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Original article

Radial growth and characterization of juvenile and adult wood in plantation grown okoumé (*Aucoumea klaineana* Pierre) from Gabon

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Abstract – The fast-growing hardwood, okoumé *(Aucoumea klaineana* Pierre), is a major forest species in Gabon and is used principally for making plywood, but research into the growth and quality of this wood is scanty. Trees from natural forests are favoured for production, yet little information exists on wood characteristics from plantation trees. Therefore, we carried out a dendrochronological study along with measurements of wood longitudinal modulus of elasticity (E_L), density (D_w), dimensional stability parameters (longitudinal, radial and tangential shrinkage and fibre saturation point) and fibre cell morphology to determine if these properties were related to age in trees from two plantations. We then used segmented regression analysis to define the limit (breakpoint) between juvenile (JW) and adult wood (AW). Using monthly precipitation data, we were able to determine that one growth ring is formed per year, composed of a large light coloured ring formed during the long rainy season and a thick, dark band formed during the major dry season. However, thinner bands, analogous to false rings, may also form during the short dry and short rainy seasons. Ring width decreases from the pith to the bark, and the breakpoint between JW and AW was at 19 years old when trees from both plantations were pooled together. No differences in D_w or radial and tangential shrinkage occurred with cambial age. E_L increased significantly up to the cambial age of 12–14 years, after which the increase with age was only slight and no breakpoint between JW and AW was found. With regard to mean longitudinal shrinkage, AW was found to form after the age of 13 years but fibre cell length was significantly longer after the age of 14.5 and 20 years, depending on the plantation of origin. Therefore, the boundary between JW and AW in plantation grown okoumé occurs between the ages of 13 and 20 years, depending on the characteristic examined.

dendrochronology / modulus of elasticity / wood density / shrinkage / fibre saturation point

Résumé – Croissance en diamètre et caractérisation de la limite entre bois juvénile et bois adulte chez l'okoumé des plantations au Gabon. L'okoumé *(Aucoumea klaineana* Pierre) est une essence à croissance rapide que l'on rencontre majoritairement au Gabon. Son bois est principalement utilisé dans la fabrication de panneaux de contreplaqué. Cependant les recherches sur la croissance et la qualité de son bois ne sont pas suffisamment avancées. L'utilisation des arbres issus des forêts naturelles est favorisée pour la production par rapport à ceux issus des plantations dont les caractéristiques sont peu connues. De ce fait, nous avons entrepris d'étudier la dendrochronologie des okoumés dans les deux plantations dans l'optique d'évaluer, en suivant l'âge cambial, le module d'élasticité longitudinal (E_L), la densité (D_w), les paramètres de stabilité dimensionnelle (retraits longitudinal, radial et tangentiel et point de saturation des fibres) et les caractéristiques morphologiques de fibres. En utilisant la régression linéaire segmentée, nous avons pu définir la limite entre le bois juvénile et le bois adulte en mettant en relation l'âge cambial et les caractéristiques mesurées. En s'aidant des données des précipitations mensuelles, nous avons déterminé l'existence d'un cerne annuel chez l'okoumé. L'accroissement annuel est composé d'une large bande claire formée pendant la longue saison de pluies et d'une large bande sombre formée pendant la grande saison sèche. Les fines bandes qui se formeraient durant les petites saisons sèches et de pluies sont assimilables aux faux cernes. La largeur du cerne d'okoumé décroît de la moelle vers l'écorce et présente une limite entre bois juvénile et bois adulte à l'âge cambial de 19 ans en considérant les deux plantations. On n'observe pas de différence avec la densité, les retraits radial et tangentiel par rapport à l'âge cambial. En revanche, le module d'élasticité longitudinal croît significativement jusqu'à l'âge cambial de 12–14 ans. Au-delà de cet âge, le module (E_L) augmente faiblement, mais aucune limite entre le bois juvénile et le bois adulte n'a été trouvé. Les moyennes de retrait longitudinal ont présenté une limite entre le bois juvénile et le bois adulte après 13 ans. Quant à la longueur de fibres, nous avons trouvé deux âges limites à 14,5 et 20 ans selon la plantation. En conclusion, suivant les caractéristiques examinées, la limite entre le bois juvénile et le bois adulte chez l'okoumé apparaît dans l'intervalle allant de l'âge cambial 13 ans à 20 ans.

dendrochronologie / module d'élasticité / densité / retrait / point de saturation de fibres

1. INTRODUCTION

Gabon, an equatorial country in Central Africa (Fig. 1), is covered with over 80% forest, of which the fast growing okoumé *(Aucoumea klaineana* Pierre) is the dominant species. Although this species is quasi-endemic to Gabon, it can also be found in Cameroon, Congo and Equatorial Guinea [8, 10, 11, 19, 27]. Of 30 000 ha of timber plantations in Gabon, 85% are okoumé [24]. Exploited when they have a mean

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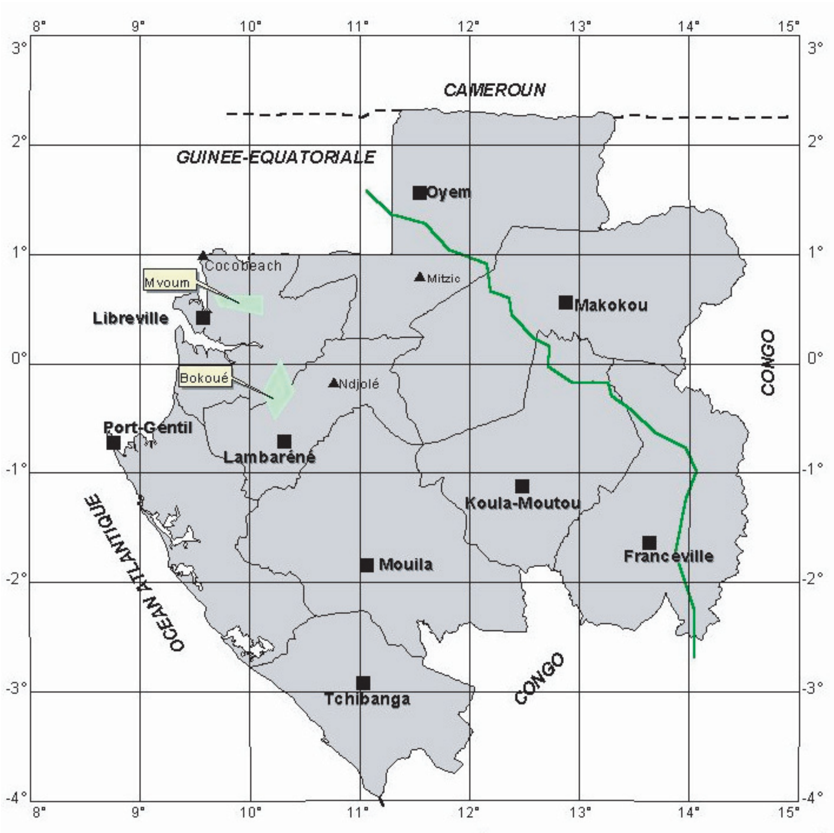

