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Basic wood density variations of *Parkia velutina* Benoist, a long-lived heliophilic Neotropical rainforest tree

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Photo 1.
Leaves, flowers and fruits of *Parkia velutina*.
Photo É. Nicolini.

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RÉSUMÉ

Variations de la densité du bois de *Parkia velutina* Benoist, essence à longue durée de vie des forêts humides néotropicales

L'analyse de la densité radiale des bois tropicaux révèle des profils linéaires et parfois curvilignes. Ce type d'étude ne prend généralement pas en compte les variations longitudinales, qui sont considérées comme similaires aux variations radiales. La présente étude vise à mettre en lumière (1) un nouveau profil curviligne de la densité radiale du bois, (2) des différences d'amplitude entre les gradients radiaux et longitudinaux et (3) à classer les variations de la densité du bois (DB) selon différentes échelles pour *Parkia velutina*, essence émergente des forêts humides néotropicales. La variabilité de la densité du bois a été évaluée sur des rondelles entières recueillies sur six arbres abattus et des carottes radiales prélevées sur dix arbres sur pied, et le taux de croissance en hauteur par des prélèvements sur un axe dominant. Cette essence montre des taux de croissance très élevés indicatifs d'un tempérament héliophile. La DB varie de 0,194 à 0,642 g/cm^3, amplitude rarement observée au sein d'un même arbre. La variation radiale de la DB est curviligne, l'amplitude radiale étant généralement plus faible qu'en longitudinal. En conséquence, pour les arbres matures, les valeurs DB dans les houppiers sont plus élevées que dans le tronc. Les variations de la DB peuvent être très significatives à différentes échelles. Le partitionnement de la variance montre également que l'estimation intra-individu de la DB pour l'essence *Parkia velutina* est plus précise si l'on prend en compte à la fois le gradient longitudinal et radial.

Mots-clés : profil curviligne, intra-arbre, essence tropicale, Guyane française.

ABSTRACT

Basic wood density variations of *Parkia velutina* Benoist, a long-lived heliophilic Neotropical rainforest tree

Investigations of basic radial wood density (WD) in tropical trees revealed linear patterns and some curvilinear patterns. Studies usually disregard longitudinal variations, which are often considered to be similar to radial variations. This study aimed to show (1) a new radial curvilinear WD pattern, (2) differences in amplitude between radial and longitudinal gradients and (3) to partition WD variations according to different scales in *Parkia velutina*, an emergent tree found in Neotropical rain forests. We collected full discs from six felled trees and radial cores from 10 standing trees to check WD variability, plus one dominant axis per tree for analysis of height growth rates. This species showed very high growth rates indicative of heliophilic habits. WD varied from 0.194 to 0.642 g/cm^3. Such amplitude is rarely observed within the same tree. Radial variation in WD was curvilinear, with an amplitude generally less than the longitudinal amplitude. Consequently, in mature trees, WD values in the crown were higher than those in the outer trunk. WD variations can be highly significant at different scales. The variance partitioning also revealed that the whole WD range of *Parkia velutina* is more accurately estimated intra-individually when both longitudinal and radial gradient are covered.

Keywords: curvilinear pattern, intra-tree, tropical species, French Guiana.

RESUMEN

Variaciones de la densidad básica de madera de *Parkia velutina* Benoist, especie longeva de las selvas neotropicales

El análisis de la densidad radial básica de las maderas tropicales revela patrones lineales y, en ocasiones, curvilíneos. Los estudios no suelen integrar las variaciones longitudinales, consideradas como similares a las variaciones radiales. Este estudio tiene como objetivo poner de manifiesto (1) un nuevo patrón curvilíneo de la densidad radial de la madera, (2) las diferencias de amplitud entre los gradientes radiales y longitudinales y (3) clasificar las variaciones de la densidad de la madera (DM), según distintas escalas, de *Parkia velutina*, especie emergente de los bosques húmedos neotropicales. Se evaluó la variabilidad de la densidad de la madera en rodajas completas sacadas de seis árboles talados y de cilindros radiales extraídos de 10 árboles en pie; además, se calculó la tasa de crecimiento de la altura mediante muestreos a lo largo de un eje dominante. Esta especie muestra unas tasas de crecimiento muy altas, indicativas de su comportamiento heliófilo. La DM varía de 0,194 a 0,642 g/cm^3, una amplitud raramente observada dentro del mismo árbol La variación radial de la DM es curvilínea, la amplitud radial suele ser menor que la longitudinal. En consecuencia, en árboles maduros, los valores de DM en la copa son más altos que en el tronco. Las variaciones de la DM pueden ser muy significativas en diferentes escalas. La distribución de la varianza muestra asimismo que la estimación intraindividuo de todo el rango de la DM de *Parkia velutina* es más precisa si se tienen en cuenta tanto el gradiente longitudinal como el radial.

PALABRAS CLAVE: patrón curvilíneo, intra-árbol, especie tropical, Guayana Francesa.

Introduction

Wood density is now considered as a major tree functional ecological trait because it includes the expression of the genome, the ecological temperament and the history of tree functioning. Among tropical trees, basic wood density (WD), defined as wood dry mass divided by fresh volume (Kollmann and Côté, 1968), varies between 0.1 to more than 1.2 g/cm^3 (Chave *et al*., 2009; Zanne *et al*., 2009). This huge variation between species is related to different stages of ecological succession. Heliophilic species have a much lower WD than sciaphilic species (Wiemann and Williamson, 1988; Nock *et al*., 2009). Although, variation in WD has been shown to be highest between species (Maniatis *et al.*, 2011), both within species and within tree variation (especially in tropical emergent species) are substantial (Nock *et al*., 2009; Osazuwa-Peters *et al*., 2014; Plourde *et al*., 2015; Wassenberg *et al*., 2015). Indeed, our knowledge about within tree WD variations and its functional significance has increased significantly in recent decades.

