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ORIGINAL ARTICLE

Radial variations in wood functional traits in a rain forest from eastern Amazonia

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Abstract

Key message **Positive radial trends in WSG were common among light-demanding species, and were mainly explained by radial shift in fiber and parenchyma traits.**

Abstract Trees can modify their wood structure in response to changes in mechanical, hydraulic and storage demands during their life-cycles. Thus, examining radial variations in wood traits is important to expand our knowledge of tree functioning and species ecological strategies. Yet, several aspects of radial changes in wood functional traits are still poorly understood, especially in angiosperm trees from tropical humid forests. Here, we examined radial shifts in wood traits in trunks of tropical forest species and explored their potential ecological implications. We first examined radial variations in wood specific gravity (WSG). Then, we asked what anatomical traits drove radial variations in WSG, and whether WSG, vessel fraction and specific hydraulic conductivity vary independently from each other along the radius gradients. We measured WSG and eight wood anatomical traits, at different radial positions along the trunks, in 19 tree species with contrasting shade-tolerance from a lowland tropical forest in eastern Amazonia. Most species had significant radials shifts in WSG. Positive radial gradients in WSG (i.e., increments from pith to bark) were common among shade-intolerant species and were explained by different combinations of fiber and parenchyma traits, while negative radial shifts in WSG (e.g., decreases towards the bark) were present in shade-tolerants, but were generally weakly related to anatomical traits. We also found that, in general, WSG was unrelated to vessel fraction and specific hydraulic conductivity in any radial position. This study illustrates the contrasting radial variations in wood functional traits that occur in tree species from a humid lowland tropical forest. In particular, our results provide valuable insights into the anatomical traits driving WSG variations during tree development. These insights are important to expand our knowledge on tree ecological strategies by providing evidence on how wood allocation varies as trees grow, which in turn can be useful in studying trait-demography associations, and in estimating tree above-ground biomass.

Keywords Wood functional traits · Radial variation · Tree functioning · Tropical trees · Wood anatomy

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Introduction

The study of wood traits has a long tradition in wood technology and wood anatomy (e.g., Zobel and van Buijtenen 1989; Carlquist 2001; Baas et al. 2016). Yet, with the emergence of trait-based ecology in the last decades (Westoby and Wright 2006; Shipley et al. 2016), there has also been an increasing interest in studying wood traits from an ecological perspective (i.e., Larjavaara and Muller-Landau 2010, Beeckman 2016). One basic assumption of trait-based ecology is that, in broad interspecific comparisons, trait variation among species would be greater than among or within-individual trait variations (Shipley et al. 2016). Hence, most trait-based studies on wood have used mean trait values per species, overlooking the often remarkable trait variation that exists within trees (i.e., Hietz et al. 2013; Olson and Rosell 2013). As a consequence, several aspects of radial (i.e., from pith to bark) changes in wood traits in individual trees, and their ecological significance, are still poorly understood (Lachenbruch et al. 2011; Hietz et al. 2016; Rungwattana and Hietz 2017). In this sense, studying these radial changes in wood traits may increase our understanding of stem allocation patterns and functioning during tree development, and consequently of life-history variations across species.

Wood specific gravity (WSG) is considered a central trait to understand tree functioning and species ecological strategies (Westoby and Wright 2006; Chave et al. 2009). For instance, WSG is generally related to biomechanical (King et al. 2006, Anten and Schieving 2010) or hydraulic properties (Santiago et al. 2004, 2018), and is hypothesized to mediate a trade-off between stem construction and maintenance costs (Larjavaara and Muller-Landau 2010). Moreover, it is well established that there can be important radial changes in WSG within trees (Hietz et al. 2013; Osazuwa-Peters et al. 2014; Plourde et al. 2015). These radial trends in WSG may reflect the combined effects of the age of the vascular cambium, which can determine the size of wood cells produced (Lachenbruch et al. 2011), or tree diameter, since trees adjust their wood anatomy in response to size-related changes in mechanical and hydraulic demands (Nock et al. 2009; Williamson and Wiemann 2010a; Rungwattana & Hietz 2017). Alternatively, these radial changes might be a consequence of the deposition of wood extractives in the inner wood during heartwood formation (Lehnbach et al. 2019, but see Larjavaara and Muller-Landau 2010).

In angiosperms, wood is composed of three main cell types: fibers that mainly provide mechanical support, vessels responsible for sap transport, and living parenchyma cells that, among others, store and transport nutrients and secondary metabolites (i.e., Carlquist 2001). As specific gravity (SG) is an emergent property of wood that is affected by the relative amount of fibers, vessels and parenchyma cells, quantifying radial shifts in their proportions and morphologies can help us attain a broader and deeper understanding of the functional bases underlying radial trends in WSG (i.e., Zieminska et al. 2015). A number of studies have examined the anatomical drivers of interspecific variations in WSG of angiosperm trees. These studies have shown that WSG can be driven by fiber traits such as fiber fraction or wall thickness (i.e., Martínez-Cabrera et al. 2009; Fortunel et al. 2013; Zieminska et al. 2013). Yet, this trend may not always hold for all species, especially for species with intermediate (*c*. 0.50–0.80) WSG, since some species with similar values of WSG may have contrasting wood anatomies (Zieminska et al. 2015).

Studies aiming at understanding the anatomical bases of radial changes in WSG have been mostly done on temperate gymnosperm species (reviewed by Lachenbruch et al. 2011), while very few studies have been conducted on tropical angiosperm forest trees (e.g., McDonald et al. 1995; Rungwattana and Hietz 2017). In one of these few studies, Rungwattana and Hietz (2017) showed that the anatomical drivers of radial shifts in WSG varied substantially among five tree species from a dry tropical forest. Yet, these results cannot be easily extrapolated to other tropical forests. First, radial variations in WSG are thought to be less pronounced in trees from dry forests compared to trees from humid forests, possibly because canopy stratification and light competition tend to be lower in dry forests (Wiemann and Williamson 1989). Second, WSG tend to be higher in dry forests than in humid ones (Chave et al. 2009), suggesting that in dry forest wood a large stem cross-sectional area is occupied by fibers. Third, trees from dryland areas also tend to have higher total parenchyma fractions than trees from humid areas (Morris et al. 2016). Thus, it is likely that radial gradients in wood traits reported for dry forest trees may differ considerably from those of humid forest trees. Despite the existence of valuable studies on WSG (i.e., Nock et al. 2009; Williamson and Wiemann 2010a; Hietz et al. 2013; Plourde et al. 2015) and vessel lumen size (i.e., Olson and Rosell 2013; Hietz et al. 2016), detailed aspects of radial variations in wood traits in trees from humid tropical forests are still unknown.