Figure 1. Map of Gabon showing location of the field sites in the districts of M'Voum and Bokoué. The eastern limit of okoumé (thick, solid line) is also indicated.

diameter at breast height (DBH) of 0.7 m, okoumé trees are used largely for plywood, but research into tree growth and wood quality of this species is negligible [3, 7, 8, 17, 20], even though it is the principal timber export in Gabon [8, 9, 14]. In the year 2000, Gabon produced > 4 million m^3 timber, of which 72% was okoumé. However, in 2004, only 1.6 million m^3 timber was produced, of which 61% was okoumé[1]. This decrease in lumber production was largely due to a change in policy concerning environmental protection and also new regulations pertaining to how timber could be transformed locally.

As wood from okoumé plantations is destined for the making of plywood, stands have been managed largely for improved stem volume, with little consideration of wood quality [8]. However, plywood is less in demand [9, 12], due mainly to the development of fibre-based composites e.g. MDF, LVL and OSB. Therefore, since 1995, the Gabonese government has been investigating new means of improving the wood industry [32]. Even though okoumé regenerates quickly in plantations, the type of exploitation carried out results in a decrease in the quantity and quality of the remaining trees [26]. Therefore, it is necessary to improve both the silvicultural management of okoumé plantations as well as determining if okoumé wood can be used for different purposes. If further information concerning the physical and mechanical properties of okoumé were available, wood from this species could have more uses than just for plywood. However, it is not always possible to date tropical hardwoods due to the difficulty in determining defined seasons and the ability of individuals to produce several growth rings, or have missing rings, in any one year [13]. Wood quality parameters change with tree age, thus the ability to determine tree age from ring width analysis would aid the forest manager and end-user to better evaluate wood quality.

According to the literature, Gabon has only two main seasons: one dry season lasting from the beginning of June to the end of August, and one rainy season for the rest of the year [12, 25]. It is therefore expected that okoumé can be correctly dated using dendrochronological techniques [29]. Although such techniques have been used successfully on individual okoumé trees growing in western Congo, cross-dating between trees of different ages needed to be checked using climatic data [3]. Correctly dating tree age is the first step to take when trying to determine wood quality parameters e.g. elasticity, strength and natural durability. Such parameters differ depending on tree age, plantation density and local climatic factors and can be manipulated to a certain extent through silvicultural techniques and improvement programs [38].

Wood quality of any tree species depends on the requirements of the end-user. In the case of okoumé, wood is used mainly for plywood manufacture. However, few data exist on the mechanical, physical and chemical properties of this species [8], therefore it is difficult to envisage other uses of the wood e.g. for construction or furniture making. It is thus necessary to better characterize both juvenile and adult okoumé

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[1] Economic data were provided by the General Direction of the Gabonese Forest Department.

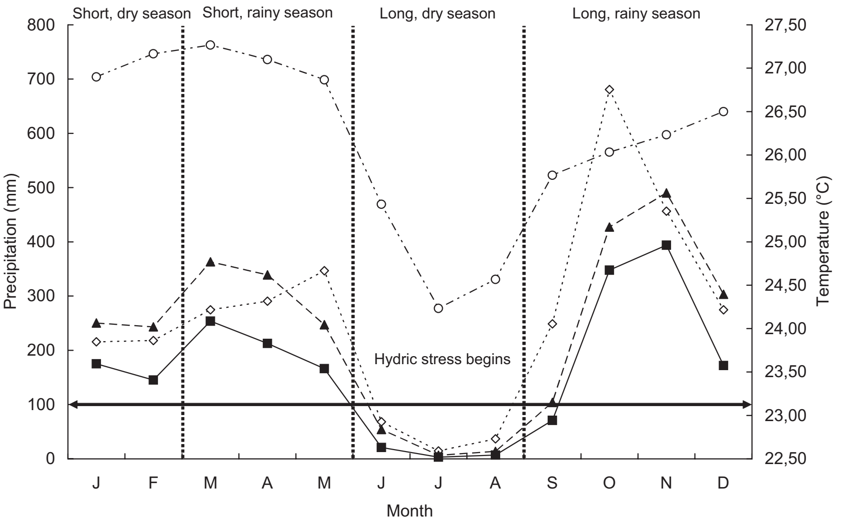

Figure 2. Monthly precipitation using data from the three meteorology stations situated near the okoumé plantations (squares = Lambarene, diamonds = Cocobeach, triangles = Libreville). For monthly temperature, little variation was observed between the three stations, therefore mean temperature (circles) is shown. The thick, solid line indicates when hydric stress begins in the trees.

wood. Juvenile wood (JW) is formed from a juvenile cambium during the early years of physiological activity [5, 38]. Adult wood (AW) is then produced and usually has thinner annual growth rings, a higher longitudinal modulus of elasticity (E_L), higher density and greater dimensional stability due to changes in xylem structure. The age at which AW begins to form depends largely on species and as far as the authors know, has not yet been determined for okoumé. Such data would enable foresters and end-users to better predict wood quality in young plantations and help decide when to carry out thinning and harvesting.

We carried out a dendrochronological study on adult okoumé trees from two plantation forests (M'Voum and Bokoué) in west Gabon. Combined with measurements of wood density, E_L, dimensional stability and xylem structure, we determined a range of ages at which JW and AW forms. The results are discussed with regard to climatic data and how wood quality from plantation trees can be improved. Such information will be highly useful when comparing plantation okoumé to that exploited from natural forest conditions and will also aid our understanding of how to improve forest production in Gabon.