Diameter at breast height (DBH), followed by WD are the best predictors of above-ground biomass (AGB) and of carbon sequestration by trees (Ketterings *et al*., 2001; Chave *et al*., 2009, 2014; Vieilledent *et al*., 2012; Zhang *et al*., 2012). Consequently, a better knowledge of radial and longitudinal variations in WD within the tree will enable to more accurate estimates of the carbon stored by a given ecosystem. This is particularly applicable in the case of tropical forests, which contain a high diversity of tree species (Whitmore, 1990) and represent the main stock of carbon (Lewis *et al*., 2009).

Reaching the canopy is challenging for an individual tree due to high stand density and strong competition for light. To face this challenge, trees have evolved different biomass allocation strategies that influence both the range and the way that WD varies radially (*i.e.* from pith to bark). At the lower end of the shade tolerance continuum, pioneers and more generally heliophilic species increase rapidly in height to reach the light as fast as possible. This rapid increase in height is enabled by the production of low WD (Woodcock and Shier, 2002). When the tree crown reaches the canopy, its environment changes and growth in height decreases in favour of the development of the crown, which, in turn, creates mechanical stresses due to the tree's increasing self-weight and/or wind forces (Woodcock and Shier, 2002). This change triggers the production of relatively higher WD in order to maintain mechanical stature (Wiemann and Williamson, 1988, 1989; Rueda and Williamson, 1992; Woodcock and Shier, 2002; Nock *et al*., 2009). Inversely, at the other end of the shade tolerance continuum, shade tolerant or sciaphilic species grow more slowly and initially produce denser, stiffer more resistant wood, which is interpreted as an adaptation to resist pests and the falling leaves/branches of taller neighbouring trees (Woodcock and Shier, 2002; Muller-Landau, 2004).

WD can thus vary radially within tree (Wiemann and Williamson, 1988, 1989; Woodcock and Shier, 2002; Nock *et al*., 2009; Hietz *et al*., 2013). This radial variation, estimated as the slope of the regression of WD on the distance from the pith, is strongly correlated with tree age but not with tree size, suggesting an ontogenetic control of radial WD variation (Rueda and Williamson, 1992; De Castro *et al.*, 1993; Nock *et al*., 2009; Williamson and Wiemann, 2010, 2011; Williamson *et al*., 2012). This assumption holds only for species with a linear pattern. However further studies illustrated substantial diversity in radial gradients: four main patterns of variation in radial WD are reported in the literature. Patterns showing a linear radial increase with low values near the pith and high density values near the bark (Panshin and De Zeeuw, 1980; Wiemann and Williamson, 1988; De Castro *et al*., 1993; Williamson and Wiemann, 2010; Osazuwa-Peters *et al*., 2014) are associated with early successional behaviour (Woodcock and Shier, 2002), whereas patterns showing a linear radial decrease with high values near the pith and lower density near the bark (Panshin and De Zeeuw, 1980) are associated with late successional behaviour (Woodcock and Shier, 2002). The two other WD radial patterns are nonlinear with a concave or convex pattern (Williamson *et al*., 2012; Osazuwa-Peters *et al*., 2014). However, any successional behaviour was seen to be associated with the last non-monotonic pattern. Still, one could think that this pattern characterizes a heliophilic strategy, as shown by Williamson *et al.* (2012) in *Schizolobium parahyba* a typical short-lived Neotropical pioneer species.

Most studies focused on radial variation in WD (Butterfield *et al*., 1993; Woodcock and Shier, 2002; Nock *et al*., 2009; Williamson and Wiemann, 2010, 2011; Williamson *et al.*, 2012; Hietz *et al*., 2013; Schüller *et al*., 2013; Osazuwa-Peters *et al*., 2014), whereas little is known about longitudinal variation in WD (Rueda and Williamson, 1992; Wiemann and Williamson, 2014; Wassenberg *et al*., 2015), probably because longitudinal pattern of wood properties has generally been considered to be similar to radial pattern (Lachenbruch *et al*., 2011) due to the same physiological age of the cambium at tree base and at tree tip.

In this paper, we show the entire WD pattern of a long-lived heliophilic forest tree by answering the two following questions: (1) What do the radial and longitudinal variations in the WD of the trees look like? (2) What is the pattern of radial variation in WD?

We chose *Parkia velutina* Benoist (Leguminosae: Mimosoideae), an emergent forest tree widely but discontinuously distributed in the Brazilian and Peruvian Amazon, French Guiana, eastern Venezuela and in Colombia west of the Andes (Hopkins, 1986). Not used in French Guiana, big trees are peeling for veneer industry in Brazil, when the heart is healthy. This species usually has low values of WD (about 0.4 g/cm^3, Zanne *et al*., 2009), but is a long-lived heliophilic species, *i.e.* intermediate between pioneer and hemi-tolerant, making this emergent Neotropical forest species particularly attractive to investigate WD variations within a tree, with respect to tree architecture and ontogeny.