An additional aspect to consider when studying the underlying anatomical drivers of radial changes in WSG is that, while WSG and fiber traits represent one major axis of variation in wood structure (Martínez-Cabrera et al. 2009; Fortunel et al. 2013; Zieminska et al. 2013), there is also substantial anatomical variation that is independent of WSG (Zieminska et al. 2015). For example, vessel fraction (F_V), i.e., the amount of stem cross-sectional area allocated to vessels, is thought to reflect an axis of variation in xylem structure that is largely orthogonal to WSG (i.e., Zanne et al.

2010). This independence between traits may be significant because it suggests that hydraulic and mechanical functions might be decoupled (Hietz et al. 2016). There are good biophysical and anatomical reasons why these functions should be independent. For example, since specific hydraulic conductivity (K_S) increases exponentially with vessel lumen area (V_A, Tyree and Zimmermann 2002), trees may adjust K_s by small increments in V_A, without considerable variations in F_V or WSG (Poorter et al. 2010; Zanne et al. 2010). Similarly, for a constant fiber fraction (F_F), trees can modulate WSG by increasing fiber wall thickness (F_{WT}) (i.e., Ziemინska et al. 2013). Hence, it appears that trees can adjust F_V or K_S independently of WSG and mechanical stability (Hietz et al. 2016). It remains unclear, however, if these orthogonal relationships between F_V, K_S and WSG are radially constant.

In this study, we quantified radial changes in wood functional traits, and analyzed correlations between these traits, in 19 tree species from a lowland humid forest in eastern Amazonia. Our general aim was to broaden our understanding of the anatomical bases of radial trends in wood specific gravity. In particular, we wanted to answer the following questions: (i) How does wood specific gravity change with tree diameter (ii) What are the main anatomical drivers of radial trends in wood specific gravity? (iii) Do vessel fraction and specific hydraulic conductivity vary independently of wood specific gravity as trees grow larger?

Materials and methods

Study site

The research took place in the Paracou field station, a lowland tropical humid forest located in northern French Guiana (5° 18' N, 52° 55' W). The site has a mean annual temperature of 28.4 ºC, and annual rainfall averages 3.000 mm with a marked dry season from August to November, and a distinct rainy season between March and June (Wagner et al. 2011). In terms of floristic composition and species richness, the forest of Paracou is representative for northeaster Amazonia (ter Steege et al. 2006) and the Guiana Shield (ter Steege et al. 2000). Detailed descriptions of soils of Paracou can be found in Ferry et al. (2010) and Vincent et al. (2011).

Species and sampling

At Paracou, a 25-ha and three 6.25-ha permanent plots were established, between 1991 and 1992, to study the dynamics of an undisturbed tropical rain forest, and censuses of all stems with DBH > 10 cm have been conducted every five years since then (Gourlet-Fleury et al. 2004). Based on 23-year census data from these plots, we selected 19 tree species with broad gradients of variation in growth rates and shade-tolerance, and belong to some of the most dominant families at the site, namely Fabaceae, Lecythidaceae and Chrysobalanaceae (Table 1; Hérault et al. 2011; Baraloto et al. 2012). Our study species also spanned a wide spectrum of mean wood specific gravity ranging from 0.30 to 0.97 (Table 2). In total, we sampled 65 mature trees (DBH > 10 cm), with two to five individuals per species (Table 1). All wood samples were collected in Paracou, except for *Cordia alliodora*, *Schefflera morototoni*, *Cecropia obtusa* and *Miconia tschudyoides*, that were collected in a nearby secondary forest. Samples of eight species (e.g., all legume species, *Cordia alliodora* and *Bagassa guianensis*) were from previous studies (Bossu 2015; Lehnebach et al. 2019).

Wood samples were collected, in 2014 and 2018, from stem discs taken at breast height, from cut-down trees. From each wood sample, wood segments of 2 × 2 cm size were cut and split every 0.5 cm from pith to bark. Whenever possible, heartwood and sapwood were distinguished based on color differences, and sapwood and heartwood lengths were measured. For each wood segment, we measured the radial position with respect to the pith, fresh volume and dry mass. Fresh volume was measured with the water displacement method, and dry mass was obtained after drying the segments at 103 ºC to a constant mass, for 24–72 h. WSG per segment was defined as dry mass over fresh volume (Kollman and Coté 1968). For each tree, wood anatomical analyses were conducted on the segments closest to the pith, and every 1.5 cm until reaching the bark. To characterize wood anatomy, the cross-sectional surface of each wood segment was sanded using a polishing machine with 1200-grit diamond discs, and then samples were cut with a GLS-1 sledge microtome (Gärtner et al. 2015) to get a plane surface. Then, photographs were taken at 5–10 × objective lenses using a reflected light (episcopic) microscope (BFMX, Olympus, Tokyo, Japan), equipped with a digital camera (Canon EOS T6i; Canon Inc., Tokyo, Japan). For each wood segment, between 10 and 20 partially focused images were taken and were then combined using Helicon Focus (Helicon Focus Ltd., Kharkov, Ukraine). Because of its very high WSG (0.97), it was not possible to obtain high-quality anatomical images of *Bocoa prouacensis* and this species was excluded from the anatomical analyses.