2. MATERIALS AND METHODS

2.1. Site description and sampling

Trees were selected from two plantations situated in the forests of M'Voum (0° 26'–0° 37' N and 9° 40'–10° 07' W) and Bokoué (0° 01' N–0°28' S and 10° 07'–10° 24' W), situated in the estuary region of western Gabon (Fig. 1), where the only okoumé plantations are grown. The two plantations were 165 km apart and the nearest meteorological stations were located at Cocobeach, Lambaréné and Libreville (Fig. 1). Mean annual precipitation is 3263mm y^{-1}, 2001 mm y^{-1} and 2859 mm y^{-1} for the three stations, respectively. At both forest sites, minimum precipitation is 100 mm mo^{-1} lower in August, and reaches a maximum of 650 mm mo^{-1}in October (Fig. 2, data from the Direction Nationale de la Climatologie, Gabon and the Centre Africain de la Météorologie Appliquée au Développement, Niger). Annual temperatures range from 22–32 °C and air humidity is fairly constant at 80–85%.

Trees were planted from seed in 1960 at a spacing of 6 × 6 m, at both plantations; therefore the initial density was 270 stems ha^{-1} [2]. No consequent thinnings were carried out. Eight dominant trees were felled for analysis from the plantation at Bokoué and 15 from M'Voum. It was not possible to harvest more trees due to logistical constraints. Mean diameter at 1.3 m (DBH) for all trees was 0.69 ± 0.01 m. Trees were healthy and the first faults noted along the trunk were at a height of 12 m upwards. If these trees were exploited, the basal log length would be at least 16 m long.

Once felled, a 1.0 m long log was removed at a height of 0.7 m from all trees. Below this height, buttressing usually occurs along the length of the stem bole, which may influence results. Boards were then cut through the centre of the log, so that the whole cross-section, from bark to pith on both sides of the tree, could be used for further sampling (Fig. 3). Strips of wood were removed from one end of the board (at a stem height of 0.7 m) for dendrochronological analysis (n = 23). Each board was then sawn in two along the length of the pith and stored at 20 ± 2 °C and 65 ± 5% humidity, until wood theoretical moisture content had reached 12% with a constant mass. The boards were then cut into smaller samples (Fig. 3). Samples (dimensions: 600 mm longitudinal × 25 mm radial × 30 mm tangential) were cut along the radial axis and the position of each sample with regard to the cambial age was noted (n = 152). The growth ring closest to the centre of the sample was used as the indicator of cambial age for that sample. These samples were used for measuring wood elastic properties and density (Fig. 3). From the remaining wood, smaller samples were cut (dimensions: 20 mm longitudinal × 20 mm radial × 20 mm tangential) along the radial direction, for determining volumetric shrinkage (n = 78). The position of each sample with regard to cambial age was again noted. Finally, samples were taken from all growth rings in five trees from each plantation for measurements of fibre cell morphology. Each sample was sawn into small blocks (dimensions: 20 mm longitudinal × 20 mm tangential × X mm radial. X corresponds to growth ring width. n = 400) and each block was then carefully cut into 1 mm thick splinters using a sharp cutter. The position of each sample with regard to heart- and sap-wood was noted, as the subsequent chemical preparation for isolating fibres differed slightly depending on wood type.

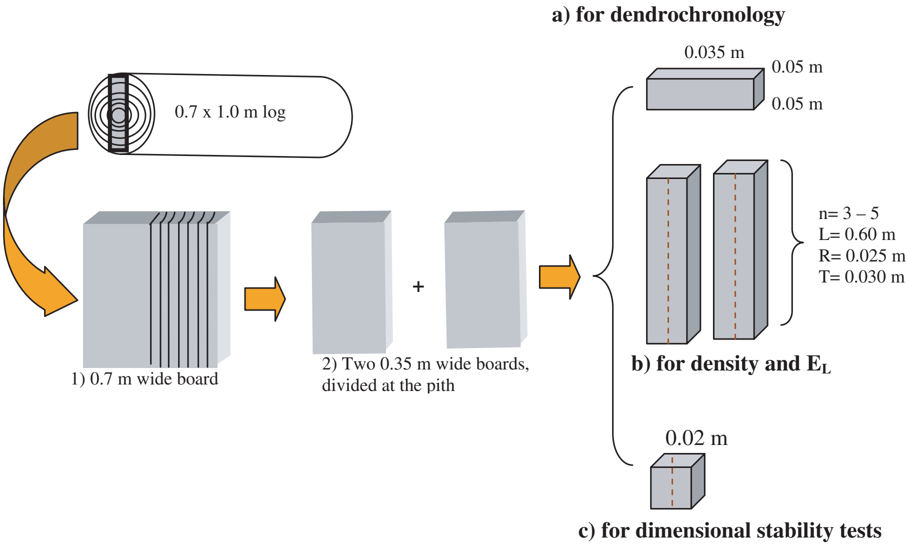

Figure 3. Samples were cut to different sizes depending on test to be carried out. (a) samples were cut for dendrochronological analysis, (b) testing of mechanical properties and (c) measurement of volumetric shrinkage. L = longitudinal, R = radial, T = tangential faces.

2.2. Growth ring width

Strips of wood were air-dried and then polished with sandpaper so that tree growth rings could be easily distinguished (Fig. 4). Visual cross-dating was carried out manually by comparing samples with each other until a reference skeleton plot could be obtained. It was also necessary to visually compare each sample with climate data for the period. Growth rings were measured to the nearest 0.01 mm using a binocular microscope and the software WinDendro© (Regent Instruments, Quebec, Canada). Ring surface area (SA) was then calculated assuming the ring was a complete annulus [1].