Material and methods

Study site and climatic typology

The study was conducted at the Paracou experimental site in the lowland tropical rainforest of French Guiana (5° 18' N, 52° 55' W) (Gourlet-Fleury *et al.*, 2004). The site receives nearly two-thirds of the annual 3,041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October. A daily mean temperature of 25.8 °C is almost constant over the year. The experimental site is a stand of old growth forest dominated by Leguminoseae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae (Sabatier and Prévost, 1989).

Tree sampling and measurements

Since we knew very little about *P. velutina*, we first measured the height, diameter, architectural stages of development, crown position in a population of 90 individual forest trees. Height was assessed using a laser meter (Haglöf Vertex Laser L400) and diameter was measured using a dendrometer placed higher than breast height (2-3 m) to avoid buttress effects. In addition, we assessed crown architecture suspected to significantly affect WD. Like many species, *P. velutina* reaches its mature stage through a reiterative process (Oldeman, 1974), which changes the tree's architecture through the duplication of the architectural unit. Three architectural stages of development (ASDs) were recorded (figure 1d): ASD1 trees with sequential branches borne by an orthotropic trunk, ASD2 trees with erect branches ("reiterated branches") forming the future fork at the top of the trunk and some sequential branches always present below the fork, and ASD3 trees with reiterated branches forming a hemispherical shaped crown, whereas sequential branches are no longer present. Among our 90 trees, we classified 42 ASD1, 19 ASD2 and 29 ASD3 trees.

Next, among the 90 trees, we selected 10: one ASD2 tree (N°4) and nine ASD3 trees (N°6, 7, 9, 10, 11, 12, 13, 14 and N°15) (table I). From each, we extracted one radial wood core above breast height (between 2 and 6 m from the base of the trunk) with a 5-mm diameter increment borer, while a climber collected one dominant branch in the crown.

In addition, to be sure of observing the entire range of WD variability, we felled three young trees (ASD1: N°1 and N°2; ASD2: N°3) and two large adult trees (ASD3; N°5 and N°8, table I) among the 90 forest trees *plus* a third adult tree (ASD3; N°16 growing in the open condition in a large logging gap created 23 years ago). It was not the biggest tree to avoid a hollow trunk (40 cm ‹ D ‹ 50 cm, figure 1). For each of these six trees, three wood discs were collected between the base of the trunk and the top of the crown: above breast height (between 2 and 6 m from the base of the trunk), below the fork and in the crown. In the field, the discs and the radial wood cores were sealed in plastic bags and plastic tubes, respectively, to prevent drying, and then stored in the refrigerator until the measurements were made.

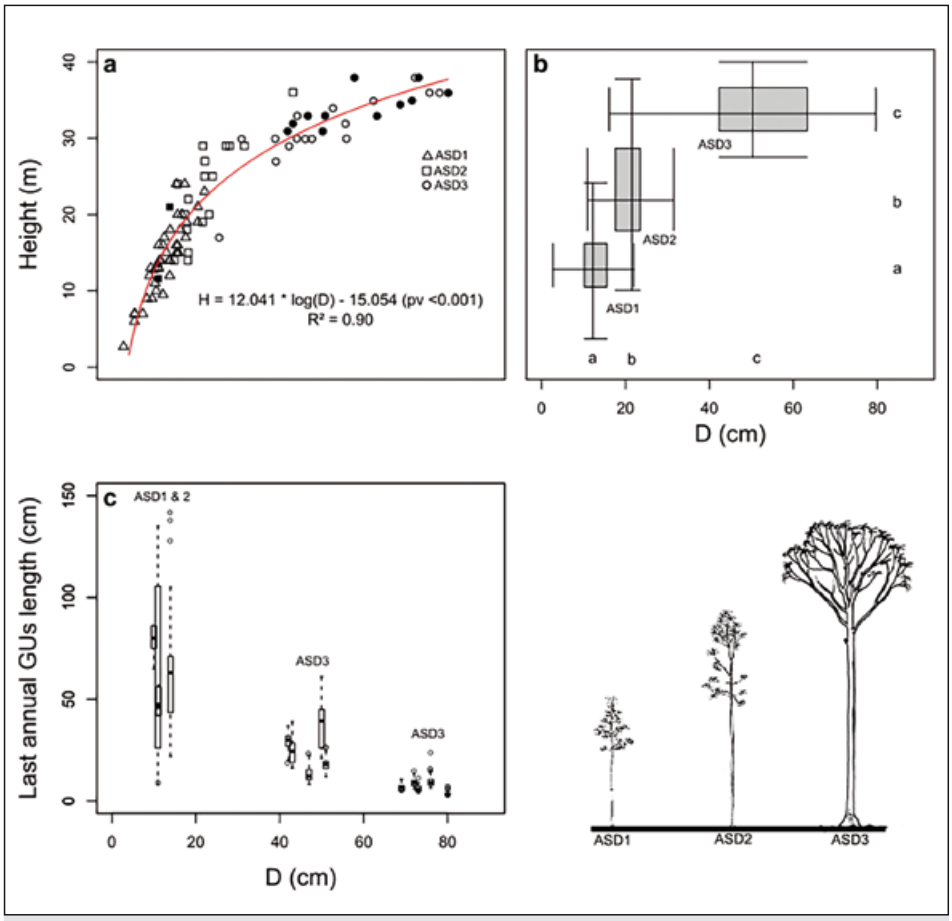

Figure 1.
a) Height as a function of diameter (D) and of the architectural stage of development (ASD) of 90 trees of *Parkia velutina*. Closed symbols represent the sampled trees. The red line represents the fitted function H=a*log(D)+b. b) Diameter (D) and height according to the architectural stage of development (ASD). Kruskal-Wallis tests are significant at $\alpha = 0.05$. The different letters correspond to significant differences between groups after *post-hoc* multiple comparison. c) Length of last annual growth units (GUs) as a function of tree diameter (D). d) Architectural stage of development (ASD) of *P. velutina*.

