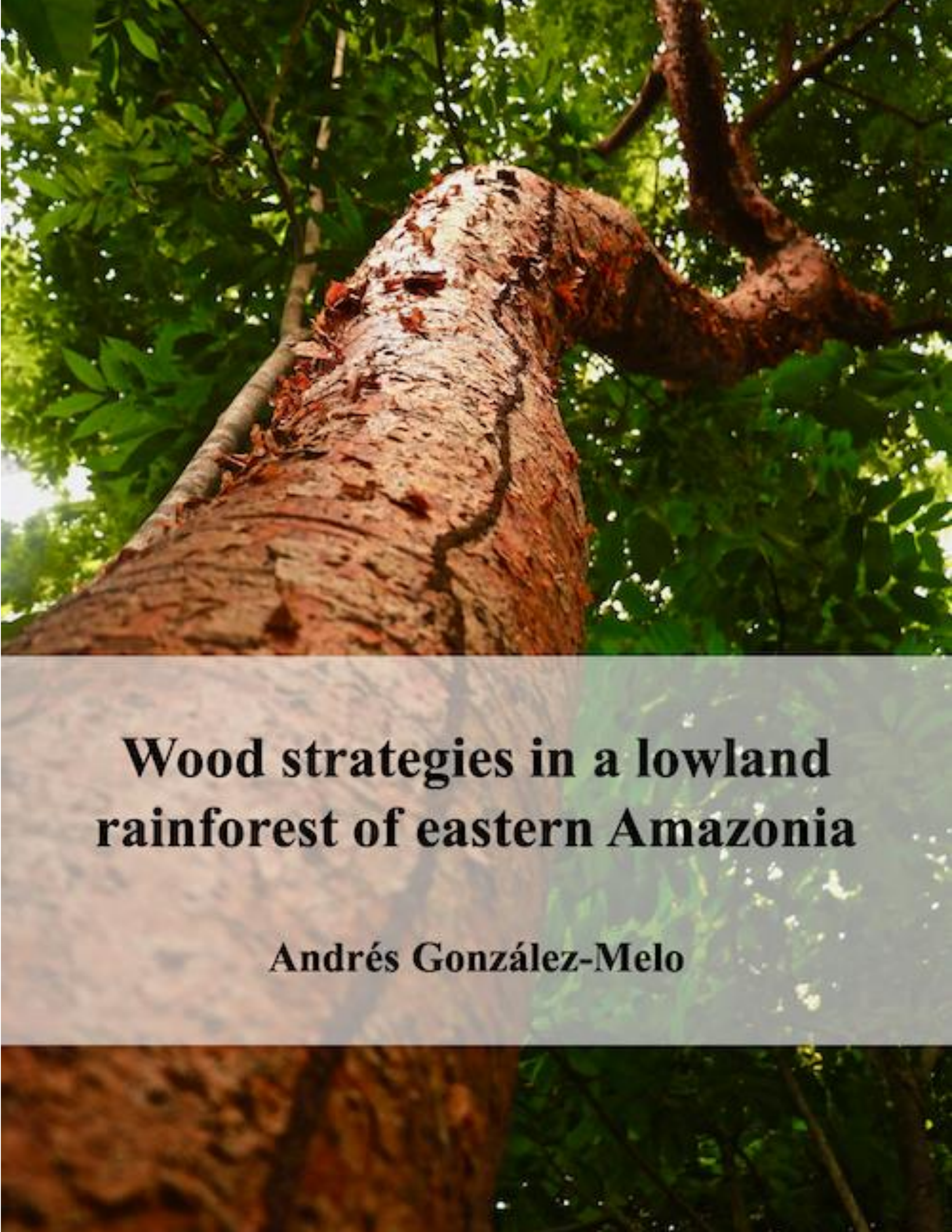

Wood strategies in a lowland rainforest of eastern Amazonia

Andrés González-Melo

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Cover picture: a tree of *Simarouba amara* (Busi kanambuli for locals) in a French Guianian forest.

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Chapter 1

General introduction

INTRODUCTION

Background

All plants need the same essential resources, namely water, CO_2, light and mineral nutrients (Westoby et al., 2002). However, even coexisting plant species can differ considerably in their ecological strategies, i.e., in the way in which individuals acquire and allocate resources to sustain populations in the long term (Grime, 2001). Plant ecological strategies can be inferred by measuring functional traits, broadly defined as any anatomical, morphological or physiological feature at the individual level that affects plant performance (Violle et al., 2007). For instance, Westoby (1998) proposed the "leaf-height-seed" scheme to quantify plant strategies based on three key functional traits: specific leaf area (SLA), plant height and seed mass. SLA (i.e., leaf area per unit of dry mass) is related to leaf photosynthetic capacity (Wright et al., 2004), plant height is linked to competitive ability (Westoby, 1998), and seed mass is considered a good predictor of dispersal and seedling establishment (Moles et al., 2004). In the last decades, there have been considerable advances in understanding leaf (e.g., Wright et al., 2004), seed (e.g., Moles et al., 2007), or whole-plant strategies (Westoby, 1998; Díaz et al., 2015). In contrast, much less is known about wood strategies (e.g., Chave et al., 2009; Beeckman et al., 2016), which limits our understanding of plant functioning and life-history variations (Westoby & Wright, 2006; Zieminska et al., 2015).

The study of wood traits has a long tradition in forestry and wood science (e.g., Zobel & Buijtenen, 1987; Carlquist, 2001; Baas et al., 2016). However, with the recent growth of trait-based ecology (Westoby & Wright, 2006; Shipley et al., 2016), there has also been an increasing interest in studying wood traits from an ecological perspective (e.g., Larjavaara & Muller-Landau, 2010; Beeckaman et al., 2016). In the ecological literature, the spectrum of interspecific variation in wood traits, which reflects trade-offs in plant functions, is often referred as the wood economics spectrum (WES, Chave et al., 2009). While the WES has established an important framework to understand life-history variations among woody species, there are still important gaps in our knowledge on wood strategies. For instance, most of our knowledge on wood traits comes from studies comparing trait variations across species or sites (e.g., Muller-Landau, 2004; Zanne et al., 2010; Chave et al.,2009; Zieminska et al., 2015; Morris et al., 2016). Yet, wood traits can also vary substantially within trees as they grow (reviewed by Lachenbruch et al., 2011). Since the structure of wood is overall conserved during tree development, the ontogenetic variations in wood structure can be studied by measuring radial (i.e., from pith to bark) shifts in wood traits (e.g., Rungwattana & Hietz, 2017). In this sense, more research is needed to better understand the anatomical traits driving radial variations in wood specific gravity (WSG), as well as the size-related variations in trait-demography associations. Similarly, the ecological research on wood traits has been focused mainly on WSG or wood anatomy, while relatively little is known on how wood nutrients covary with other wood traits. Addressing these knowledge gaps can help us attain a broader understanding of wood strategies and make more informed comparisons of traits among species or sites.

Specific gravity is an emergent property of wood that is affected, in angiosperms, by the relative proportions and morphologies of vessels, fibers and parenchyma cells (e.g., Zieminska et al., 2015). This raises the question of what are the main anatomical drivers underlying variations in WSG. Several studies have indicated that fibers, which are the most abundant cell type and tend to have thicker walls compared to other wood cells (e.g., Zieminska et al., 2015), are the major determinants of WSG variations across species (e.g., Martínez-Cabrera et al., 2009; Fortunel et al., 2013). However, it is uncertain whether, and to what extent, this pattern holds true for radial variations in WSG in trees from tropical humid forests, since very few studies have examined the radial variations of wood anatomical traits in angiosperm forest trees, and also because similar values of WSG, particularly intermediate ones (*c.* 0.50-0.80), can be underpinned by different wood anatomies (e.g., Zieminska et al., 2015).

Nutrients are key resources for plants because they are needed to maintain physiological functions (e.g., Jiang et al., 2019), and can be limiting in some plant communities (Wright et al., 2011; Turner et al., 2018). Although wood contains roughly half of the nutrients in live vegetation of tropical forests (e.g., Tanner, 1985), our knowledge on wood nutrient allocation of tropical trees is limited. Wood nutrients are hypothesized to covary along the WES (Martin et al., 2014). Yet, how wood nutrients are related to wood economics traits, such as WSG or parenchyma fractions, is poorly understood (Martin et al., 2014; Heineman et al., 2016). Moreover, the remobilization of nutrients in tree stems, from inner to outer wood, remains unclear, particularly for trees from lowland tropical forests (e.g., Heinemann et al., 2016). As a consequence, we are lacking an overall understanding on the ecological significance of wood nutrients.

In addition, radial changes in wood traits are expected to have important implications on tree demography (e.g., Osazuwa-Peters et al., 2017) and tree biomass estimations (e.g., Hietz et al., 2013; Nock et al., 2009). In particular, it has been shown that the strength of the relationships between traits and demographic rates can vary with tree size (e.g., Visser et al., 2016; Yang et al., 2018). This suggests that the predictive power of wood traits in explaining tree demographic rates may change during tree development. A number of recent studies have confirmed this trend for “easy-to measure” traits like WSG (e.g., Iida et al., 2014; Visser et al., 2016), but it is not clear if this can be assumed for “hard-traits” such as wood anatomical or chemical traits. Moreover, as WSG is an important predictor of above-ground biomass (AGB, Chave et al., 2014), the magnitude and direction of radial trends in WSG may affect AGB and biomass growth rates (BGR) estimations at both the species and stand level. However, the effects of radial shifts in WSG on AGB and BGR estimations have been barely considered in lowland humid forests.

Objectives of this study

This thesis aims to broaden our understanding of wood functional traits (i.e., WSG, anatomical and chemical traits) of coexisting tree species varying in their shade-tolerance. It focuses on the study of wood traits variations at the individual, species or guild level; and how these traits explain tree demography and influence biomass estimations. The specific objectives are:

1. To examine how wood specific gravity change radially in trunks during tree development, and how these radial shifts can be explained by wood anatomical traits (chapter 2).
2. To analyze how WSG, wood nutrients concentrations and parenchyma fractions are interrelated, and whether wood nutrients concentrations are higher in outer than in inner wood (i.e., nutrient remobilization) among species and ecological guilds (chapter 3).
3. To assess the predictive power of wood traits in explaining species demographic rates, and how trait-demography associations change during tree development (chapter 4).
4. To evaluate the effects of radial shifts in WSG on above-ground biomass and biomass growth rates estimations at the species and stand level (chapter 5).

General research approach

To achieve the research objectives, I obtained a comprehensive set of wood functional traits and long-term plot data. Wood functional traits were measured on a set of 22 tree species from a lowland humid forest in eastern Amazonia. These species spanned a wide spectrum of wood functional traits, and reflected a broad gradient of variation in shade-tolerance, ranging from light-demanding species to shade-tolerant ones. My dissertation had a strong focus on radial changes in wood traits to understand different aspects of life-history variations across species. In chapter 2, I collected wood trait data along radial profiles (i.e., from pith to bark) to infer shifts in tree functioning during tree development. In chapter 3, I looked at within-stem variations in wood nutrients, examined the associations between wood nutrients, wood anatomical traits and ecological guilds for 22 species. Chapter 4 focused on determining if wood traits were related to size-dependent demographic data from the Guyafor network of forest permanent plots, and from an independent demographic dataset collected by Molino & Sabatier (2001). Finally, in chapter 5, I combined radial measurements of WSG and tree-growth data, to evaluate the effects of radial variations in WSG on above-ground biomass and biomass growth rates estimations at the species and stand level.

Thesis outline

This thesis consists of six chapters: the general introduction (this chapter), four research chapters (chapters 2-5), and a synthesis chapter (chapter 6). I first focused on WSG and wood anatomical traits (chapter 2), then looked at wood chemical traits (chapter 3), and then combined data on wood traits and species demography to assess the links between traits and demographic rates (chapter 4). Finally, I examined the implications of within-stem variations in WSG on biomass estimations at both the species and stand level (chapter 5).

It is well established that wood specific gravity (WSG) can vary substantially from pith to bark (Williamson & Wiemann, 2010), which can reflect ontogenetic shifts in hydraulic, mechanical and storage demands during tree development (Hietz et al., 2013). However, the wood anatomical traits underlying these radial variations in WSG are not well understood, particularly for angiosperm tree species from humid tropical forests. In ***chapter 2***, I used a set of wood functional traits, measured along the stem radial profile, to explain the anatomical drivers of radial shifts in WSG.

Wood nutrients are expected to play a central role in tree functioning and life-history variations among woody species (Martin et al., 2014; Heinemann et al., 2016). Yet, very few studies have investigated how wood nutrients are related to other wood functional traits, or how they vary radially within stems, or across species and ecological guilds. In ***chapter 3,*** I related wood nutrients (i.e., phosphorous, calcium, potassium and magnesium) to WSG and xylem parenchyma fractions in inner and outer wood, and evaluated nutrient resorption rates at the species and ecological guilds level.

One central assumption in trait-based ecology is that traits can predict species demography (Shipley et al., 2016). However, the predictive power of most traits on tree demographic rates is in general low. This pattern may be explained by two reasons: the use of "soft traits", which might not fully capture some plant functions (Yang et al., 2018), and the lack of consideration of size-related changes in both traits and demographic rates (Iida & Swenson, 2019). In ***chapter 4***, I combined demographic rates (i.e., diameter growth and mortality rates) of trees of different sizes and "hard traits" (i.e., chemical and anatomical traits) measured at different radial positions to explain the associations between wood traits and species demography during tree development.

Besides its functional significance, wood specific gravity is also an important predictor of above-ground biomass (AGB) and, consequently, of biomass growth rates (BGR) estimations. Although radial shifts in WSG may have considerable effects on AGB and BGR estimations, at both the species and stand level, most regional and local studies do not consider these possible effects. In ***chapter 5,*** I quantified species percentage errors in AGB and BGR estimations that resulted from not taking into account radial trends in WSG, and extrapolated these species percentage errors to the stand level.

Finally, in the last chapter (***chapter 6***), I synthesized the results of this thesis, and discussed how they complement existing knowledge on trait-based ecology. Furthermore, I outlined the limitations of this study and proposed future research directions.

Chapter 2

Radial variations in wood functional traits in a rainforest from eastern Amazonia

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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 on 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 radial 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.

Key words: Wood functional traits, radial variation, tree functioning, tropical trees, wood anatomy.

INTRODUCTION

The study of wood traits has a long tradition in wood technology and wood anatomy (e.g., Zobel & Buijtenen, 1987; Carlquist, 2001; Baas et al., 2016). Yet, with the emergence of trait-based ecology in the last decades (Westoby & Wright, 2006; Shipley et al., 2016), there has also been an increasing interest in studying wood traits from an ecological perspective (e.g., Larjavaara & Muller-Landau, 2010; Beeckman et al., 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 (e.g., Hietz et al., 2013; Olson & 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 & Hietz, 2017). Thus, 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 & Wright, 2006; Chave et al., 2009). For instance, WSG is generally related to biomechanical (King et al., 2006; Anten & Shieving, 2010) or hydraulic properties (Santiago et al., 2004, 2018), and is hypothesized to mediate a trade-off between stem construction and maintenance costs (Larjavaara & 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 structure in response to size-related changes in mechanical and hydraulic demands (Nock et al., 2009; Williamson & 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 (Lehnebach et al., 2019; but see Larjavaara & 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 (e.g., 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 (e.g., 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 (e.g., 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 different 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 & Hietz, 2017). In one of these few studies, Rungwattana & 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 & 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 radial shifts in WSG (e.g., Nock et al., 2009; Williamson & Wiemann, 2010a, Hietz et al., 2013; Plourde et al., 2015) and vessel lumen size (e.g., Olson et al., 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 (e.g., 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 & Zimmerman, 2002), trees may adjust Ks 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}) (e.g., Zieminska 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, South America (5° 18' N, 52° 55' W). During pre-Columbian times, the forests of French Guiana were inhabited by different indigenous communities, also known as *Amerindians*, such as the Wayana, the Wayampi and the Teko. Later, during the eighteenth and nineteenth centuries, the *Maroons*, who are descendants of slaves brought from Africa, took refuge in these forests and established autonomous societies (Gulon, 2020). Mean annual temperature in Paracou is 28.4ºC, 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 northeastern

Amazonia (ter Steege et al., 2006) and the Guiana Shield (ter Steege et al., 2000). See Chapter 3, as well as Ferry et al., (2010) and Vincent et al., (2011), for detailed descriptions of soils of Paracou.

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 20-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 (i.e., all legume species, *Cordia alliodora* and *Bagassa guianensis*) were from previous studies (Bossu, 2015; Lehnebach et al., 2019).

Wood trait measurements— Wood samples were collected, in 2014 and 2018, from stem discs taken, at breast height, from cut-down trees (Fig. S1). From each wood sample, wood segments of 2 x 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 103ºC to a constant mass, for 72 h. WSG per segment was defined as dry mass over fresh volume (Kollman & 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 x 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 10-20 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, 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 (see Fig. S2, S3 and S4). 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 (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 20º C (998.2 kg m^{-3}) and η is the viscosity of water at 20º C (1.002 x 10^{-9} MPa s); Dh is the mean hydraulically weighted vessel diameter given by

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

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 & Zimmermann 2002; Hietz et al., 2016). Fiber wall thickness (F_{WT}, µm) was measured by taking photographs with a 100x objective lens using a laser microscope (VK 9710, Keyence). Each cross-sectional image (see Fig. S3) 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, 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 & Wiemann, 2010a; Osazuwa-Peters et al., 2014). Previous studies examining non-linear radial trends in WSG have considered mainly quadratic equations (e.g., Ozazuwa-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 & 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 few radial anatomical measurements.

After examining radial trends in WSG, we studied the anatomical drivers of those trends. 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 & Anderson, 2002), and it was as follows:

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

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. In these models, 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 holds radially within trees. 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 (*D*x*WSG*). Both F_V and K_S were log-transformed to meet regression assumptions. Lack of significance of the *D*x*WSG* 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 & Ripley, 2002) in the software R 3.6.1 (R Development Core Team, 2019).

Table 1. Study species, family, number of trees sampled (n), mean diameter at breast height of trees sampled (DBH$_{S}$), mean and maximum diameter at breast height of each species (DBH$_{M\ \mathrm{and}}$ DBH$_{MAX,}$ respectively), ecological guilds according to Favrichon (1994), and relative growth rates (RGR, mm.mm^{-1} y^{-1}), for 19 tree species from eastern Amazonia. RGR, DBH$_{M}$ and DBH$_{MAX}$ were calculated based on 20-year census data from one 25-ha and three 6.25-ha permanent plots established in Paracou (see Materials and Methods). DBH$_{M}$ of *C. alliodora* were obtained from Bossu (2015), while DBH$_{MAX}$ were obtained from Vega (1977). DBH$_{MAX}$ for each species was estimated averaging values of the five largest individuals.

Species	**Family**	**Local name**	**n**	**DBH$_{S}$ (cm)**	**DBH$_{M}$ (cm)**	**DBH$_{MAX}$ (cm)**	**Ecological guild**	**RGR**
Bagassa guianensis	Moraceae	Bagasse	5	25.1	35.8	105.7	Long-lived pioneer-Canopy	
Bocoa prouacensis	Fabaceae	Boco	3	12.3	28.6	52.7	Shade-tolerant-Understory	3.81
Cecropia obtusa	Urticaceae	Diapapaire	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	
Dicorynia guianensis	Fabaceae	Angelique	5	22.2	47.3	94.7	Semi shade-tolerant-Canopy	2.76
Eperua falcata	Fabaceae	Wapa	5	45.5	47.7	71.8	Semi shade-tolerant-Canopy	1.91
Eschweilera coriacea	Lecythidaceae	Maho noir	2	30.3	38.2	63.3	Shade-tolerant-Canopy	1.55
Eschweilera sagotiana	Lecythidaceae	Maho noir	3	20.8	41.4	69.2	Shade-tolerant-Canopy	1.41
Hirtella glandulosa	Chrysobalanaceae	Santi koko	2	30.3	17.1	40.3	Shade-tolerant-Understory	1.78
Lecythis persistens	Lecythidaceae	Maho rouge	5	22.3	35.9	65.8	Shade-tolerant-Understory	0.91
Licania alba	Chrysobalanaceae	Lebi koko	5	23.7	28.8	49.3	Shade-tolerant-Canopy	0.82
Miconia tschudyoides	Melastomataceae	Mesepu	2	21.2	15.7	25.8	Pioneer-Understory	1.90
Oxandra asbeckii	Annonaceae	Muamba	2	24.6	19.5	33.3	Shade-tolerant-Understory	0.72
Parkia nitida	Fabaceae	Dodomisinga	5	23.5	63.1	101.3	Pioneer-Canopy	6.98
Recordoxylon speciosum	Fabaceae	Wakapu gitin	3	14.3	38.2	64.4	Semi shade-tolerant-Canopy	2.18
Schefflera morototoni	Araliaceae	Bois saint jean	3	41.2	38.6	49.3	Pioneer-Canopy	4.3
Sextonia rubra	Lauraceae	Grignon franc	3	42.4	50.5	100.2	Semi shade-tolerant-Canopy	2.15
Swartzia panacoco	Fabaceae	Bugu bugu	3	20.5	25.4	51.3	Shade-tolerant-Canopy	0.76
Virola michelii	Myristicaceae	Yayamadou	3	31.5	31.8	64.5	Pioneer-Canopy	2.37

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).

Table 2. Summary characteristics of wood traits measured on 18 tree species from a lowland tropical forest in eastern Amazonia. Mean, standard deviation (SD), range and n-fold variation are shown.

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

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 (i.e., *C. obtusa*, *S. morototoni*) or semi shade-tolerants (sensu Favrichon, 1994; *Dicorynia guianensis* or *Eperua falcata*); while negative gradients were present in five species (i.e., *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 coefficients 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}) (i.e., *Bagassa guianensis* or *Schefflera morototoni*), or increasing both F_{WT} and fiber fraction (F_F) (i.e., *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 (*D*x*WSG*) was significant in only one species, indicating that these radial changes in F_V were largely independent from WSG (Table 5, Fig. 3). Specific hydraulic conductivity (K_S) increased significantly with stem diameter in ten species (Table 5). In three of these species, the *D*x*WSG* interaction term was significant, which indicates that variations in K_S were in general independent of shifts in WSG.

DISCUSSION

Positive radial gradients in WSG and their anatomical drivers— Similar to previous research (e.g., Hietz et al., 2013; Plourde et al., 2015), we found significant and positive radial gradients of WSG in all fast-growing 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 (e.g., Woodcock & 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 & 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).

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

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 ***

In contrast, our knowledge on the radial changes in wood anatomy underlying this growth strategy is still limited (Rungwattana & 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. 1 and 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 & Hietz, et al., 2017). Here, we extend these findings by showing that there are two alternative ways in which trees can adjust fibers in order 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 (F_{AP}) and radial (F_{RP}) parenchyma fractions 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 radial parenchyma cells tend to have thin walls of low tissue densities (e.g., 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 (e.g., 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 & 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

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. (+) 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 (DxWSG) indicate that radial shifts of F_V or K_S are unrelated to WSG.

Species	**F_V**		**K_S**	
	D	DxWSG	D	DxWSG
	R^2	X^2	R^2	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
Schefflera 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

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 which 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 & 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 radial changes in both stem construction and maintenance costs in order 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). 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; Lehnebach et al., 2019). Wood extractives are secondary compounds involved in defense (Hillis, 1987), which can affect WSG via increments in wood dry mass. For example, Lehnebach 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 all the five species that had negative trends in WSG, heartwood was clearly distinguished. 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 two 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.

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. (+) 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 (DxWSG) indicate that radial shifts of F_V or K_S are unrelated to WSG.