2.3. Wood density at 12% moisture content

To determine if wood density at 12% moisture content (D_w) varies with age, the mean D_w for each cambial age was calculated. Each sample was weighed (M), and the exact dimensions measured with a pair of Vernier callipers at three points along the length of the sample so that volume (V) can be determined. D_w was calculated using Equation (1):

$$D_w = \frac{M}{V} \tag{1}$$

2.4. Longitudinal modulus of elasticity E_L

Using the same samples as those for which D_w was measured, mean E_L for each cambial age was determined using a vibration analysis system, VibraPann, described elsewhere [6]. The dynamic E_L in flexion was calculated using mechanical principles that state a relationship between the natural vibration frequencies and the elastic properties of a material [22].

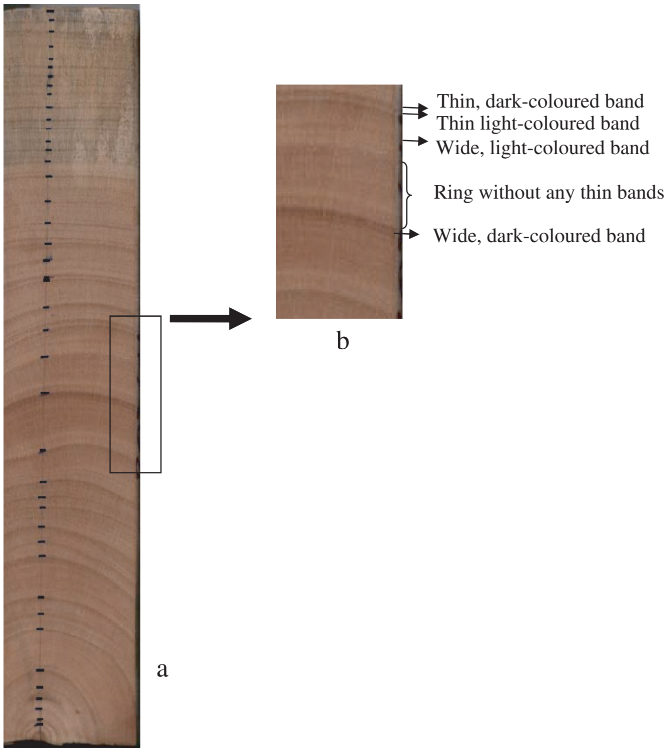

Figure 4. Cross-section of the transversal face of okoumé wood: (a) the limit of each growth ring is shown by a black line and (b) one growth ring is made up of distinct wide, light-coloured bands and thin dark-coloured bands. Thin bands can also be missing within one growth ring.

2.5. Dimensional stability

Dimensional stability was measured on 55 samples from 11 trees (five from the Bokoué forest and six from the M'Voum site). Due to limited time and resources, it was not possible to test enough samples so that both plantations could be compared. Samples were placed in environments with different levels of air temperature and relative humidity until a constant mass for each sample was obtained in each thermal state. After each state was reached, all samples were weighed (M), and the exact dimensions of each face (longitudinal, radial and tangential) measured with a pair of Vernier callipers. Initially, samples were immersed in water until full saturation was attained (H_{sat}).

Then, each sample was stored at 20 ± 2 °C temperature and 65 ± 5% relative humidity, until the theoretical moisture content had reached 12% (H_{12}). Samples were then transferred to an oven, and kept at a temperature of 20 ± 2 °C and 50 ± 5% relative humidity, until the theoretical moisture content of the samples had reached 9% (H_9). Finally, samples were brought to the anhydrous state, by oven drying them at 103 ± 2 °C ($H_{anhydrous}$).

The differences in dimensions, i.e. shrinkage (α) between the saturated state and the three other states of moisture content were determined using Equations (2), (3) and (4):

$$\alpha_1 = H_{sat} - H_{12} \tag{2}$$

$$\alpha_2 = H_{sat} - H_9 \tag{3}$$

$$\alpha_{Total} = H_{sat} - H_{anhydrous}. \tag{4}$$

These variations in dimensions regress linearly with the moisture content of wood [20]. It is thus possible to determine numerically the fibre saturation point (FSP). The FSP is the stage in the drying or wetting of wood at which the cell walls are saturated and the cell cavities free from water [37]. The FSP is determined by plotting the regression line obtained between the values of $\alpha_{1,}\alpha_2$ and α_{Total} (Yi) and wood moisture content (x). The point at which the line $Y = ax + b$ crosses the Y axis (intercept = b) is the FSP [20].

2.6. Fibre cell morphology

Length and width of fibre cells were measured using a MorFi LB-01 fibre analyser (Techpap, France). Wood splinters from each growth ring were first treated so that fibres could be isolated in a suspension, which is then analysed by MorFi LB-01. This suspension was prepared by air-drying the wood splinters and then adding 50 mL acetic acid (CH_3COOH) and 50 mL hydrogen peroxide (H_2O_2) to samples weighing 4.0 g. This bleaching treatment discolours wood lignin. This solution was placed into a pyrex reactor equipped with a reflux condenser and kept at a temperature of 75 °C in an oil bath during 5.5 h for heartwood samples and 3.0h for sapwood samples. The solution was then filtered twice, washed in tap water and air-dried for 4–5 h.

Fibre dimensions were automatically measured by MorFi LB-01 via computerized image analysis of the fibre suspension. Fibres may be damaged during the preparation of wood samples, therefore the arithmetical mean length of fibres was calculated using Equation (5):

$$FL = \frac{\Sigma z_i l_i}{\Sigma z_i} \tag{5}$$

where z_i is the number of fibres in a class of a given length and l_i is the mean length of fibres in the given class [36].

2.7. Statistical analysis

A two-sample T-test was used to determine if differences in mean DBH existed between plantations. Analysis of variance with cambial age as a covariate was used to determine if differences in growth ring width, D_w, E_L dimensional stability and fibre morphological parameters existed between the two plantations. If no significant differences were found between plantations, the mean of both sets of data were used for subsequent statistical analysis. Power and linear regressions between D_w, E_L, dimensional stability and fibre morphological parameters and cambial age were also performed to find the best model fitting the data. The program SegReg [34] was used to carry out segmented linear regression analysis on these parameters with cambial age, to estimate the age limit between the formation of JW and AW [1,5]. The model consists of finding two linear regressions to characterize wood characteristics as a function of cambial age. The threshold or breakpoint between JW and AW can be considered as the transition age between the two and is considered as Equation (6) for JW and Equation (7) for AW:

$$Y = aX + b + \varepsilon \text{ for } X \leqslant X_o \tag{6}$$

$$Y = cX + d + \varepsilon \text{ for } X > X_o \tag{7}$$

where Y is the wood characteristic and a, b, c and d are the coefficients and X is cambial age. X_o is unknown and determined with an iterative method to estimate the best statistical coefficient of determination of the model including the two regressions by a numerical optimization method [1,34]. Although other authors have used different models to estimate the limit between JW and AW, segmented linear regression analysis appears to be the most useful [1,5], especially on specimens with a low number of annual growth rings, as is the case in our study. Mean data presented are ± standard error.

