three goals of this study were to: (1) compare wood density (WD) between and within nine harvested tropical tree species; (2) find out how leaf phenology and shade tolerance may affect potential changes in WD; and (3) assess the discrepancy between estimated WD and database values.

II. MATERIALS AND METHODS

a) Study Site

The study was conducted around the city of Gari-Gombo in the eastern region of Cameroon. Stem discs were collected inside the 2013 cutting block in the Forest Management Unit (FMU) 10 025 of the "Société Forestière Industrielle de la Lokoundjié (SFIL)" of the Decolvenaere Group Cameroon (DC). This FMU has been partially or fully exploited previously (1990–1997); its approximate boundaries are 3° 30' N and 3° 55' N latitudes and 14° 45' E and 15° 00' E longitudes. Its area is 49 595 ha, and the area of the 2013 cutting block (3-3) is 1586 ha (SFIL 2009). Soils are mainly ferralitic type, reddish-brown to yellow (Jones et al. 2013), and rest on a geological base consisting of metamorphic rocks with a high content of clay oxides iron and aluminum, formed from materials such as mica schists and chlorous schists (Martin & Segalen 1966). The climate of the site is equatorial rainforest, fully humid (Köppen 1936), with a unimodal rainfall distribution and a dry season from December to February: monthly rainfall less than 60mm (Worbes 1995). Rainfall amounts vary between nearby weather stations. The Yokadouma (85 km to the southeast of the study area) has four seasons, including a long dry season (mid-November to mid-March). The average annual rainfall is 1471.78 mm, and the annual average temperature is about 24 °C (21.94–24.56 °C). The annual average air humidity is 80 percent, with ranges of elevation between 600 and 680 meters above sea level. (Fig. 1.)

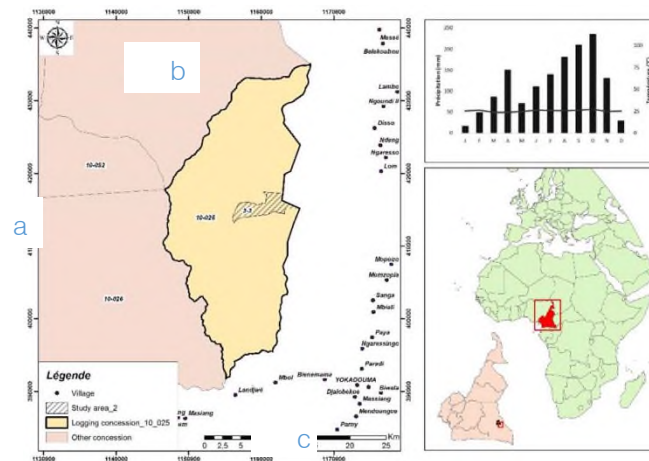


Fig. 1: a. Map of Study Site: 2013 cutting block (hatched) of Forest Management Unit 10 025 (wheat), the neighboring Forest Management Unit (pink), and the major village are also shown, b. the climate diagram for the meteorological station in Yokadouma town (1961-2013), c. the inlay shows the location of the study site in Cameroon

The vegetation of the region is the Guineo-Congolese dense forest (White 1983). For Letouzey (1968), FMU 10 025 is in the transition zone between dense, moist evergreen forest and semi-evergreen forest. This FMU was certified by the Forest Stewardship Council (FSC) until 2014, and now it only has a traceability and legality certificate. This study concerned nine legally harvested tree species. In 2013 cutting block of Forest Management Unit 10 025 of SFIL-GDC logging company (SFIL 2009). The selection of these species was based on their commercial potential, the availability of the resource, and the visibility of growth rings among the eighteen species harvested

b) Study Species

The following species were examined: *Azelia bipendensis* Harms, *Cylicodiscus gabunensis* Harms, *Erythrophleum suaveolens* A. Chev. and *Pterocarpus soyauxii* Taub. (Fabaceae); *Entandrophragma cylindricum* Sprague and *Entandrophragma utile* (Dawe & Sprague) Sprague (Meliaceae); *Milicia excelsa* (Welw.) C. C. Berg (Moraceae); *Mansonia altissima* (A. Chev.) A. Chev. and *Triplochiton scleroxylon* K.Schum (Malvaceae) (Amougou et al. 2022). The specific wood density was extracted from the Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009). Leaf phenology at the adult stage, regeneration guilds (Hawthorne 1995; Bénédet et al. 2019), and dispersal mode (Hawthorne 1995) at the species level.

c) Tree Logging and Sample Collection

Tree DBH was measured before trees were felled by a diameter tape. One stem disc was collected at the base of the trunk of each tree (around 0.5 m from the ground or more if buttresses were observed). All stem discs were collected with a chainsaw and immediately they were divided into two halves and each half was divided into three fragments by ensuring that all

parts of the stem discs were taken (pith-to-bark). Randomly, a total of 20 fragments of stem discs were collected: 3 fragments of stem discs for *M. excelsa*, *P. soyauxii*, and *T. scleroxylon*; 2 for *A. bipendensis*, *C. gabunensis*, *E. cylindricum*, *E. ivorensis*, and 1 for *E. utile*. The samples were transported by plane to the Royal Museum of Central Africa in Tervuren, Belgium, where they received unique Tervuren wood (Tw) identification numbers and were stored in the Xylarium. (Table 1).