From each anatomical image (see Fig. S1), fractions of fibers (F_F), vessels (i.e., vessel lumen, F_V), axial parenchyma (F_{AP}), radial parenchyma (F_{RP}) and total parenchyma (F_{TP}: $F_{AP} + F_{RP}$) per cross-section were measured in the whole image. To calculate cell fractions, wood cell types were manually colored using Photoshop (Adobe Systems Incorporated, USA) and then added automatically using the batch function in the software ImageJ (https://imagej.nih.gov/ij/). Moreover, in each anatomical image, three metrics related to xylem vascular strategies were measured: Vessel lumen area

Table 1 Study species, family, number of trees sampled (n), mean diameter at breast height of trees sampled ($\mathrm{DBH_S}$), mean and maximum diameter at breast height of each species ($\mathrm{DBH_M}$ and $\mathrm{DBH_{MAX}}$, respectively), ecological guilds according to Favrichon (1994), relative growth rates (RGR, mm mm^{-1} year^{-1}), and leaf habit; for 19 tree species from eastern Amazonia. $\mathrm{DBH_M}$ and $\mathrm{DBH_{MAX}}$ were calculated based on data from one 25-ha and three 6.25-ha permanent plots established in Paracou (see Materials and methods)

Species	Family	n	$\mathrm{DBH_S}$ (cm)	$\mathrm{DBH_M}$ (cm)	$\mathrm{DBH_{MAX}}$ (cm)	Ecological guild	RGR	Leaf habit
Bagassa guianensis	Moraceae	5	25.1	35.8	105.7	Long-lived pioneer-Canopy		Deciduous (Loubry 1994)
Bocoa prouacensis	Fabaceae	3	12.3	28.6	52.7	Shade-tolerant-Understory	3.81	Evergreen (Levionnois et al. 2020)
Cecropia obtusa	Urticaceae	3	23.1	15.7	33.3	Pioneer-Understory	5.30	
Cordia alliodora	Boraginaceae	3	44.4	38.9	85.2	Long-lived pioneer-Canopy		Deciduous (Loubry 1994)
Dicorynia guianensis	Fabaceae	5	22.2	47.3	94.7	Semi shade-tolerant-Canopy	2.76	Deciduous (Loubry 1994)
Eperua falcata	Fabaceae	5	45.5	47.7	71.8	Semi shade-tolerant-Canopy	1.91	Deciduous (Loubry 1994)
Eschweilera coriacea	Lecythidaceae	2	30.3	38.2	63.3	Shade-tolerant-Canopy	1.55	Evergreen (Levionnois et al. 2020)
Eschweilera sagotiana	Lecythidaceae	3	20.8	41.4	69.2	Shade-tolerant-Canopy	1.41	Evergreen (Levionnois et al. 2020)
Hirtella glandulosa	Chrysobalanaceae	2	30.3	17.1	40.3	Shade-tolerant-Understory	1.78	Evergreen (Carneiro de Oliveira et al. 2021)
Lecythis persistens	Lecythidaceae	5	22.3	35.9	65.8	Shade-tolerant-Understory	0.91	Evergreen (Levionnois et al. 2020)
Licania alba	Chrysobalanaceae	5	23.7	28.8	49.3	Shade-tolerant-Canopy	0.82	Evergreen (Levionnois et al. 2020)
Miconia tschudyoides	Melastomataceae	2	21.2	15.7	25.8	Pioneer-Understory	1.90	
Oxandra asbeckii	Annonaceae	2	24.6	19.5	33.3	Shade-tolerant-Understory	0.72	
Parkia nitida	Fabaceae	5	23.5	63.1	101.3	Pioneer-Canopy	6.98	Deciduous (Loubry 1994)
Recordoxylon speciosum	Fabaceae	3	14.3	38.2	64.4	Semi shade-tolerant-Canopy	2.18	Deciduous (Loubry 1994)
Schefflera morototoni	Araliaceae	3	41.2	38.6	49.3	Pioneer-Canopy	4.3	Deciduous (Loubry 1994)
Sextonia rubra	Lauraceae	3	42.4	50.5	100.2	Semi shade-tolerant-Canopy	2.15	Deciduous (van der Werff 1997)
Swartzia panacoco	Fabaceae	3	20.5	25.4	51.3	Shade-tolerant-Canopy	0.76	Deciduous (Loubry 1994)
Virola michelii	Myristicaceae	3	31.5	31.8	64.5	Pioneer-Canopy	2.37	Deciduous (Loubry 1994)

$\mathrm{DBH_M}$ of *C. alliodora* were obtained from Bossu (2015), while $\mathrm{DBH_{MAX}}$ were obtained from Vega (1977). $\mathrm{DBH_{MAX}}$ for each species was estimated averaging values of the five largest individuals. RGR were calculated based on 20-year census data from permanent plots established in Paracou

(V_A, mm^2), vessel number (V_N, number of vessels per mm^{-2}) and specific hydraulic conductivity (K_S, kg m MPa^{-1} s^{-1} h). To calculate V_A and V_N, all conduits within each anatomical image were manually colored, counted and measured. K_S was estimated according to the Hagen–Poiseuille equation as

$$K_S = \rho w/(128\eta)\, V_D Dh^4 10^6,$$

where ρw is the density of water at 20° C (998.2 kg m^{-3}) and η is the viscosity of water at 20 °C (1.002×10^{-9} MPa s); Dh is the mean hydraulically weighted vessel diameter given by

$$Dh = \left(\Sigma D^4/n\right)^{1/4}$$

where D is the average of the major and minor axis for each vessel cross-section (in mm) and n is the total number vessels (Tyree and Zimmermann 2002; Hietz et al. 2016). Fiber wall thickness (F_{WT}, µm) was measured by taking

Table 2 Summary characteristics of wood traits measured on 18 tree species from a lowland tropical forest in eastern Amazonia