	F_V		**K_S**	
Species	D R^2	DxWSG X^2	D R^2	DxWSG 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

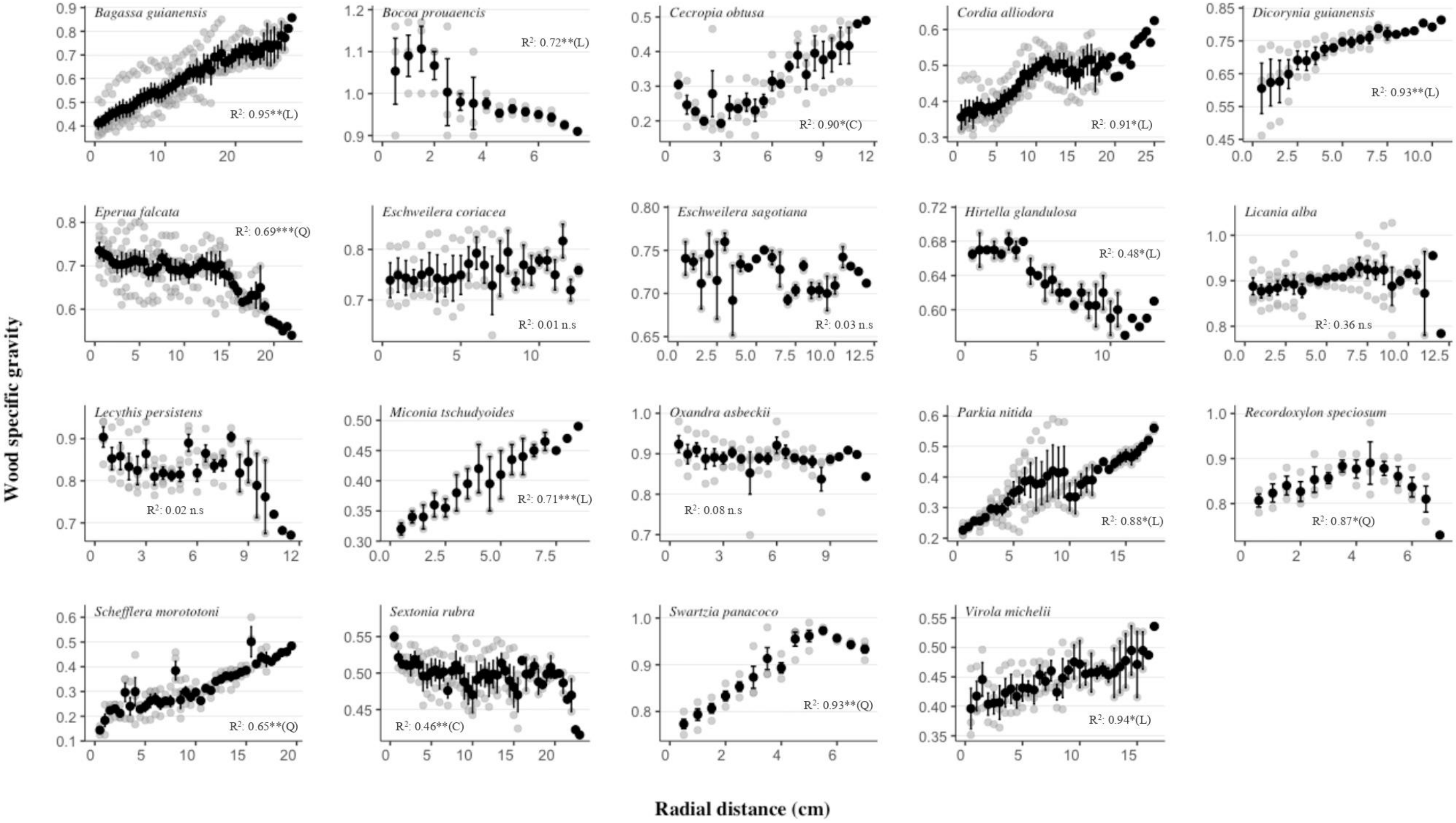

Fig. 1. Radial trends in WSG in 19 tree species from a lowland tropical forest in eastern Amazonia. Grey and black dots represent individual trees and species-mean values, respectively. Error bars denote standard deviation. Coefficients of determination (R^2), significance levels (n.s: $P > 0.05$; $P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

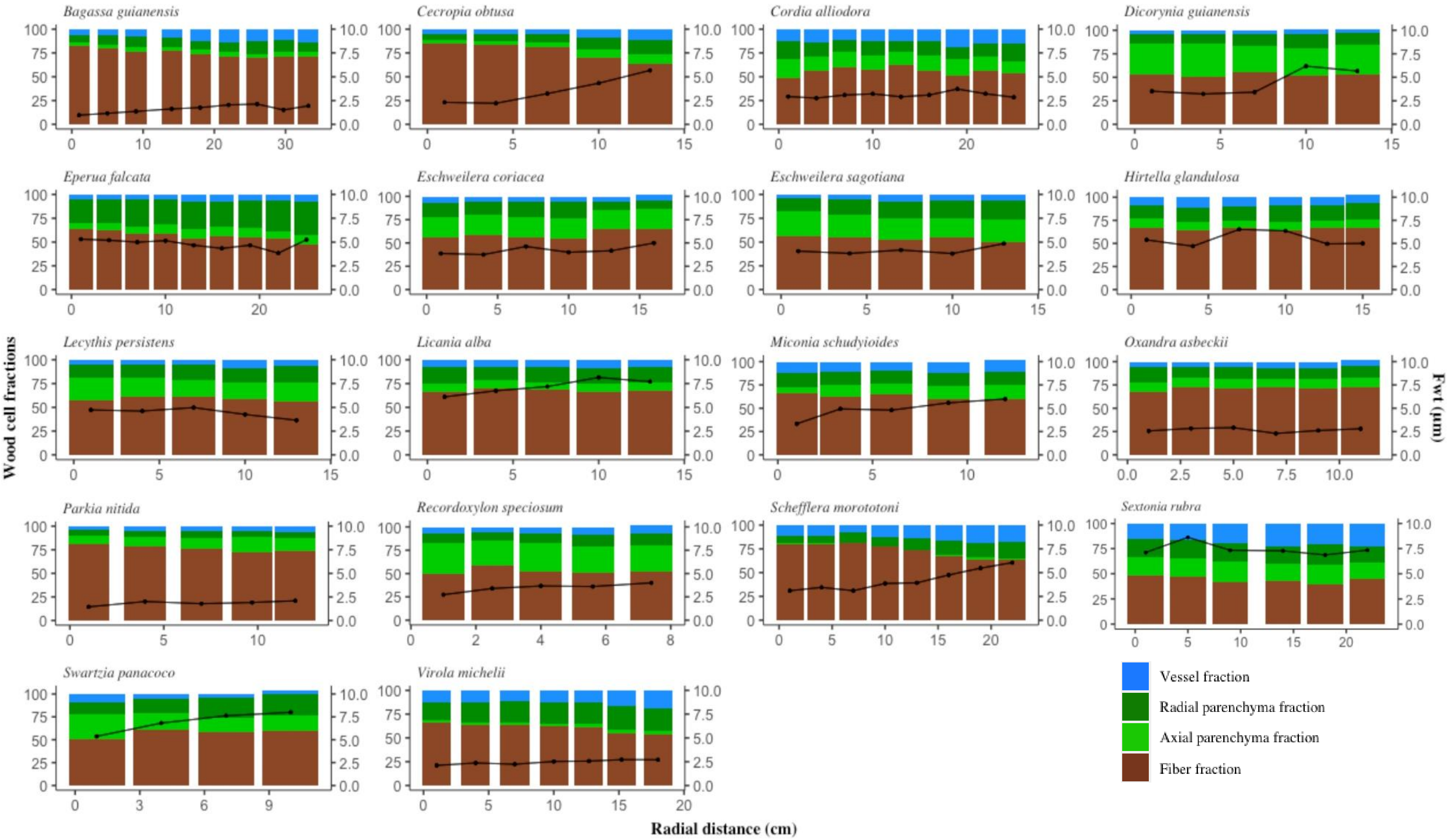

Fig. 2. Radial variations in wood cell fractions and fiber wall thickness (black line; F_{WT}) for 18 tree species from eastern Amazonia.

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 (e.g., 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., 2002; Rozendal et al., 2006). In our study, shade-tolerant species had negative (i.e., *B. prouacensis*) or no (i.e., *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 & Sabatier, 2001), and thus 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 the 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 & 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 & Shieving, 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 & 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 that allocate a similar stem cross-sectional area to vessels may have either positive (i.e., *P. nitida*), negative (i.e., *E. falcata*) or even absent radial trends in WSG (i.e., *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 in the inner wood. 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 rainforest tree species. These radial changes in wood traits are likely to be important to expand our knowledge on 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 (see Chapter 4), which are frequent among different forest ecosystems. Lastly, as WSG is an important predictor of above-ground biomass (AGB), considering radial trends in WSG may increase the accuracy of AGB estimations at both the tree and stand level (see Chapter 5).

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SUPPORTING INFORMATION

Table S1. Linear or generalized linear models predicting wood anatomical fractions (see Table 2 for trait abbreviation) based on radial distance. (+) or (-) gives the sign of the radial trends. Coefficient of determination (R^2) of each model are shown. Significance levels are: *, $P < 0.05$; **$P < 0.01$; ***, $P < 0.001$. Significant radial trends ($P < 0.05$) are given in bold.

Species	$\mathbf{F_F}$	$\mathbf{F_{WT}}$	$\mathbf{F_{AP}}$	$\mathbf{F_{RP}}$	$\mathbf{F_{TP}}$
	R^2	R^2	R^2	R^2	R^2
Bagassa guianensis	**0.58 (-) ** **	**0.24 (+) * **	0.09	**0.20 (+) * **	**0.24 (+) * **
Cecropia obtusa	**0.96 (+) ** **	**0.61 (-) ** **	**0.24 (+) * **	0.09	**0.21 (+) * **
Cordia alliodora	**0.71 (-) ** **	**0.31 (-) ** **	**0.72 (+) * **	**0.04 (+) * **	**0.32 (+) ** **
Dicorynia guianensis	**0.90 (+) * **	0.028	0.06	0.03	0.10
Eperua falcata	**0.95 (+) ** **	**0.16 (+) * **	0.03	-0.03	**0.19 (-) * **
Eschweilera coriacea	**0.73 (-) *** **	0.13	-0.21	0.008	0.22
Eschweilera sagotiana	**0.93 (+) *** **	0.22	0.08	**0.13 (+) * **	**0.23 (+) ** **
Hirtella glandulosa	0.05	0.05	0.06	-0.12	-0.04
Lecythis persistens	0.01	-0.19	-0.02	0.23	0.04
Licania alba	0.06	0.06	0.07	**0.09 (-) * **	0.10
Miconia tschudyoides	0.03	-0.05	0.24	-0.05	0.03
Oxandra asbeckii	0.35	**0.04 (+) * **	**0.68 (+) * **	**0.16 (+) * **	**-0.04 (-)**
Parkia nitida	**0.71 (+) ** **	0.19	-0.09	-0.03	0.32
Recordoxylon speciosum	0.11	**0.09 (-) * **	0.10	**0.04 (+) * **	0.04
Schefflera morototoni	**0.93 (+) ** **	-0.07	0.001	-0.03	0.11
Sextonia rubra	**0.90 (-) ** **	**0.38 (-) * **	**0.58 (+) * **	**-0.08 (-)**	**0.23 (+) * **
Swartzia panacoco	**0.67 (+) ** **	**0.06 (-) * **	0.08	**0.06 (-) * **	**-0.04 (+)**
Virola michelii	**0.44 (+) ** **	**0.39 (+) * **	**0.24 (-) * **	0.47	**0.49 (+) * **

Fig. S1. Stem cross-section of the fast-growing species *Baggasa guianensis*

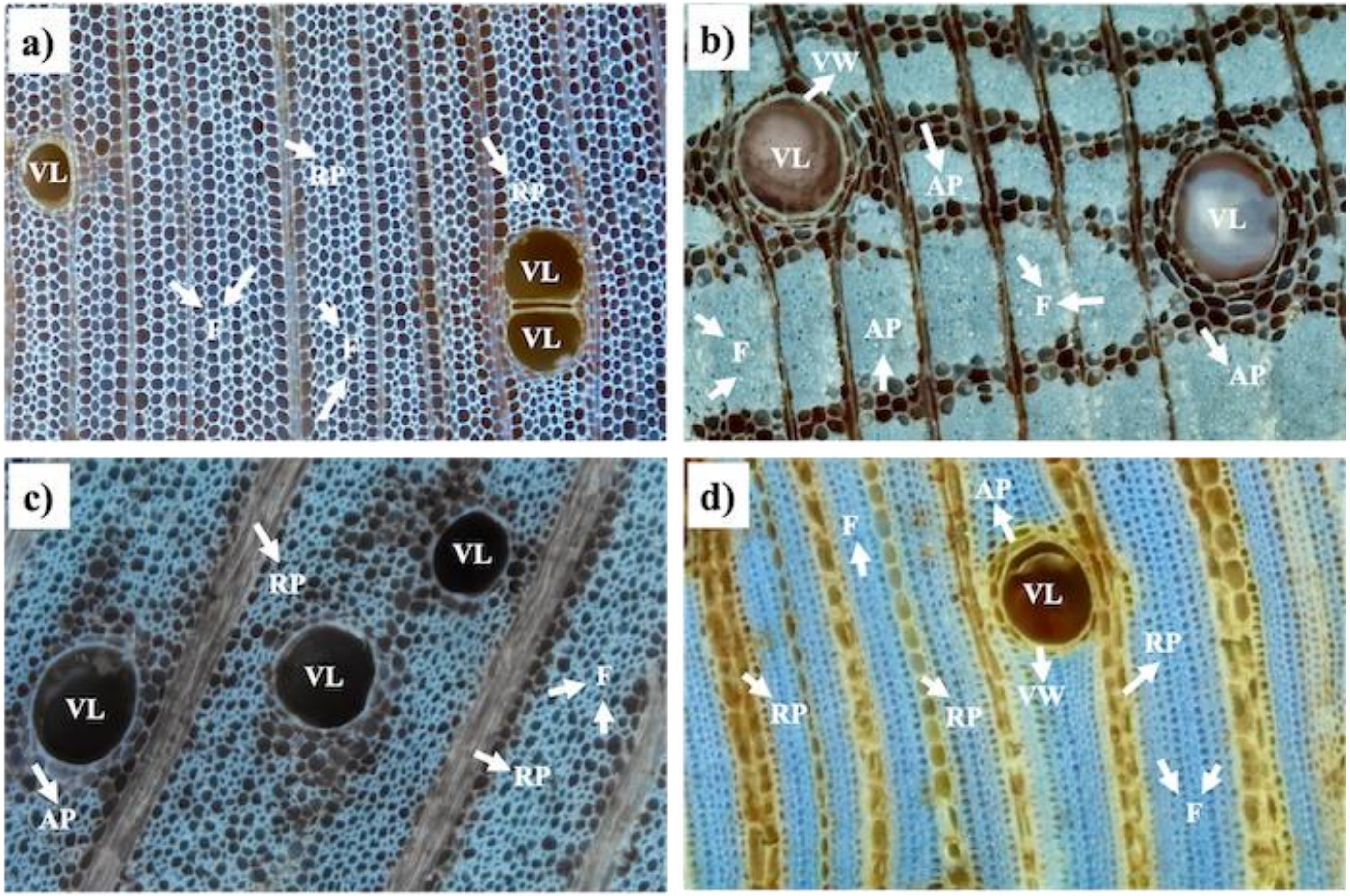


Fig. S2. Wood anatomical images of four tropical tree species: a) *Cecropia obtusa*, b) *Dicorynia guianensis*, c) *Cordial alliodora*, and d) *Eperua falcata*. AP: axial parenchyma cells, RP: radial parenchyma cells, VL: vessel lumen, VW: vessel wall, and F: fibers.

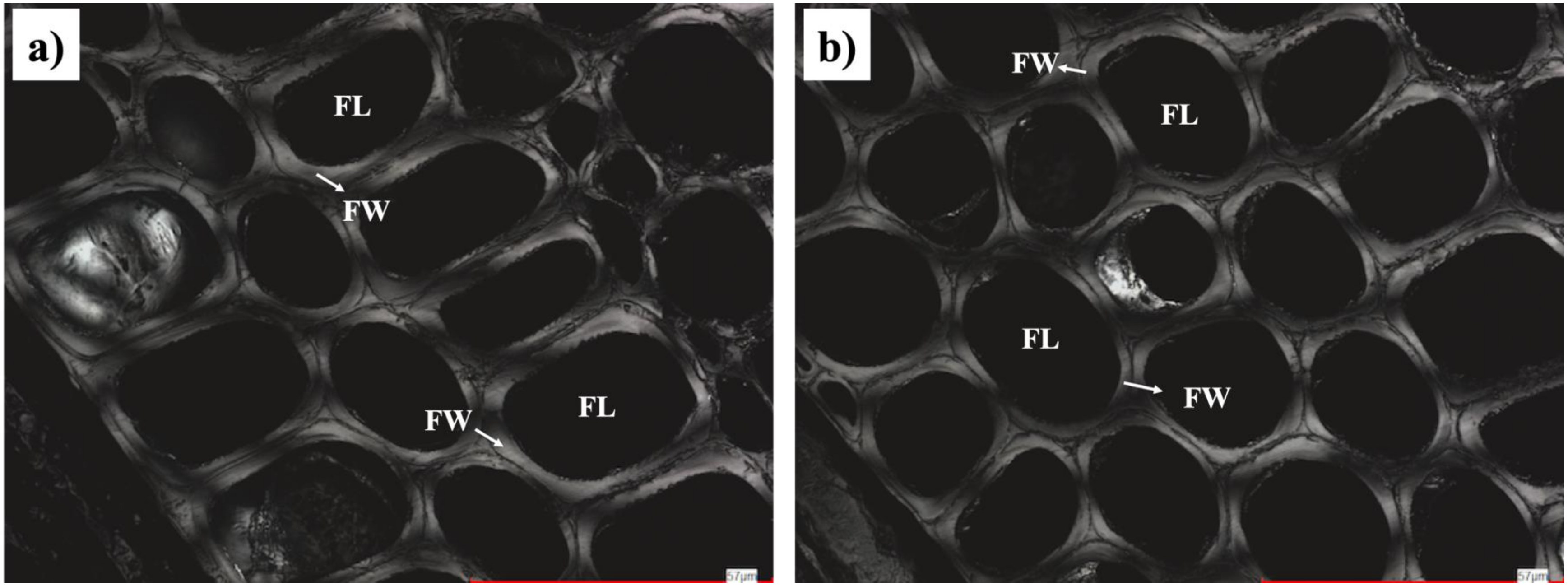
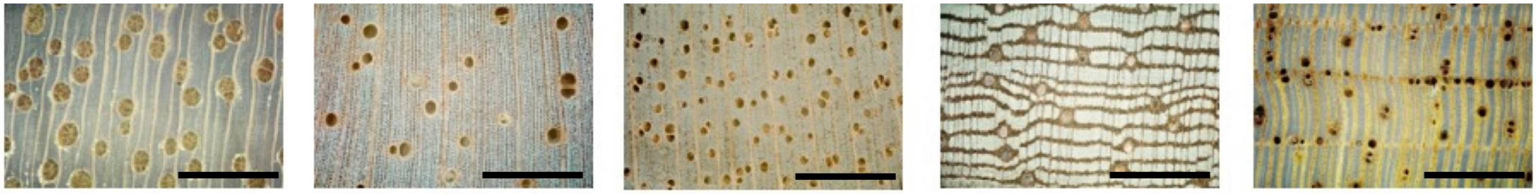
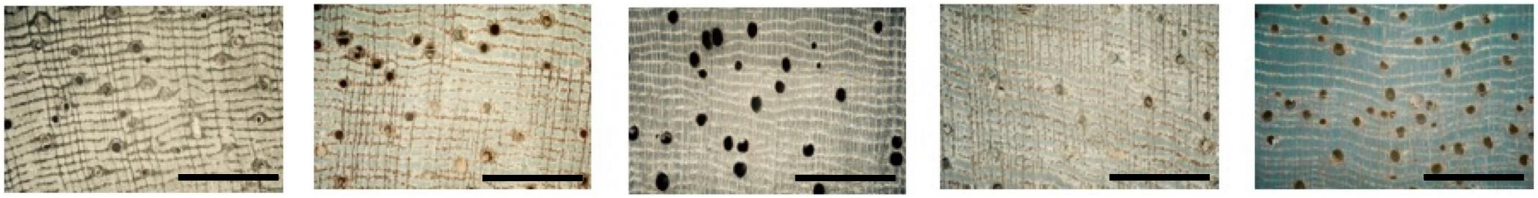


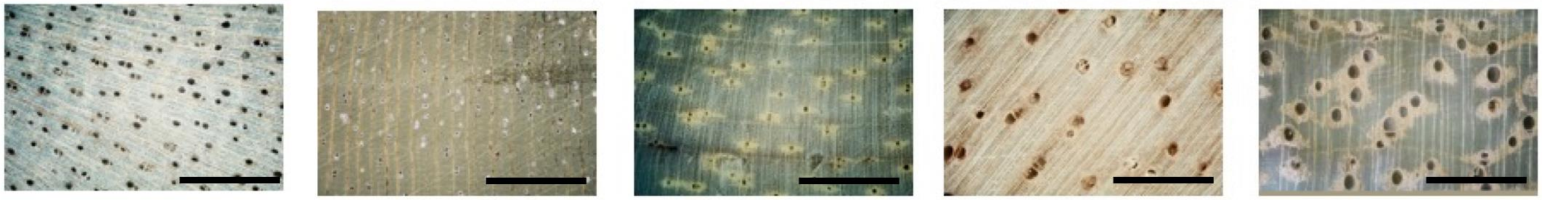
Fig. S3. Wood anatomical images, taken with a laser microscope, of two tropical tree species: a) *Virola michelii*, and b) *Schefflera morototoni*. FL: fiber lumen, and FW: fiber wall.