Table 1: List of the 9 Studied Species with Their Botanical Family, Commercial Name, and Local Name, Tervuren Wood Identification Number (Tw); Diameter at Breast Height (DBH) of the Sampled Tree; Wood Density at the Species Level (Zanne et al. 2009), Dispersal Mode (Meunier et al. 2015), for the Regeneration Guild, P: Pioneer, NPLD: Non-Pioneer Light Demander, and SB: Shade Bearer, and for the Leaf Phenology, Dec.: Deciduous, Brevi.: Brevidciduous, and ev.: Evergreen (Bénédet et al. 2019)

Species	Family	Commercial/Local name	Tw number	DBH (cm)	Specific wood density (g.cm ³)	Dispersal mode	Regeneration guild	Phenology
<i>Azelia bipendensis</i>	Fabaceae	Doussié/ M'bang	Tw65080, Tw69081	85	0.73 ± 0.05	Animal	NPLD	Dec.
<i>Cylicodiscus gabunensis</i>	Fabaceae	Okan/Adoum	Tw65078, Tw69079	65	0.79 ± 0.07	Wind	NPLD	Brevi.
<i>Entandrophragma cylindricum</i>	Meliaceae	Sapele/Assié	Tw65076, Tw69077	115	0.57 ± 0.04	Wind	NPLD	Dec.
<i>Entandrophragma utile</i>	Meliaceae	Sipo/Asseng-Assié	Tw65086	84	0.54 ± 0.04	Wind	NPLD	Dec.
<i>Erythroleum suaveolens</i>	Fabaceae	Tali/Elon	Tw65082, Tw65083	52	0.77 ± 0.06	Unassisted	P	Dec.
<i>Mansonia altissima</i>	Malvaceae	Bété/Koul	Tw65084, Tw69085	64	0.56 ± 0.03	Wind	NPLD	Dec.
<i>Milicia excelsa</i>	Moraceae	Iroko/Abang	Tw65067, Tw67068, Tw67069	102	0.58 ± 0.06	Animal	P	Dec.
<i>Pterocarpus soyauxii</i>	Fabaceae	Padouk/Mbel	Tw65073, Tw65074, Tw65075	62	0.66 ± 0.07	Wind	NPLD	Brevi.
<i>Triplochiton scleroxylon</i>	Malvaceae	Ayous/Ayus	Tw65070, Tw69071, Tw69072	92.1	0.33 ± 0.03	Wind	P	Dec.

d) Assignment of radial position

On the longest radius section of the fixed fragment of the stem disc (i.e., bark to pith), a piece of 1 cm wide wood was extracted from each stem disc using different hand saws (basic, flat, Japanese, splitter, hack, coping, and square) and two clamps (fixed and mobile) (Fig. 2.a, b, c). This piece of 1 cm was immobilized in a fixed clamp and cut using the same saws into ten (10)

small pieces of roughly the same size, reporting the Tw number of the stem disc followed by the numbers 1 (at the bark piece) to 10 (at the pith piece) from the bark-to-the-pith for the ten small pieces (Fig. 2.d). Finally, using chisels and a wooden mallet, these small pieces were finely carved on the sides to have uniform pieces (Fig. 2.d.).

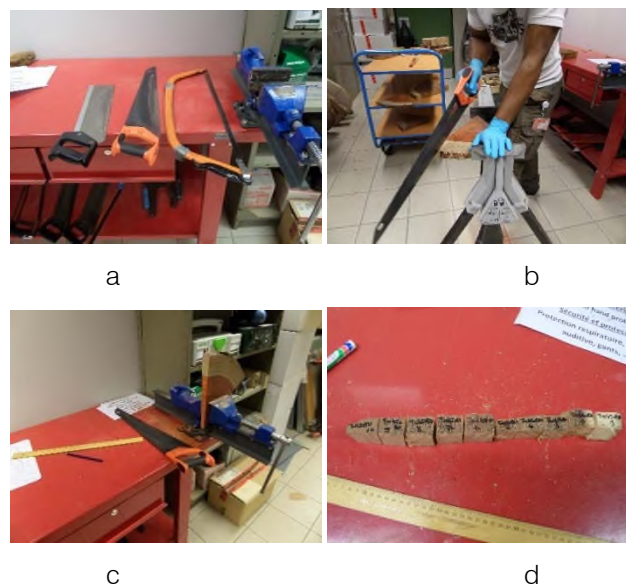


Fig. 2: Preparation of Wood Fragments for Density Testing, a. Various Saws and a Fixed Clamp, b. Removal using a Saw of a 1 cm Fragment Lamella on the Longest Section Held Fixed on a Mobile Clamp, C. Removal Using a Saw of a 1 cm Fragment Lamella on the Longest Section of a Fragment of Stem Disc Held Fixed on an Immobile Clamp, and d. 1 cm Fragment Slice Taken, Subdivided, and Numbered from 1 to 10 in Direction (Bark-to-Pith)

e) Density Determination

Density tests were performed on these smaller fragments (pieces). The methodology used for these tests was water displacement, and it was based on the Archimedes principle by displacement water: the volume of a sample is estimated by the mass of the volume that is moved while the sample is immersed in deionized water, according to (Olesen 1971; Williamson & Wiemann 2010). This method is also called the hydrostatic method.

To regain its green condition, the small piece of wood (that had naturally dried) was immersed or soaked in a container filled with demineralized water for a few minutes to the point of saturation of the fibers. This container was under a digital balance, SCLATECSPB53

(max. 610; 0.01 g precision), and was calibrated and tared before and after measurement in the digital balance (Fig.3. a, b.). And those samples were immediately weighed. Then the dry weight or mass was obtained by introducing the samples to a Memmert UN75 oven for 48 h (2 h at 60° C, 4 h at 80°C, and 42 h at 103°C) (Fig.3.b,c.). To achieve constant mass, the oven temperature is gradually increased. To avoid the risks of burst or cracked samples, the dry weights were immediately taken out of the oven. At ambient moisture within the wood laboratory in the RMCA-Tervuren, it was 8 percent. To avoid a constant dry weight, samples were measured on a digital balance KERN₅₇₂ (up to 2,100 g; 0.1 g) three times successively (Fig. 3.a.).