Trait	Abbrev	Unit	Mean	SD	Range	*n*-fold variation
Wood specific gravity	WSG	unitless	0.61	0.07	0.30–0.97	2.9
Fiber fraction	F_F	% area	63.3	6.89	42–77	1.83
Fiber wall thickness	F_{WT}	µm	4.15	1.29	1.72–7.47	4.34
Vessel fraction	F_V	% area	8.94	2.96	4.30–21,2	4.9
Axial parenchyma fraction	F_{AP}	% area	11.5	9.06	1.68–29.1	17.3
Radial parenchyma fraction	F_{RP}	% area	15.8	3.69	6,09–27,7	4.54
Total parenchyma fraction	F_{TP}	% area	27.6	5.33	12.6–44.2	3.5
Vessel lumen area	V_A	mm^2	0.015	0.006	0.01–0.03	3
Vessel number	V_N	mm^{-2}	5.68	4.12	0.87–21.1	26
Specific hydraulic conductivity	K_S	kg m s^{-1} MPa^{-1} / mm^2	147.7	18.1	46.9–330.1	7.17

Mean, standard deviation (SD), range and n-fold variation are shown

photographs with a 100 × objective lens using a laser microscope (VK 9710, Keyence). Each cross-sectional image (see Fig. S2) was divided in four equal sections and 8 pairs of fibers were randomly selected in each section, for a total of 32 pairs of fibers per image. To obtain F_{WT}, double wall thickness was measured and then divided by two, using ImageJ.

Data analyses

To analyze radial gradients in WSG (question 1), we fitted separate linear models (LM) per species predicting WSG based on radial distance. We also evaluated non-linear equations in these LM, as curvilinear gradients in WSG are common among tropical trees (e.g., Williamson and Wiemann 2010a; Osazuwa-Peters et al. 2014). Previous studies examining non-linear radial trends in WSG have considered mainly quadratic equations (e.g.,Osazuwa-Peters et al. 2014) which, although widely used and flexible, cannot describe some patterns commonly observed during tree growth. Therefore, we fitted linear or curvilinear functions (i.e., quadratic, logistic and cubic) to each WSG-radial distance species plot and compared these models based on Akaike's Information Criterion corrected for small sample sizes (AIC_C), with lower AIC_C scores indicating a better fit to the data. When the difference in AIC_C scores between two models was ≤ 2, we selected the simpler model with fewer parameters (Burnham and Anderson 2002). Finally, we examined residual plots to confirm linear or non-linear trends. We also analyzed radial trends in wood anatomical traits for each species (see Table S1), we used linear or generalized linear models (GLM) to predict each anatomical trait based on radial distance. Yet, in these models we were not able to reliably test non-linear terms because for several trees, particularly the small-to-medium-sized ones, we had only a few radial anatomical measurements.

Table 3 Linear and non-linear models predicting WSG based on radial distance

Species	WSG	
	Best-fit model	R^2
Bagassa guianensis	Linear	**0.95****
Bocoa prouacensis	Linear	**0.72****
Cecropia obtusa	Cubic	**0.90***
Cordia alliodora	Linear	**0.91***
Dicorynia guianensis	Linear	**0.93****
Eperua falcata	Quadratic	**0.69****
Eschweilera coriacea	Linear	0.01
Eschweilera sagotiana	Linear	0.03
Hirtella glandulosa	Linear	**0.48***
Lecythis persistens	Linear	0.02
Licania alba	Linear	0.35
Miconia tschudyoides	Linear	**0.71*****
Oxandra asbeckii	Linear	0.08
Parkia nitida	Linear	**0.88****
Recordoxylon speciosum	Quadratic	**0.87***
Schefflera morototoni	Quadratic	**0.65****
Sextonia rubra	Cubic	**0.46****
Swartzia panacoco	Quadratic	**0.93****
Virola michelii	Linear	**0.94***

Best fit model and its parameters are shown for each species

Coefficient of determination (R^2) of each model is provided

Significance levels are: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Significant radial trends ($P < 0.05$) are given in bold

After examining radial trends in WSG, we studied the anatomical drivers of those trends (question 2). To do so, we analyzed a subset of our dataset consisting of 13 (excluding *B. prouacensis*) species that had significant radial trends in WSG (Table 3). First, we fitted linear mixed models with all possible predictors (i.e., anatomical traits) and species and individuals as random factors. The best-fit model based was selected based on AIC_C, which penalizes models with additional parameters (Burnham and Anderson 2002), and it was as follows:

$$WSG \sim F_F + F_{WT} + F_{AP} + F_{RP} + (1\ |\text{Species Individuals}).$$

We then fitted separate multiple regression models for each of the 13 species, predicting radial shifts in WSG based on F_F, F_{WT}, F_{AP} and F_{RP}. F_{AP} was log-transformed to meet normality assumptions.

As F_V and K_S may vary independently from WSG across species (Zanne et al. 2010; Hietz et al. 2016), we tested if this assumption still holds radially within trees (question 3). To do this, we fitted separate LM per species predicting these traits (i.e., F_V and K_S) based on radial distance. In these models, we included a radial distance-WSG interaction term (DxWSG). Both F_V and K_S were $\log_{10}$ transformed to meet regression assumptions. Lack of significance of the DxWSG interaction term, accompanied by a significant radial change in F_V or K_S, would mean that the radial trend of a given hydraulic trait was independent of WSG. All LM, GLM and multiple regression models were fitted using the "MASS" package (Venables and Ripley 2002) in the software R 3.6.1 (RCore Development Team 2019).

Results

Overall, there was substantial variation in mean wood trait values across species (Table 2). Mean WSG ranged from 0.30 in *S. morototoni* to 0.97 in *B. prouacensis* (2.9-fold variation, Table 2). Fibers, the most abundant cell type, occupied on average 63.3% of wood cross-section and had the lowest variation between traits (1.83-fold variation). Fiber wall thickness averaged 4.15 µm and varied 4.34-fold between species. Total parenchyma (axial + radial) was the second most abundant cell type with a mean fraction of 27.6% and a 3.5-fold variation. Vessel fraction averaged at 8.94% (with 4.9-fold variation). Mean K_S varied from 46.9 to 330.1 (kg m MPa^{-1} s^{-1}) with 7.17-fold variation (Table 2).