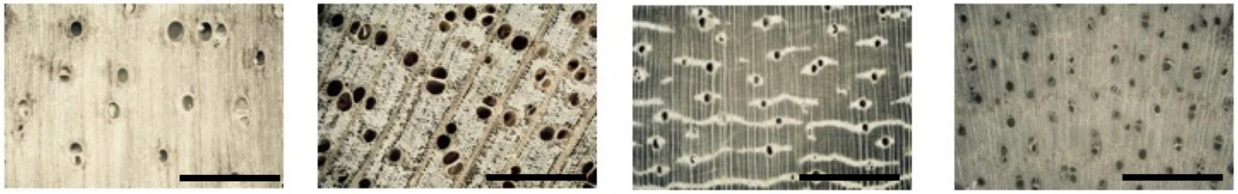
Bagassa guianensis *Cecropia obtusa* *Cordia alliodora* *Dicorynia guianensis* *Eperua falcata*



Eschweilera coriacea *Eschweilera sagotiana* *Hirtella glandulosa* *Lecythis persistens* *Licania alba*

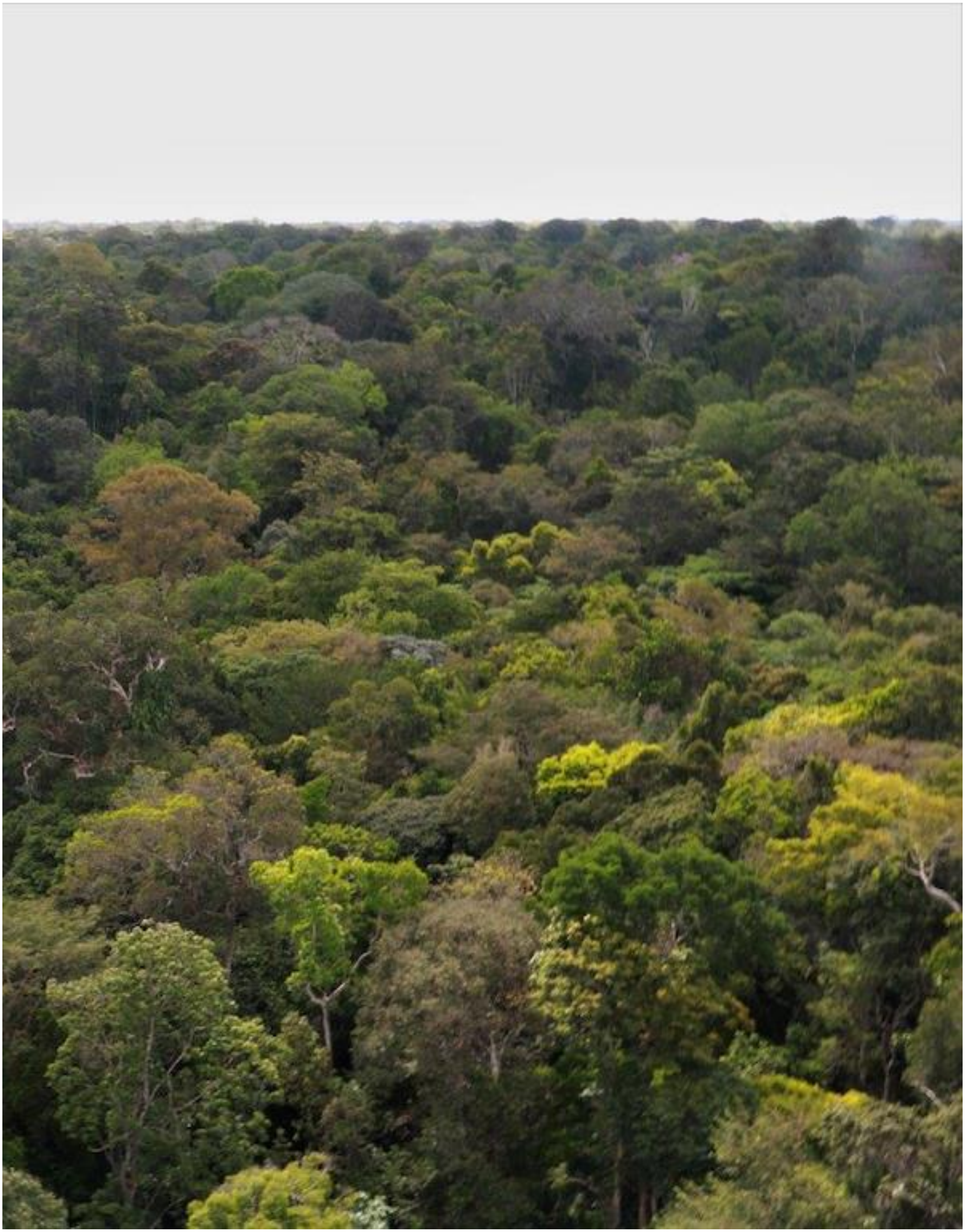


Miconia tschudyoides *Oxandra asbeckii* *Parkia nitida* *Parkia velutina* *Recordoxylon speciosum*



Schefflera morototoni *Sextonia rubra* *Swartzia panacoco* *Virola michelii*

Fig. S4. Wood anatomical images (5x amplifications) of 19 tropical tree species from a rainforest in eastern Amazonia. Scale bars are 1 mm.



Chapter 3

Variation of wood nutrients along the wood economics spectrum in a lowland tropical forest

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ABSTRACT

Wood nutrients are expected to play important roles in the functioning of trees, and are essential components of the wood economics spectrum. However, relatively little is known, particularly in tropical trees, about the interspecific variation of wood nutrients concentrations, the relationships of wood nutrients with other wood functional traits, and the resorption of nutrients within tree stems.

Here we measured four wood nutrients concentrations (i.e., P, K, Ca and Mg), wood specific gravity (WSG) and xylem parenchyma fractions, in both inner and outer wood, in 22 tree species from a tropical forest in eastern Amazonia. We first examined the associations between wood nutrients concentrations, WSG and parenchyma fractions, and whether these relationships are consistent in inner and outer wood. We also examined nutrient resorption rates, as the difference between sapwood and heartwood wood nutrient concentrations.

WSG was positively related to wood P concentrations in outer wood, but it was negatively related to Mg in inner wood, and to K in both inner and outer wood. WSG scaled positively with fractions of axial parenchyma in inner and outer wood. Overall, nutrients were unrelated or negatively related to wood parenchyma fractions, except for wood P, which was positively related to axial parenchyma fractions in outer wood. Nutrient resorption rates did not differ significantly when species where pooled, nor when they were grouped into functional groups.

This study illustrates that the relationships of wood nutrients concentrations with WSG can be both nutrient-and size-specific. It also suggests that axial parenchyma cells, in outer wood, may play a central role in the storage of P in species with high WSG, and that nutrient resorption from senescing woody tissues might be species-specific at our study site. These insights are important to increase our understanding on wood nutrient allocation patterns and tree ecological strategies in lowland tropical forests.

Key words: Wood nutrients, xylem parenchyma, wood specific gravity, tropical trees, ecological strategies.

INTRODUCTION

The wood economics spectrum (WES, Chave et al., 2009) describes global patterns of covariation among wood traits that reflect trade-offs in plant functions (Chave et al., 2009; Martin et al., 2014). A central idea in the WES is that wood functional traits covary consistently with wood specific gravity (WSG) across species (Chave et al., 2009). The patterns of covariation between WSG and wood anatomical traits (e.g., Zanne et al., 2010; Fortunel et al., 2013; Zieminska et al., 2015), or among WSG and wood carbon concentrations (e.g., Chave et al., 2009; Martin & Thomas 2015), are relatively well studied. In contrast, although wood contains roughly half of the nutrients in live vegetation of tropical forests (e.g., Tanner, 1985), few studies have investigated how wood nutrients are related to other wood traits, and how they vary both within stems and among species (Chave et al., 2009; Heineman et al., 2016). Consequently, there are still important gaps in our knowledge on wood nutrients, particularly on their variation within stems, among species, and with other wood traits (Martin et al., 2014; Heineman et al., 2016).

Phosphorus (P) is an essential element for plants because it plays central roles in photosynthesis and respiration (Santiago & Goldstein 2016; Jiang et al., 2019), and hence can limit primary productivity in some plant communities such as lowland tropical forests (Vitousek, 1984; Chapin et al., 2011; Dalling et al., 2016; Turner et al., 2018). In addition, base cations such as calcium (Ca), potassium (K) and magnesium (Mg) are thought to play a key role in wood formation, hydraulic balance and tree growth (Lautner et al., 2007; Ache et al., 2010; Fromm, 2010, Sardans & Peñuelas, 2015). Therefore, broadening our understanding on how wood nutrients concentrations vary among species and within stems, as well as in relation to other wood traits, may provide important insights into tree functioning and life-history variations (Martin et al., 2014).

Life history theory predicts that there is a trade-off between plant growth and survival (Wright et al., 2010; but see Russo et al., 2020), which may be mediated by allocation to storage (Chapin et al., 1990; Kitajima & Poorter, 2007). A greater investment in storage of non-structural carbohydrates (NSC) or nutrients may increase plant survival, particularly when water and light are limiting, but at the same time it might reduce growth because storage may increase maintenance costs (Chapin et al., 1990). As shade-tolerant species have inherently slow growth rates (e.g., Wright et al., 2010), the reduction in growth derived from a high investment in storage should be relatively low in these species (Kitajima & Poorter, 2007). Shade-tolerants are therefore expected to have higher investments in storage than fast-growing, pioneer species (Kitajima & Poorter, 2007). In this sense, Martin et al.,

(2014) hypothesized that shade-tolerant species, which typically have dense woods (e.g., Poorter et al., 2008; Wright et al., 2010), should store more nutrients in wood than fast-growing species. However, evidence supporting this hypothesis is mixed. For example, Heineman et al., (2016) found that wood P concentration was negatively correlated to WSG across 106 tree species from Panama. Becker et al., (2012), on the other hand, reported that WSG was unrelated to wood nitrogen (N) in 23 species from Uganda, while Martin et al., (2014) showed that wood N scaled positively with WSG among 59 Panamanian tree species. These contrasting patterns demonstrate that more information is needed to clarify the relationships among wood nutrients concentrations, WSG and plant ecological strategies.

The variation of wood nutrients concentrations among species can be better understood by considering how nutrients are allocated within tree stems. In xylem, a substantial fraction of some nutrients, particularly P and K, is thought to be deposited in parenchyma cells (Merril & Cowling, 1966; Meerts. 2002), which are mainly involved in storage, but can also participate in defense and water transport (e.g., Morris et al., 2016). Evidence indicates that low-WSG species have larger fractions of total parenchyma (F_{TP}) compared to species with dense wood (e.g., Martínez-Cabrera et al., 2009; Zieminska et al., 2013). Moreover, it has been suggested that F_{TP} reflects the storage capacity of NSC (Plavcová & Jansen 2015; Placová et al., 2016). Taken together, these observations suggest that low-WSG species should allocate more resources to storage of P and K than high-density species, consistent with a recent study that found a negative correlation between WSG and wood P (Heineman et al., 2016). In contrast, it seems that most wood Ca and Mg tend to be allocated primarily to cell walls (Lautner et al., 2007). As high-WSG species have in general thicker fiber walls and larger fiber fractions than low-WSG species (Zieminska et al., 2013), it is likely that high-WSG species have higher concentrations of wood Ca and Mg, compared to light-wooded, pioneer species. Thus, the relationship between nutrients concentrations and WSG might be nutrient-specific.

Wood nutrients concentrations might vary not only across species, but also radially within trees, from pith to bark (e.g., Meerts, 2002; Millard & Grelet, 2010; Heineman et al., 2016). The studies that have examined how wood nutrients shift radially within the stem have found that, when heartwood is present, nutrient concentrations tend to be higher in sapwood than in heartwood (reviewed by Meerts, 2002). This pattern has been interpreted in several studies as evidence that trees resorb nutrients to sapwood once heartwood formation begins (Millard & Grelet, 2010; Sette et al., 2013; Heineman et al., 2016). Resorption rates, however, might differ considerably among nutrients depending on their allocation and environmental availability, as well as in relation to species ecological strategies (Meerts, 2002; Sardans & Peñuelas, 2014). For example, the role of Ca and Mg in cell walls (Lautner et al., 2007) means that they are likely to be less mobile than P or K, which are mainly located in parenchyma cells and can be easily mobilized to be used in metabolism (e.g., Meerts, 2002). Consequently, Ca and Mg are generally resorbed at lower rates than P and K (Sette *et al.*, 2013; Urbina et al., 2021). In addition, it has been suggested that the resorption of limiting nutrients should be greater than of the non-limiting ones (McGroddy et al., 2004; Posada & Schuur 2011; Sardans & Peñueñas, 2015). Since tropical lowland forests tend to be mainly P-limited (Vitousek, 1984; Dalling et al., 2016; Turner et al., 2018), one may expect higher resorption of wood P than most base cations in tropical lowland trees (Sardans & Peñuelas, 2014; Heineman et al., 2016). Furthermore, nutrient resorption is suggested to be particularly advantageous for shade-tolerant species, because they live longer and will have to counteract nutrient limitations for longer periods in comparison to fast-growing species (Sardans & Peñuela, 2014).

In this study, we quantified interspecific and within-individual tree variations in the wood concentrations of four nutrients (i.e., P, Ca, K, and Mg), and related them to WSG and xylem parenchyma fractions, across 22 tree species. We aimed to answer the following questions: (i) What are the relationships between WSG, wood nutrients concentrations and parenchyma fractions (i.e., axial, radial and total), and do these relationships change between inner and outer wood? We hypothesized that the concentration of P and K would be greater in species with large fractions of total parenchyma (i.e., fast-growing, low-WSG species; Martínez-Cabrera et al., 2009), as these nutrients are expected to be deposited mainly in xylem parenchyma cells (e.g., Meerts, 2002). This would agree with studies that have found a negative correlation between WSG and wood P in tropical trees (e.g., Heineman et al., 2016). On the other hand, we anticipated higher concentrations of wood Ca and Mg in high WSG species (i.e., shade-tolerant species) than low WSG species, because these nutrients are mostly present in cell walls (Lautner et al., 2007), and high WSG species typically have thicker fiber walls and larger fiber fractions (Zieminska et al., 2013). (ii) Are there differences in resorption rates among nutrients, and do nutrient resorption rates differ between ecological guilds? Since K and P tend to be more mobile than Ca and Mg (e.g., Meerts, 2002; Urbina et al., 2021), we expected higher resorption rates (i.e., higher differences in nutrient concentrations between heartwood and sapwood) of K and P in comparison to Ca and Mg. Higher resorption rates of P are also expected because it is a limiting nutrient at our study site (Grau et al., 2016), and resorption rates are suggested to be higher for limiting nutrients (e.g., Sardans & Peñuelas, 2014). Finally, we anticipated that nutrient resorption rates will be more common and pronounced in shade-tolerant species (Sardans & Peñuelas, 2014).

MATERIALS AND METHODS

Study site — The study was conducted in the Paracou research station in northern French Guiana (5° 18' N, 52° 55' W). Mean annual temperature in Paracou is 28.4ºC. Annual rainfall averages *c*. 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). Vegetation at Paracou is lowland tropical rain forest, representative of northeastern Amazonia (ter Steege et al., 2006) and the Guiana Shield (ter Steege et al., 2000) in terms of diversity and floristic composition. The landscape is dominated by moderate hills separated by narrow streams (Ferry et al., 2010). Evidence indicates that soils at Paracou are strongly P-limited (Grau et al., 2016; Urbina et al., 2021). First, these soils, as most soils of the Guiana Shield (Hammond, 2005), are ancient and have been subjected to long-term weathering of primary minerals during soil development (Urbina et al., 2021). Second, stocks of P in soils, leaves and litter are low (Quesada et al., 2012; Urbina et al., 2021). Third, P resorption rates from senescing leaves are high at Paracou (Uribina et al., 2021), which can be interpreted as evidence of P scarcity (e.g., Sardans & Peñuelas, 2015).

Species and sampling— In Paracou, one 25-ha and three 6.25-ha permanent forest dynamics plots were established between 1991 and 1992 to study the dynamics of an undisturbed tropical rain forest. 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 22 tree species that represent a range of growth rates and shade-tolerance, and belong to some of the most dominant families at the site, namely Fabaceae, Lecythidaceae and Chrysobalanaceae (Table 1, Baraloto et al., 2012). We classified our study species into two ecological guilds: shade-tolerants and fast-growing species, according to Favrichon (1994). In the later guild, we included both short (i.e., *Cecropia obtusa*) and long-lived (i.e., *Cordia alliodora*) pioneers (Table 1). Overall, we sampled 75 mature trees, with two to five individuals per species. Most wood samples were collected in Paracou, except for *Cordia alliodora*, *Schefflera morototoni*, *Cecropia obtusa* and *Miconia tschudyoides*, which were collected in nearby secondary forests on comparable soils Samples of ten species (i.e., all legume species, *C. alliodora* and *Bagassa guianensis*) were collected and used in previous studies (Bossu et al., 2016; Lehnebach et al., 2019).

Wood trait measurements— Wood samples were collected from stem discs taken, at breast height, from trees that had been cut down. Two wood segments (*c*. 2x2x2 cm) were cut from each stem disc:

one at 2 cm from the pith (i.e., inner wood), and the other at 2 cm from the bark (e.g., outer wood). In 14 of the study species (see Table 1), sapwood and heartwood were distinguished based on color differences (i.e, heartwood is typically dark-colored). For these species, inner wood corresponds to heartwood, and outer wood to sapwood. For each wood segment, we measured fresh volume and dry mass. Fresh volume was measured by the water displacement method, and dry mass was obtained after drying the segments at 103ºC to a constant weight for 72 h. WSG per segment was defined as dry weight over fresh volume (Kollman & Coté, 1968).

For analyses, cross-sectional surfaces were 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. Photographs were taken at 5-10 x 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 10-20 partially focused images were taken and combined using Helicon Focus (Helicon Focus Ltd., Kharkov, Ukraine). It was not possible to obtain high-quality anatomical images of *Bocoa prouacensis* because of its very high WSG, and this species was excluded from the analysis that included parenchyma fractions. Fractions of axial (Fap) and radial parenchyma (Frp), and total parenchyma (Ftp: Fap + Frp) per cross-sectional area, were obtained from the anatomical images. To calculate these fractions, parenchyma cells were first manually colored using Photoshop (Adobe Systems Incorporated, USA), and then fractions were calculated automatically using the batch function in the software ImageJ (https://imagej.nih.gov/ij/). After taking the anatomical images, wood segments were ground and ashed at 550ºC for 1 h, and then the ash was dissolved in 1M HNO_3. Wood base cations and P were quantified using inductively coupled plasma-optimal emission spectrometry (ICP-OES) on an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA), with apple leaves (NIST 1515) as a certified reference sample.

Statistical analyses— All statistical analyses were performed in R 3.6.1 (R Development Core Team, 2019). The relationships between WSG, wood nutrients and parenchyma fractions were analyzed using standardized major axis (SMA) regression in the "*smatr*" package for R (Warton et al., 2006). We conducted separate SMA for inner and outer wood data, and the differences in the SMA slopes, between inner and outer wood, were examined using likelihood ratio tests (LRT). Then, principal component analyses (PCA) were conducted, for inner and outer wood separately, in order to describe the associations between wood functional traits. As nutrients are resorbed from senescing tissues (e.g., Meerts, 2002), we calculated nutrient resorption rates only for the 14 species for which we distinguished heartwood based on color differences (see Table 1). We calculated resorption rates for all species pooled (n=14), as well as for each species and ecological guild, as: (outer-inner)/outer x 100 (Heineman et al., 2016), where *outer* and *inner* are wood nutrients concentrations in sapwood and heartwood, respectively. Finally, we used analyses of variance (ANOVA) and *post-hoc* tests (i.e., Tukey's HSD test) to evaluate the variation of resorption rates among nutrients, and nutrient resorption rates between ecological guilds. Wood K, Mg and Ca were log-transformed to meet the assumption of normality.

Table 1. Study species, family, number of trees sampled (n), mean diameter at breast height of trees sampled (DBH, standard deviation in brackets), ecological guilds, canopy position and heartwood presence (HP) for 22 Amazonian tree species from a lowland forest in eastern Amazonia. Ecological guilds, and canopy positions, were assigned based on Favrichon (1994).

Species	**Code**	**Family**	**Local name**	**n**	**DBH (cm)**	**Ecological guild**	**Canopy position**	**HP**
Bagassa guianensis	Bag gui	Moraceae	Bagasse	5	25.1 (2.53)	Semi-tolerant	Canopy	Yes
Bocoa prouacensis	Boc pro	Fabaceae	Boco	4	12.3 (1.87)	Shade-tolerant	Understory	Yes
Cecropia obtusa	Cec obt	Urticaceae	Diapapaire	3	16.1 (0.89)	Fast-growing	Understory	
Cordia alliodora	Cor all	Cordiaceae		4	26.4 (1.86)	Fast-growing	Canopy	Yes
Dicorynia guianensis	Dic gui	Fabaceae	Angelique	5	18.2 (2.41)	Semi-tolerant	Canopy	Yes
Eperua falcata	Epe fal	Fabaceae	Wapa	5	19.5 (2.54)	Semi-tolerant	Canopy	Yes
Eperua grandiflora	Epe gra	Fabaceae	Wapa courbaril	3	12.4 (3.55)	Semi-tolerant	Canopy	Yes
Eschweilera coriacea	Esc cor	Lecythidaceae	Maho noir	2	16.3 (2.64)	Shade-tolerant	Canopy	
Eschweilera sagotiana	Esc sag	Lecythidaceae	Maho noir	2	17.8 (2.92)	Shade-tolerant	Canopy	
Hirtella glandulosa	Hir gla	Chrysobalanaceae	Santi koko	2	15.3 (3.12)	Shade-tolerant	Understory	
Lecythis persistens	Lec per	Lecythidaceae	Maho rouge	5	16.3 (3.52)	Shade-tolerant	Understory	Yes
Licania alba	Lic alb	Chrysobalanaceae	Lebi koko	4	14.7 (2,37)	Shade-tolerant	Canopy	Yes
Miconia tschudyoides	Mic tsc	Melastomataceae	Mesepu	2	13.2 (1,37)	Fast-growing	Understory	
Oxandra asbeckii	Oxa asb	Annonaceae	Muamba	4	14.6 (2.36)	Shade-tolerant	Understory	Yes
Parkia nitida	Par nit	Fabaceae	Dodomisinga	4	18.5 (3,78)	Fast-growing	Canopy	
Parkia velutina	Par pen	Fabaceae	Dodomisinga	3	12.4 (3.14)	Semi-tolerant	Canopy	
Peltogyne venosa	Pel ven	Fabaceae	Amarante	3	13.1 (2.62)	Shade-tolerant	Understory	Yes
Recordoxylon speciosum	Rec spe	Fabaceae	Wakapu gitin	3	12.3 (1.60)	Semi-tolerant	Canopy	Yes
Schefflera morototoni	Sch mor	Araliaceae	Bois saint jean	3	21.2 (3.22)	Fast-growing	Canopy	
Sextonia rubra	Sex rub	Lauraceae	Grignon franc	3	22.4 (2.74)	Semi-tolerant	Canopy	Yes
Swartzia panacoco	Swa pan	Fabaceae	Bugu bugu	3	12.5 (2,16)	Shade-tolerant	Canopy	Yes
Virola michelii	Vir mic	Myristicaceae	Yayamadou	3	20.5 (3,86)	Fast-growing	Canopy	Yes

RESULTS

Wood nutrient concentrations varied considerably among species (Table 2). The least variable element in inner (15.2-fold) and outer wood (4.67-fold variation) was P, whereas the most variable was K (54.3 and 33.1-fold variation, respectively). When pooling species, wood P concentrations were higher in outer than in inner wood ($P<0.001$; t: 4.00), while the concentrations of K ($P>0.05$; t:1.35), Ca ($P>0.05$; t: -0.33) and Mg ($P>0.05$; t: 0.61) did not differ significantly between inner and outer wood (see also Table 2).

Relationships between wood nutrients, parenchyma fractions and WSG— The functional space between wood traits and nutrients concentrations were summarized by PCAs (Fig. 1 a, b). In the PCA reflecting inner wood (Fig. 1a), the first axis accounted for 38.4% of all variation, and was defined by WSG, F_{TP} and wood Mg. The second axis of the PCA accounted for 19.5% of the variation and was dominated by F_{RP}, wood Ca and K. In the PCA summarizing outer wood (Fig. 1b), the first axis (43.2%) was defined by WSG, F_{AP} as well as wood K and Mg, whereas the second axis (23.2%) was mainly determined by F_{RP}, wood P and Ca.