Table I.
Description of 16 sampled trees for WD measurements. ASD: Architectural stages of development. CP: Crown position. Trees with an asterisk are felled trees.

Tree	Diameter (cm)	Height (m)	ASD	CP
1*	10	12.7	1	4
2*	11	13.5	1	3
3*	11	11.6	2	3
4	14	21	2	3
5*	42	31	3	4
6	43	32	3	4
7	47	33	3	4
8*	50	31	3	5
9	51	33	3	4
10	58	38	3	4
11	69	34.5	3	4
12	72	35	3	4
13	73	38	3	5
14	76	36	3	4
15	80	36	3	5
16*	52	26	3	5

Measurements of basic wood density (WD)

A diametral sample (*i.e.* bark to bark through the pith) of 2*2 cm section was extracted from each wood disc taken from the six felled trees (N°1, 2, 3, 5, 8 and 16) and tangentially cut into 0.5 cm segments from bark to bark for the young trees (N°1, 2 and 3) and into 1.5 cm segments for the adult's trees (N°5, 8, 16), in such way that ensured the pith was included in a single segment.

A 2 cm long outer segment (close to the bark) was taken from the core of each 10 additional trees (N° 4, 6, 7, 9, 10, 11, 12, 13, 14 and N°15). In addition, for these 10 trees, complete wood discs (~ 4 cm in diameter) were also collected from the higher part of dominant branches.

In all cases, the bark and the pith were discarded. Within 24 h of sampling, the green volume of each segment was determined using the water displacement method. The wood samples were oven-dried at 103 °C for 72 h before weighing on a 0.2 mg precision SARTORIUS balance. The WD of each sample was calculated as the ratio of dry mass to green volume (g/cm^3, Kollmann and Côté, 1968).

Measurement of longitudinal growth rates

As the height growth rate is indicative of the development stage of the tree (juvenile, adult mature and senescent), we investigated the height growth rate of the branches of each tree sampled. The limits of the growth units (GUs) making up the axes were located by recognizing morpho-anatomical markers that result from the rhythmic activity of the primary meristems, and which persist in the bark and pith for several years (Barthélémy and Caraglio, 2007). According to a study by Nicolini *et al.* (2012) on *P. velutina*, we retrospectively identified, for different axes per tree, the last successive GUs and measured their lengths.

Statistical analysis

We compared the basal diameter and height of the three different architectural stages (ASD1, ASD2 and ASD3) in 90 trees using a nonparametric Kruskal-Wallis test followed by Tukey's honest significant difference test if the Kruskal-Wallis test was significant. The same procedure was used to compare mean WDs among three heights (basal, under the fork and in the crown) within each felled tree (N°1, 2, 3, 5, 8). Tree N°16 was excluded from this analysis because of its hollow trunk.

Because we wanted to study tree behaviour according to tree size, the trees were classified in three groups as a function of basal diameter and the mean length of the last annual GUs. The first group (1) was composed of four trees (ASD1 and ASD2: N°1, 2, 3 and 4) whose basal diameter was ‹ 20 cm, and whose mean length of the last annual GUs was 68 cm. The second group (2) was composed of five trees (N°5, 6, 7, 8 and 9) whose basal diameter ranged between 40 and 55 cm, and whose mean length of the last annual GUs was 25 cm. The last group (3) was composed of the five largest trees (N°11, 12, 13, 14 and 15) whose basal diameter ranged between 65 and 85 cm, and whose mean length of the last annual Gus was 7 cm. Tree N°10 was excluded since it clearly did not fit in any group. We compared the WD in the crowns and trunks of the three groups with a nonparametric Kruskal-Wallis test followed by Tukey's honest significant difference test if the Kruskal-Wallis test was significant.

We performed a variance component analysis in order to assess the contribution of WD variation among measurement radius, measurement heights and individuals. A random effects model with three nested levels of random effects (individuals/height/radius) was used to estimate the proportion of variation in WD associated with individuals, height and radius. The residual variation included variation associated with segments plus measurement error.

Radial patterns of WD variations at different heights and in different individuals were modelled using multilevel linear mixed effect models (Pinheiro and Bates, 2000). As WD varies radially, we used distance from the pith as a fixed effect and selected three nested random factor levels that enabled modelling of WD at different scales: between and within individuals. These three nested random factors levels were (1) individual, (2) height within an individual and (3) sampled radius within height.

As a curvilinear pattern exists (Williamson *et al.*, 2012; Osazuwa-Peters *et al*., 2014), we first specified a full multilevel mixed-effects quadratic model, for which all terms have random effects at all nested levels considered (table II). Let WD_{ijkd} be the WD value of the d^{th} 0.5 cm interval from the pith of the k^{th} radius within the j^{th} height within i^{th} individual, our full species-level model is expressed as follow:

$WD_{ijkd} = (\beta0+\beta0_i+\beta0_{ij}+\beta0_{ijk}) + (\beta1+\beta1_i+\beta1_{ij}+\beta1_{ijk})*x_{ijkd} + (\beta2+\beta2_i+\beta2_{ij}+\beta2_{ijk})*x_{ijkd}^2 + \varepsilon_{ijkd}$

where x is the distance from the pith, and ε_{ijkd} is the within group error.