Radial gradients in WSG and wood anatomical traits

We found significant radial changes in WSG in 14 out of the 19 study species (74%; Fig. 1, Table 3). Among them, positive gradients in WSG were observed in nine species, mostly corresponding to fast-growing species (e.g., *C. obtusa, S.*

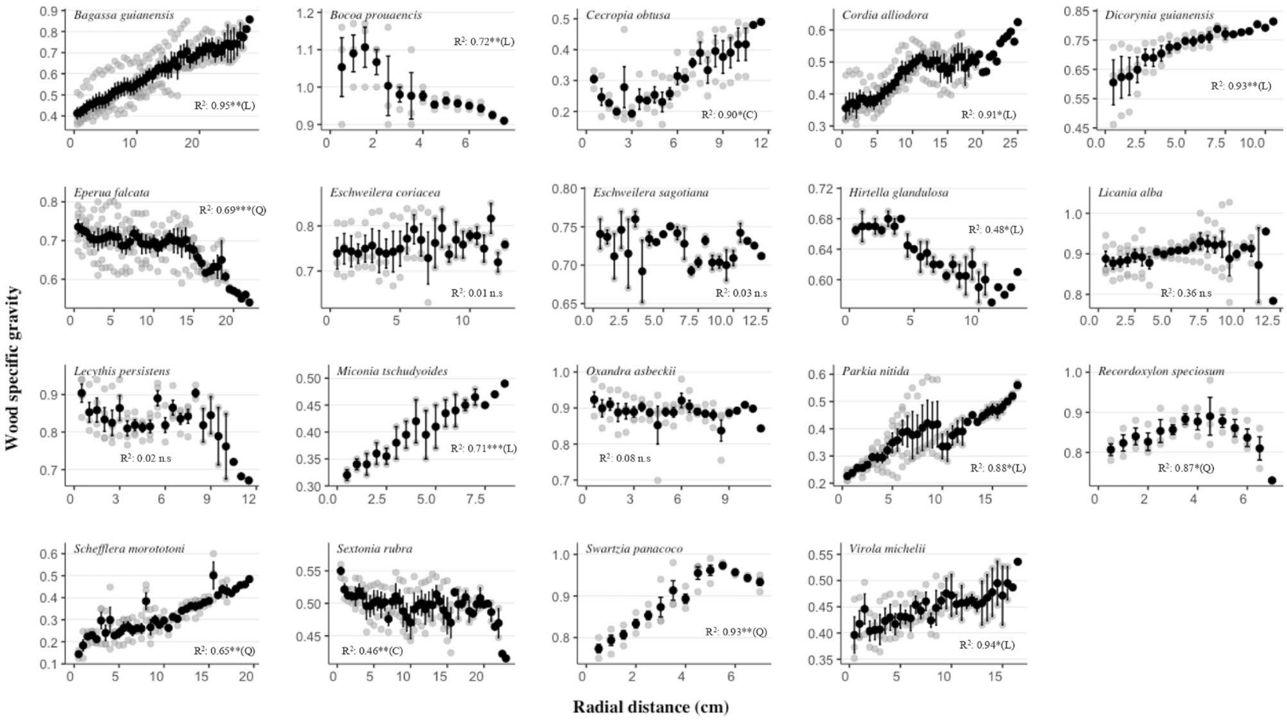

Fig. 1 Radial trends in WSG in 19 tree species from a lowland tropical forest in eastern Amazonia. Grey and black dots represent individual trees and species-mean values, respectively. Error bars denote standard deviation. Coefficients of determination (R^2), significance levels (n.s: $P > 0.05$; $P < 0.05$; $**P < 0.01$; $***P < 0.001$), and best-fit models (C, cubic; L, linear; and Q, quadratic) are provided (see Table 3)

morototoni) or semi shade-tolerants (sensu Favrichon 1994; *Dicorynia guianensis* or *Eperua falcata*); while negative gradients were present in five species (e.g., *B. prouacensis* or *Swartzia panacoco*; three of them are shade-tolerants). Radial gradients in WSG were best fitted by linear models in eight species (57.1%), while quadratic and cubic models best explained radial gradients in WSG in four (28.5%) and two (14.2%) species, respectively (Fig. 1, Table 3). The coefficients of determination of these models (Table 3) suggest that radial trends in WSG are not only common in the study site, but also substantial. Five species had no significant radial shifts in WSG. Not all species showed significant trends in wood anatomical traits, and the signs and coefficient of determination of these trends, when significant, usually varied between species. In general, F_F, F_{AP} and F_{TP} tended to increase with increasing radial distance (Fig. 2, Table S1).

Anatomical drivers of radial gradients in WSG

For the 13 species that had significant radial changes in WSG (Table 3), we examined the anatomical traits underlying those trends by fitting multiple regression models. These models predicted radial changes in WSG in only six species. Among these six species, radial variations in WSG were predicted by different combinations of fiber and parenchyma traits (Table 4). There were two main ways in which trees modulated fiber fractions and morphologies in order to increase WSG radially: increasing fiber wall thickness (F_{WT}) (e.g., *Bagassa guianensis* or *Schefflera morototoni*), or increasing both F_{WT} and fiber fraction (F_F) (e.g., *Virola michelii* or *Miconia tschudyoides*). F_{AP} and F_{RP} had either positive or negative effects on positive radial trends in WSG (Table 4).

Links between vessel related traits and WSG

Vessel fraction (F_V) changed significantly from pith to bark in nine species (Table 5). Of these species, the radial distance-WSG interaction term (DxWSG) was significant in only one species, indicating that these radial changes in F_V were largely independent from WSG (Table 5). Specific hydraulic conductivity (K_S) increased significantly with stem diameter in ten species (Table 5). In three of these species, the DxWSG interaction term was significant, which indicates that variations in K_S were in general independent of shifts in WSG.