Wood P and WSG scaled positively in outer wood ($R^2=0.58$, $P<0.001$), but were unrelated in inner wood ($R^2=0.035$, $P>0.05$; Fig. 2a). The slopes of this relationship in inner and outer wood differed significantly (LRT: 7.61; $P=<0.05$). Wood K was negatively related to WSG in both inner ($R^2=0.18$, $P<0.05$) and outer wood ($R^2=0.31$, $P<0.01$; Fig 2b). By contrast, Ca concentrations were unrelated to WSG in both inner and outer wood ($R^2=0.07$, $P>0.05$; $R^2=0.04$, $P>0.05$, respectively, Fig. 2c). Wood Mg decreased with WSG in inner wood ($R^2=0.20$, $P<0.05$), and was unrelated to WSG in outer wood ($R^2=0.11$, $P>0.05$; Fig. 2d). The slopes of the relationships of WSG with K, Ca and Mg did not differ significantly between inner and outer wood (see Fig. 2 b,c,d).

Table 2. Summary characteristics of wood traits, of inner and outer wood, measured on 22 tree species from a lowland tropical forest in French Guiana. Mean, standard deviation (SD), range and n-fold variation are shown.

Trait	**Abbrev.**	**Unit**	**Inner wood**				**Outer wood**			
			Mean	**SD**	**Range**	***n*-fold variation**	**Mean**	**SD**	**Range**	***n*-fold variation**
Wood specific gravity	WSG	unitless	0.63	0.21	0.21-0.99	4.58	0.65	0.178	0.38-0.98	2.55
Wood phosphorus concentration	P	$\mu g\ g^{-1}$	54.1	31.7	8.90-135.7	15.2	70.67	31.5	29.0-135.7	4.67
Wood calcium concentration	Ca	$\mu g\ g^{-1}$	2166.7	1719.1	281.5-7239.6	25.7	2227.8	2016.0	281.5-7239.6	25.7
Wood potassium concentration	K	$\mu g\ g^{-1}$	232.8	281.1	25.3-1379.8	54.3	172.7	154.4	19.4-643.5	33.1
Wood magnesium concentration	Mg	$\mu g\ g^{-1}$	400.8	317.0	59.9-1269.7	21.1	374.3	209.1	63.2-1269.7	20.0
Total parenchyma fraction	Ftp	unitless	28.4	9.2	8.55-47.8	5.59	30.0	9.27	15.4-47.8	3.09
Axial parenchyma fraction	Fap	unitless	14.6	8.87	0.46-32.4	70.0	14.7	7.95	1.34-31.4	23.4
Radial parenchyma fraction	Frp	unitless	13.7	6.46	2-32.9	16.4	15.0	7.44	2-32.9	16.4

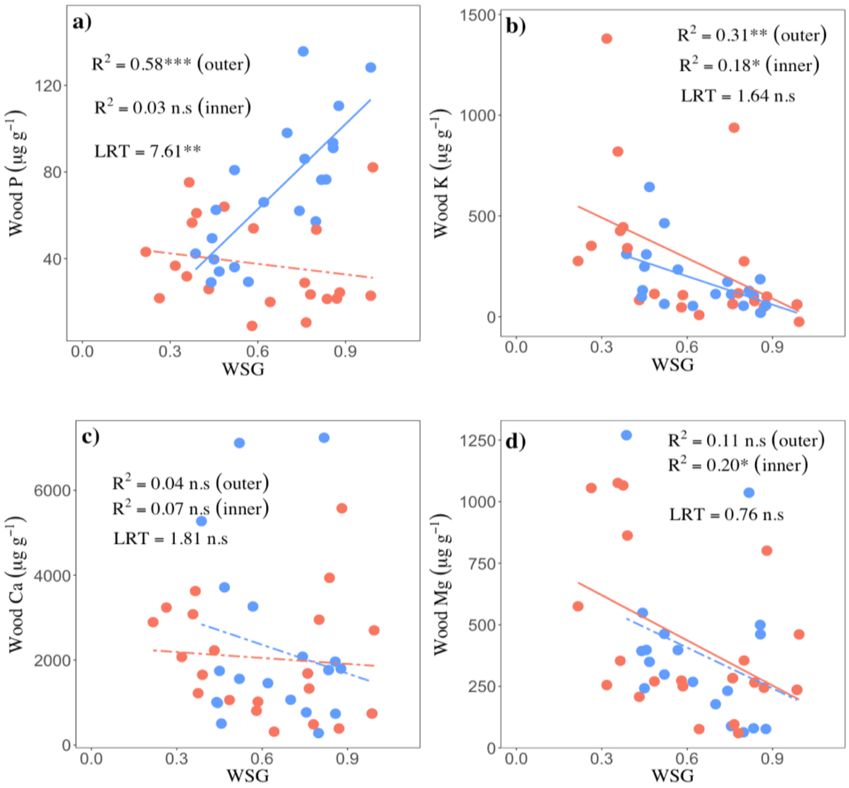

Figure 2. Relationships between wood specific gravity (WSG) and wood nutrients concentrations in inner (red circles) and outer wood (blue circles) for 22 species from a lowland forest in eastern Amazonia. (a-d) Phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). Solid and dashed lined represent significant ($P<0.05$) and non-significant major axis regression model fits, respectively. Coefficients of determination (R^2) and significance levels (n.s, $P>0.05$; $^{**}P<0.01$; ***, $P<0.001$) of the corresponding major axis regressions are shown. The differences between slopes of inner and outer wood were examined using likelihood ratio tests (LRT). Significant differences ($P<0.05$) indicate that the slopes differ.

Inner and outer WSG were significantly, and positively, related to F_{AP} (R^2=0.21, $P<0.05$; R^2=0.29, $P<0.05$, Fig S1a). In contrast, WSG in both inner and outer wood was unrelated to F_{RP} (R^2=0.015, $P>0.05$; R^2=0.16, $P>0.05$) and F_{TP} (R^2=0.13, $P>0.05$; R^2=0.08, $P>0.05$) across species (Fig. S1 b, c). The slopes of the relationships of WSG with parenchyma fractions did not vary significantly between inner and outer wood (Fig. S1). Phosphorus was positively related to F_{AP} in outer wood (R^2=0.21, $P<0.05$; Fig. 3a), and the slope of this relationship differ significantly from the

P-F_{AP} association in inner wood (Fig. 3a). Interestingly, this was the only positive relationship between nutrient concentrations and parenchyma fractions. Mg and Ca in outer wood were negatively related to F_{AP} and F_{TP}, respectively (R^2=0.19, $P<0.05$; R^2=0.55, $P<0.05$; respectively, Fig. 3d, k). Similarly, inner and outer wood Mg were negatively associated to F_{TP} (R^2=0.32, $P<0.01$; R^2=0.241, $P<0.05$, Fig. 3 l). The slopes of these associations of parenchyma fractions with Mg and Ca did not differ between inner and outer wood (Fig. 3). F_{RP} was unrelated to all wood nutrients in both inner and outer wood (Fig. 3e-h).

Resorption of wood nutrients— When pooling species, resorption rates did not differ significantly among nutrients (F= 1.63; P>0.05). Similarly, ecological guilds did not show significant differences in the resorption rates of P (F= 0.08; P>0.05), K (F=3.73; P>0.05), Ca (F=0.38; P>0.05), or Mg (F=1.13; P>0.05). Yet, at the species level, the occurrence and magnitude of nutrient resorption varied considerably (Fig. S2).

DISCUSSION

Relationships between wood nutrients, WSG and parenchyma fractions— We found that wood Mg decreased with WSG in inner wood (Fig. 2d). Similarly, our results show that wood K is negatively related to WSG in both inner and outer wood (Fig. 2b). Furthermore, wood K concentrations were not related to parenchyma fractions (Fig.3 b, f, j), while wood Mg concentrations were unrelated to F_{RP} in inner and outer wood (Fig. 3 h), and negatively related to F_{AP} and F_{TP} in both inner and outer wood (Fig. 3 d, l). Together, these findings indicate that low-WSG species tend to have higher concentrations of wood K in both inner and outer wood, and of Mg in inner wood, and that these species may allocate a large fraction of these nutrients to wood xylem cells other than parenchyma. One possible explanation was that most K and Mg was allocated to vessel walls (Langer et al., 2002). However, we found that vessel fractions were unrelated to wood K in inner (R^2=0.02, P=>0.05) and outer (R^2=0.07, P=>0.05) wood, and to inner wood Mg (R^2=0.02; P=>0.05). It is likely that low WSG species allocate K, and inner Mg, to both parenchyma cells and vessel walls, which makes it statistically harder to detect significant associations. Further studies on wood nutrients using techniques such as scanning electron microscopy would be valuable to have a more mechanistic understanding of wood nutrient allocation in wood cells.

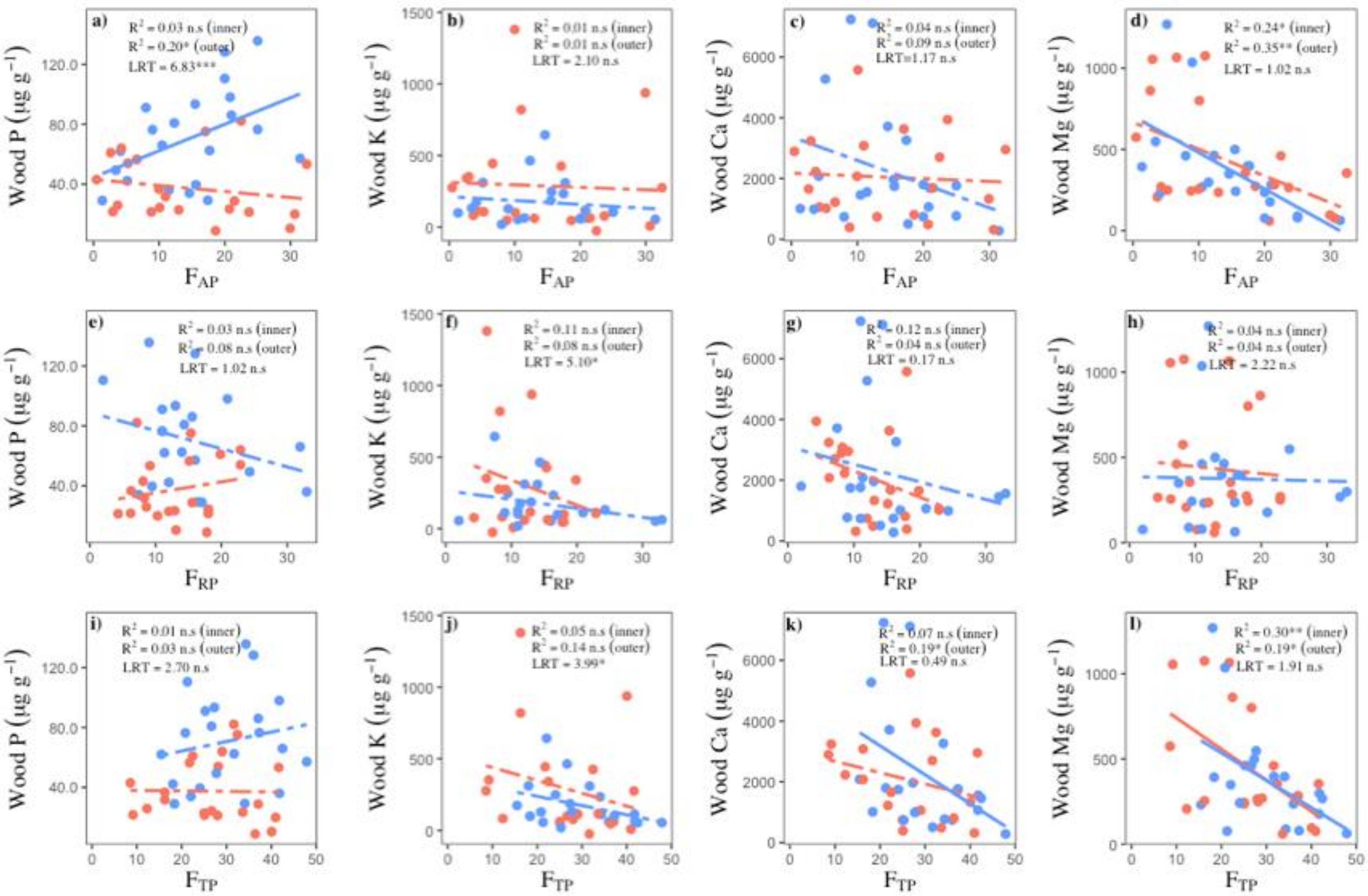

Figure 3. Relationships between wood nutrient concentrations and xylem parenchyma fractions, in inner (red circles) and outer wood (blue circles), across tree species (n=21) from a lowland forest in Eastern Amazonia. (e-d) Axial parenchyma fraction, Fap. (e-h) Radial parenchyma fractions, Frp. (i-l) Total parenchyma fraction, Ftp (Fap+Frp). Solid and dashed lined represent significanT ($P<0.05$) and non-significant major axis regression model fits, respectively. Coefficients of etermination (R^2) and significance levels (*, P=<0.05; **P=<0.01; ***, P=<0.001) of the corresponding major axis regressions are shown. The differences between slopes of inner and outer wood were examined using likelihood ratio tests (LRT). Significant differences ($P<0.05$) indicate that the slopes differ.

The positive relationship between WSG and wood P concentrations, in outer wood (Fig.2a), supports the notion that high-WSG species have higher concentration of wood nutrients (Martin et al., 2014). In our study species, WSG scaled positively with F_{AP} (Fig. S1) and, in turn, F_{AP} was positively related to wood P concentrations in outer wood (Fig. 3a). Taken together, these results suggest that axial parenchyma cells may play a central role in the storage of P in high-density species (Fig. 1b). Previous studies have reported positive relationships between wood nitrogen concentrations and total (Merrill & Cowling, 1966) and axial parenchyma fractions (Kotowska et al., 2020), but to our knowledge this is the first study to demonstrate a link between F_{AP} and wood P concentrations. It can be difficult to separate the functions of axial (AP) and radial (RP) parenchyma cells, as they can perform simultaneously different functions and are ultimately interlinked forming a complex three-dimensional network (Morris et al., 2016 a, b). However, previous studies have suggested that AP and RP cells might be functionally different to some extent (Zheng & Martinez Cabrera, 2013; Morris et al., 2017). In general, the mechanical role of parenchyma cells is thought to be more related to RP cells, while hydraulics tends to be more closely associated to AP (Zheng & Martinez Cabrera, 2013; Morris et al., 2016b; Morris et al., 2017). For example, the fraction and width of RP cells have been positively related to mechanical properties such as radial modulus of elasticity and tensile strength (Beery et al., 1983; Reiterer et al., 2002), while AP associated to vessels (i.e., paratracheal parenchyma) could play an important role in xylem water transport by presumably avoiding and/or refilling embolized conduits (Zheng & Martínez-Cabrera 2013; Morris et al., 2017; Jansen et al., 2020; Pratt et al., 2021). In this sense, our results, together with those reported recently by Kotowska et al., (2020), suggest that axial parenchyma cells may serve as an important reservoir of mineral nutrients.

At our study site, P is the most limiting nutrient (Grau et al., 2016), and its soil total concentration is lower than in several forests from the Amazon basin (Quesada et al., 2012). P storage is likely to be particularly relevant for shade-tolerant species because they have long-life cycles and will have to counteract nutrient limitations for long periods (Sardans & Peñuela, 2014). In contrast, P storage might be less important for fast-growing species that grow in gaps with relatively higher nutrient availability, and which tend to prioritize short-term over long-term benefits. In general, forests of the Guiana Shield have lower rates of disturbance (i.e., gap openings) compared to other Amazonian or Neotropical forests (Molino & Sabatier, 2001; ter Steege et al., 2006). As a consequence, most tree species from Guianan forests are shade-tolerants that typically have large seeds and dense woods (ter Steege et al., 2000; 2006), traits that may confer a competitive advantage in the shaded understory (Kitajima & Poorter, 2007). We suggest that the dominance of shade-tolerant species in these forests may also be related to higher storage of P in species with high WSG. Possibly, soil P limitation may have acted as a strong selective pressure favoring the abundance of species that are efficient at storing P (Lovelock et al., 2007; Grau et al., 2016).

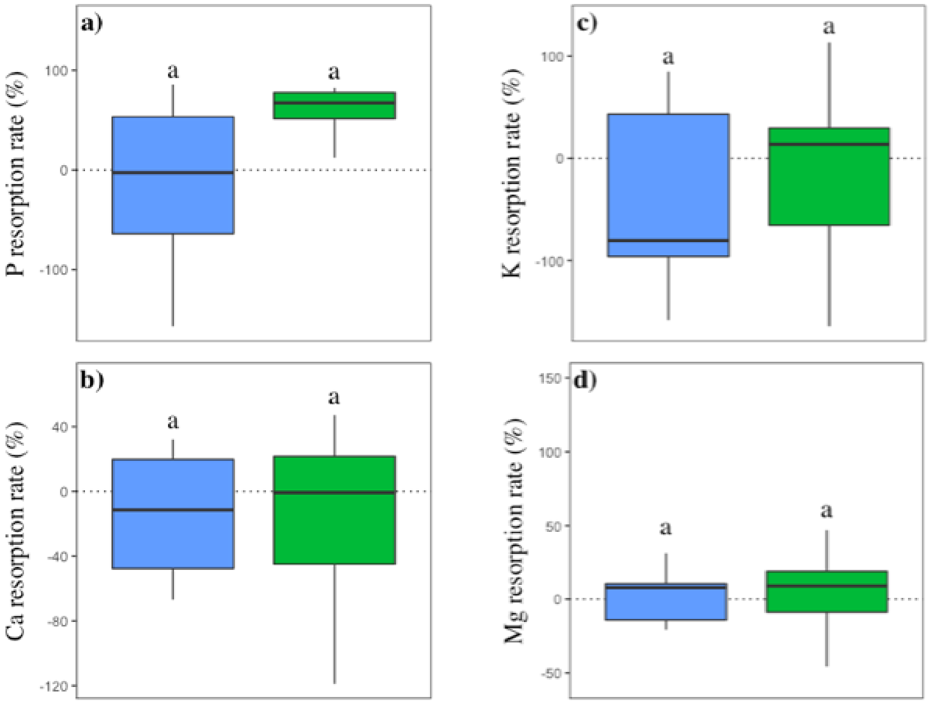

Figure 4. Nutrient resorption rates (%) of tree species (n=21) belonging to different ecological guilds: fast-growing (blue) and shade-tolerant species (green) in a lowland forest from eastern Amazonia. a) phosphorus, b) potassium, c) calcium and d) magnesium. Letters above bars indicate significant differences (P<0.05) among ecological guilds.

Besides some significant associations between wood nutrients and parenchyma fractions, mainly in outer wood, wood nutrients were commonly unrelated to parenchyma fractions (Fig. 3). One possible explanation for this result is the occurrence of living-septate fibers, which we did not quantify, in three of our study species, namely *Shefflera morototoni*, *Sextonia rubra* and *Cecropia* *obtusa*. Living fibers are frequent in species with scanty or absent parenchyma and are suggested to play an important role in storage (Carlquist, 2015; Plavcová et al., 2016). However, we ruled out this explanation since excluding these three species from the analyses did not change the results (data not shown). Then, we suggest two alternative explanations that may not necessarily be mutually exclusive. The first and most likely explanation is that, among our study species, an important fraction of wood nutrients is allocated to other cells, like fibers and vessels (see above). Second, our study was focused on xylem nutrient concentrations, but bark may also be an important reservoir of nutrients as has been suggested for some tropical (Jones et al., 2019) and temperate trees (Wetzel & Greenwood, 1989). This might be particularly true for plant Ca concentrations. For instance, in a study conducted in a tropical premontane forest, Jones et al., (2019) showed that bark accounted for the largest percent of Ca (up to 82%) in above-ground biomass nutrient pools. Thus, further studies should examine nutrient allocation to bark and its role in the economy of trees.

A common prediction derived from the wood economic spectrum (WES) is that wood functional traits covary with WSG across species (Chave et al., 2009; Martin et al., 2014; Heinemann et al., 2016). In line with this prediction, we found that in outer wood WSG, F_{AP} and wood P concentrations were positively correlated (Fig. 1b, Fig. 2a, Fig. 3a). The main benefits of high specific gravity wood are suggested to be high decay resistance (i.e., Chave et al., 2009; Hérault et al., 2010) and lower stem maintenance costs (Larjavaara & Muller-Landau, 2010). At our study site, high WSG is also thought to increase stem hydraulic resistance, as it is negatively related to xylem turgor loss points (Santiago et al., 2018). Our finding that WSG, F_{AP} and P concentrations are positively related in outer wood suggest that, at least for our study species, an additional benefit of high WSG may be higher fractions of axial parenchyma cells, which may possibly favor higher storage of wood P. However, our findings also suggest that the variation of wood traits along the WES is more complex than previously assumed. Part of this complexity in wood trait covariation relates to inner and outer wood. For instance, in contrast to outer wood, in inner wood WSG, F_{AP} and P were unrelated (Fig. 1a, Fig. 2a, Fig. 3a). This may reflect the presence of sapwood and heartwood, since a close association between traits is expected in sapwood (i.e., outer wood), which is the physiologically active part of the trunk. Moreover, we found that radial parenchyma fractions (F_{RP}) and Ca concentrations were unrelated to WSG in both inner and outer wood. These results indicate that WSG is not always a good proxy for F_{RP} and wood Ca concentrations, which in turn suggests that these wood traits may represent axes of functional variation that are independent from WSG.

Nutrients reabsorption among species and ecological guilds— We hypothesized that nutrients resorption rates would be higher for limiting nutrients (Sardans & Peñuelas, 2014). Yet, contrary to this hypothesis, P resorption rate was not significantly higher than that of other nutrients. In Paracou, P resorption from senescing leaves is more common and higher than N resorption (Urbina et al., 2021), suggesting that tree species at our study site are more efficient at resorbing P from leaf than from woody senescing tissues. On the other hand, nutrients resorption rates did not differ significantly among ecological guilds, which is in agreement with a recent study on leaf nutrient resorption conducted in Paracou (Urbina et al., 2021). These findings suggest that the resorption of nutrients in the forest of Paracou might be species-specific. In this sense, future studies should examine the role of competition or species growing conditions on nutrient resorption rates.

We also anticipated that nutrients resorption rates would be more common and accentuated in shade-tolerant species (Sardans & Peñuelas, 2014). While ecological guilds did not differ in terms of nutrient resorption rates, we found evidence of nutrient resorption in several species (Fig. S2). Nutrient resorption is a key mechanism to increase nutrient use efficiency, that might be especially prevalent in species growing on poor nutrient soils (Sardans & Peñuela, 2014; Turner et al., 2018). This would be probably the case of many tree species in the forest of Paracou, which grow on strongly weathered soils with low concentrations of nutrients (Grau et al., 2016; Soong et al., 2020). Our knowledge on nutrient resorption in wood lags far behind that for leaves (Kotowska et al., 2020), then its ecological significance is still uncertain. Yet, nutrient resorption in woody tissues may have important implications in forest community dynamics. For example, at Paracou, soil characteristics are generally weak predictors of biomass and demographic rates (Grau et al., 2016), suggesting that mechanisms such as nutrient resorption from senescing tissues might influence forests structure and dynamics (Grau et al., 2016).

At the species level, the resorption of P and K tended to be more common and pronounced than that of other nutrients (Fig. S2), which is partially in line with some studies on leaf nutrient resorption at both regional (e.g., Sardans & Peñuela, 2014) and local scales (e.g., Urbina et al., 2021). A more frequent resorption of wood P may suggest, to some extent, a possible plant adaptation to soil P limitation at our study site (Sardans & Peñuela, 2014). Furthermore, this trend may also be explained by differences in nutrients functional roles and storage forms. For instance, whereas K is a free cation in plant cells (Sardans & Peñuelas, 2014) Ca and Mg are typically found in cell walls (Meerts, 2002) and thus they are harder to remobilized. Since K is involved in many mechanisms that mitigate water stress (Sardans & Peñuelas, 2015), the use and resorption of K is expected to become increasingly important in plant communities under drought stress.