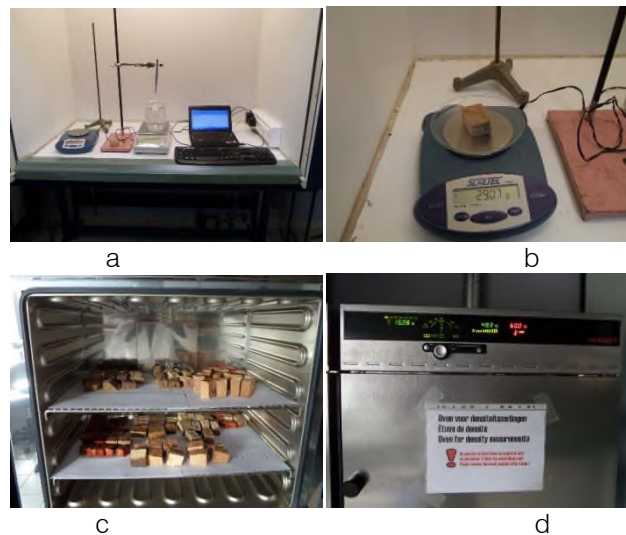


Fig. 3: Process of Density Tests a. Experimental Apparatus; b. Weighing Of Sub-Fragments To Obtain Fresh Mass; c. Removal of Fragments Dried in an Oven for Weighing of Dry Mass; and d. Drying of Wood Fragments in an Oven for 48 Hours

Using the formula, wood-specific gravity was computed as the ratio of each wood's dry mass to its corrected dry volume (Williamson & Wiemann 2010a).

$$\text{WSG (8\%)} = (\text{Md}) / (\text{Vcd})$$

$$[\text{W}_{\text{SG}}]_{(8\%)} = (\text{M}_d) / (\text{V}_{\text{cd}})$$

Where Wsd is the wood-specific gravity in g/cm³, Md is the anhydrous weight in g, and Vcd is the corrected dry volume in cm³.

III. RESULTS

a) Wood Density Intra and Inter-Radial Variation

ANOVA test results ($P > 0.05$) showed that there was radial variation in wood density (WD) for each tree species and between tree species. These inter- and intra-specific radial variations in WD were as follows: *A. bipendensis* range, 0.65-0.75 g.cm³; and the average were 0.70 ± 0.05 g.cm³; *C. gabunensis* range, 0.65-0.93 g.cm³; and the average were 0.79 ± 0.14 g.cm³; *E. cylindricum* range, 0.64-0.74 and the average were 0.

69 ± 0.05 g.cm³; *E. utile* range, 0.51-0.58 and the average were 0.55 ± 0.03 g.cm³; *E. suaveolens* range, 0.78-0.84 g.cm³ and the average were 0.81 ± 0.03 g.cm³; *M. altissima* range, 0.61-0.65 g.cm³ and the average were 0.63 ± 0.08 g.cm³; *M. excelsa* range, 0.45-0.73 g.cm³ and the average were 0.65 ± 0.08 g.cm³; *P. soyauxii* range, 0.59-0.69 g.cm³ and the average were 0.64 ± 0.05 g.cm³ and finally for *T. scleroxylon* range, 0.37 - 0.63 g.cm³ and the average were 0.44 ± 0.07 g.cm³ (Fig.2).

The observation of variations in WD from bark-to-pith enabled three qualitative types of radial patterns to be distinguished (Fig. 2.). Type 1 was represented by a tree species in which WD increased from bark to pith: *A. bipendensis*. Type 2 corresponded to tree species in which WD decreased from the bark to the pith: *C. gabunensis*; *E. cylindricum*; *E. utile*; *E. suaveolens*; *M. excelsa*; and *P. soyauxii*. And type 3 was represented by tree species in which WD values were substantially equal from bark-to-pith: *M. altissima* and *T. scleroxylon* (Figure 3, Table 2).

At the family species level, there was a significant difference between the WD of Fabaceae: *E. suaveolens*, with a WD of $0.81 \pm 0.03 \text{ g.cm}^3$, was less similar to the WD of *C. gabunensis* ($0.79 \pm 0.14 \text{ g.cm}^3$), and those two timber tree species were not similar with WD of *A. bipendensis* ($0.70 \pm 0.05 \text{ g.cm}^3$) and with WD of *P. soyauxii* ($0.64 \pm 0.05 \text{ g.cm}^3$), who is less dense wood species in this family. There was also a significant difference in the WD of Meliaceae: *E. cylindricum* with a WD of ($0.69 \pm 0.05 \text{ g.cm}^3$) which was not similar to the WD of *E. utile* ($0.55 \pm 0.03 \text{ g.cm}^3$). The WD of Moraceae was only for *M. excelsa* ($0.65 \pm 0.08 \text{ g.cm}^3$). And finally, there was also a significant difference between WD Malvaceae (*M. altissima* with a WSG of $0.63 \pm 0.02 \text{ g.cm}^3$) and WD *T. scleroxylon* ($0.44 \pm 0.07 \text{ g.cm}^3$) (Figure 3).

b) Wood Density Shade Tolerance and Phenology

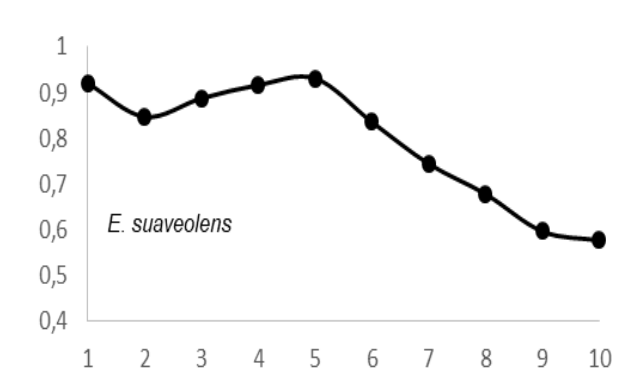
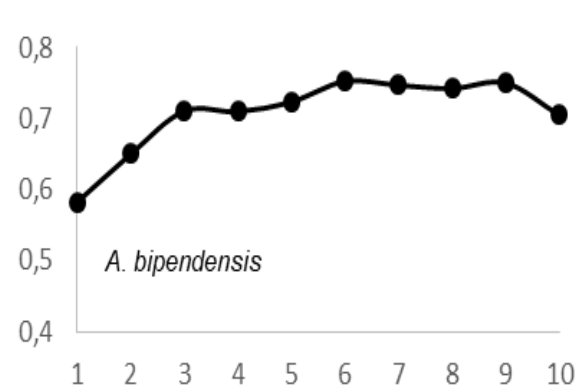
These timber tree species were classified into three leaf phenological types: brevideciduous, deciduous, and evergreen for drought tolerance (Bénédet et al. 2019). All these nine timber tree species were deciduous and were classified as heavy for the lower WSG: *E. suaveolens* ($0.81 \pm 0.03 \text{ g.cm}^3$); *C. gabunensis* ($0.79 \pm 0.14 \text{ g.cm}^3$); *A. bipendensis* ($0.70 \pm 0.05 \text{ g.cm}^3$); *E. cylindricum* (0.69 ± 0.05); *P. soyauxii* ($0.64 \pm 0.05 \text{ g.cm}^3$); *M. altissima* (0.63 ± 0.02); *M. excelsa* ($0.58 \pm 0.06 \text{ g.cm}^3$); *E. utile* ($0.55 \pm 0.03 \text{ g.cm}^3$); and *T. scleroxylon* ($0.44 \pm 0.07 \text{ g.cm}^3$). Particularly *A. bipendensis*, *C. gabunensis*, *E. cylindricum*, *E. utile*, and *E. suaveolens* were all deciduous; meanwhile, *C. gabunensis* and *P. soyauxii* were brevideciduous (Table 1; Table 2).