We also specified a full multilevel mixed-effects linear model:

$WD_{ijkd} = (\beta0+\beta0_i+\beta0_{ij}+\beta0_{ijk}) + (\beta1+\beta1_i+\beta1_{ij}+\beta1_{ijk})* x_{ijkd} + \varepsilon_{ijkd}$

The most parsimonious model was selected using a series of reduced models that vary in their inclusion of random effects (table II). We derived both quadratic and linear models and computed the corrected Akaike information criterion (AICc) for each derived model. We selected the model with the lowest AICc.

All analyses were conducted in R version 3.2 .2 (R Core Team, 2012) using the "base" (R Core Team, 2012) and "nlme" (Pinheiro *et al.*, 2013) packages.

Results

Allometry, architecture and longitudinal growth rates at the population scale

The diameter and height of the measured trees ranged from 3 to 80 cm and from 3 to 38 m, respectively (figure 1a). The height/diameter relationship for *P. velutina* trees of Paracou was fitted by a linear model involving log(D) (figure 1a, red line). In small trees (D ‹ 25 cm), height increased sharply with increasing diameter but slowed down in bigger trees (D › 25 cm). Height and diameter efficiently distinguished the different development stages of our samples. Only ASD1 trees were observed in the first part of the curve (D mean = 12.6 ± 4.3 cm and H mean = 14.2 ± 4.8 m), whereas ASD3 trees were found only in the second part of the curve (D mean = 52.2 ± 16.1 cm and H mean = 31.6 ± 5.1 m). ASD2 trees symbolized the transition between the two other stages (D mean = 21.5 ± 7.3 cm and H mean = 22.5 ± 6.5 m). Although the different architectural stages overlapped a little, we observed significant differences in diameter (Kruskal-Wallis test; p-value ‹ 0.001) and in height (Kruskal-Wallis test; p-value ‹ 0.001) in the ASD classes (figure 1b). On the basis of the mean length of the last annual GU as a function of tree diameter (figure 1c), we also distinguished three groups that differed significantly both in trunk diameter (Kruskal-Wallis test; p-value ‹ 0.001) and in the length of the last annual GU (Kruskal-Wallis test; p-value ‹ 0.001). To sum up, trees with the biggest diameters had the shortest GU and conversely. So, we were able to distinguish two vigour groups among the ASD3 trees: young adult trees and pre-senescent adult trees.

Contribution of WD variation among individuals, heights, and radius

Variance component analysis depicted the contribution of the three nested factors (individual/height/radius) to the overall variation of WD (figure 2). Surprisingly, the measurement height within individuals contributes to the bulk

Table II.
Description of the fitted linear mixed-effects models. The table presents the inclusion of both fixed and random effects for each model (X). For each model, the number of freedom degrees as well as the corrected Akaike Information criterion (AICc) are presented. The ΔAICc is equal to the difference between the AICc of the model and the lower AICc.

	Fixed effects			Random effects: Individual			Random effects: Height			Random effects: Radius			df	AICc	ΔAICc
	$\beta0$	$\beta1$	$\beta2$	$\beta0_i$	$\beta1_i$	$\beta2_i$	$\beta0_{ij}$	$\beta1_{ij}$	$\beta2_{ij}$	$\beta0_{ijk}$	$\beta1_{ijk}$	$\beta2_{ijk}$			
full	x	x	x	x	x	x	x	x	x	x	x	x	13	-912,36	1,9
m1	x	x	x	x	x	x	x	x	x		x	x	12	-912,45	1,82
m2	x	x	x	x	x	x	x	x	x				10	-827,34	86,92
m3	x	x	x	x	x	x		x	x		x	x	11	-734,42	179,85
m4	x	x	x		x	x	x	x	x		x	x	11	-914,27	0
m5	x	x	x				x	x	x		x	x	9	-710,77	203,49
m6	x	x	x		x	x					x	x	8	-497,73	416,53
fulls	x	x		x	x		x	x		x	x		9	-862,97	51,3
m1s	x	x		x	x		x	x			x		8	-864,97	49,3
m2s	x	x		x	x		x	x					7	-812,88	101,39
m3s	x	x		x	x			x			x		7	-619,81	294,46
m4s	x	x			x		x	x			x		7	-866,97	47,3
m5s	x	x					x	x			x		6	-708,76	205,51
m6s	x	x			x						x		5	-490,18	424,08

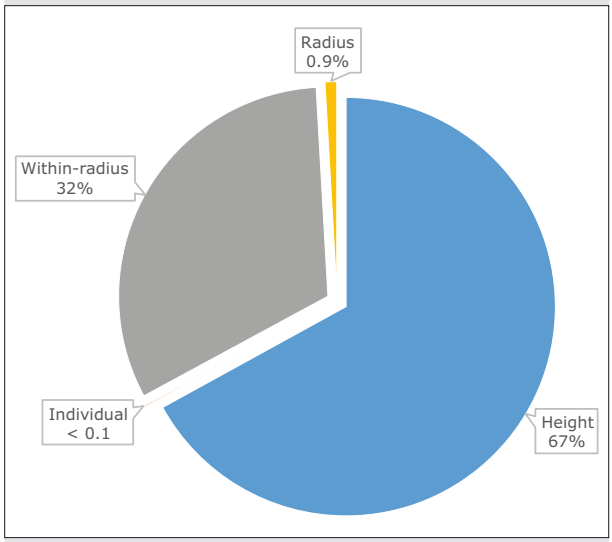

Figure 2.
Variance component analysis depicting the contribution of the three nested factors (individual/height/radius) to the overall variation of WD.