CONCLUSIONS

This study illustrates that wood nutrients can have different patterns of associations with WSG and parenchyma fractions, and that some of these associations change between inner and outer wood. Our results suggest that axial parenchyma fractions, in outer wood, play an important role in the storage of P in species with high WSG. They also suggest that the resorption of nutrients from senescing woody tissues might be species-specific. These findings represent valuable insights into how wood nutrients vary along the wood economic spectrum in tropical trees, which in turn may help to broaden our understanding on the functional significance of wood specific gravity and tree ecological strategies in lowland tropical forests.

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SUPPORTING INFORMATION

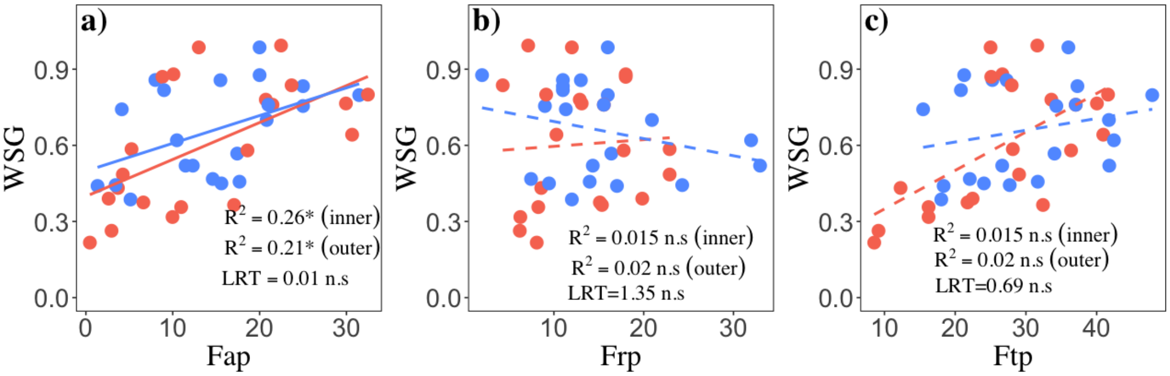


Figure S1. Relationships between wood specific gravity (WSG) and xylem parenchyma fractions, for inner (red circles) and outer wood (blue circles), across tree species (n=21) from Paracou, French Guiana. a) Axial parenchyma fraction, Fap. b) Radial parenchyma fraction, Frp. c) Total parenchyma fraction, Ftp (Fap+Frp). Solid and dashed lines represent significant ($P<0.05$) and non-significant major axis regression fits, respectively. Coefficients of determination (R^2) and significance levels (n.s, $P>0.05$; *, $P<0.05$;) of the corresponding major axis regressions are shown. The differences between slopes of inner and outer wood were examined using likelihood ratio tests (LRT). Significant differences ($P<0.05$) in LRT indicate that the slopes are different.

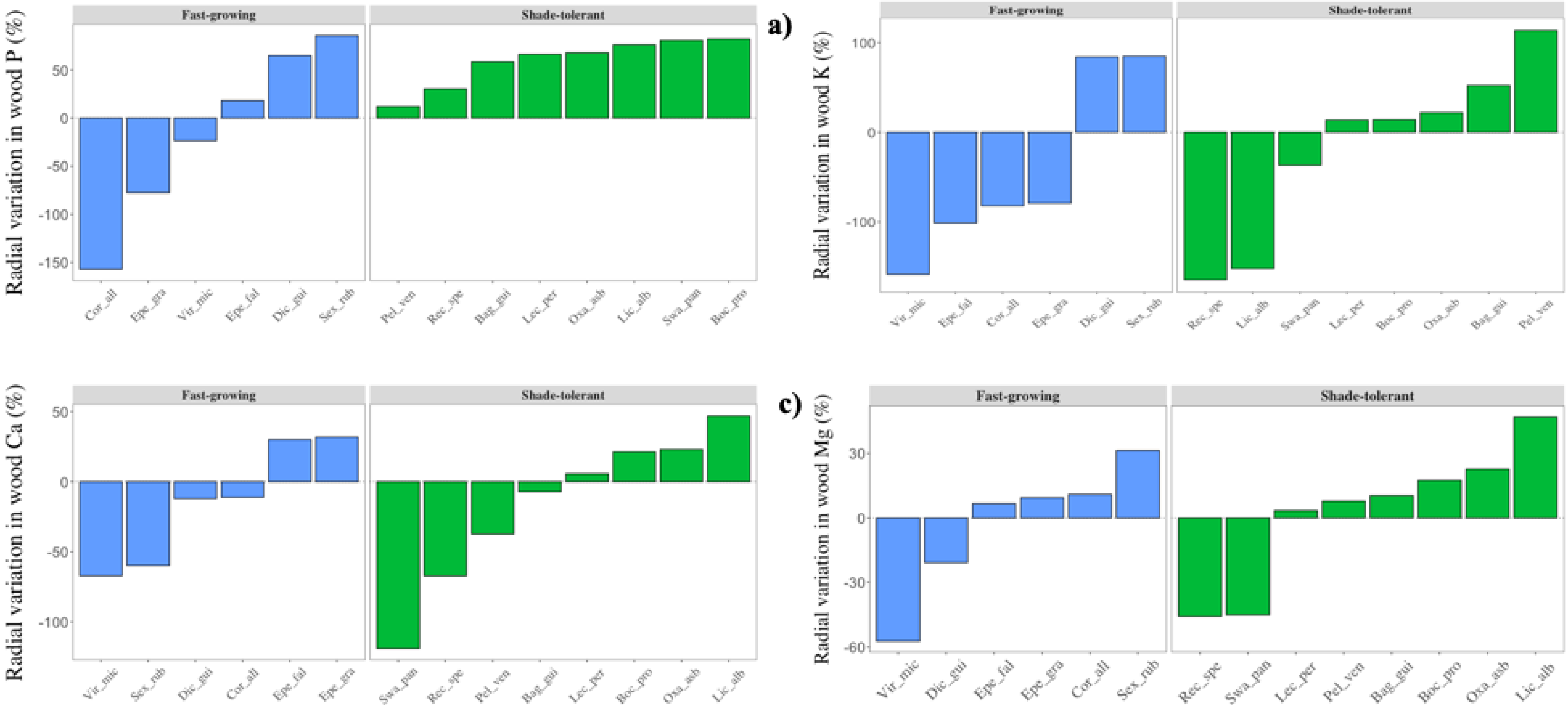
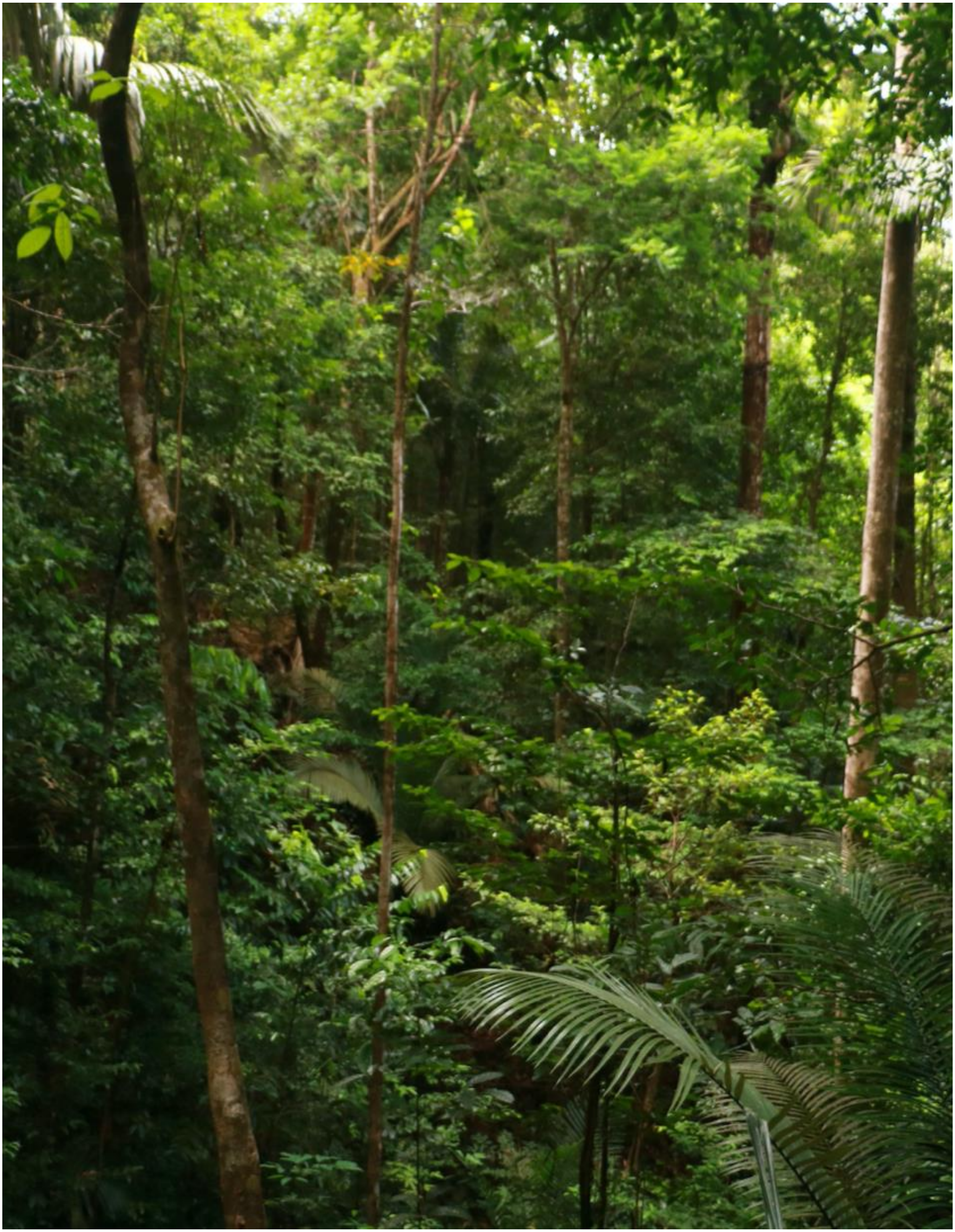


Figure S2. Resorption rates of wood phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg), for 14 tree species belonging to two ecological guilds (a-d). Species mean values and standard deviations are shown. See Table 1 for species codes.



Chapter 4

The relationships between wood traits and species demography change during tree development in a lowland tropical forest

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ABSTRACT

One foundational assumption of trait-based ecology is that functional traits are related to species demography. However, the links between traits and demographic rates are, in general, not as strong as expected. These weak associations may be due to the use of soft traits that are distantly related to performance, and/or the lack of consideration of size-related variations in both traits and demographic rates.

Here, we examined how wood functional traits were related to demographic rates in 19 tree species from eastern Amazonia. We measured eleven wood traits (i.e., structural, anatomical and chemical traits) in sapling, juvenile and adult wood, and related them to growth and mortality rates at different life stages.

The relative role of wood traits in explaining demographic rates changed during tree development. At the sapling stage, relative growth rates (RGR) were negatively related to wood specific gravity (WSG) and total parenchyma fractions (F_{TP}), while mortality rates (MR) decreased with radial parenchyma fractions but increased with vessel lumen area (V_A). Juvenile RGR were unrelated to wood traits, whereas juvenile MR were negatively related to WSG and axial parenchyma fractions (F_{AP}). At the adult stage, RGR scaled positively with V_A and wood potassium concentrations. Adult MR were not predicted by any trait. Overall, the strength of the trait-demography associations decreased at later ontogenetic stages.

Our results indicate that the associations between traits and demographic rates can change as trees age. Also, hard traits, such as wood chemical or anatomical traits, may be better predictors of growth and mortality rates than WSG. Our findings are important to expand our knowledge on tree life-history variations and community dynamics in tropical forests, by broadening our understanding on the links between wood traits and demography during tree development.

Key words: wood traits, demographic rates, tree size, tropical trees, ontogeny

INTRODUCTION

A main goal of trait-based ecology is to understand how functional traits are related to species demography (Shipley et al., 2016). This is of central importance for understanding life-history variations and mechanisms of community assembly (Gilbert et al., 2006; Wright et al., 2010), as well as to improve dynamic global vegetation models (e.g., Worthy & Swenson, 2019). Although significant advances have been made in the last decades in explaining the links between traits and demographic rates (e.g., Poorter et al., 2010; Wright et al., 2010; Hérault et al., 2011; Aubry-Kietz et al., 2015; Paine et al., 2015; Visser et al., 2016), the relationships of most functional traits with species demography are generally weak (e.g., Visser et al., 2016; Yang et al., 2018). Two main reasons may explain this pattern. First, research on this topic has focused largely on few and relatively easy to measure traits (i.e., "soft traits"), which may not fully capture some plant functions (Yang et al., 2018). This leads to the question of whether, and how, "hard traits" (i.e., traits that would be more mechanistically linked to plant functions, despite being more difficult to measure) can be more strongly related to species demographic rates (Russo et al., 2010; Poorter et al., 2010; Fan et al., 2012). Second, most previous studies on trait-demography relationships have considered either only one stem size class or have averaged broad stem size classes (e.g., Russo et al., 2010; Wright et al., 2010), overlooking size-related variations in both traits and performance (e.g., Visser et al., 2016; Rungwattana & Hietz, 2017). Therefore, it remains unclear to what extent the effects of traits on demography change during tree development (Iida et al., 2014).

A number of studies have shown that wood specific gravity (WSG) can predict, to some extent, species demographic rates (Poorter et al., 2010; Wright et al., 2010; Hietz et al., 2016; Visser et al., 2016). In general, WSG is negatively related to mortality and diameter growth rates (Poorter et al., 2008; Wright et al., 2010; but see Russo et al., 2010). Yet, specific gravity is an emergent property of wood that is affected, in angiosperms, by the fractions and morphologies of fibers, vessels and parenchyma cells (e.g., Zieminska et al., 2013, 2015). The main functions of these cell types are related to mechanical strength, water transport and storage, respectively (e.g., Carlquist, 2001). Therefore, the relationships of WSG with growth and mortality rates may be better understood by considering wood anatomy (e.g., Poorter et al., 2010; Russo et al., 2010).

The anatomical traits underlying the relationship between WSG and diameter growth rates are relatively well studied (e.g., Russo et al., 2010; Fan et al., 2012; Hietz et al., 2016). For example, low-WSG species grow fast in part because they generally have lower fiber fractions and/or thinner fiber walls (Zieminska et al., 2013), which may reduce stem construction costs (King et al., 2006). They also build wider vessels which favor high xylem hydraulic conductivity and support high leaf-photosynthetic carbon gain (Santiago et al., 2004; Poorter et al., 2010; Hietz et al., 2016). In addition, tree growth may also depend on wood nutrient concentrations (Martin et al., 2014). For instance, physiological studies have shown that calcium (Ca), potassium (K) and magnesium (Mg) are involved in wood formation, particularly during cell expansion and differentiation (Ache et al., 2010; Fromm, 2010). Phosphorous (P), on the other hand, plays critical roles in plant metabolism since it is a structural component in ribonucleic acid (RNA), and acts as a metabolic energy unit in adenosine triphosphate (ATP, Jiang et al., 2019), among others. Furthermore, nutrient addition experiments in lowland tropical forests have shown that tree growth is commonly limited by soil P (Vitousek, 1984; Turner et al., 2018) or K availability (Wright et al., 2011; Wright et al., 2018). Thus, there are good reasons to think wood nutrient concentrations should be related to growth rates. Yet, the extent to which wood nutrients influence growth is unclear, especially in diverse tropical forests, since studies examining the links between wood nutrient concentrations and growth rates in tropical trees have been scarce and show seemingly contradictory results (Martin et al., 2014; Heineman et al., 2016).

On the other hand, it is well known that species with higher WSG tend to have lower mortality rates (e.g., Wright et al., 2010; Visser et al., 2016). However, the anatomical mechanisms driving this relationship are still unclear (but see Poorter et al., 2010; Osazuwa-Peters et al., 2017). This is due to the fact that similar values of WSG can be the product of different wood anatomies (e.g., Zieminska et al., 2015) and also, and more importantly, because tree mortality tends to be a slow and stochastic process (Poorter et al., 2008) which can be simultaneously influenced by different processes (Russo et al., 2010; Hietz et al., 2016; Osazuwa-Peters et al., 2017). For instance, the lower mortality rates that characterize high-WSG tree species may be due to high fiber fractions and thicker fiber walls that may increase structural strength (Poorter et al., 2010) and resistance to pathogen attacks (Álvarez-Clare & Kitajima, 2007), and/or low xylem turgor loss points that might counteract the adverse effects of water deficits on living cells (Santiago et al., 2018).

In addition, there are possible links between xylem parenchyma cells and species mortality, but they remain poorly understood (Poorter et al., 2010; Morris et al., 2016a). For instance, a higher allocation to axial (AP) and radial (RP) parenchyma cells could reduce mortality (Poorter et al., 2010), because these cells store non-structural carbohydrates and nutrients (Plavcová & Jansen, 2015) which might enable faster recovery from disturbances (Kitajima & Poorter, 2007; Martin et al., 2014), or can provide an active response to xylem infections and mechanical damage (Carlquist, 2001; Morris et al., 2016b, 2019). The effects of parenchyma cells on mortality rates may depend, to some extent, on their stem cross-sectional fractions (Poorter et al., 2010; Morris et al., 2016b). While total parenchyma fractions (i.e., AP+RP) tend to be lower in high-WSG species (e.g., Fortunel et al., 2013; Zieminska et al., 2015), AP (Gonzalez-Melo et al., unpublished results) or RP (Zheng & Martínez-Cabrera, 2013) fractions can scale positively with WSG. This suggest that AP and RP cells may have different patterns of associations with WSG and mortality rates. However, very few studies have formally examined the possible links between xylem parenchyma cells and mortality rates across tropical tree species (but see Herrera-Ramírez et al., 2021).

Since wood functional traits (e.g., Marin & Thomas, 2013; Rungwatanna & Hietz, 2017) and demographic rates (e.g., Hérault et al., 2011; Visser et al., 2016) can vary substantially with tree size, it is likely that both the sign and the strength of the trait-demography links may change accordingly. For instance, seed size and stature are important to predict seedling performance, while WSG seems to be the best predictor of demography of small, but not of large trees (Lida et al., 2014; Visser et al., 2016). Similarly, in a recent study conducted in a tropical semi-deciduous forest, Osazuwa-Peters et al., (2017) found that species demography was more strongly related to wood anatomical traits, such as cell fractions, in small than in large trees (Osazuwa-Peters et al., 2017). However, it is unclear if this trend holds true for other forest types. To our knowledge, no previous studies have examined the extent to which the relationships between wood anatomical traits and demographic rates change during tree development in lowland tropical humid forests.

Here, we studied how wood functional traits (i.e., WSG, and wood anatomical and chemical traits) are related to growth and mortality rates in 19 tree species from a lowland forest in eastern Amazonia. In particular, we wanted to answer the following questions: (i) Are wood functional traits related to growth and mortality rates? We hypothesized that diameter growth rates will increase with wood nutrient concentrations (i.e., P, K, Mg and Ca) and xylem water transport capacity (i.e., vessel lumen area), and decrease with stem construction costs (i.e., higher WSG, fiber fraction or fiber wall thickness). We also predicted that mortality rates will be negatively related to traits linked to stem structural strength (i.e., WSG, fiber fraction and fiber wall thickness) and either to AP or RP fractions. (ii) How does the strength of the relationships between wood functional traits and demographic rates vary with tree size? We expected that the associations between wood traits and species demographic rates will be stronger for sapling and juvenile wood, in comparison to adult wood.

MATERIALS AND METHODS

Study site— The research was conducted in the Paracou research station, a lowland tropical rainforest located in northern French Guiana (https://paracou.cirad.fr/; 5° 18' N, 52° 55' W). At Paracou, mean annual temperature is 28.4ºC, and annual rainfall averages *c.* 3.000 mm with a marked dry season occurring between August and November, and a distinct rainy season from March to June (Wagner et al., 2011). Dominant families in the forests of Paracou include Fabaceae, Lecythidaceae, Sapotaceae and Chrysobalanaceae (Hérault et al., 2011). The landscape is characterized by moderate hills separated by narrow streams (Ferry et al., 2010), and soils are strongly P-limited (Grau et al., 2016).

Species and sampling— We selected 19 tree species that represent a broad gradient of variation in shade-tolerance, ranging from pioneers to understory or canopy shade-tolerants (Table 1). These species also spanned a wide range of WSG and wood anatomical traits (Table 2). We sampled 75 large trees (i.e., > 10 cm DBH), with two to five individuals per species (Table 1). Stem discs were collected, at breast height (*c.* 1.3 m), from previously cut-down trees. All wood samples were collected in Paracou, except for *Schefflera morototoni*, *Cecropia obtusa* and *Miconia tschudyoides* that were collected in nearby secondary forests.

Since wood structure is conserved as trees age, ontogenetic shifts in wood structure can be analyzed by measuring radial (i.e., from pith to bark) changes in wood traits. Consequently, in each stem disc, radial segments were cut and then divided in three radial sections: (i) 1-5 cm, (ii) 5-10 cm, and (iii) >10 <50 cm. Hereafter, we refer to these radial sections as sapling, juvenile and adult wood, respectively. It is important to note that here we used stem diameter to define these three ontogenetic stages (i.e., sapling, juvenile and adult wood). Yet, we acknowledge that this categorization of ontogenetic stages can differ from others found in the literature, and may not always reflect real ontogeny because species can attain maturity at different stem diameters (e.g., Wright et al., 2005).

Wood trait measurements— In each sapling, juvenile and adult wood section, samples of *c.* 2x2x1 cm were cut every 1 cm. In these wood samples, we measured fresh volume and dry mass. Fresh volume was measured with the water displacement method, and dry mass was obtained after drying the segments at 103ºC to a constant mass for 72 h. WSG per sample was defined as dry mass over fresh volume (Kollman & Coté, 1968). Then, mean WSG values for sapling, juvenile and adult wood was calculated averaging values from the 1-cm samples. Since the deposition of wood extractives

Table 1. Study species, family, number of trees sampled (n), mean diameter at breast height (DBH) of sampled individuals, and ecological guilds for 19 Amazonian tree species from a lowland forest in eastern Amazonia. Ecological guilds were assigned based on Favrichon (1994), Uriarte et al., (2005), Scotti et al., (2010) and Bossu et al., (2015).