At the level of light requirement succession, these timber tree species were classified into three regeneration guilds: pioneer, non-pioneer light

demand, and shade bearer (Hawthorne 1995; Bénédet et al. 2019). The pioneer species were: *E. suaveolens*, with its highest wood density ($0.81 \pm 0.03 \text{ g.cm}^3$); *M. excelsa*, with its medium wood density ($0.65 \pm 0.08 \text{ g/cm}^3$); and *T. scleroxylon*, with its weakest wood density ($0.44 \pm 0.07 \text{ g.cm}^3$). And non-pioneer light demander species were: *C. gabunensis*, with its very highest wood density ($0.79 \pm 0.14 \text{ g.cm}^3$); *A. bipendensis*, with its highest wood density ($0.70 \pm 0.05 \text{ g.cm}^3$); *E. cylindricum*, with its highest wood density ($0.69 \pm 0.05 \text{ g.cm}^3$); *P. soyauxii*, with its medium wood density ($0.64 \pm 0.05 \text{ g.cm}^3$); *M. altissima*, with its medium wood density ($0.63 \pm 0.02 \text{ g.cm}^3$) and *E. utile*, with its lowest wood density ($0.55 \pm 0.03 \text{ g.cm}^3$) (Table 1; Table 2)

c) Comparison between Estimated Wood Density and Database Values

The difference was not significant between the calculated and measured WD and those of the Global Wood Density Database (Zane et al. 2009), particularly for tree species who's calculated WD were lower than the WD of the GWDD base: *A. bipendensis*, $0.70 \pm 0.05 / 0.73 \pm 0.05 \text{ g.cm}^3$; *P. soyauxii*, $0.64 \pm 0.05 / 0.66 \pm 0.07 \text{ g.cm}^3$. The calculated WD were greater than the WD value of the GWDD: *E. utile*, $0.55 \pm 0.03 / 0.54 \pm 0.04 \text{ g.cm}^3$. And the calculated WSG were equal to the WD of the GWDD: *C. gabunensis*, $0.79 \pm 0.14 / 0.79 \pm 0.07 \text{ g.cm}^3$. In contrast, the difference was very significant for the following species: *E. cylindricum* $0.69 \pm 0.05 / 0.57 \pm 0.04 \text{ g.cm}^3$; *E. suaveolens* $0.81 \pm 0.03 / 0.77 \pm 0.06 \text{ g.cm}^3$; *M. altissima* $0.63 \pm 0.02 / 0.56 \pm 0.03 \text{ g.cm}^3$; *M. excelsa* $0.65 \pm 0.08 / 0.58 \pm 0.06 \text{ g.cm}^3$ and *T. scleroxylon* $0.44 \pm 0.07 / 0.33 \pm 0.03 \text{ g.cm}^3$ (Table 2).