of the variation in WD (67%). Variation among segments within radius is the second contributor to WD variations with 32%. Finally, the variation attributed to the individual level and between radius within height are marginal, with ‹ 1% and ‹ 0.1 % respectively. Height and among-segments levels being the most important, this variance partitioning analysis suggests strong longitudinal and radial variation in WD.

Longitudinal variations in WD with ontogeny and within the sampled trees

The outer WD at the base of the trunk increased gradually from group 1 to group 3 (figure 3), while the WD values in the crown top increased significantly from group 1 to group 2 but not from group 2 to group 3 (figure 3). Finally, the WD at the top of the crown was significantly higher than outer WD at the base of the trunk in both groups 2 and 3 (ASD3 trees), but not in group 1 (ASD1 and ASD2, figure 3).

In the six felled trees, WD ranged from 0.194 to 0.642 g/cm^3 with an average of 0.392 g/cm^3, however the same range was also observed in a single tree (figure 4). Mean WD in the crown was higher than mean WD at the base of the trunk and under the fork. Above all, in three adult trees (N°5, 8 and 16), the WD under the fork was between WD at the base of the trunk and WD in the crown. A visual assessment was sufficient to state that the within disc variability in the crown was less than that in the trunk.

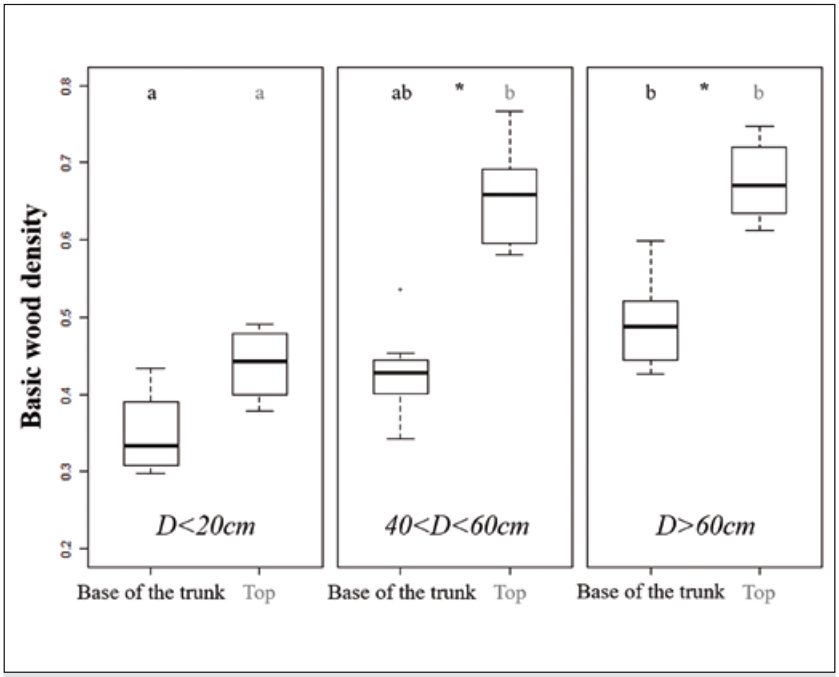

Figure 3.
Mean basic wood density (WD, in g/cm^3) at the base of the trunk and at the top of the crown from the 2 cm outermost segments of the three ontogeny groups (Group 1: n = 4, diameter ‹ 20 cm, Group 2: n = 5, diameter between 40-55 cm, Group 3: n = 5, diameter between 65-85) of trees of *Parkia velutina*. For each group, a Kruskal-Wallis test was used to compare the two heights; the star indicates a significant difference (P › 0.05). For each height, a Kruskal-Wallis test was used to compare the three groups; pairs with the same letter are not significantly different (P › 0.05). Kruskal-Wallis test was followed by *post-hoc* multiple comparison tests if the Kruskal-Wallis test was significant.

Mixed-effects modelling of radial variations in WD

The radial gradient in WD was best fitted by the quadratic regression model (figure 4). AICc is the lowest for the m4 model (AICc = -914.27, table II). This model includes random effect on both linear and quadratic terms for all levels considered. Nevertheless, it only includes random effect on intercept for height, suggesting that the WD at stem centre varies with measurement height. In counterpart, the absence of random effect on intercept for the individual level suggests that the mean WD along the stem centre does not varies between trees.

According to the mixed-effect modelling and the visual assessment of WD variations (figure 4), the lowest values of WD were observed in the inner wood at the base of the trunk whereas highest values were recorded in the crown.

In *P. velutina* N°16, which was an isolated tree, all the outer parts of the basal trunk reached values similar to those observed in the top of the crown (figure 4). This observation agrees with the observed non-significant differences in WD between the base of the trunk and under the fork in this individual.