Species	Family	Local name	n	DBH (cm)	Ecological guild	Reference
Bagassa guianensis	Moraceae	Bagasse	5	25.1	Light-demanding/Canopy	Bossu et al., (2015)
Cecropia obtusa	Urticaceae	Diapapaire	3	16.1	Light-demanding/Understory	Favrichon (1994)
Dicorynia guianensis	Fabaceae	Angelique	5	18.2	Semi hade-tolerant/Canopy	Favrichon (1994)
Eperua falcata	Fabaceae	Wapa	5	19.5	Semis hade-tolerant/Canopy	Favrichon (1994)
Eperua grandiflora	Fabaceae	Wapa courbaril	3	12.4	Semis hade-tolerant/Canopy	Favrichon (1994)
Eschweilera coriacea	Lecythidaceae	Maho noir	3	16.3	Shade-tolerant/Canopy	Favrichon (1994)
Eschweilera sagotiana	Lecythidaceae	Maho noir	2	17.8	Shade-tolerant/Canopy	Favrichon (1994)
Hirtella glandulosa	Chrysobalanaceae	Santi koko	2	15.3	Shade-tolerant/Understory	Favrichon (1994)
Lecythis persistens	Lecythidaceae	Maho rouge	5	16.3	Shade-tolerant/Understory	Favrichon (1994)
Licania alba	Chrysobalanaceae	Lebi koko	4	14.7	Shade-tolerant/Canopy	Favrichon (1994)
Miconia tschudyoides	Melastomataceae	Mesepu	2	13.2	Light-demanding/Understory	Favrichon (1994)
Oxandra asbeckii	Annonaceae	Muamba	4	14.6	Shade-tolerant/Understory	Favrichon (1994)
Parkia nitida	Fabaceae	Dodomisinga	4	18.5	Light-demanding/Canopy	Favrichon (1994)
Parkia velutina	Fabaceae	Dodomisinga	3	12.4	Light-demanding/Canopy	Favrichon (1994)
Recordoxylon speciosum	Fabaceae	Wakapu gitin	3	12.3	Semi-shade-tolerant/Canopy	Favrichon (1994)
Schefflera morototoni	Araliaceae	Bois saint jean	3	21.2	Light-demanding/Canopy	Uriarte et al., (2005)
Sextonia rubra	Lauraceae	Grignon franc	3	22.4	Semi-shade-tolerant/Canopy	Scotti et al.,(2010)
Swartzia panacoco	Fabaceae	Bugu bugu	3	12.5	Shade-tolerant/Canopy	Favrichon (1994)
Virola michelii	Myristicaceae	Yayamodou	3	20.5	Light-demanding/Canopy	Favrichon (1994)

(WE) in heartwood or sapwood can increase wood dry mass and then alter WSG values (e.g., Lehnebach et al., 2019), it is possible that the links between WSG and demographic rates may be affected by the concentration of WE. To examine the effects of WE on the WSG-demography associations, we recalculated sapling, juvenile and adult WSG (i.e., WSG_{REC}) of five species (*Bocoa prouacensis*, *Virola michelii*, *Sextonia rubra*, *Bagassa guianensis* and *Dicorynia guianensis*) by removing the effect of WE concentrations on wood dry mass, and run analyses (see below) using

WSG_{REC} values. We obtained WE concentrations from both published (Amusant et al., 2014) and unpublished studies (Rodrigues, 2010).

In sapling and juvenile wood, anatomical analyses were conducted on one wood sample (*c.* 2x2x1 cm); whereas in adult wood, anatomy was analyzed every 1.5 cm until reaching the bark, and an averaged value was calculated. To characterize wood anatomy, cross-sectional surfaces were sanded using a polishing machine with 1200-grit diamond discs, and then samples were cut with a GLS-1 sledge microtome to get a plane surface (Gärtner et al., 2015). Photographs were taken at 5-10 x 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 sample, between 10-20 partially focused images were taken and were then combined using Helicon Focus (Helicon Focus Ltd., Kharkov, Ukraine). From these anatomical images, vessel lumen area (V_A, mm^2) and cross-sectional area fractions of fibers (F_F), vessels (F_V, lumen+wall), axial (F_{AP}), radial (F_{RP}), and total parenchyma cells ($F_{TP}= F_{AP} + F_{RP}$), were measured.

To calculate cell fractions and V_A, wood cell types were manually colored using Photoshop (Adobe Systems Incorporated, USA), and traits were calculated automatically using the batch function in the software ImageJ (https://imagej.nih.gov/ij/). Fiber wall thickness (F_{WT}, μm) was measured by taking photographs at 50-100x objective lenses using a laser microscope (VK 8850, Keyence). To do so, each anatomical image 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. In total, we measured eight wood anatomical traits (Table 2).

We measured wood nutrients concentrations in both sapling and adult wood. Yet, as wood nutrients tend to be reabsorbed from inner to outer wood, during heartwood formation, in several of our study species (A. Gonzalez-Melo, et al., unpublished results), nutrient concentrations from sapling wood were not considered reliable for this study. Therefore, here we only considered values of wood nutrient concentrations from adult wood. Wood nutrient concentrations were estimated on the sample closest to the bark. Whenever possible, nutrient analyses were conducted on the same wood samples that were used to calculate WSG and anatomical traits. To calculate wood nutrient concentrations, wood samples were grinded and dry-ashed at 550ºC for 1 h, and then the ash was dissolved in HNO_3 (1M). Wood base cations and P were calculated using inductively coupled plasma-optimal emission spectrometry (ICP-OES) on an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA), with apple leaves (NIST 1515) as reference samples.

Demographic rates— To calculate adult (i.e., >10 cm DHB) demographic rates, we used two datasets belonging to the Guyafor network of forest permanent plots (https://paracou.cirad.fr/). The first dataset is based on eight permanent plots: one 25-ha and seven 6.25-ha plots (plots 9-15) set up between 1991 and 1992 to monitor the functioning and dynamics of both disturbed and undisturbed forests in Paracou (Gourlet-Fleury et al., 2004). Between 1992 and 2015, censuses of all stems with a DBH>10 cm were conducted every five years in the 25-ha plot, and every two years in the seven 6.25-ha permanent plots. The second dataset is from five 1-ha permanent plots established in undisturbed forests in Nouragues, a research station located *c.* 120 km from Paracou. In these plots, all stems with a DBH > 10 cm have been monitored at 2-4-year intervals since 1993.

To calculate sapling (1-5 cm DBH) and juvenile (5-10 cm DBH) demographic rates, we used two datasets: the first dataset belongs to the Guyafor network and is based on *c.* 750 eight-m radii circular subplots established in twelve 6.25-ha permanent plots to monitor forest regeneration dynamics in Paracou. Diameter increments and mortality rates of saplings and juveniles have been monitored in these circular subplots at 3 or 5-year intervals between 1992 and 2016. The second dataset is from ten 20x250 m transects established in Paracou in 1994 by Molino & Sabatier (2001). In these transects, inventories of diameter growth and mortality rates of saplings and juveniles were conducted for a seven-year period (1995-2002).

Diameter relative growth rates (RGR, $mm \cdot mm^{-1} y^{-1}$) were calculated as: $\ln(DBH_f/DBH_i)/\Delta t$, where DBH_f and DBH_i refer to final and initial diameters, respectively and Δt is the time in years between the latest and earlier censuses. Mortality rates (MR, % y^{-1}) were calculated as $100 \times (1-(N_f/N_i))^{1/t}$, where N_i is the initial number of individuals, N_f is the number of survivors, and t is the time in years between measurements (Sheil & May, 1996). RGR and MR were calculated separately for sapling (1-5 cm DBH), juvenile (5-10 cm DBH), and adult wood (10-50 cm DBH). The number of individuals and census intervals used to calculate species demographic rates at each ontogenetic stage are shown in Table S1.

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$(N_f/N_i))^{1/t}$, where N_i is the initial number of individuals, N_f is the number of survivors, and t is the time in years between measurements (Sheil & May, 1996). RGR and MR were calculated separately for sapling (1-5 cm DBH), juvenile (5-10 cm DBH), and adult wood (10-50 cm DBH). The number of individuals and census intervals used to calculate species demographic rates at each ontogenetic stage are shown in Table S1.

Statistical analyses— Trait-demography relationships, for each ontogenetic stage, were examined using pairwise Pearson correlations. We also analyzed growth-mortality and trait-trait relationships, for each ontogenetic stage, using linear regressions and pairwise Pearson correlations, respectively. All statistical analyses were conducted in R (R Development Core Team, 2019).

RESULTS

Overall, there was substantial variation in mean trait values both among species and ontogenetic stages. Most mean trait values were higher in adults, than in juveniles or sapling wood, except for fiber fraction (F_F) and vessel number (V_N), which were higher in sapling wood. Overall, the ranges of variation in wood traits were higher for sapling than for adult or juvenile wood. RGR was higher for adults, while MR was larger for saplings (Table 2).

Relationships between wood traits and mortality rates— Sapling and juvenile mortality rates (MR) were significantly related to different wood traits. In contrast, adult MR was unrelated to wood traits. The traits that explained MR differed between sapling and juvenile wood. Sapling MR decreased with radial parenchyma fractions (F_{RP}; Fig. 1c), but increased with vessel lumen area (V_A; Fig. 1d); while juvenile MR decreased with both WSG (Fig. 2a) and axial parenchyma fractions (Fig. 2b).

Table 2. Summary characteristics of wood functional traits measured on sapling, juvenile and adult wood for 19 tree species from a lowland tropical forest in eastern Amazonia. Mean, standard deviation (SD) and range of variation are shown.

Trait	Abbrev.	Unit	Sapling wood			Juvenile wood			Adult wood		
			Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Wood specific gravity	WSG	unitless	0.60	0.23	0.21-0.97	0.63	0.22	0.23-0.92	0.67	0.15	0.36-0.92
Fiber wall thickness	F_{WT}	μm	4.10	1.86	1.05-7.87	4.44	1.88	1.48-7.73	4.80	1.83	2.01-7.71
Fiber fraction	F_F	unitless	65.1	11.2	47.4-84.3	63.9	10.9	41.8-79.5	60.7	9.04	41.2-72.8
Vessel lumen area	V_A	mm^2	0.010	0.05	0.002-0.02	0.017	0.08	0.003-0.03	0.019	0.09	0.002-0.03
Vessel number	V_N	mm^{-2}	6.95	3.67	2.07-17.1	4.52	3.20	1.60-14.5	5.17	3.89	2.28-15.7
Vessel fraction	Fv	unitless	7.26	3.3	3.91-16.0	7.86	3.84	4.27-20.9	9.39	5.06	3.49-23.3
Specific hydraulic conductivity	Ks	kg m s^{-1} MPa^{-1} / mm²	98.8	45.2	54.4-224.5	108.1	58.2	53.4-297.5	131.9	73.9	63.8-333.7
Total parenchyma fraction	F_{TP}	unitless	21.1	10.4	8.55-14.6	28.2	10.1	10.6-41.5	29.9	9.34	15.5-49.0
Axial parenchyma fraction	F_{AP}	unitless	13.2	10.3	0.46-32.4	13.0	8.45	0.84-30.8	13.5	8.11	1.93-32.8
Radial parenchyma fraction	F_{RP}	unitless	13.1	5.79	4.30-22.8	15.1	5.99	7.35-26.6	16.3	6.04	7.70-28.8
Wood phosphorous	P	μg g^{-1}							65.1	31.3	20.6-153.7
Wood calcium	Ca	μg g^{-1}							2152	2059	281-7239
Wood potassium	Mg	μg g^{-1}							162.5	164.2	19.4-643.5
Wood magnesium	K	μg g^{-1}							359.2	306.0	63.2-1269
Relative growth rate	RGR	mm·mm yr^{-1}	0.83	1.04	0.01-3.71	0.98	0.59	0.39-2.57	2.49	1.73	0.72-6.98
Mortality rate	MR	% yr^{-1}	3.62	6.14	0.61-23.7	2.10	2.09	0.23-7.29	0.82	1.66	0.1-7.27

Relationships between wood traits and diameter growth rates— Sapling and adult relative growth rates (RGR) were significantly related to different wood traits, while juvenile RGR were unrelated to wood traits. Sapling and adult RGR were explained by different wood traits. Sapling RGR were negatively related to both WSG (Fig. 1a) and total parenchyma fractions (F_{TP}; Fig. 1b). Adult RGR scaled positively with V_A (Fig. 3a) and wood K concentrations (Fig. 3b)

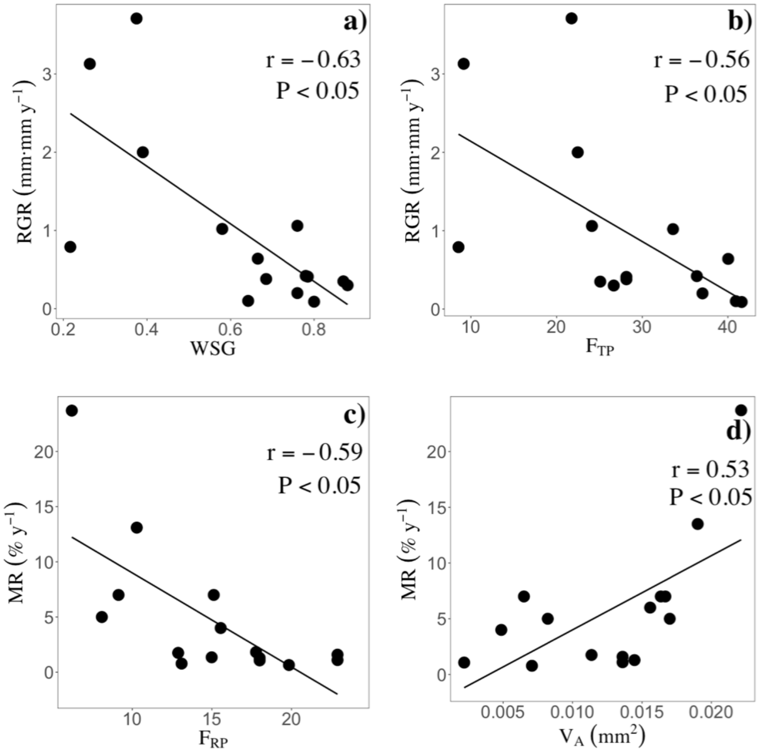

Fig. 1. Significant bivariate relationships between demographic rates and wood traits at the sapling stage. a) wood specific gravity, b) total parenchyma fractions, c) radial parenchyma fractions, and e) fiber lumen area. Black and solid lines represent significant ($p<0.05$) relationships. Pearson correlation coefficients (r) are shown for each trait-demography relationship.

Effect of wood extractives on WSG-demography associations— The concentration (i.e., % wood dry mass) of wood extractives (WE), in both heartwood and sapwood, is known for five of our study species (i.e., *Bocoa prouacensis*, *Virola michelii*, *Sextonia rubra*, *Bagassa guianensis* and *Dicorynia* *guianensis*). In these species, WE concentrations are low (< 7%), and the differences between heartwood and sapwood WE concentrations are small (< 3%, Rodrigues, 2010; Amusant et al., 2014). The multiple regressions that included WSG_{REC} (see Materials and methods) did not differ, in terms of the coefficient of determination or p-value, from the multiple regressions ran using WSG (data not shown).

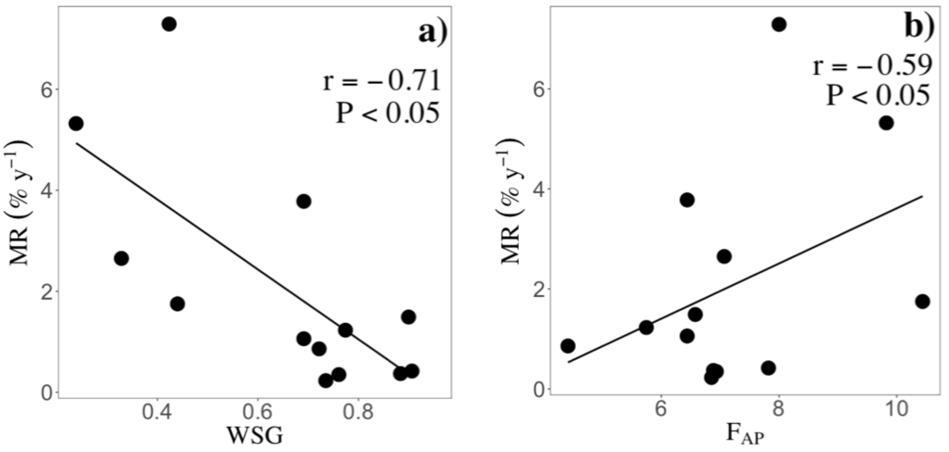

Fig. 2. Significant bivariate relationships between demographic rates and wood traits at the juvenile stage. a) wood specific gravity and b) axial parenchyma fractions. Black and solid lines represent significant ($p<0.05$) relationships. Pearson correlation coefficients (r) values are shown for each bivariate relationship.

DISCUSSION

Relationships between wood traits and mortality rates— We hypothesized that mortality rates (MR) decrease with stem traits related to wood strength (i.e., WSG, fiber fractions or fiber wall thickness) and the fractions of either axial (AP) or radial (RP) parenchyma. In line with this expectation, we found that juvenile MR were negatively related to WSG (Fig. 2a). This is in agreement with a number of studies showing a negative relationship between WSG and juvenile MR in closed-canopy tropical forests (e.g., Wright et al., 2010; Philipson et al., 2014). Different and non-exclusive reasons may explain this finding. First, in the shaded understory, where carbon gain is limited by low light availability, selection should favor denser tissues which increase survival due to reduced mechanical damages from falling debris or lower risk of pathogen attacks (Alvarez-Clare & Kitaima, 2007; Kitajima et al., 2012; Reich, 2014). For instance, stem tissue density was strongly correlated

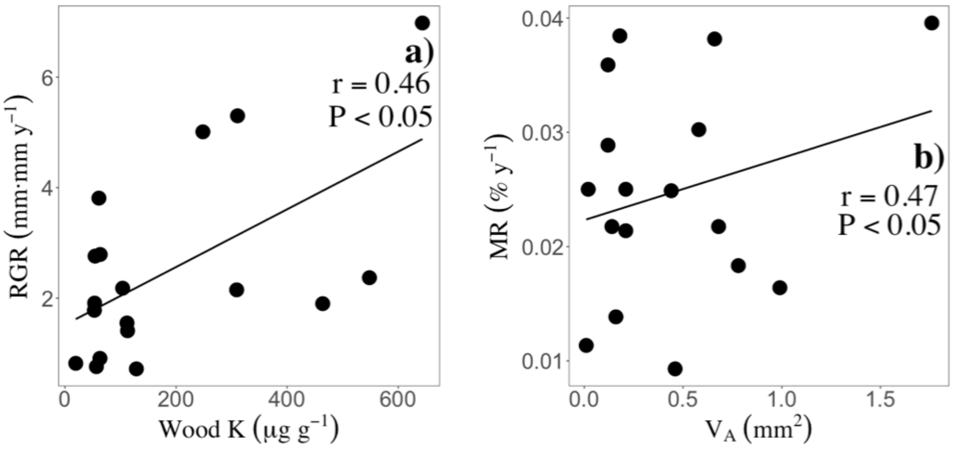

Fig. 3. Significant bivariate relationships between demographic rates and wood traits at the adult stage. a) wood potassium concentrations and b) vessel lumen area. Black and solid lines represent significant ($p<0.05$) relationships. Pearson correlation coefficients (r) are shown for each bivariate relationship.

with the modulus of elasticity and toughness of stems, and was the best predictor of species mortality rates in saplings of eight lowland tropical tree species (Álvarez-Clare & Kitajima, 2007). It is likely that fiber wall thickness (F_{WT}) mediates the relationship between WSG and MR, since WSG scaled positively with (F_{WT}) in juvenile wood (Fig. S2-b). Second, in juvenile wood, WSG is positively related to total parenchyma fractions (Fig. S2-b), which can increase survival because parenchyma cells provide an active response against pathogens (e.g., Morris et al., 2016b). Third, high-WSG species may have lower mortality rates because they can be more tolerant to drought events. For example, at Paracou, high-WSG species tend to have lower xylem turgor loss points than low-WSG species, which may reduce the detrimental effects of water deficits on living cells (Santiago et al., 2018).

We also found a significant and positive relationship between vessel lumen area (V_A) and sapling MR (Fig. 1d). This finding agrees with that of Osazuwa-Peters et al., (2017), who showed that sapling MR increased with vessel lumen size in a semi-deciduous forest in Panama. According to the "rare pith hypothesis", wider conduits can have more interconduit pits and pit membranes and, therefore, should be potentially more vulnerable than narrow conduits to air-seeding through pits (Wheeler et al., 2005). Therefore, one possible explanation to this result should be that species with wider conduits have a higher risk of drought-induced xylem embolisms, that may eventually cause mortality. Yet, we ruled out this possibility since at our study site vessel lumen size was found to be independent from pit traits, and is weakly associated to xylem cavitation (Levionnois et al., 2021). Instead, we suggest that the observed association between V_A and MR, at the sapling stage, can reflect allocation and demographic differences between species. Fast-growing species typically have wider conduits because they favor water transport and ultimately growth (e.g., Santiago et al., 2004; Russo et al., 2010; Hietz et al., 2016; see bellow). Yet, at the same time, species that grow faster tend to have higher mortality rates (e.g., Poorter et al., 2008; Russo et al., 2020). For instance, among our study species, growth rates were traded-off against mortality rates at the sapling stage (Fig. S1a). Evidence suggests that saplings of fast-growing species have higher mortality rates because they tend to have poorly-defended tissues (Alvarez-Clare & Kitajima, 2007; Kitajima et al., 2012; see above). It is likely, then, that saplings with wider conduits (i.e., fast-growing saplings) die more often because they are more susceptible to pathogen or herbivores (e.g., Zhu et al., 2018; Alvarez-Clare & Kitajima, 2007), rather than as a consequence of hydraulic failure.

In line with our expectation, sapling and juvenile MR were negatively related to radial ($F_{RP;}$ Fig. 1c) and axial (F_{AP}; Fig. 2a) parenchyma fractions, respectively. Storage of nutrients and non-structural carbohydrates (NSC; i.e., starch, soluble sugars and lipids) is thought to be one of the main functions of xylem parenchyma cells (e.g., Morris et al., 2016). For example, both axial and radial parenchyma fractions have been positively related to the concentrations of NSC (e.g., Plavcová et al., 2015; Godfrey et al., 2019). Therefore, a higher allocation of wood volume to F_{RP} or F_{AP} might enable higher storage of NSC, which in turn may increase survival because NSC favor a faster recovery from periods of drought, defoliation or shading (Poorter & Kitajima, 2007; Myers & Kitajima, 2007; Herrera-Ramirez et al., 2021). An alternative, but not mutually exclusive explanation, is that radial and axial parenchyma cells increase survival since they play a critical role in plant defense by providing an active response against xylem infections and mechanical damages (Morris et al., 2016b). Although F_{RP} and F_{AP} were significantly related to sapling and juvenile MR, parenchyma fractions were unrelated to MR at the adult stage. This may be due to the possibility that other parenchyma traits, such as spatial arrangement and morphology, can have effects on tree functioning, in addition to the cross-sectional fractions measured here. For instance, axial parenchyma associated to vessels (i.e., paratracheal AP) is suggested to be of central importance in hydraulic balance (e.g., Morris et al., 2017; Aritsara et al., 2020), while banded axial parenchyma (i.e., AP arranged in bands) may play a role in limiting the spreading of decay (Morris et al., 2016, 2019). Moreover, the morphology of radial parenchyma cells (i.e., uniseriate or multiseriate rays) may affect stem hydraulics and, to some extent, mechanics (e.g., Zheng & Martinez-Cabrera, 2013). Thus, future studies should consider measuring the spatial arrangements and classify parenchyma cells into more specific categories.

Relationships between wood traits and relative growth rates— As expected, adult RGR scaled positively with wood K (Fig. 3a). This result is in line with fertilization experiments in lowland tropical forests showing that tree growth is strongly limited by soil K availability (e.g., Wright et al., 2011), although differed from those of Heineman et al., (2016), that reported no association between wood K and RGR. Potassium is suggested to play an important role in wood formation, mainly during cell expansion and osmoregulation (Ache et al., 2007; Fromm, 2010). Specifically, K is thought to be a driver of vessel formation (Fromm, 2010), and studies using secondary ion mass spectrometry have reported higher concentrations of K in vessels than in other xylem cells (e.g., Langer et al., 2002). Since fast-growing species need large vessels to increase xylem hydraulic conductivity and sustain high growth rates (e.g., Hietz et al., 2016), it is likely that they allocate proportionally more K to grow vessels than slow-growing species.