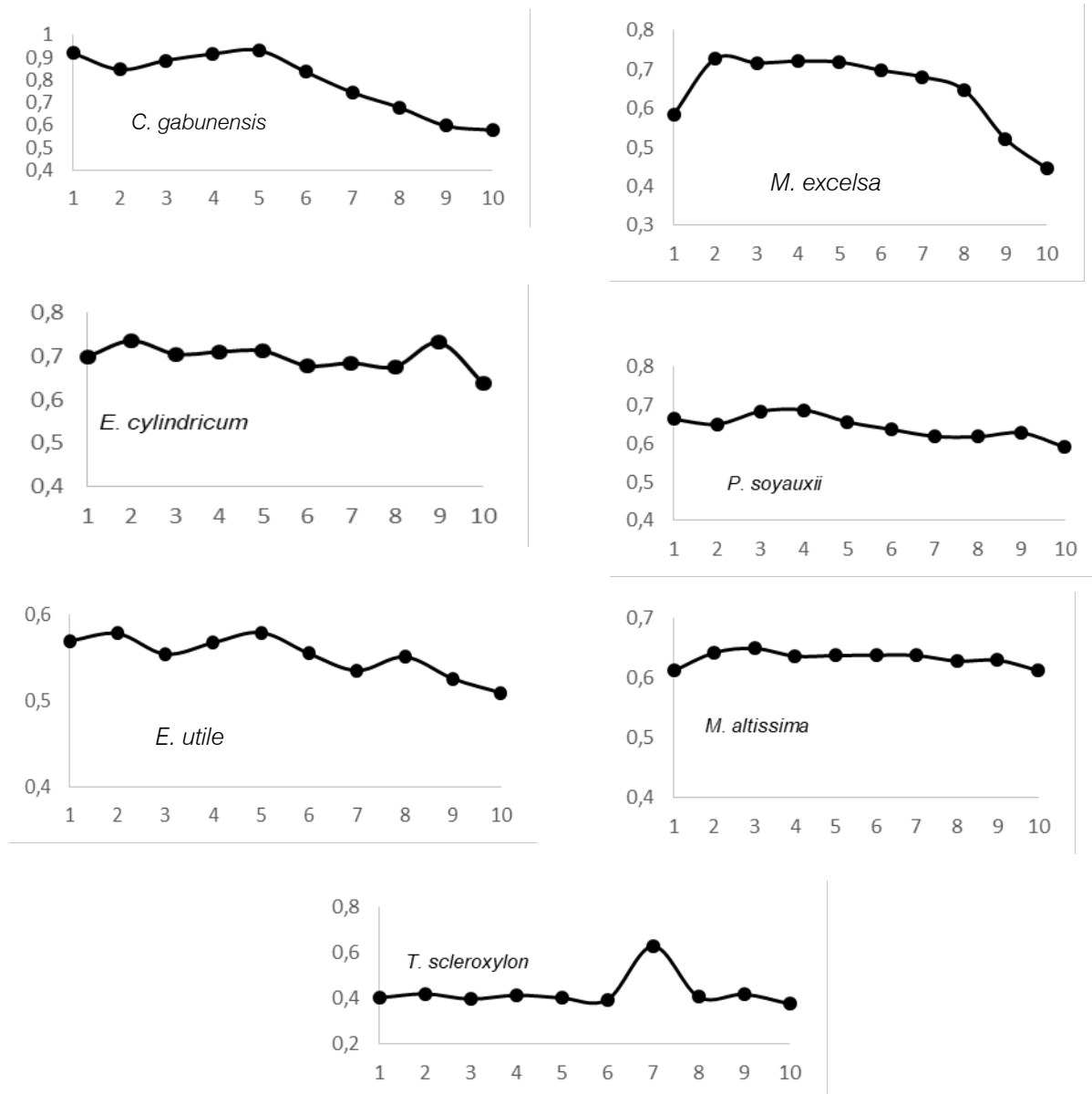


Fig. 4: Variation in Wood Density Measured (G.Cm⁻³) at 8 Percent Moisture Content Along the Distance from Bark (1) to Pith (10) for the 09 Species Investigated in SFIL, Cameroon

d) Comparison between Estimated Wood Density and Database Values

The difference was not significant between the calculated/measured WD and those of the Global Wood Density Database (Zane et al. 2009), particularly for tree species whose calculated WD were lower than the WD of the GWDD base: *A. bipendensis* 0.70 (\pm 0.05) / 0.73 \pm 0.05 g.cm³; *P. soyauxii* 0.64 (\pm 0.05) / 0.66 \pm 0.07 g.cm³; the calculated WD were greater than the WD of the GWDD and *E. utile* 0.55 (\pm 0.03) / 0.54 \pm 0.04 g.cm³ and the calculated WSG were equal to the WD of the GWDD *C. gabunensis* 0.79 (\pm 0.14) / 0.79 \pm 0.07

g.cm³. And in contrast, the difference was very significant for the following species: *E. cylindricum* 0.69 (\pm 0.05) / 0.57 \pm 0.04; *E. suaveolens* 0.81 (\pm 0.03) / 0.77 \pm 0.06 g.cm³; *M. altissima* 0.63 (\pm 0.02) / 0.56 \pm 0.03 g.cm³; *M. excelsa* 0.65 (\pm 0.08) / 0.58 \pm 0.06 g.cm³ and *T. scleroxylon* 0.44 (\pm 0.07) / 0.33 \pm 0.03 g.cm³ (Table 2).

Table 2: WD of the Measured Samples Per Species Compared to the WD Values in the GWDD. WD Values from the GWDD Were Taken for Species Occurring in Africa, as the Measured Species all Originate From Central Africa. an Asterisk (*) Next to a Species Name Indicates a Significant Difference ($P < 0.05$) Between the Mean of the Measured Values and the Mean of That Species in the GWDD

Species	No. Samples/Stem discs measured	Average WD \pm STD (g.cm^{-3}) at humidity 8 %	Range WD (g.cm^{-3}) [Min-Max]	No. values are given in GWDD	WD value GWDD \pm STD (g.cm^{-3})	WD value GWDD range (g.cm^{-3})
<i>Atzelia bipendensis</i> (Fabaceae)	01/02	0.70 (± 0.05)	[0.65 – 0.75]	11	0.73 \pm 0.05	0.66 – 0.82
<i>Cylicodiscus gabunensis</i> (Fabaceae)	01/02	0.79 (± 0.14)	[0.65 – 0.93]	18	0.79 \pm 0.07	0.62 – 0.97
<i>Entandrophragma cylindricum</i> (Meliaceae)*	01/02	0.69 (± 0.05)	[0.64 – 0.74]	16	0.57 \pm 0.04	0.50 – 0.63
<i>Entandrophragma utile</i> (Meliaceae)	01/01	0.55 (± 0.03)	[0.51 – 0.58]	18	0.54 \pm 0.04	0.44 – 0.58
<i>Erythrophloeum suaveolens</i> (Fabaceae)*	01/02	0.81 (± 0.03)	[0.78 – 0.84]	20	0.77 \pm 0.06	0.69 – 0.87
<i>Mansonia altissima</i> (Malvaceae)*	01/03	0.63 (± 0.02)	[0.61 – 0.65]	23	0.56 \pm 0.03	0.47 – 0.63
<i>Milicia excelsa</i> (Moraceae)*	01/03	0.65 (± 0.08)	[0.45 – 0.73]	24	0.58 \pm 0.06	0.44 – 0.67
<i>Pterocarpus soyauxii</i> (Fabaceae)	01/03	0.64 (± 0.05)	[0.59 – 0.69]	14	0.66 \pm 0.07	0.57 – 0.81
<i>Triplochiton scleroxylon</i> (Malvaceae)*	01/03	0.44 (± 0.07)	[0.37 – 0.63]	24	0.33 \pm 0.03	0.28 – 0.41

IV. DISCUSSION

a) Wood Density Intra and Inter-Radial Variation

The first aim of our study was to compare the variation in WD among and within nine harvested tropical tree species, including radial variation within individuals. At the light of this analysis conducted on stem discs. This results show that species's explained most wood density radial variance whereas individuals explained only a minor part from pith-to-bark. These results were consistent with previous observations in different part of world (Parolin 2002 Woodcock & Sheir 2002; Nock et al. 2009; Onada et al. 2010; Hietz et al. 2013; Osazuwa-Peters et al. 2014; Bastin et al. 2015; Plourde et al. 2015; Lehnebach et al. 2019). And globally among tropical tree species (Zanne et al. 2009). Importantly, the WD values between 0.44 and 0.81 g.cm^{-3} from this present study were within the range (0.11 to 1.39 g.cm^{-3}) reported for 2,456 tropical forest tree species (Chave et al. 2006). The differences in WD between our study and other studies may be due to aspects of the growing environment (biotic and abiotic) factors.