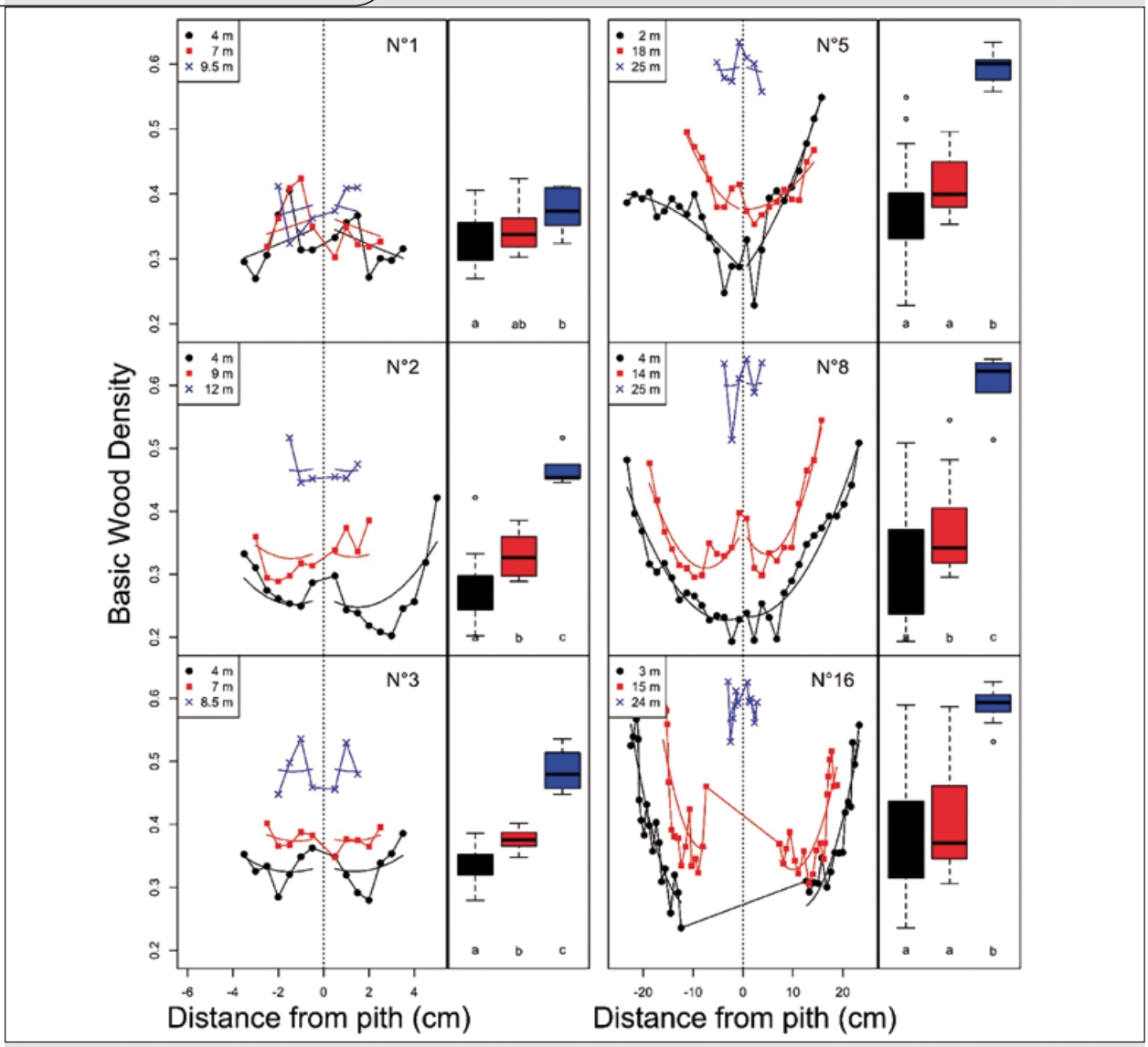

Figure 4.
Radial and longitudinal variation in basic wood density (WD, in g/cm^3) according to distance from the pith in six *Parkia velutina* trees (N°1, 2, 3, 5, 8 and 16). Mean basic wood density (WD) for the three heights (on the trunk (between 2 and 6 m, in black), under the fork (in red) and in the crown (in blue) for the six felled trees. Kruskal-Wallis tests were used to compare the three groups within each individual; pairs with the same letter are not significantly different (P › 0.05). Kruskal-Wallis tests were followed by *post-hoc* multiple comparison tests if the Kruskal-Wallis test was significant.

Discussion

Parkia velutina, a heliophilic long lived trees

In our study, we combined a precise description and fine-scale measurement of WD variability according to the tree ontogenic development and architecture. These approaches allowed us to highlight the fact that growth rate varies considerably with tree diameter and height. These notable variations can be explained by the ecological temperament of *P. velutina*, which is between that of a strictly heliophilic species like *Cecropia obtusa*, for example, and a hemi-tolerant species like *Dicorynia guianensis*.

Like a pioneer species, *P. velutina* reaches the canopy as rapidly as possible, as reflected in the very long successive GUs (more than 150 cm) observed in young trees (*e.g.* in ASD1) (figure 1). Rapid longitudinal growth is enabled by the production of wood with low inertia (low density) (figure 4) and high growth rate as previously reported in tropical pioneers (Williamson *et al.*, 2012). When the tree reaches a sufficient height, and can intercept sufficient light, longitudinal growth starts to slow down in favour of crown expansion (*i.e.* the reiteration process, ASD2-3). At this time, the tree produces denser wood in the peripheral part of the trunk in order to maintain its mechanical stature (Fournier *et al.*, 1991). Therefore, both the strong competition in height growth in the juvenile stages (*heliophilic temperament*) and the crown emergence/lateral expansion in the adult stages (*long lived tree*) may be the main factors that explain the strong radial range of WD encountered in this species.