We found that V_A had a significant and positive effect on adult RGR (Fig. 3b). This result is in agreement with our hypothesis and with the results of several other studies (Russo et al., 2010; Fan et al., 2012; Hietz et al., 2016) which indicate that, everything else being equal, species with wider vessels grow faster. Since xylem-specific hydraulic conductivity (Ks) increases exponentially with vessel lumen area, but only linearly with vessel number (Tyre & Zimmerman, 2002), Ks is expected to be significantly higher in species that build large conduits. In turn, Ks tends to be positively related to stomatal conductance and leaf maximum photosynthetic carbon gain (Santiago et al., 2004), which ultimately favors diameter growth rates (Poorter et al., 2010; Russo et al., 2010). We also predicted that RGR would decrease with traits related to stem structural strength (i.e., WSG, F_F or F_{WT}). Consistent with this prediction, we found that sapling RGR was negatively related to WSG (Fig. 1a), which is in agreement with other studies in tropical forests (Poorter et al., 2008; Wright et al., 2010). One main reason to explain this result is the fact that, in sapling wood, species with high WSG have thicker fiber walls (Fig. S2-a), which represent higher stem construction costs.

We also found that total parenchyma fractions (F_{TP}) were negatively related to sapling RGR (Fig. 1b). We are aware of only one study that has shown a significant, although positive, link between F_{TP} and RGR (Poorter et al., 2010). Parenchyma cells represent the majority of living cells in wood (Morris et al., 2016), besides living-fibers (Carlquist, 2015). Living parenchyma cells, and in particular contact cells (i.e., cells having functional connections with vessels), are metabolically highly active (Spicer & Holbrook, 2007). Therefore, although living parenchyma have been linked to several simultaneous functions such as storage, defense and transport (e.g., Pfautsch et al., 2015, Morris et al., 2016, 2019), they may also represent a significant maintenance cost for trees. Thus, stem maintenance costs could be mediating the negative relationship between F_{TP} with growth RGR in adult wood (Fig. 3, Table 3).

Changes in trait-demography relationships during tree development— A number of studies have shown that both traits (Hietz et al., 2016, Rungwattana & Hietz, 2017) and demographic rates (Wright et al., 2010; Hérault et al., 2011) can vary considerably during tree development. Thus, we expected that the trait-demography relationships may change accordingly. In line with this expectation, we found that WSG explained MR only at the juvenile stage (Fig. 1d). High-WSG may represent a competitive advantage for individuals growing in the shaded-understory (see discussion above), but not for adult trees that have reached the sunlit canopy. At Paracou, adult tree mortality tends to increase during the rainy season when storms are common (Aubry-Kientz et al., 2015; but see Pillet et al., 2017), and is also strongly associated to soil topography and drainage, with higher treefall rates in bottomlands with waterlogged soils where root anchorage is limited (Ferry et al., 2010). It is reasonable to expect, then, that traits determining tree biomechanical stability, such as rooting depth, crown architecture, or the presence of buttressed roots may be better predictors of adult tree mortality in Paracou than WSG.

The Pearson correlation coefficients of the growth-trait relationships tended to be higher at the sapling compared to the adult stage (Fig. 1 and 2). This, together with the fact that adult MR were unrelated to wood traits, suggests that wood traits tend to be more weakly related, or unrelated, to demographic rates at later ontogenetic stages. This agrees with previous findings at local (Visser et al., 2016; Osazuwa-Peters et al., 2017) and regional scales (Poorter et al., 2008; Wright et al., 2010). One main factor explaining this result is the strong gradient in light availability that characterizes our study site (e.g., Baraloto et al., 2005; Laurans et al., 2012). In closed-canopy forests, light availability is an important factor mediating morphological and demographic variations across species, because it limits carbon gain (Wright et al., 2010). In general, saplings growing in the understory experience lower and more variable light availability than adult trees that grow in the canopy or subcanopy (Wright et al., 2010). As a consequence, interspecific differences in traits and demographic rates are expected to be higher in saplings than in adults (e.g., Poorter et al., 2010). Among our study species, the range of variation of most traits, as well as of MR, is higher for saplings than for juveniles or adults (Table 2). This may have favored the detection of stronger relationships between traits and demographic at early ontogenetic stages. Another factor that may contribute to the observed changes in the strength of the trait-growth relationships during tree development may be related to size-related shifts in growth rates. For instance, in Paracou, most tree species attain higher growth rates at intermediate stem sizes, likely when they have reached favorable canopy layers (Hérault et al., 2011). Yet, growth rates in larger trees of Paracou is typically lower (Hérault et al., 2011), possibly due to a shift in resource allocation from diameter growth to reproduction (Thomas, 1996).

A large body of literature has shown that WSG is in general a good proxy of growth and mortality rates (e.g., Poorter et al., 2008; Wright et al., 2010; Hérault et al., 2011). Yet, our results indicate that the associations between WSG and demographic rates are not always supported for different ontogenetic stages. For instance, at the sapling stage, WSG explained RGR but not sapling MR; while the opposite trend was found at the juvenile stage. Similarly, WSG was unrelated to both adult growth and mortality rates. These findings add to recent studies showing that demographic rates may be better explained by wood anatomical (Poorter et al., 2010; Russo et al., 2010; Fan et al., 2012; Osazuwa-Peters et al., 2017) or chemical traits (Martin et al., 2014) than by WSG. This may be due to the fact that "hard traits" are more closely related to performance than WSG. For example, vessel lumen area is more directly related to water transport capacity, and consequently to growth rates, than WSG (e.g., Fan et al., 2012). Furthermore, species with similar values of WSG may be functionally different, because similar values of WSG may be product of different wood anatomies (Zieminska et al., 2015).

Finally, it is important to note that while our study species reflect a wide spectrum of ecological strategies, the number of species we sampled is low which might affect the strength of the trait-demography associations we found and limits their generalizability. Thus, we suggest that further studies should examine whether the trait-demography associations reported in this study are consistent for larger sets of species and for different forest types as well.

CONCLUSIONS

In this study, we examined trait-demography associations of sapling, juvenile and adult wood of 19 tree species from eastern Amazonia. We found that, in general, growth and mortality rates of saplings, juveniles and adults were predicted by different combinations of wood traits. We also showed that the strength of the trait-demography associations decreased at later ontogenetic stages. Overall, our results support the growing evidence that the relationships of functional traits on species demographic rates can change during tree development. Moreover, our findings indicate that WSG may not always be a good proxy of growth and mortality, particularly when hard traits, such as wood chemical or anatomical traits are considered. These findings also support the general expectation that functional traits con be related to species demographic rates and, hence, that traits are important to increase our understanding of life-history variations and community dynamics in lowland tropical forests.

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SUPPORTING INFORMATION

Table S1. Relative growth rates (RGR, mm·mm^{-1} y^{-1}) and mortality rates (MR, % y^{-1}) for saplings, juveniles and adults of 19 tree species from a lowland forest in eastern Amazonia. Sample sizes (n), years of measurement (years), and datasets (data, see Material and methods) used to calculate demographic rates are shown for each species.

Species	**Saplings**				**Juveniles**				**Adults**			
	Growth		**Mortality**		**Growth**		**Mortality**		**Growth**		**Mortality**	
	RGR	n/years/data	MR	n/years/data	RGR	n/years/data	MR	n/years/data	RGR	n/years/data	MR	n/years/data
Bagassa guianensis									3.81	12/25/2nd	0.18	12/25/2nd
Cecropia obtusa	3.13	10/7/4th	23.7	40/7/4th	2.57	27/7/4th	2.65	35/7/4th	5.30	14/5/1st	7.27	19/23/1st
Dicorynia guianensis	0.10	20/24/3rd	13.1	307/7/3rd	0.83	30/5/3rd	0.86	17/6/3th	2.76	87/23/1st	0.66	147/23/1st
Eperua falcata	0.38	105/24/3rd	1.59	188/7/4th	0.93	26/5/3rd	1.06	69/7/4th	1.91	46/23/1st	0.46	105/23/1st
Eperua grandiflora	0.41	67/24/3rd	1.10	40/7/4th	0.45	12/24/3rd	3.78	57/5/3th	2.79	110/23/1st	0.02	147/23/1st
Eschweilera coriacea	1.02	43/6/4th	1.75	43/7/4th	0.95	12/6/4th	1.23	12/7/4th	1.55	146/23/1st	0.21	525/23/1st
Eschweilera sagotiana	0.64	136/25/4th	0.78	167/7/4th	0.93	50/24/4th	0.23	61/7/4th	1.41	245/23/1st	0.16	262/23/1st
Hirtella glandulosa	1.06	10/7/4th	1.35	11/7/4th					1.78	30/25/2nd	0.01	544/25/2nd
Lecythis persistens	0.20	74/5/3rd	0.75	271/7/4th	0.83	176/5/3rd	0.35	122/7/4th	0.91	251/23/1st	0.14	571/23/1st
Licania alba	0.35	19/5/3rd	1.29	172/23/4th	0.77	23/5/3rd	0.42	68/7/4th	0.82	109/23/1st	0.68	559/23/1st
Miconia tschudyoides	3.71	51/7/4th	1.32	503/7/4th	1.8	254/7/4th	1.75	86/7/4th	1.90	14/7/1st	0.21	40/5/1st
Oxandra asbeckii	0.30	99/5/3rd	1.07	328/5/3rd	1.13	41/5/3rd	0.37	154/5/3th	0.72	117/23/1st	0.78	733/23/1st
Parkia nitida			3.13	11/7/4th					6.98	10/10/1st	0.12	17/23/1st
Parkia velutina									5.01	11/23/1st	0.12	16/23/1st
Recordoxylon speciosum	0.09	12/24/3rd	2.71	40/7/4th	0.39	11/7/4th	1.49	11/5/3th	2.18	28/23/1st	0.44	32/23/1st
Schefflera morototoni	0.79	14/24/3rd	1.66	54/7/4th	0.98	16/7/4th	5.32	22/7/4th	4.3	12/23/1st		
Sextonia rubra	0.42	19/5/3rd	1.82	33/7/3rd			2.57	18/7/3rd	2.15	101/23/1st	0.99	108/23/1st
Swartzia panacoco	0.83	11/7/4th							0.76	14/23/1st	0.58	24/23/1st
Virola michelii	0.48	138/24/3rd	0.65	111/7/4th	0.48	19/24/3rd	7.29	22/5/3rd	2.37	61/23/1st	1.76	79/23/1st

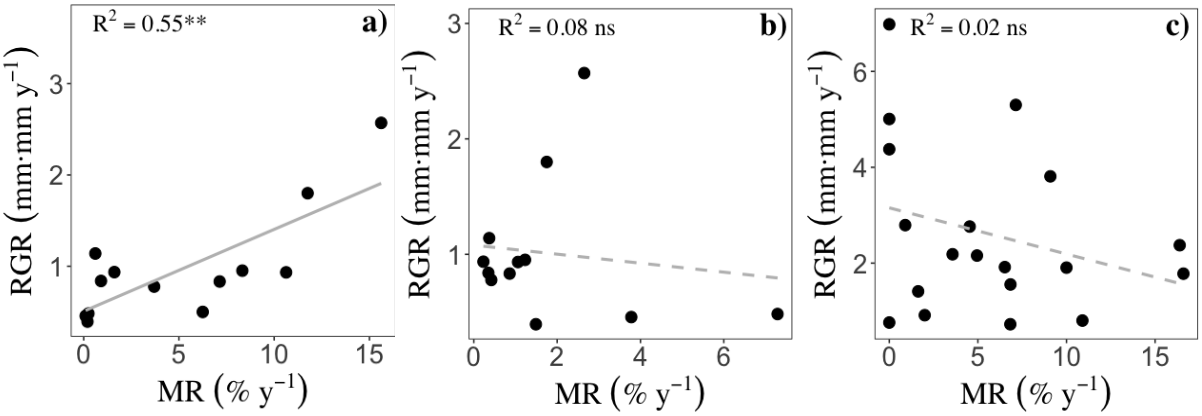

Fig. S1. Relationships between relative growth (RGR) and mortality rates (MR) for tree species in a lowland forest in Eastern Amazonia. a) saplings, b) juveniles and c) adults. Coefficients of determination (R^2) and P values are given. Solid and dashed lines represent significant (*P*<0.05) and non-significant regression fits, respectively. Significant levels are: **: P<0.01, and ns: P>0.05.

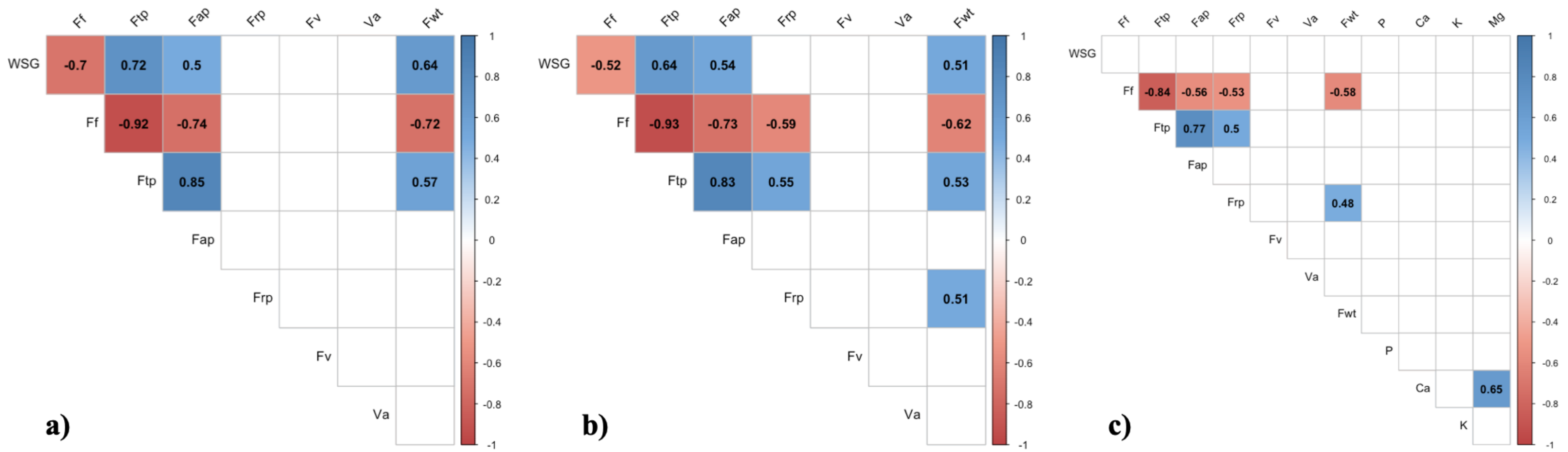

Fig. S2. Correlation matrices, using Pearson correlation coefficients, between wood traits measured on sapling (a), juvenile (b) and adult wood (c) of 19 tree species from a lowland forest in French Guiana. Significant correlations ($P<0.05$) are colored, where blue shades represent positive correlations and red shadows negative ones. Wood nutrient contents were not measured on juvenile wood (See Materials and methods). See Table 2 for trait abbreviation.

Chapter 5

The effects of radial variations in wood specific gravity on above-ground biomass and biomass growth rates estimations in a lowland tropical rainforest.

Andrés González-Melo & Juan Manuel Posada

ABSTRACT

Wood specific gravity (WSG) is a key trait to predict above-ground biomass (AGB) and biomass growth rates (BGR) of woody plants. It is well known that WSG can vary substantially within stems, from pith to bark. Yet, these radial trends in WSG are not usually taken into account, despite the fact they can have considerable effects on AGB and BGR estimations.

Here, we examined the effects that radial trends in WSG have on these estimations. We did radial measurements of WSG on 18 tree species with contrasting shade-tolerance, in a lowland forest in eastern Amazonia. Then, we estimated the percentage errors in AGB and BGR estimations that resulted from not considering radial gradients in WSG.

Not taking into account radial trends in WSG led to an average over-estimation of 17.1 % in AGB for fast-growing, low WSG, species; and an average under-estimation of -9.2 % for slow-growing, high WSG, species. A similar pattern of percentage errors in species BGR estimations were found among fast (13.3 % on average) and slow (-5.9 % on average) growing species. At the stand level, not considering radial trends in WSG led to underestimations of both AGB (-3.2% in undisturbed forests, and -4.9% in disturbed forests) and BGR (-3.5 in undisturbed forests).

These results are important to reduce uncertainties associated to AGB and BGR estimations in lowland tropical forests. The findings of this study suggest that the forest of Paracou may store and capture more biomass carbon than previously assumed. Moreover, they also suggest that uncertainties in AGB, BGR and carbon stocks estimations would be particularly relevant in the case of secondary forests, since these forests are becoming widespread in the tropics and tend to be dominated by fast-growing species for which errors in biomass estimations are higher.

Key words: Wood specific gravity; radial changes; above-ground biomass; biomass growth rates; lowland tropical trees.

INTRODUCTION

Wood specific gravity (WSG) is one of the most widely measured of all plant traits (e.g., Kattge et al., 2011), and it is considered a good proxy of plant functioning and ecological strategies (King et al., 2006; Chave et al., 2009; Anten & Shieving, 2010; Santiago et al., 2018). Besides its ecological importance, WSG also represents the carbon storage per unit volume of stem (Chave et al., 2009), and is a central trait to estimate above-ground biomass (AGB). For instance, after stem size, WSG is generally the second most important predictor of AGB (Chave et al., 2014). In addition, it is well established that WSG can vary considerably along the stem radial profile (i.e., from pith to bark) during tree development (e.g., Lachenbruch et al., 2011; Hietz et al., 2013; Plourde et al., 2015), which may have important implications for AGB estimations. Thus, the lack of consideration of radial trends in WSG may potentially lead to errors in AGB estimations (Bastin et al., 2015; Plourde et al., 2015). Yet, most regional and local studies on forest biomass do not consider radial shifts in WSG. Instead, they frequently use WSG values either from the outer part of the trunk (e.g., Baraloto et al., 2012b; Bastin et al., 2015) or averaged WSG values, at the genus or family level, obtained from global datasets (e.g., Malhi et al., 2004; Baker et al., 2004; Grau et al., 2016).

The percentage errors in tree biomass estimations that result from not taking into account radial shifts in WSG, depend mainly on the magnitude and direction of radial trends in WSG (e.g., Nock et al., 2009; Plourde et al., 2015). In general, there are two main patterns of radial trends in WSG (Woodcock & Shier, 2002; but see Williamson et al., 2012; Osazuwa-Peters et al., 2014): positive gradients in WSG (i.e., increments from pith to bark) that are common among fast-growing species, and negative trends (i.e., decreases in WSG towards the bark) that are frequent in slow-growing species (Hietz et al., 2013; Osazuwa-Peters et al., 2014; Plourde et al., 2015). As a consequence, not considering radial trends in WSG will result in an over-estimation of biomass in the case of fast-growing species (up to 31%; e.g., Nock et al., 2009), and an under-estimation in slow-growing species (up to -12%; e.g., Plourde et al., 2015). Similarly, not considering radial trends in WSG may lead to errors in the estimation of biomass growth rates (BGR), and potentially to misinterpretations of species biomass allocation patterns. Yet, the extent to which radial trends in WSG affect BGR estimations is still unclear for many forest ecosystems. These species-level errors in AGB and BGR estimations can also be propagated to stand level estimations of carbon stocks and fixation. The error will in part depend on the relative abundance of fast-or slow-growing species. For instance, since radial shifts in WSG tend to be less common and pronounced in shade-tolerant species (e.g., Hietz et al., 2013; Plourde et al., 2015), stand-level errors in AGB or BGR estimations are expected to be lower for old-growth forests that tend to be dominated by shade-tolerant, slow-growing species.

Tropical forests play a central role in the global biogeochemical carbon (C) cycle, because they represent two-thirds of terrestrial biomass C stocks, and have been subjected to massive deforestation in the last decades (Pan et al., 2013; Pennisi, 2020). Since AGB and BGR are two major components of forest C stocks and fluxes (Clark, 2001; Malhi et al., 2004; Muller-Landau et al., 2020), increasing the accuracy in AGB and BGR estimations is of central importance for ground-based carbon monitoring protocols (Chave et al., 2014). While forest biomass estimations and monitoring are expected to be increasingly based on remote-sensing techniques (e.g., Chave et al., 2014; Réjou-Mechain et al., 2017), accuracy in AGB and BGR estimations at large spatial scales will still depend on reliable ground data at the species or stand level (Bastin et al., 2015). Considering this overall context, the objective of our study was to examined the effects of radial trends in WSG on biomass estimations in a lowland tropical rainforest. In particular, we intended to study the extent to which radial changes in WSG lead to errors in individual species above-ground biomass (ABG) and biomass growth rates (BGR) estimations, and explore their possible implications on biomass estimations at the stand level.

METHODS

Study area— The study was conducted in Paracou, a tropical rainforest located in eastern Amazonia, French Guiana (5° 18' N, 52° 55' W; https://paracou.cirad.fr/). Paracou is a research station covered by extensive old-growth forest growing on smooth hills and nutrient poor soils (Baraloto et al., 20212b; Grau et al., 2016; Urbina et al., 2021). The climate is typical of seasonally tropical forest, with a dry season from August to November, and a rainy season from December to July. Mean annual temperature is 28.4ºC and annual rainfall averages c. 3000 mm (Wagner et al., 2011). Above-ground biomass in the northern forests of French Guiana range from 310 to 470 t ha^{-1} (Grau et al., 2016).

Species and sampling— In Paracou, we selected 18 tree species that represent a broad gradient of variation in shade-tolerance (Table 1), ranging from pioneers to shade-tolerant species (Table 1). These species also reflect a wide spectrum of mean WSG, from 0.30 to 0.97 (Table 2), that encompass most of the range of WSG values reported for trees in Paracou to date (Baraloto et al., 2010; Sarmiento et al., 2011). In total, we sampled 62 mature trees (DBH >10 cm), with two to five individuals per species (Table 1).

Wood specific gravity measurement —Radial wood samples (i.e., from pith to bark) were collected from stem discs taken at breast height from cut-down trees. These samples were cut and split every 1 cm. For each 1-cm 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 103ºC to a constant mass, for 24-72 h. WSG per each segment was defined as dry mass over fresh volume (Kollman & Coté, 1968).

We calculated three different values of WSG for each tree and species: (i) mean WSG (WSG_M), which corresponded to the average of all radial WSG values per tree; (ii) outer WSG (WSG_O), which was the average of WSG values from the outer part (i.e., 3 cm) of each trunk; and weighted WSG (WSG_W), that represented the average WSG weighted by the cross-sectional area of the trunk that corresponded to each individual wood segment, and assuming a cylindrical trunk (Muller-Landau, 2004). Here, WSG_W is a more accurate estimation of tree WSG in comparison to WSG_M or WSG_O, because it takes into account that outer wood segments contribute more to the whole WSG of each tree.

Above-ground biomass estimations— Tree above-ground biomass (AGB) was calculated, using a general allometric equation for tropical humid forests (Chave et al., 2014), as:

$$AGB= \exp (-1.803-0.9769 \text{ x } E + 0.9769 \text{ x } \log (WSG) + 2.6739 \text{ x } \log (DBH)-0.0299 \text{ x } \log (DBH)^2$$

where DBH is given in cm and E is a parameter that depend on climate. We calculated, for each individual tree and species, mean AGB (AGB_M), outer AGB (AGB_O), and weighted AGB (AGB_W) using WSG_M, WSG_O and WSG_W values, respectively (Table 2). We then estimated the percentage errors in AGB per species by comparing AGB_O and AGB_M with AGB_W, as follows:

$$\% \text{ error } AGB = ((AGB-AGB_W)\ ^{\cdot}\ *100)/AGB_W \qquad (1)$$

where AGB is AGB_O or AGB_M.