Particularly, the observation of variations in WD from bark to pith enabled three qualitative types of radial patterns to be distinguished. Type 1 was represented by a tree species in which WD increased from bark to pith: *A. bipendensis*. Type 2 corresponded to tree species in

which WD decreased from the bark to the pith: *C. gabunensis*; *E. cylindricum*; *E. utile*; *E. suaveolens*; *M. excelsa*; and *P. soyauxii*. And type 3 was represented by tree species in which WD values were substantially equal from bark-to-pith: *M. altissima* and *T. scleroxylon*. These results confirms the effect of heartwood on WD radial variations already suspected (Parolin 2002; Hietz et al. 2013).

These findings contrast with the bulk of studies on WD radial variations (Parolin 2002; Woodcock & Sheir 2002; Nock et al. 2009; Hietz et al. 2013; Osazuwa-Peters et al. 2014; Plourde et al. 2015), which reported both negative and positive gradients. We presume that this difference is mainly due to the failure to take into account the presence of heartwood that was previously hypothesized by several authors (Parolin 2002; Hietz et al. 2013).

b) Wood Density Shade Tolerance and Phenology

Wood density profiles with a decreasing trend from bark to pith and a low wood density were not systematic for pioneer and non-pioneer light-demanding species, but our results demonstrated that the pioneer species *E. suaveolens* showed the very highest wood density value, the second highest wood density value was for *C. gabunensis*, and the lowest wood density value was found for the pioneer species *T. scleroxylon*. For the nine tree species studied, this assertion was true

For the nine tree species studied, this assertion was true for Type 2: *C. gabunensis*; *E. cylindricum*; *E. utile*; *E. suaveolens*; *M. excelsa* and *P. soyauxii*. The opposite shade-tolerant species systematically showed high wood density values. In our study, shade-tolerant species were not available. But Chao et al. (2008) and King et al. (2006) formulated the hypothesis that slow-growing species that invest in dense wood were shade-tolerant, in particular during the early stages of their lives. Other studies also reported that shade tolerant species tend to have a much higher WD than do pioneer species (King et al. 2006; Ramanantoandro et al. 2016). One explanation were that pioneer species produce a low WD to grow taller than their neighbors, thereby acquiring more resources (i.e., light) quickly (Woodcock & Shier 2002). The observations of these six listed tree species were unlikely to persist in old-growth forests, supporting the assumption that strictly light-demanding species present decreasing trends in wood density from bark to pith (Nock et al. 2009; Wiemann & Williamson 1988). Type 1: *A. bipendensis* presents an increasing trend in wood density from bark-to-pith. This observation was confirmed by Woodcock & Shier (2002), who corroborated that the increase in wood density from bark-to-pith is often attributed to increased light exposure and improved growth conditions in the later stages. With possible access to the canopy for some trees during ontogeny (Brienen & Zuidema 2006). All of this supports the idea that a species' regeneration guild may differ between places (Hawthorne 1985) and should only be assigned with care. This finding emphasises the significant correlation between wood density and regeneration guild and backs up the notion of a comprehensive wood economic spectrum (Chave et al. 2009).

It's clear that the evergreen species invest in denser wood, the production of this denser wood induct the difficulty of detection of tree ring boundaries in wood samples of this species. And the evergreen species growth in entire year and during the drought periods. All these nine studied timber tree species, were deciduous, and there were no a significant difference between them (brevidecidious and deciduous). Only two: *C. gabunensis* and *P. soyauxii* were brevidecidious with a second highest density for *C. gabunensis*: $0.79 \pm 0.14 \text{ g.cm}^3$. The other seven timber tree species were deciduous with highest density for *E. suaveolens* $0.81 \pm 0.03 \text{ g.cm}^3$; and lowest density for *T. scleroxylon* $0.44 \pm 0.07 \text{ g.cm}^3$. At the light of this exception and results, it's appeared clear that brevidecidious present more heavy wood than deciduous species.

c) Comparison between Different Wood Densities

The specific wood density of *A. bipendensis* in this study is 83 percent lower than the value obtained by (Sallenave 1964; 1971), 96 percent lower than that

obtained by Zanne et al. (2009), and 106 percent higher than that obtained by Fayolle et al. (2013). For *C. gabunensis*, these values were 94 percent lower than those of Sallenave (1955) and were equal to the value obtained by Zanne et al. (2009). In *E. cylindricum*, they were equal to the value obtained by Sallenave (1955), 113 percent higher than those of Fayolle et al. (2013), and 121 percent higher than those of Zanne et al. (2009). For *E. utile*, the value obtained was 80 percent lower than that of Sallenave (1955), 91 percent lower than that of Sallenave (1964), and 101 percent higher than that of Zanne et al. (2009). The WD value of *E. suaveolens* was 102 percent higher than Sallenave (1971), 82 percent lower than the value of Fayolle et al. (2013), and 105 percent higher than the value of Zanne et al. (2009). In *M. altissima*, the WD values obtained in this study were 106 percent higher than those of Sallenave (1964), 85 percent lower than those of Fayolle et al. (2013), and 112 percent higher than the value of Zanne et al. (2009). In *M. excelsa*, they were 103 percent higher than those of Sallenave (1964) and 112 percent higher than those of Zanne et al. (2009). The WD value in *P. soyauxii* was 95 percent lower than that of Sallenave (1964) and 97 percent lower than that of Zanne et al. (2009). Finally, the WD values obtained in *T. scleroxylon* were 118 percent higher than those of Sallenave (1955), 125 percent higher, and 133 percent higher, respectively, than those of Fayolle et al. (2013) and Zanne et al. (2009).

V. CONCLUSION

In this study, we characterised detailed bark-to-pith WD profiles between and within nine harvested tropical tree species. Our study on WD radial gradients in Congo Basin tropical tree species showed an exclusively significant positive, neutral, and negative pith-to-bark WD gradient. These unique, site-specific details are not included in the global databases that are currently in use, which could result in assessments of species' functional attributes and estimates of tree biomass that are inadequate and erroneous.