3. RESULTS

Trees at Bokoué had a significantly greater mean DBH (0.74 ± 0.03 m) than those at M'Voum (0.67 ± 0.02 m; $T = 2.51, P = 0.028$).

3.1. Growth ring width

Within a growth ring, several bands could sometimes be observed (Fig. 4). These bands corresponded to mean monthly precipitation (Fig. 2), in that the large, light-coloured band, present in every growth ring, forms during the long rainy season (September to May). A thinner dark-coloured band then forms during the main dry season, from June to August (Fig. 4). From September to the beginning of December, precipitation is very high, and a thin, light-coloured band can form during this "short" rainy season, (Fig. 2). This thin band is similar to the "false" rings often found in tropical species [13]. Between December and February, the weather is drier, and a very thin dark band can form (Fig. 4), also analogous to a false ring. Therefore, one annual growth ring may be composed of several bands, depending on local climate. Such "false" rings appeared in greater quantities closer to the pith where ring width was wider. When a thin band was present on one side of the sample face, it was not necessarily present on the underside of the sample, however, the thick bands were always present on both faces. Therefore, a much higher variability in the presence and absence of thin bands exists in okoumé.

When both plantations were considered separately, growth ring width was significantly larger in trees from Bokoué, compared to those from M'Voum, using cambial age as a covariate ($P < 0.001$). In trees from the M'Voum plantation, the breakpoint between JW and AW was determined at 9.8 y. However, no breakpoint nor significant relationship between growth ring width and cambial age was found in trees from the Bokoué plantation. When both plantations were considered together,

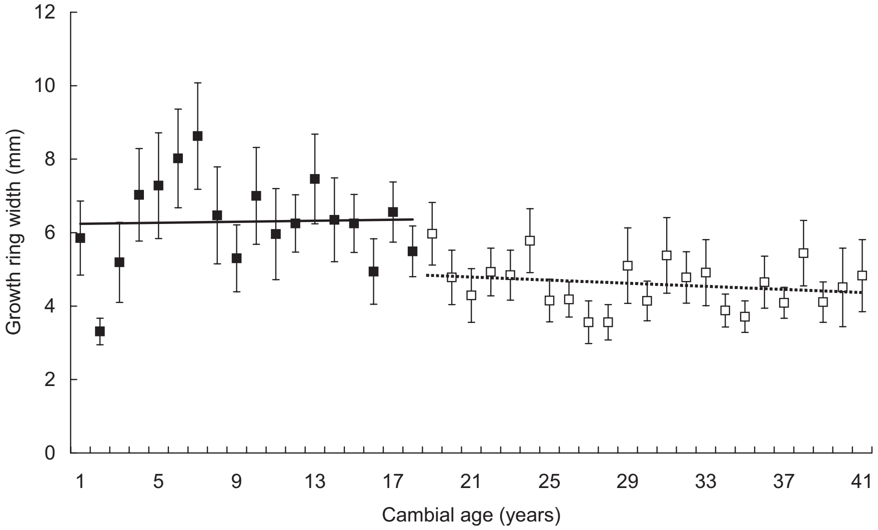

Figure 5. Growth ring width decreases slightly with cambial age. Two plateaux can be seen, with a significant breakpoint at the age of 19 y (black squares, solid line: 0–18 y: $y = -0.0212x + 5.22$, $R^2 = 0.05$, $P = 0.33$. White squares, dashed line: 19–41 y: $y = 0.007x+6.23$, $R^2 = 0.01$, $P = 0.91$). Data are means ± standard error.

growth ring width at the centre of the tree was highly variable, ranging from 3.3 ± 0.4 mm in cambial year 2 to 8.6 ± 1.5 mm in cambial year 7 (Fig. 5). After the cambial age of 8 y, ring width decreased steadily, reaching a minimum at the age of 19 y and the significant breakpoint between JW and AW was determined at 19.2 y. When the SA of growth rings was examined, no breakpoint was found and the regression was considered as significantly linear ($y = 132x + 897$, $R^2 = 0.85$, $P < 0.001$). No significant differences in ring width or SA between plantations were found.

3.2. Wood density at 12% moisture content

Mean D_w at 12% moisture content was 450.8 ± 3.7 kg/m^3 and did not change significantly with cambial age. No significant differences between plantations were found, nor was any relationship found with cambial age (Fig. 6).

3.3. Longitudinal modulus of elasticity E_L

Mean E_L was 8626 ± 119 MPa and increased rapidly with cambial age up to the age of 12–14 y, and then only slightly afterwards (Fig. 6). No breakpoint was found between JW and AW and the best relationship was a power regression (Fig. 6). No significant differences between plantations were found. Although no significant relationship occurred between mean D_w and cambial age, a significant positive relationship existed between E_L and D_w (Fig. 7).

3.4. Dimensional stability

No significant differences in total radial or tangential shrinkage were found with cambial age (Tab. I, Fig. 8). However, a highly significant relationship was found between total longitudinal shrinkage and cambial age (Tab. I, Fig. 8). The breakpoint between JW and AW was found to be at 12.7 y, after which a plateau was reached. Significant linear regression relationships were found between E_L and total longitudinal ($y = -2E - 06x + 0.02$, $R^2 = 0.25$, $P = 0.01$), radial ($y = 2E - 06x + 0.018$, $R^2 = 0.18$, $P = 0.034$) and tangential shrinkage ($y = 4E - 06x + 0.026$, $R^2 = 0.26$, $P = 0.009$). No significant relationships were found between total shrinkage in any direction and D_w. Mean radial FSP was significantly smaller than that in the tangential direction (Tab. I, $T = -4.47$, $P < 0.001$) and was negatively regressed with E_L only ($y = -2E - 05x + 0.51$, $R^2 = 0.17$, $P = 0.039$), but no relationship was found with cambial age. No significant relationships were found between FSP measured in the tangential direction and any other parameter.