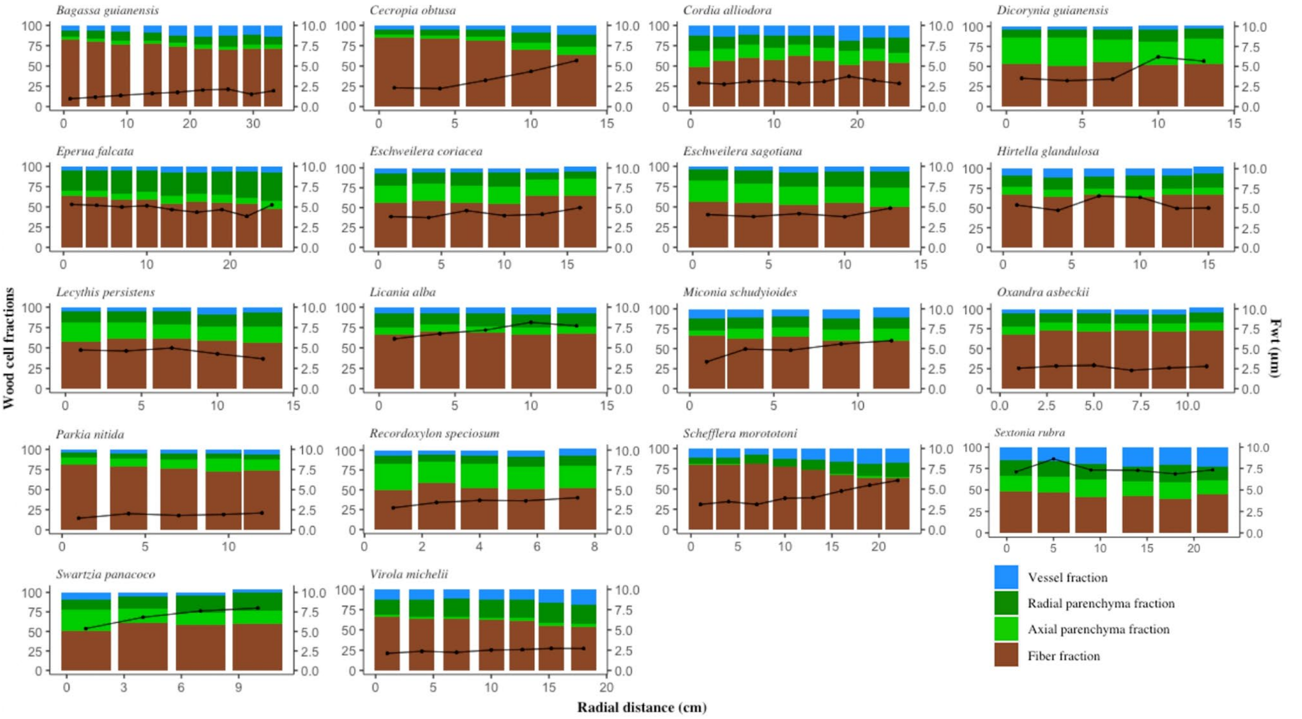

Fig. 2 Radial variations in wood cell fractions and fiber wall thickness (black line; F_{WT}) of 18 tree species from eastern Amazonia

Table 4 Effects of wood anatomical fractions on radial variations of WSG variations for species ($n = 13$) that had significant radial trends in WSG (see Table 3)

Species	Wood anatomical fractions				R^2
	F_F	F_{WT}	F_{RP}	F_{AP}	
Bagassa guianensis	**2.41(–)***	**3.56(+)****	**1.69 (+)***	0.59	0.77
Cecropia obtusa	0.21	0.24	0.51	0.46	0.45
Cordia alliodora	1.52	0.56	0.32	1.21	0.34
Dicorynia guianensis	0.65	0.21	0.03	1.14	0.64
Eperua falcata	0.31	0.41	0.98	1.04	0.53
Hirtella glandulosa	0.14	0.32	1.02	1,71	0.51
Miconia tschudyoides	**2.48(+)***	**3.76(+)****	**2.05(–)***	0.87	0.79
Parkia nitida	**2.15(–)***	0.06	1.25	**3.95(+)****	0.72
Recordoxylon speciosum	1.12	0.03	0.72	1.46	0.62
Schefflera morototoni	**2.63(–)***	**2.37(+)***	1.42	**2.47(–)***	0.92
Sextonia rubra	**2.41(–)***	0.02	**2.31(+)***	**3.22(–)****	0.36
Swartzia panacoco	1.41	0.51	1.11	0.45	0.85
Virola michelii	**2.70(+)***	**3.75(+)****	0.72	**2.92(–)****	0.82

B. prouacensis was excluded from anatomical analyses, see Material and meth

Multiple R^2 values of the corresponding multiple regression models, and *t*-values for each trait are shown

(+) or (−) gives the sign of the effects of wood anatomical traits on WSG variations. Significance levels are: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

Significant effects ($P < 0.05$) are given in bold

Table 5 Linear models predicting vessel fraction (F_V) and specific hydraulic conductivity (K_S) based on radial distance (D), and effects of WSG on significant radial trends in F_V and K_S

Species	F_V		K_S	
	D R^2	$D \times$ WSG X^2	D R^2	$D \times$ WSG X^2
Bagassa guianensis	**0.62(+)*****	**30.1*****	**0.58(+)*****	**1.29*****
Cecropia obtusa	**0.47(+)****	0.04	0.08(+)	3.21
Cordia alliodora	0.24	0.45	– 0.02	4.72
Dicorynia guianensis	0.14	0.71	**– 0.09(+)***	1.72
Eperua falcata	**0.14 ***	0.82	**0.30(+)****	**4.24***
Eschweilera coriácea	**0.47(+)***	1.88	**0.69 ****	1.37
Eschweilera sagotiana	0.22	0.15	**0.94(+)****	**12.6***
Hirtella glandulosa	– 0.04	0.05	– 0.16	0.87
Lecythis persistens	**0.08(+)***	0.95	0.41(+)	0.14
Licania alba	0.10	1.43	**0.07 ****	3.21
Miconia tschuyoides	0.03	0.28	**0.56 ***	2.84
Oxandra asbeckii	**0.17(+)***	1.12	**0.32 ***	1.37
Parkia nitida	0.32	0.11	– 0.09(+)	0.98
Recordoxylon speciosum	0.04	0.17	0.04	1.56
Scheflera morototoni	**0.51(+)***	0.21	**0.30(+)***	2.61
Sextonia rubra	**0.54(+)****	0. 38	**0.54(+)****	2.71
Swartzia panacoco	– 0.03	0.31	0.47	5.21
Virola michelii	**0.15 ***	0.26	0.12	1.07