We advise extreme caution when performing meta-analyses based on global functional trait databases to prevent mistakes brought on by insufficient data collection and storage. Regional biomass estimates will be improved, and our understanding of the functional strategies and successional behaviour of tropical tree species will be increased by future studies documenting trends in WD variance in new locations and forest types.

Particularly, this study recommends that future studies of wood density include the analysis of the effect of vertical variation with long-term phenological data and anatomical analysis in the same species and use a large sampling size including individuals of both the same

and different species to facilitate the analysis of the radial and vertical structure.

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REFERENCES RÉFÉRENCES REFERENCIAS

1. Amougou Ndi YA, Mbolu M, Amougou Amougou FB, Ndongo Din (2022) Potentiel d'analyse des cernes de croissance: cas de 09 essences forestières en Afrique Centrale. *Inter. J. of In no. and App. Scie.* 37 (1): 49-60. ISSN: 2028-9324.
2. ASTM International (2011) ASTM D2395 - 07ae1 Standard test methods for specific gravity of wood and wood-based materials. Web page. <http://www.astm.org/Standards/D2395.htm>. Accessed 04 March 2019
3. Bastin JF, Fayolle A, Tarelkin Y, Van Den Bulcke J, De Haulleville, T, Mortier F, Beeckman H, Van Acker J, Serckx A, Bogaert J, et al. (2015) Wood specific gravity variations and biomass of Central African tree species: The simple choice of the outer wood. *PLoS ONE* 10(11): e0142146. doi:10.1371/journal.pone.0142146.
4. Beeckman H (2016) Wood anatomy and trait-based ecology. *IAWA J* 37:127–151.
5. Bénédet F, Doucet JL, Fayolle A, Gourlet-Fleury S, Vincke D (2019) Cofortraits, African Plant Traits Information Database. Version 1.0. Available online: http://coforchange.cirad.fr/african_plant_trait. (accessed on 6 November 2020). doi:10.18167/DVN1/Y2BIZK. CIRAD Dataverse, V1.
6. Brien RJW, Zuidema PA (2006) Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *J. Ecol.* 94: 481–493. doi: 10.1111/j.1365-2745.2005.01080.x
7. Chao KJ, Phillips OL, Gloor E, Monteagudo A, Torres-Lezama A, Martínez RV (2008) Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology* 96: 281–292. doi: 10.1111/j.1365-2745.2007.01343.x
8. Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, Lescure J.-P, Nelson BW, Ogawa H, Puig H, Riéra B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99. doi 10.1007/s00442-005-0100-x.
9. Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R. (2004) Error propagation and scaling for tropical forest biomass estimates. *Philos Trans R Soc Lond B Biol Sci.* 359: 409–20. doi:10.1098/rstb.2003.1425.
10. Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366. doi: 10.1111/j.1461-0248.2009.01285.x
11. Chave J, Muller-Landau HC, Baker T, Easdale T, ter Steege H, Webb, CO (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecol. Appl.* 16(6): 2356–2367.
12. Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Wellington BC, Delitti, Duque A, Eid T, Fearnside P, Goodman RC, Henry M, Martínez-Yrizar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Péliissier R, Ploton P, Ryan CM, Saldarriaga J, Vieilledent G (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* 20: 3177– 3190. doi: 10.1111/gcb.12629.
13. De Mil T, Tarelkin Y, Hahn S, Hubeau W, Deklerck V, Debeir O, Van Acker J, De Cannière C, Beeckman H, Van den Bulcke Jan (2018) Wood density profiles and their corresponding tissue fractions in tropical angiosperm trees. *Forests*. 9 (12) 763: 1-14. doi: 10.3390/f9120763.
14. Détienné P, Chanson B. (1996) L'éventail de la densité du bois des feuillus : Comparaison entre différentes régions du monde. *Bois forêts des Tropiques*, CIRAD—Forêt; 19–30.
15. Fayolle A, Doucet JL, Gillet JF, Bourland N, and Lejeune P (2013) Tree allometry in Central Africa: Testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. *For. Ecol. and Man.* 305: 29–37.
16. Hawthorne WD (1995) Ecological profiles of Ghanaian forest trees, Tropical Forestry Papers. Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, Oxford- United Kingdom.
17. Hietz P, Valencia R, Joseph Wright S (2013) Strong radial variation in wood density follows a uniform pattern in two neotropical rain forests. *Funct. Ecol.* 27: 684–692.
18. Henry M, Besnard A, Asante WA, Eshun J, Adu-Bredu S, Valentini R, Bernoux M, Saint-André M (2010) Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. *For. Eco. and Manag.* 260 (8): 1375-1388.
19. Houghton RA (1985) Net flux of carbon dioxide from tropical forest in 1980. *Nature* 316.