3.5. Fibre cell morphology

Fibre length was significantly longer in trees from the M'Voum plantation, when cambial age was considered as a covariate ($P = 0.052$). In trees from the M'Voum and Bokoué plantations, the breakpoints between JW and AW were 14.5 and 20 years, respectively (Fig. 9). When fibre lengths from both plantations were pooled together, a significant negative relationship existed with growth ring width, although variability was high ($y = -28.4x + 1188$, $R^2 = 0.25$, $P = 0.001$) and a significant positive relationship existed with growth ring SA ($y = 0.037x + 901$, $R^2 = 0.76$, $P < 0.001$). Fibre length was significantly positively regressed with E_L and negatively regressed with longitudinal shrinkage (Fig. 10), but not with any other shrinkage values. Mean fibre width was 21.8 ± 0.1 µm. No significant differences in fibre width were found with age or between plantations and no significant relationships were found with any other wood characteristics.

4. DISCUSSION

We were able to measure stem annual radial growth using basic dendrochronological techniques. Nevertheless, care must be taken when interpreting growth ring data in okoumé. According to Mariaux [29] and Belingard et al. [3], the presence/absence of wide and thin bands can lead to confusion, particularly when cross-dating several trees of different ages. Mariaux [29] suggested that a normal growth ring

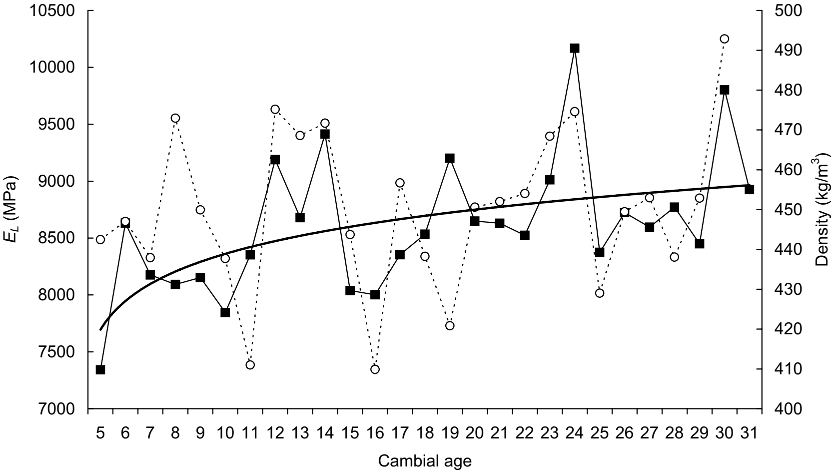

Figure 6. Mean longitudinal modulus of elasticity (E_L, black squares, solid lines) increased significantly with cambial age ($y = 7695.4x^{0.0463}$, $R^2 = 0.33$, $P = 0.008$), but no breakpoint was found between JW and AW. No significant relationship was found between mean wood density at 12% moisture content and cambial age (white circles, dotted line).

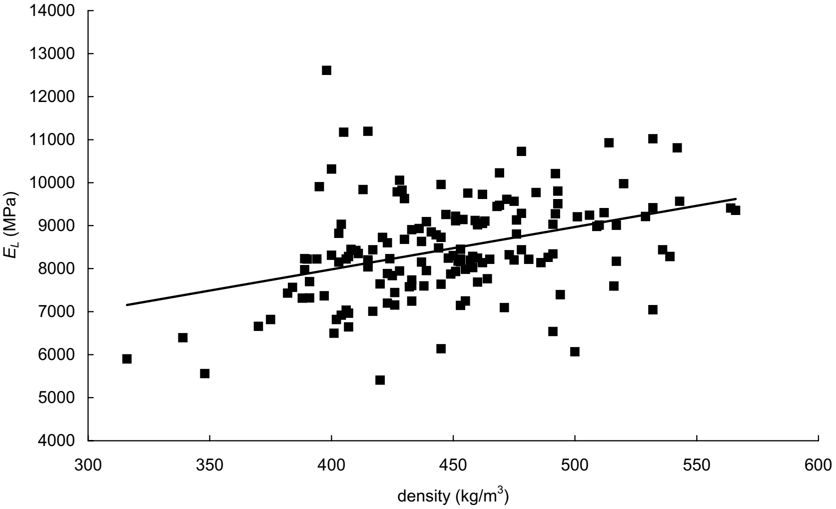

Figure 7. Longitudinal modulus of elasticity (E_L) increased significantly with wood density at 12% moisture content ($y = 9.86x + 4038$, $R^2 = 0.14$, $P < 0.001$).

Table I. Total percent variation in dimensional stability parameters. Data are means ± standard error.

Dimensional stability parameter	Total variation in parameter (%)
Longitudinal shrinkage	0.36 ± 0.05
Radial shrinkage	3.47 ± 0.06
Tangential shrinkage	5.91 ± 0.1
Radial FSP	30.1 ± 0.75
Tangential FSP	33.9 ± 0.70

should be contained within two thin, dark bands which form in December–January (short dry season). However, we did not always find these bands clearly marked and quite often they were absent, especially in the older wood. Therefore, we propose that an annual growth ring in the okoumé we studied should contain one large, light-coloured band (formed during the long, rainy season) and one thick dark band (formed during the main dry season). Any thin bands formed during the 'short' seasons should be contained within this annual growth ring.

The thin bands observed within the annual growth rings can be considered as analogous to 'false' growth rings. False rings occur as a result of tree response to different environmental and physical factors e.g. drought during the growing season or excess rainfall during the dry period [35]. In certain species, e.g. *Acer saccharum* Marsh, the number of ring anomalies are inversely related to growth rate and vigor. In this species, dominant trees had only a mean percentage of 1.3% anomalies, including false rings, whereas all the overtopped trees had partial or missing rings [28]. We did not examine if anomalies occurred with regard to crown position, nor did we have access to detailed, monthly climatological data for the period studied. Therefore, future studies on this species should consider how ring formation differs depending on the position of the tree within the stand and canopy, and how climatic factors affect false ring formation.