(+) or (−) gives the sign of F_V and K_S radial trends

Significance levels are: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

Significant radial trends ($P < 0.05$) in K_S and K_S are given in bold. Coefficient of determination (R^2) for each model, and Chi-square statistic (X^2) for each interaction term, are provided. Non-significant effects of the interaction term ($D \times$ WSG) indicate that radial shifts of F_V or K_S are unrelated to WSG

Discussion

Positive radial gradients in WSG and their anatomical drivers

Similar to previous research (i.e., Hietz et al. 2013; Plourde et al. 2015), we found significant and positive radial gradients in WSG in all pioneer and semi shade-tolerant species (Fig. 1, Table 3). A number of studies have suggested that radial gradients in WSG in fast-growing species reflect their growth and allocation strategy (i.e., Woodcock and Shier 2002; Hietz et al. 2013; Plourde et al. 2015). For instance, juveniles of fast-growing species tend to produce low specific gravity (SG) wood to favor high growth rates; and later, when they reach more favorable canopy layers, they produce high SG wood, probably to enable crown expansion and to increase mechanical stability (Woodcock and Shier 2002; Nock et al. 2009; Osazuwa-Peters et al. 2014). Then, positive radial gradients in WSG have been interpreted as providing mechanical advantage, since trees with high SG wood in the outer part of the trunk can achieve needed strength, at a lower construction cost, than trees with high SG in inner wood (Hietz et al. 2013, Schüller et al. 2016, Bossu et al. 2018).

In contrast, our knowledge on the radial changes in wood anatomy underlying this growth strategy is still limited (Rungwattana and Hietz 2017). Zieminska et al. (2013, 2015) have shown that similar values of WSG, particularly intermediate ones (c. 0.50–0.80), might be the product of different combinations of wood anatomies. Likewise, we found that positive radial gradients in WSG were driven by different combinations of fiber and parenchyma traits (Table 4, Fig. 2). Previous studies on fast-growing species have found that radial increments in WSG can be explained either by increments in fiver fractions (McDonald et al. 1995) or in fiber wall thickness (Rungwattana and Hietz 2017). Here, we extend these findings by showing that there are two alternative ways in which trees can adjust fibers to increase WSG radially: (i) by simultaneously increasing fiber fractions (F_F) and fiber wall thickness (F_{WT}) (i.e., *Virola michelii* or *Miconia tschudyoides*, Table 4, Fig. 2), or (ii) by increasing F_{WT} (i.e., *Bagassa guianensis* or *Schefflera morototoni*, Table 4, Fig. 2). Fibers are the most abundant cell type and tend to have thicker walls compared to other wood cells (Zieminska et al. 2013), and thus are expected to contribute to a large extent to WSG variations (Jacobsen et al. 2007; Martínez-Cabrera et al. 2009). On the other hand, we found that axial parenchyma fractions (F_{AP}) and fiber fractions (F_{RP}) can have either positive or negative effects on radial changes in WSG (Table 4). However, their overall influence on radial WSG variations should be small, since both axial and parenchyma cells tend to have thin walls of low tissue densities (i.e., Fujiwara 1992). The fact that positive radial gradients in WSG were underpinned by different radial shifts in fiber and parenchyma traits suggests that species with similar shade-tolerance may differ in their stem allocation patterns and functioning. For instance, species that increase WSG radially by increasing F_{WT}, also tend to decrease F_{F} towards the bark (Table 4). This suggests that these species might achieve needed strength while leaving more wood volume available for vessels or parenchyma cells, in comparison to species that adjust WSG radially by increasing both F_F and F_{WT}.

While there is a growing consensus that positive radial gradients in WSG represent a benefit in terms mechanical stability (i.e., Hietz et al. 2013, Schüller et al. 2016, Bossu et al. 2018), it is still less clear what are the potential disadvantages of this growth strategy. Larjavaara and Muller-Landau (2010) showed that low-WSG species can achieve greater strength than high WSG species, at a lower construction cost, by building thicker stems. Yet, they also hypothesized that, for the same strength, low-WSG species would have higher maintenance costs compared to high-WSG species, because stem respiration is thought to be proportional to stem surface area. This hypothesis would hold in general for our study species, given that low WSG species usually attain larger stem diameters compared to high-density species (Table 2). However, although this hypothesis has received considerable interest and is partially supported by recent experimental evidence (e.g., Rodríguez-Calcerrada et al. 2019), it does not consider radial variations in WSG that are prevalent in several forest types. The occurrence of these radial trends in WSG suggests that stem construction costs may change as trees grow. Moreover, while stem maintenance costs may be proportional to stem surface area (Larjavaara and Muller-Landau 2010), it is likely that stem respiration will be more linked to the fraction of living parenchyma cells (Rodríguez-Calcerrada et al. 2019). We observed contrasting radial trends in total parenchyma fractions among our study species (Table S1, Fig. 2), indicating that species might also have distinct radial changes in stem respiration. We suggest that future studies should explore both radial changes in stem construction and maintenance costs to better understand the ecological significance of radial WSG variations.