20. Jones A, Breuning-Madsen H, Brossard M, Dampha A, Deckers J, Dewitte O, Gallali T, Hallett S, Jones R, Kilasara M (2013) Soil atlas of Africa. European Commission, Office of the European Union. 173p.
21. Ketterings QM, Coe R, Van Noordwijk M, Ambagau Y, Palm CA (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *For. Ecol. and Manag.* 146: 199–209. doi:10.1016/S0378-1127(00)00460-6.
22. King DA, Davies SJ, Supardi MNN, Tan S. (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct. Ecol.* 19: 445–453. doi: 10.1111/j.1365-2435.2005.00982.x
23. King DA, Davies SJ, Tan S, Noor NSMD (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. *Jor of Ecol.* 94 (3): 670–680. doi:10.1111/j.1365-2745.2006.01112.x.
24. Köppen W (1936) Das geographische System der Klimate, in: *Handbuch der Klimatologie*, edited by: Köppen, W. and Geiger, G., 1. C. "Gebr. Borntraeger, pp 1–44.
25. Lachenbruch B, McCulloh K (2014) Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. *New Phytologist.* 204:747–764. Doi
26. Lehnebach R, Bossu J, Va S, Morel H, Amusan N, Nicolini E, Beauchêne J. (2018) Wood Density Variations of Legume Trees in French Guiana along the Shade Tolerance Continuum: Heartwood Effects on Radial Patterns and Gradients. *Forests.* 10, 80: 1-22 doi:10.3390/f10020080
27. Letouzey R (1968) *Etude phytogéographique du Cameroun*. Editions Paul Lechevalier, Paris, France 511 p.
28. Maniatis D, Saint AL, Temmerman M, Malhi Y, Beeckman H (2011) The potential of using xylarium wood samples for wood density calculations: A comparison of approaches for volume measurement. *iForest—Bioge and For.* 4(4): 150-159. doi: 10.3832/for0575-004.
29. Martin D, Segalen P (1966) Notice explicative. Carte pédologique du Cameroun oriental au 1/1000000. Centre O.R.S.T.O.M. de Yaoundé, Cameroun. O.R.S.T.O.M., Paris, France. 134p.
30. Meunier Q, Moumougou C, Doucet JL (2015) *Les Arbres Utiles du Gabon*. Les presses Agronomiques de Gembloux, Gembloux
31. Nock CA, Geihofer D, Grabner M, Baker PJ, Bunyavejchewin S, Hietz P (2009) Wood density and its radial variation in six canopy tree species differing in shade-tolerance in western Thailand. *Annals of Botany.* 104: 297–306. doi:10.1093/aob/mcp118.
32. Olesen PO (1971) The water displacement method: a fast and accurate method of determining the green volume of wood samples. *Forest Tree Improvement.* 3: 3–23.
33. Onoda Y, Richards AE, Westoby M (2010) The relationship between stem biomechanics and wood density is modified by rainfall in 32 Australian woody plant species. *New Phytol.* 185: 493–501. doi: 10.1111/j.1469-8137.2009.03088.x
34. Osazuwa-Peters OL, Wright SJ, Zanne AE. (2014) Radial variation in wood specific gravity of tropical tree species differing in growth-mortality strategies. *Am J Bot.* 101: 803-811. doi: 10.3732/ajb.1400040.
35. Panshin AJ, de Zeeuw C (1970) *Textbook of wood technology, Volume 1: structure, identification, properties, and uses of the commercial woods of the United States and Canada*. 3rd ed. McGraw-Hill, New York-USA.
36. Panshin AJ, de Zeeuw C (1980) *Textbook of wood technology: structure, identification, properties, and uses of the commercial woods of the United States and Canada*. 4th ed. McGraw-Hill, New York-USA
37. Parolin P. 2002. Radial gradients in wood specific gravity in trees of central Amazonian floodplains. *IAWA Journal* 23: 449–457.
38. Plourde BT, Boukili VK, Chazdon RL (2015) Radial changes in wood specific gravity of tropical trees: inter- and intraspecific variation during secondary succession. *Func. Ecol.* 29: 111-120. doi: 10.1111/1365-2435.12305.
39. Putz FE, Coley PD, Lu K, Montalvo A, Aiello A (1983). Uprooting and snapping of trees: Structural determinants and ecological consequences. *Can. J. of For. Res.* 13(5): 1011–1020.
40. Ramanantoandro T, Rafidimanantsoa HP, Ramanakoto MF (2015) Forest aboveground biomass estimates in a tropical rainforest in Madagascar: new insights from the use of wood specific gravity data. *J For Res.* 26: 47–55. doi: 10.1007/s11676-015-0029-9.
41. Ramanantoandro T., Ramanakoto, M. F., Rajoelison, G. L., Randriamboavonjy, J. C., & Rafidimanantsoa, H. P. (2016). Influence of tree species, tree diameter and soil types on wood density and its radial variation in a mid-altitude rainforest in Madagascar. *Annals of Forest Science.* 73(4): 1–12.
42. Roque RM, Filho MT (2007) Relationships between anatomical features and intra-ring wood density profiles in *Gmelina arborea* applying x-ray densitometry. *Cerne* 13 (4): 384–392.

43. Sallenave P (1971) Propriétés Physiques et Mécaniques des Bois Tropicaux. Deuxième Supplément, CTFT. Nogent sur Marne, France .125 p.
44. Sallenave P (1955) Propriétés Physiques et Mécaniques des Bois Tropicaux de l'Union Française. CTFT, Nogent sur Marn, France. 144 p.
45. Sallenave P (1964) Propriétés Physiques et Mécaniques des Bois Tropicaux. Premier Supplément, CTFT. Nogent sur Marne, France. 81 p.
46. SFIL (2009) Société Forestière Industrielle de la Lekoundjé - plan d'aménagement de l'UFA 10 025 - Concession n°1070 Douala - Cameroun. SFIL. 142 p.
47. Tarelkin Y, Delvaux C, De Ridder M, El Berkani T, De Cannière C, Beeckman H (2016) Growth-ring distinctness and boundary anatomy variability in tropical trees. *IAWA J.*37:S1–S7.
48. Turner IM (2001) The Ecology of Trees in the Tropical Rain Forest. Cambridge: Cambridge University Press, United Kingdom.
49. Wassenberg M, Chiu H-S, Guo W, Spiecker H (2014) Analysis of wood density profiles of tree stems: incorporating vertical variations to optimize wood sampling strategies for density and biomass estimations. *Trees*. 29: 51–561. doi: 10.1007/s00468-014-1134-7
50. White F (1983) The Vegetation of Africa. A Descriptive Memoir to accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa.In: Natural Resources Research Report XX. Paris, France. 351p.
51. Wiemann MC, Williamson GB (1988) Extreme radial changes in wood specific gravity in some tropical pioneers. *Wood and Fiber Science*. 20: 344–349
52. Wiemann, MC, Williamson, GB (1989) Radial gradients in the specific gravity of wood in some tropical and temperate trees. *Forest Sci*. 35: 197–210.
53. Williamson GB, Wiemann MC (2010) Measuring wood specific gravity...Correctly. *American Journal of Botany*. 97: 519-524.
54. Woodcock DW, Shier AD (2002) Wood specific gravity and its radial variations: the many ways to make a tree. *Trees*. 16: 437–443. doi: 10.1007/s00468-002-0173-7.
55. Worbes, M (1995) How to Measure Growth Dynamics in Tropical Trees. *IAWA J*. 16: 337–351.
56. Zanne AE, Lopez-Gonzalez G, Coomes D A, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC, Chave J (2009) Global wood density database. Dryad. Identifier: <http://hdl.handle.net/10255/dryad.235>.