When both plantations were considered together, a decrease in stem radial growth occurred between the ages of 2–4 y and was probably due to a change in allocation of resources within the tree. After the initial burst of growth in the year after germination, more resources are allocated to the root system for increased nutrient uptake and anchorage, therefore, radial stem growth decreases. Once the plants are established, stem radial growth augments significantly up to the age of 7 y and

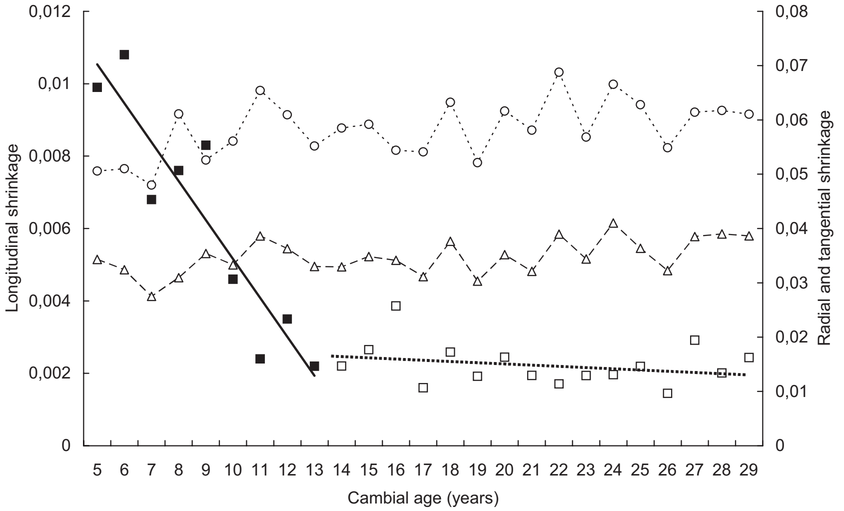

Figure 8. Longitudinal shrinkage decreased significantly up to the cambial age of 12.7 years (black squares, solid line: $y = -0.011x + 0.016$, $R^2 = 0.85$, $P < 0.001$). After this age, a plateau can be seen, (white squares, dashed line: $y = -0.000031x + 0.003$, $R^2 = 0.062$, $P = 0.36$). No relationship was found between radial (white triangles and dashed line) and tangential (white circles and dotted line) shrinkage with cambial age.

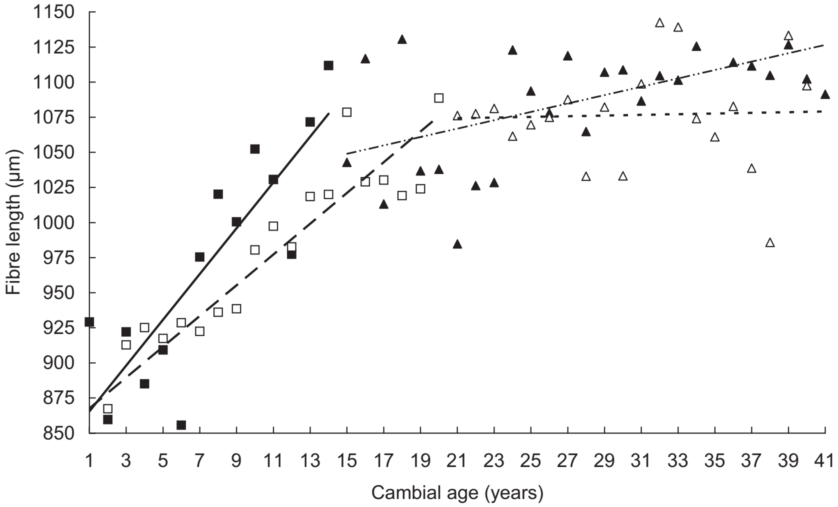

Figure 9. Fibre length increased significantly with cambial age. In trees from the M'voum plantation, the breakpoint between JW and AW was 14.5 y (black squares, solid line: 0–14.5 y: $y = 16.30x + 849.4$, $R^2 = 0.71$, $P < 0.001$. Black triangles, solid + dotted line: 15–41 y: $y = 2.45x + 1069.1$, $R^2 = 0.001$, P = ns). In trees from the Bokoué plantation, the breakpoint between JW and AW was 20 y (white squares, hatched line: 0–20 y: $y = 10.96x + 856.7$, $R^2 = 0.87$, $P < 0.001$. White triangles, dotted line: 21–41 y: $y = 2.96x+1003.6$, $R^2 = 0.31$, $P = 0.003$).

then decreases between the ages of 8–16 y. After the cambial age of 19 y, which was found to be the breakpoint between JW and AW, ring width was fairly constant. When the two plantations were considered separately, only in trees from M'Voum was a significant relationship between cambial age and growth ring width found, with a much earlier breakpoint between JW and AW at 10 y. Variability was very high in data from trees at Bokoué, therefore no breakpoint could be determined. Nevertheless, trees from Bokoué had significantly larger growth rings than those from M'Voum, thus explaining the larger DBH also found at Bokoué. Mean annual precipitation is 500–1000 mm y^{-1} higher at Bokoué than at M'Voum, and would account for the higher radial growth rate observed. The provenance of trees in our study is also not known, and genetic background also influences growth rate in okoumé, although it seems unlikely that morphological and structural traits are influenced by provenance [23].