A very wide range of wood density

The very low initial values of WD (0.2 g/cm³) also point to its heliophilic nature. This is one of the species with the lowest WD values recorded in French Guiana, since only balsa wood (*Ochroma pyramidale*) has a lower value (0.13 g/cm³) (Rueda and Williamson, 1992). However, *P. velutina* also has a relatively high WD, *i.e.* around 0.64 g/cm³, a value frequently encountered in middle successional forest species. In *P. velutina*, we thus found very high WD variability rarely reported in the literature except in *Schizolobium parahyba* (Williamson *et al*., 2012). On the other hand, such variations as we found in this species are not reported in the world wood density database (Zanne *et al*., 2009) which gives a WD value of about 0.40 g/cm³ for *P. velutina*, whereas we found a very wide range of WD variability. This difference between studies is due to the fact that measurements are usually limited to the trunk, and, as a result the real variability of this pattern is probably not observed. In the present study on *P. velutina*, WD variability in the trunk (in the axes below the main fork supporting the crown) mainly ranged between 0.19 and 0.45 g/cm³, whereas WD values inside the crown ranged from 0.45 to 0.64 g/cm³. In studies that only consider certain parts of the tree, wide variability is usually not reported. In our opinion, WD amplitude may often be under-evaluated, since the crown has never previously been included in studies of the WD in this species.

A significant difference between height at the base and top of the trunk

In *P. velutina*, WD values in the crowns were significantly higher than values found in the trunks. Two possible explanations are that the canopy axes are (i) more exposed to wind, and (ii) more ramified than the trunk, as the foliage of each branch subject to strong windage. Stimulation of the branches by the wind may lead to the biosynthesis of stiffer and less fragile wood. In fact, like in *Schizolobium parahyba* (Williamson *et al*., 2012), in *P. velutina*, monopodial growth partially reduces the risk of stem collapse and bending or breakage. The difference in WD in the trunk and the crown observed in the big trees is more rarely observed in small trees. In fact, in our sample, the crowns of the three small trees were not dominant and not been exposed to wind, so an increase in the WD of the crown would not have been necessary. Conversely, tree N°16 had grown in the open (emergent tree), and had to stiffen its structures by increasing its WD to stand up to the wind. This development resulted in a radial gradient mainly observed in the trunk of the trees and less in the crown. Contrary to the majority of previous studies in tropical pioneer species (De Castro, 1993; Williamson and Wiemann, 2010), this gradient was clearly non-linear in the trunk. Extreme radial increases in tropical trees were first reported in *Ochroma pyramidale* (Whitmore, 1973). Since then, the number of internationally published studies on radial variation in tropical trees has drastically increased and the total number of species studied is now about 100 (Wiemann and Williamson, 1988, 1989; Rueda and Williamson, 1992; Butterfield *et al*., 1993; De Castro *et al*., 1993; Woodcock *et al*., 2000; Nock *et al*., 2009; Williamson and Wiemann, 2010, 2011), except Williamson *et al*. (2012) and Osazuwa-Peters *et al*. (2014) and the present study, few showed a curvilinear radial increase. In fact, tree growth is rarely symmetric around the trunk (Williamson and Wiemann, 2011). We observed differences in the pattern of radial variation between two radii within one tree. These differences are due to how the tree responds to local environmental conditions, the reorientation of the stems for better access to light often leads to eccentric growth and the production of tension wood (Pruyn *et al*., 2000).

Variation of WD is essentially explained at the within tree level

Whereas some results show that the bulk of WD variations is first explained at the inter-specific level followed by within-radius level and among-conspecific level (Osazuwa *et al*., 2014), our variance component analysis underlines a different pattern. We assume that this difference is afforded by the integration of samples from different height. As this study focused on a single species, our results are not directly comparable with studies involving several species but can be compared in a relative way. Osazuwa *et al*. (2014) found higher percentage of WD variance explained by the within-radius level than among conspecific level. Here, the longitudinal factor is such important in explaining WD variation that the within radius variation becomes secondary. We can first hypothesise that WD variation in *P. velutina* follows a particular pattern not generalizable to other species. However, Lehnebach (2015) showed the same trend in 16 Fabaceae species sampled at different heights, including *P. velutina* and other representatives of the same genus. More interestingly, as both longitudinal and radial variations explained almost all the variation of WD (~ 99%), the variance explained between individuals, although already weak in other studies (*i.e.* 4% in Osazuwa *et al*. 2014), is negligible when accounting for variation with height. This observation provides interesting perspectives regarding the estimation of the whole range of WD covered by a species. Indeed, WD variations being essentially covered by the intra-tree level, the whole range of WD would be better estimated by replicating measurement at different positions within few individuals than estimating few WD values on a lot of individuals.

Conclusion

Variations in basic wood density (WD) were high at different scales: between sites, between ages, between trees and within individual trees. Our very selective sampling, based on the ontogenic development of the species, enabled us to access the expression of all this variability. Contrary to a local measure of WD, the complete pattern of WD provides satisfactory information on the temperament of the species. It also makes it possible to propose a model of the local density necessary for a better prediction of biomass / carbon models.

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