Negative radial trends in WSG

We found significant and negative radial trends in WSG in five species (*B. prouacensis*, *Recordoxylon speciosum, E. falcata, Hirtella glandulosa* and *Sextonia rubra*; Fig. 1, Table 3). In all of these species, heartwood was clearly distinguished on the basis of color difference. It has been suggested that the deposition of wood extractives in the inner stem, during heartwood formation, may explain the occurrence of negative radial trends in WSG (Hietz et al. 2013, Lehnbach et al. 2019). Wood extractives are secondary compounds involved in defense (Hillis 1987), that can affect WSG via increments in wood dry mass. For example, Lehnbach et al. (2019) showed that heartwood extractives changed the magnitude of radial trends in WSG in *R. speciosum*, and both the magnitude and direction of radial shifts in WSG in *B. prouacencis* and *E. falcata.* In the case of *E. falcata* and *R. speciosum*, our results showed that radial shifts of WSG were unrelated to anatomical traits (Table 3), which indicates that heartwood extractives would be the main drivers of those trends. Thus, the negative radial shifts in WSG observed in these species likely reflect defensive needs, rather than mechanical requirements. Yet, the contribution of wood extractives to WSG variations may change considerably among species depending on their concentration (i.e., % of wood dry mass) and radial distribution. For instance, in *S. rubra* and *B. prouacensis* extractives contents are only slightly higher in heartwood compared to sapwood (Rodrigues 2010; Amusant et al. 2014), suggesting that their contribution to radial changes in WSG are small.

For some species, especially shade-tolerants, we did not find any significant radial shift in WSG (Table 3, Fig. 1) nor in wood anatomical fractions (Table S1, Fig. 2). This is in agreement with prior studies showing that radial shifts in WSG are less common and pronounced in shade-tolerant than in pioneer species (i.e., Plourde et al. 2015). One possible explanation to this trend is that shade-tolerants have no, or modest, radial shifts in wood traits because they tend to have inherent low trait plasticity (Valladares et al. 2000; Popma et al. 1992; Rozendaal et al. 2006). In our study, shade-tolerant species had negative (i.e., *B. prouacensis*) or no (e.g., *Lecythis persistens*) radial trends in WSG or wood anatomical traits. These stem characteristics may be particularly common in the forests of the Guiana Shield that have lower rates of gap formation than other Amazonian forests (Molino and Sabatier 2001) and are typically dominated by shade-tolerant species (ter Steege et al. 2000, 2006). Alternatively, the fact that we did not observe significant radial changes in wood traits for some species might be due to our measurement strategy. Since we measured anatomical traits every 1.5 cm from pith to bark, we may not be able to properly capture the radial anatomical variation, when present, in some trees with low or intermediate stem diameters. Moreover, for most species we sampled trees with stem diameters lower than the mean diameters that species attain at our study site (Table 1). Then, much remains to be known on the magnitude, and ecological implications, of radial variations in wood functional traits at our study site.

Radial variations in vascular strategies

Our results show that, in general, F_V and K_S vary independently of WSG from pith to bark (Table 5). These findings add to growing evidence indicating that these traits would be decoupled across species (Zanne et al. 2010; Fortunel et al. 2013; Hietz et al. 2016), and also radially within trees from tropical dry forests (Rungwattana and Hietz 2017). These results may have distinct, but non-mutually exclusive explanations. First, in our study species, a direct trade-off between F_V and WSG is unlikely since vessel lumens occupied, on average, a relatively small fraction of stem cross-sectional area (range: 4.30–21.1, average: 8.94; Table 2). Second, at least in humid forests, trees can modulate their WSG and K_S, without significant increments in fiber and vessel fractions, by producing thicker fibers and wider vessels, respectively (Zieminska et al. 2013; Hietz et al. 2016). Since WSG is considered in general a good indicator of biomechanical properties (King et al. 2006, Anten and Schieving 2010), the orthogonal relationship of F_V and K_S with WSG has been interpreted as evidence that hydraulic and mechanical functions are decoupled (Hietz et al. 2016). This independence between functions may have important implications for understanding resource allocation patterns in high-diversity forests (Marks and Lechowicz 2006; Li et al. 2015). If trees can modulate hydraulics independently from mechanics during their life-cycles, then different trait combinations and ecological strategies might be possible among coexisting species. For instance, species with similar means and ranges of F_V (roughly 5.77 and 2.72–11.3, respectively) may have either positive (e.g., *P. nitida*), negative (i.e., *E. falcata*) or even absent radial trends in WSG (e.g., *Eschweilera sagotiana*).

Conclusions

This study illustrates the contrasting radial variations in WSG and wood anatomical traits that occurs in several tree species from a humid tropical forest in eastern Amazonia. Most of the species showed significant radial shifts in WSG and/or in wood anatomical traits. Our results indicate that positive radial gradients in WSG were mostly present in fast growing species and that these gradients were driven by different combinations of fiber and parenchyma traits. In contrast, negative radial trends in WSG were mostly present in shade-tolerant species, but were unrelated to radial changes in wood anatomy and appear to be more related, in some cases, to the accumulation of secondary compounds. Interestingly, some species, mostly shade-tolerants, did not exhibit significant radial changes in WSG nor in wood anatomical fractions. Previous studies at global and local scales have shown that, across species, WSG, vessel fraction and specific hydraulic conductivity vary independently from one another. Here we confirm that independence between these traits is in general maintained radially within stems.

Overall, our study provides valuable insights into radial variations in wood functional traits across tropical, humid forest tree species. These radial changes in wood traits are likely to be important to expand our knowledge of stem allocation patterns and tree life-history strategies. First, given that some wood traits can vary substantially from pith to bark, the study of wood trait variations across species or along environmental gradients would be improved by taking into account the effect of tree stem diameter. For instance, the common assumption that community WSG decreases with soil fertility or with mean annual precipitation may be partially explained by possible differences in stem diameters between sites. Second, radial changes in wood traits can be of central importance in explaining size-related variations in species demographic rates that are frequent among different forest ecosystems. Lastly, as WSG is an important predictor of above-ground biomass (AGB) estimations, considering radial trends in WSG may increase the accuracy of AGB estimations at both the tree and stand level.

Author contribution statement The study was designed by AGM, JMP, BC and JB. Most wood samples were collected by RL and AGM. Additional samples were provided by BC, JB and SL Anatomical images were processed by AGM and KR. Data analyses were performed by AGM with contributions from JMP. The first draft of the manuscript was written by AGM with inputs from JMP. All authors contributed equally to the writing and interpretation of advanced versions of the manuscript.

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Availability of data The datasets analyzed during the current study are available in the OSF repository, [https://doi.org/10.17605/OSF.IO/HS3MA].

Code availability No.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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