Unlike ring-porous tropical hardwoods e.g. teak (*Tectona grandis* L.), it is not easy to determine the demarcation age between JW and AW in the diffuse porous species okoumé. Relatively little radial variation exists in xylem structure, and the sharp peak in JW properties followed by a plateau in AW, which is often distinct in other species [5], is not always evident in okoumé wood. For example, E_L increased up to the cambial age of 12–14 y, after which the increase with age was only slight, but no significant breakpoint was found between JW and AW. Nor were any significant changes found in D_w at 12% moisture content with cambial age. With regard to the dimensional stability parameters, only longitudinal shrinkage (for both plantations together) differed significantly with cambial age. A sharp decrease in shrinkage occurred up to the breakpoint age of 13 y, after which little variation with age was observed. This variation in longitudinal shrinkage was significantly related to mean fibre cell length, although the significant threshold value between JW and AW for fibre length was 14.5 and 20 y in trees from Bokoué and M'voum plantations, respectively. Fibre cell length is influenced by changes in monthly precipitation with a time lag of up to four months [21] and when precipitation and hence growth rate are high, fibres are shorter. Fertilisation has also been found to reduce

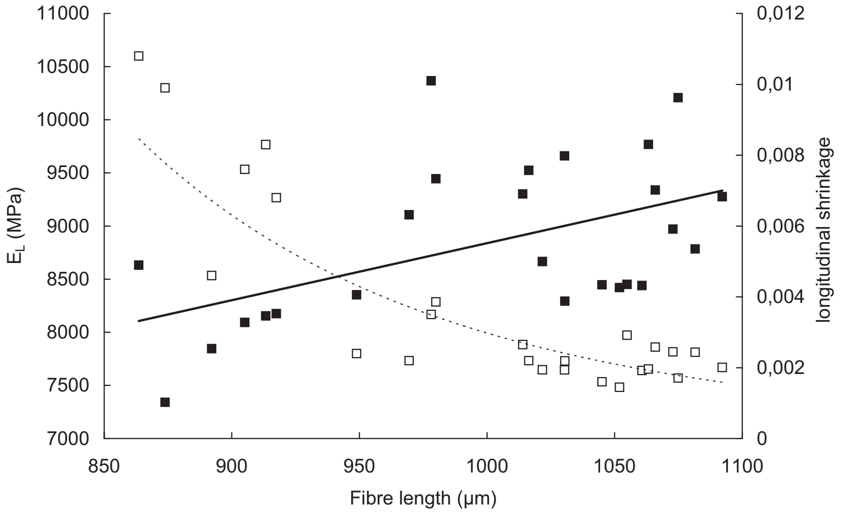

Figure 10. Fibre length was significantly positively regressed with E_L (black squares, solid line: $y = 5.37x + 3473$, $R^2 = 0.27$, $P = 0.008$) and negatively related to longitudinal shrinkage (white squares, dashed line: $y = 7E + 18x^{-7.12}$, $R^2 = 0.76$, $P < 0.001$).

Table II. Comparison of wood mechanical and physical characteristics from the present study on plantation-grown trees with those from the literature on trees harvested from the natural forest.

Source	E_L (MPa)	D_w(kg/m^3)
Brunck et al. [8]	7800	440
Christy et al. [12]	7800	440
Bakraji et al. 2002 [2]	–	550-650
Ngavoura [33]	9360	374
MatWeb [31]	9100	430
Present study	8626	451

fibre length in temperate conifers [30], but soil chemical properties of the two plantations were not measured in our study.

As there are few differences in mechanical and physical properties between JW and AW, it could be considered that wood from young trees (short rotation stands) has a similar economical value to that from older trees. However, short rotation stands for okoumé do not yet exist in Gabon. Trees are harvested when DBH reaches 0.7 m, usually around the age of 70 y in natural forest conditions. Nevertheless, in our study, trees from the Bokoué plantation had already attained this DBH by the age of 41 y, and trees from the M'voum stand had almost reached this size. Hence, plantation-grown trees appear to have faster growth rates compared to trees from the natural forest, but a comparative study should be carried out to confirm this. It should also be possible to reduce rotation lengths in plantations of okoumé to around 45–50 y, particularly as it seems wood characteristics remain fairly homogenous.

Radial growth was significantly greater in trees from the Bokoué plantation, even though wood physical and mechanical properties varied little between the two plantations, although more parameters should be evaluated. Comparing our data with those from trees harvested in the natural forest, it can be seen that wood mechanical characteristics are similar and in some cases, E_L and D_w are greater in plantation-grown trees (Tab. II). Therefore, plantation-grown okoumé can be considered as a viable alternative to the more costly method of extracting trees from natural forests, which may also be potentially damaging to the ecosystem in which these trees grow. Nevertheless, plantation grown trees also need to be suitable for harvest in terms of stem volume and straightness.

It is surprising that no significant relationship existed between mean D_w at 12% moisture content and cambial age, as a significant positive relationship existed between D_w and mean E_L. Similarly, no significant relationship existed between FSP calculated for either radial or tangential directions and D_w, yet a significant negative regression was found between radial FSP and E_L. FSP has been found to decrease in denser wood [4], however, variability in D_w across the radial stem sections was extremely high (Fig. 6), therefore it was too difficult to observe any relationships with either cambial age or FSP. It is not known why D_w is so variable within okoumé and this phenomenon could be the focus of future studies. Although D_w has been found to increase with age in other tropical species e.g. Togolese teak, [22], this is not always the case, e.g. in teak from Kerala, radial variation in specific gravity was fairly uniform [5] and in some species e.g. *Eperua* spp., actually decreased with age [16]. Dumonceaud [15] also found that in the temperate species *Castanea sativa* Mill., wood density was higher in JW. In okoumé, mean D_w was low at only 450.8 ± 3.7 kg/m^3 thus can be considered as a lightweight wood [18]. This property is a major factor influencing wood quality [1], and in particular, is one of the characteristics governing natural durability, along with extractive content. The natural durability of okoumé wood has not yet been determined, but should be quantified in future studies if this species is to be valorised for uses other than plywood.

Segmented linear regression analysis show that JW forms up to the ages of 10–20 y in okoumé. However, more wood properties should be measured in okoumé, which could better define the boundary between JW and AW e.g. microfibril angle, cell wall thickness, compression and bending strength, vessel density and diameter. Bhat et al. [5] found that the best indicators of demarcation between JW and AW in teak were microfibril angle and vessel density. Nevertheless, our results suggest that although plantation-grown okoumé wood is fairly homoxylous, ring width, fibre cell length and longitudinal shrinkage may be used as indicators of the demarcation between JW and AW, although differences may depend on the plantation's geographical location. Our results also show that plantation grown okoumé is comparable to that from natural forest conditions, both in terms of growth and mechanical/physical properties. Therefore, by carrying out a sustainable management of okoumé plantations, exploitation of natural forests will be lessened. Plantations could also be extended beyond the Estuary region.

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