Table 1. Study species, family, number of trees sampled (n), mean diameter at breast height of trees sampled (DBH$_s$), mean and maximum diameter at breast height of each species (DBH$_{m\text{ and}}$ DBH$_{max,}$ respectively), and ecological guilds according to Favrichon (1994), for 18 Amazonian tree species from Paracou, French Guiana. DBH$_M$ and DBH$_{MAX}$ were calculated based on demographic data from one 25-ha and three 6.25-ha permanent plots established in Paracou (see Materials and methods). For *C. alliodora*, DBH$_M$ and DBH$_{MAX}$ were obtained from Bossu (2015) and Vega (1977), respectively. DBH$_{MAX}$ for each species was estimated averaging values of the five largest individuals.

Species	**Codes**	**Family**	**n**	**DBH (cm)**	**DBH$_M$ (cm)**	**DBH$_{MAX}$ (cm)**	**Ecological guild**
Bagassa guianensis	Bag_gui	Moraceae	5	25.1	35.8	105.7	Long-lived pioneer-Canopy
Bocoa prouacensis	Boc_pro	Fabaceae	3	12.3	28.6	52.7	Shade-tolerant-Understory
Cecropia obtuse	Cec_obt	Urticaceae	3	16.1	15.7	33.3	Pioneer-Understory
Cordia alliodora	Cor_all	Boraginaceae	3	26.4	38.9	85.2	Long-lived pioneer-Canopy
Dicorynia guianensis	Dic_gui	Fabaceae	5	18.2	47.3	94.7	Semi shade-tolerant-Canopy
Eperua falcata	Epe_fal	Fabaceae	5	19.5	47.7	71.8	Semi shade-tolerant-Canopy
Eschweilera coriacea	Esc_cor	Lecythidaceae	2	16.3	38.2	63.3	Shade-tolerant-Canopy
Eschweilera sagotiana	Esc_sag	Lecythidaceae	3	17.8	41.4	69.2	Shade-tolerant-Canopy
Hirtella glandulosa	Hir_gla	Chrysobalanaceae	2	15.3	17.1	40.3	Shade-tolerant-Understory
Lecythis persistens	Lec_per	Lecythidaceae	5	16.3	35.9	65.8	Shade-tolerant-Understory
Licania alba	Lic_alb	Chrysobalanaceae	5	14.7	28.8	49.3	Shade-tolerant-Canopy
Miconia tschudyoides	Mic_tsc	Melastomataceae	2	13.2	11.7	15.8	Pioneer-Understory
Oxandra asbeckii	Oxa_asb	Annonaceae	2	14.6	16.5	33.3	Shade-tolerant-Understory
Parkia nitida	Par_nit	Fabaceae	5	18.5	63.1	101.3	Pioneer-Canopy
Recordoxylon speciosum	Rec_spe	Fabaceae	3	12.3	38.2	64.4	Semi shade-tolerant-Canopy
Schefflera morototoni	Sch_mor	Araliaceae	3	21.2	28.6	45.3	Pioneer-Canopy
Swartzia panacoco	Swa_pan	Fabaceae	3	12.5	25.4	51.3	Shade-tolerant-Canopy
Virola michelii	Vir_mic	Myristicaceae	3	20.5	31.8	64.5	Pioneer-Canopy

We also estimated stand-level errors in AGB estimations in both undisturbed and disturbed forests in Paracou. To do this, we first calculated total stand AGB (AGB_T), for disturbed and undisturbed forests, as the sum of AGB values of all stems within permanent plots, and then recalculated the total corrected AGB (AGB_{TC}) considering estimated errors in AGB per species (see Appendix A for details). Errors in AGB estimations at the stand level (AGB_{STAND}), at disturbed and undisturbed forests, were calculated as:

$$\% \text{ error } ABG_{STAND} = (AGB_T - AGB_{TC}) \cdot 100)/AGB_{TC} \qquad (2)$$

Biomass growth rates estimations— We calculated biomass growth rates (BGR, kg y^{-1}) using demographic data from two datasets. The first dataset belonged to the Guyafor network of forest permanent plots (https://paracou.cirad.fr/), and it is based on one 25-ha and three 6.25-ha plots (plots 13,14,15) that were set-up in 1991-1992 to monitor the functioning and dynamics of undisturbed forests in Paracou (Gourlet-Fleury *et al.*, 2004). Between 1992 and 2015, censuses of all stems with DBH>10 cm have been conducted every five years in the 25-ha plot, and every two years in the three 6.25-ha permanent plots. The second dataset is from five 1-ha permanent plots established in undisturbed forests in Nouragues, a research station located c. 150 km from Paracou. In these plots, all stems with a DBH > 10 cm have been monitored at 2-4-year intervals since 1993. BGR per species was calculated as: (AGB_F-AGB_I)/ (time interval), where AGB_F and AGB_I are above-ground biomass at the first and last measurement, respectively.

Following an analogous procedure than the one described above, we calculated three values of BGR per species, using 20-year census data: (i) outer BGR (BGR_O), that is BGR calculated with AGB_O values; (ii) mean BGR (BGR_M), which is BGR based on AGM_M; and (iii) weighted BGR (BGR_W), that is BGR calculated with AGB_W values (Table 2). We also estimated the percentage error in BGR for each individual species by comparing BGR_O and BGR_M with BGR_W, as follows:

$$\% \text{ error } BGR= ((BGR-BGR_W) \cdot 100)/BGR_W. \qquad (3)$$

where BGR is BGR_O or BGR_M.

Moreover, we calculated stand-level error in BGR estimations using census data from the 25-ha plot set up in an undisturbed forest. We first calculated total stand BGR (BGR_T) as: (AGB_F-AGB_I)/ (time interval), where AGB_F and AGB_I are above-ground biomass at the first and last measurement, respectively. Then, we assigned a percentage error in BGR per species in the 25-ha permanent plot and calculated corrected total BGR (BGR_{TC}), taking into account the estimated errors in BGR_O (see Appendix A for details). Errors in BGR estimations at the stand level (BGR_{STAND}) were calculated as:

$$\% \text{ error } BGR_{STAND} = (BGR_T\text{-}BGR_{TC}) *100)/BGR_{TC} \qquad (4)$$

Data analyses— The linear models predicting errors in species AGB and BGR (i.e., AGB_O, AGB_M, BGR_O, BGR_M) estimations based on WSG (i.e., WSG_O and WSG_M) values (see Appendix A) were fitted using the "lme4" package (Bates et al., 2015) in the software R (R Development Core Team 2019).

RESULTS

Errors in AGB estimations at the species level— In most of our study species, the use of outer values of WSG (WSG_O) led to considerable errors in AGB estimations (Fig.1). Errors ranged from -18.2% in *Eperua falcata* to 36% in *Schefflera morototoni*. In general, pioneer and long-lived pioneer species had positive percentage errors in AGB_O estimations, while shade-tolerant species had systematically negative ones. The two semi-tolerant species were intermediate with one with a positive error (*Dicorynia guianensis* 3.4%) and one with a negative value (*E. falcata* -18.2%). In comparison, the percentage errors in species AGB estimations derived from using WSG_M were lower and relatively similar across species (range: -3 to -12%). In contrast to calculations based on WSG_O, the percentage errors in AGB estimations derived from using WSG_M were all negative (i.e., ABG was systematically sub-estimated).

Errors in AGB estimations at the stand level— Radial trends in WSG had a relatively small effect on AGB estimations for both the undisturbed and disturbed forests. In the undisturbed plot, AGB_T was 435 Mg ha^{-1} while AGB_{TC} was 448.9 Mg ha^{-1}. In this plot, the percentage error in AGB estimations was c. -3.2%. In the plots subjected to selective logging, AGB_T

was 390 Mg ha^{-1}, and AGB_{TC} was 409,1 Mg ha^{-1}, corresponding to a percentage error in AGB estimations of -4,9%.

Table 2. Summary characteristics of variables measured on 18 tree species from a lowland tropical forest in French Guiana. Mean, standard deviation (SD) and range of variation are shown. These values were calculated based on mean values per species, which in turn, were estimated from all samples measured for each individual.

Trait	Abbrev.	Unit	Mean	SD	Range
Mean wood specific gravity	WSG_M	Unitless	0.65	3.48	0.29-1.01
Outer wood specific gravity	WSG_O	Unitless	0.68	2.70	0.37-1.0
Weighted wood specific gravity	WSG_W	Unitless	0.70	3.40	0.32-1.09
Mean aboveground biomass	AGB_M	kg	657.58	805.22	37.46-4062.95
Outer aboveground biomass	AGB_O	kg	726.92	964.75	49.22-5487.57
Weighted aboveground biomass	AGB_W	kg	696.16	837.41	48.05-4257.86
Outer biomass growth rate	BGR_O	kg y^{-1}	6.54	4.41	1.30-17.99
Weighted biomass growth rate	BGR_W	kg y^{-1}	7.32	4.85	1.20-18.66
Mean biomass growth rate	BGR_M	Kg y^{-1}	6.72	4.12	1.41-18.02

Errors in BGR estimations at the species level— Using WSG_O led to substantial errors in BGR (BGR_O) estimations in most of our study species (Fig. 2). The percentage errors in BGR_O estimations ranged from -7% in *Bocoa prouacensis* to 18% in *Hirtella glandulosa*. Overall, pioneer and long-lived pioneer species had positive percentage errors in BGR_O, while semi-tolerant and shade-tolerant species had either positive or negative ones. On the other hand, the percentage errors in BGR_M (i.e., using WSG_M) varied considerably among ecological guilds, but were in general lower than for BGR_O.

Errors in BGR estimations at the stand level— The percentage error in BGR_O estimations at the undisturbed plot was modest (-3.5%). BGR_T in this plot was 105 Mg y^{-1} (4.2 Mg ha^{-1} y^{-1}), and BGR_{TC} was 108,75 Mg y^{-1} (4.35 Mg ha^{-1} y^{-1}).

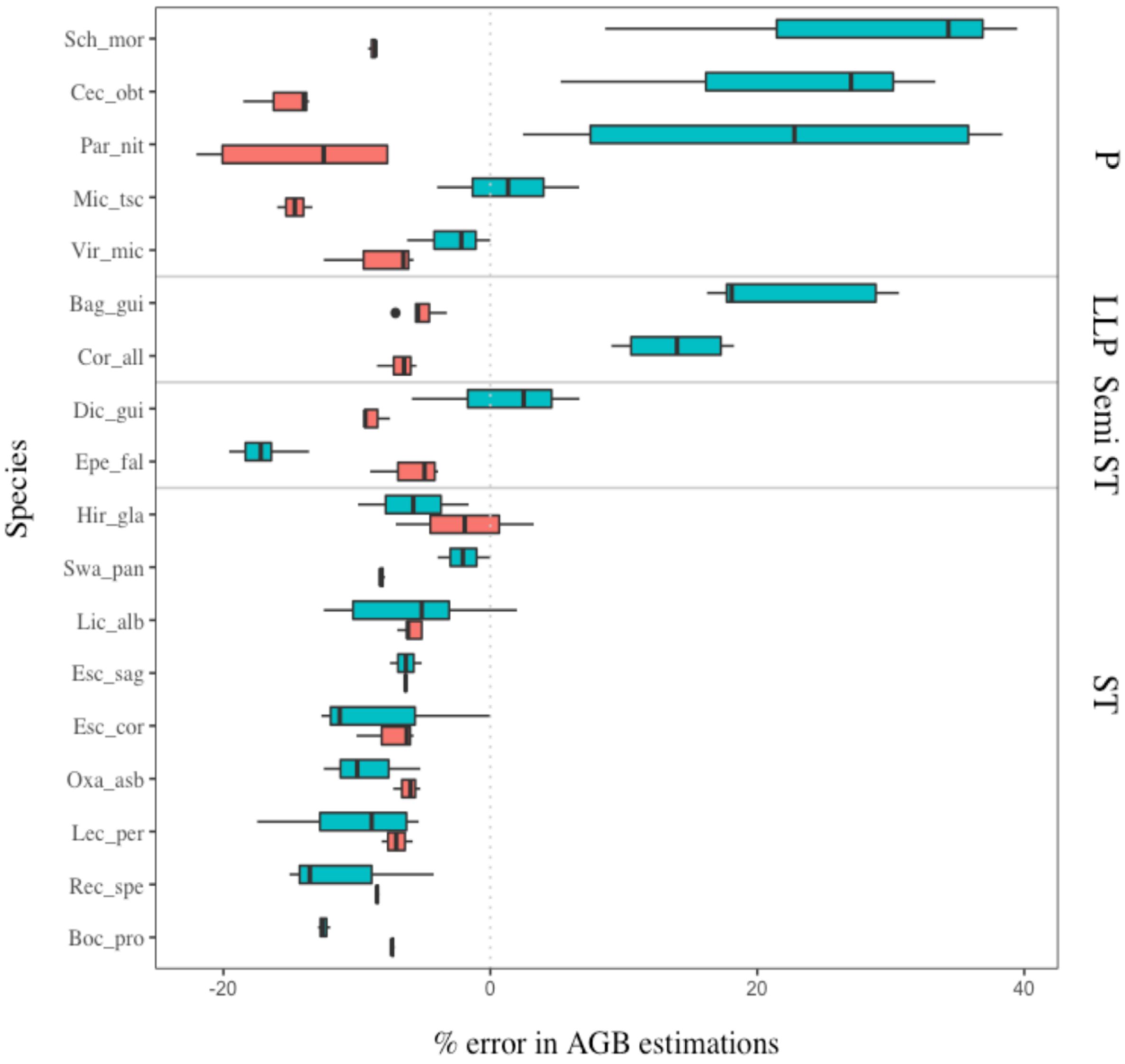

Figure 2. Percentage errors in BGR estimations for 18 tree species belonging to four ecological guilds: Pioneers (P), long-lived pioneers (LLP), semi shade-tolerants (Semi ST) and shade-tolerants (ST). Green boxplots: % errors resulted from using WSG_O in biomass estimations (i.e., BGR_O), and dark blue boxplots: % errors resulted from using WSG_M (i.e., BGR_M). See Table 1 for species codes.

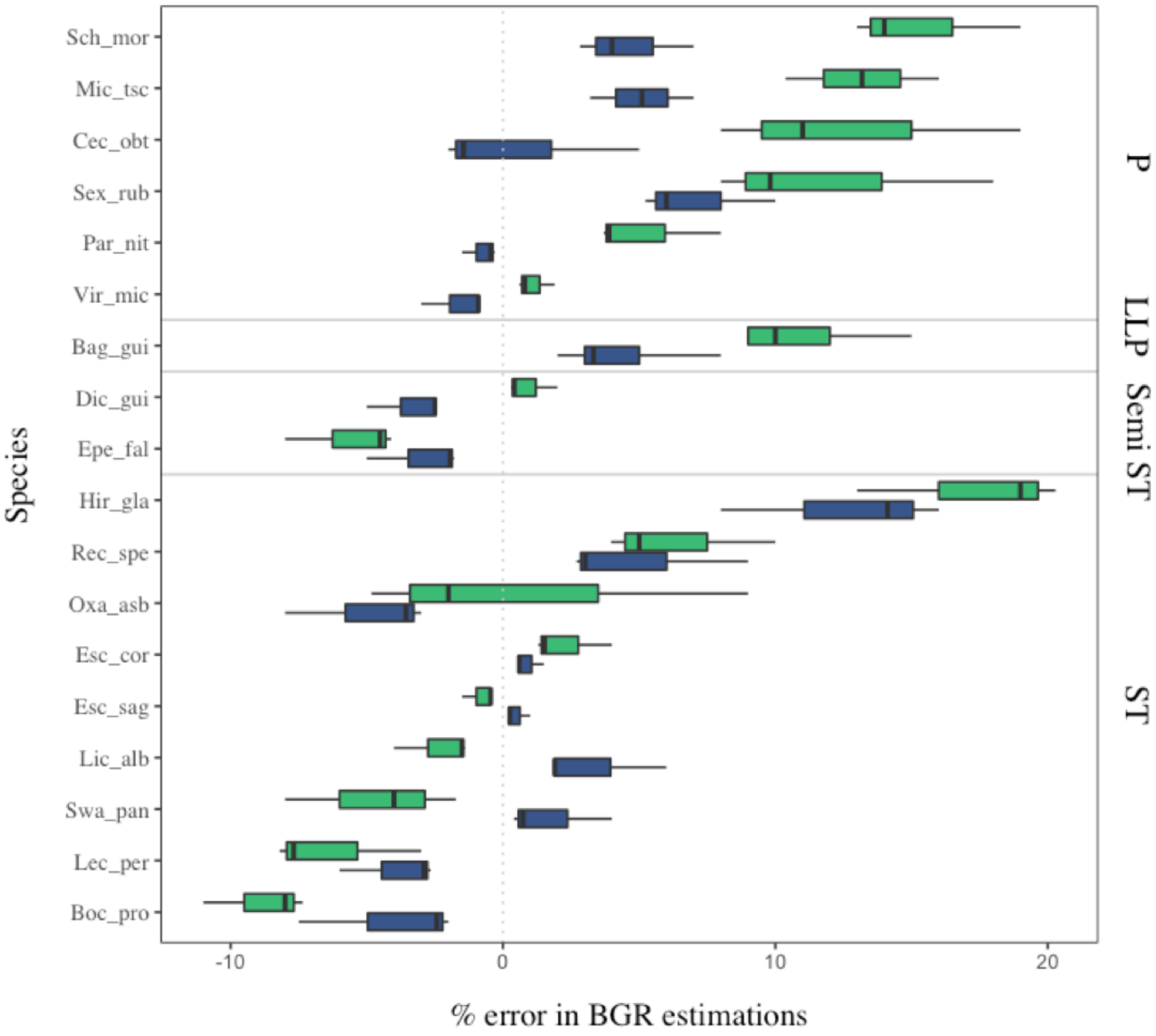

Figure 2. Percentage errors in BGR estimations for 18 tree species belonging to four ecological guilds: Pioneers (P), long-lived pioneers (LLP), semi shade-tolerants (Semi ST) and shade-tolerants (ST). Green boxplots: % errors resulted from using WSG_O in biomass estimations (i.e., BGR_O), and dark blue boxplots: % errors resulted from using WSG_M (i.e., BGR_M). See Table 1 for species codes.

DISCUSSION

Errors in AGB and BGR estimations for individual species— Radial shifts in WSG are widespread among different forest ecosystems (e.g., Nock et al., 2009; Hietz et al., 2013; Plourde et al., 2015; Lehnebach et al., 2019), but their effects on tree biomass estimations are not usually considered. Our results indicate that these radial changes in WSG can have considerable effects on AGB estimations at the species level, and that these effects vary between ecological guilds. In particular, since fast-growing species typically show radial increments in WSG (i.e., WSG increases from pith to bark; Williamson & Wiemann, 2010), the use of WSG values measured at the outer part of the trunk (WSG_O) usually introduce an over-estimation of AGB, which can be as high as 36% (Fig. 1, *S. morototoni*). On the contrary, many shade-tolerant species show negative gradients in WSG (i.e., a decrease of WSG towards the bark; Plourde et al., 2015), which are usually less pronounced than those of fast-growing species in our study species (González-Melo et al., 2021), and other tropical species (e.g., Plourde et al., 2015). These negative radial trends in WSG led to under-estimations of AGB in shade-tolerant species when WSG_O was used (Fig. 1). Thus, these findings highlight the potential errors in AGB estimations derived from the common practice of using WSG from the outer part of the trunk.

An alternative is to take tree cores all the way to the center of the trunk and use mean WSG values (WSG_M). We found that this method led to lower percentage errors in AGB estimations compared to WSG_O values (Fig. 1), but it still caused a systematic under-estimation of AGB in all of our study species. Thus, a desirable procedure to reduce errors is to measure WSG along the whole stem radial profile (e.g., estimating WSG every 2 cm or less) and then weight it by its corresponding cross-sectional area. Knowing the radial trend in WSG of a species may allow to calculate more accurate WSG values at any given stem size. Yet, although radial gradients in WSG can be described for some species with a linear function (e.g., Hietz et al., 2013), non-linear radial gradients in WSG are common in our study species (González-Melo et al., 2021), and in other tropical tree species as well (i.e., Williamson et al., 2012; Osazuwa-Peters et al., 2014). Thus, obtaining these radial gradients in WSG can be impractical in some cases, particularly in studies that include a large number of species. Another methodological option is to establish empirical relationships between the percentage error in AGB and WSG for a set of species that reflect a wide spectrum in mean WSG, and then assign percentage errors in AGB estimations for all species based on measure of WSG that are simpler to obtain, such as WSGo (Fig. xx Appendix A). This approach may be useful to increase the accuracy of non-destructive methods, such as terrestrial LiDAR scanner, that are used to estimate tree volume and biomass at large spatial scales (Momo et al., 2020).

Similarly, radial trends in WSG also influenced BGR estimations. In particular, we found that the use of WSG_O and WSG_M generally led to over-estimations of BGR in pioneer and long-lived pioneers, and under-estimations in most semi shade-tolerant and shade-tolerant species (Fig. 3). These trends in the errors of BGR estimations reflected the radial shifts in WSG that typically characterize fast and slow growing species (see above). Among our study species, BGR were higher for faster than for slower growing species (Fig. S2). This agrees with studies on saplings of tropical trees (e.g., Kitajima, 1994), but it is contrary to research on adult trees from a semi-deciduous forest in Panama (Rüger et al., 2012; Hietz et al., 2016), and a humid forest from the Peruvian Amazon (Keeling et al., 2008), which show that shade-tolerant species, that typically have dense woods, produce more biomass than fast-growing species. Fast-growing species generally have higher photosynthetic rates than shade-tolerants (e.g., Kitajima, 1994; Santiago et al., 2004; Poorter & Bongers, 2006) and, at least in our species, tend to attain larger stem diameters than shade-tolerant species (Table 1). This may explain the greater biomass increments that we found in fast-growing species (see Appendix B).

Implications for forest biomass estimations— Although radial trends in WSG may have significant effects on AGB and BGR estimations at the tree or species level (Fig 1), they had smaller effects on stand AGB and BGR estimations at our study site. We found that not taking into account radial shifts in WSG lead to under-estimations in stand AGB (AGB_{STAND}) in both undisturbed (-3.2 %; 2007.8 Mg) and logged forests (-4.9 %; 358.3 Mg). Since the patterns of radial changes in WSG vary among species from different ecological guilds (Nock et al., 2009; Hietz et al., 2013; Plourde et al., 2015), the overall effect of these radial changes on AGB estimations at the stand level will ultimately depend on the relative abundance of fast-or slow-growing species. The forests of Paracou, and the Guiana Shield in general, are typically dominated by shade-tolerant species that tend to have dense woods (ter Steege et al., 2000; 2006), and show no or modest negative radial variations in WSG (e.g., Lehnebach et al., 2019; Gonzalez-Melo et al., 2021). This explains why we found a relatively small, and negative, percentage errors in AGB estimations at the stand level in both disturbed and undisturbed forests.

Likewise, we found that not considering radial shifts in WSG caused under-estimations (-3.5%) in BGR estimations at the stand level (BGR_{STAND}), which may again be related to the dominance of shade-tolerant species in our study site (see above). This suggests that the forests of Paracou may store and capture more biomass C than previously assumed. On the other hand, while not taking into account radial trends in WSG may not have strong effects on stand AGB and BGR estimations in old-growth forests dominated by late-successional species, it can potentially lead to substantial errors in stand biomass estimations in second-growth forests with a high proportion of fast-growing species. For instance, these errors in biomass estimations would be particularly relevant in Neotropical secondary forests that represent at least one-third of all Neotropical forests, and are suggested to play a key role in carbon sequestration and climate change mitigation (Chazdon et al., 2016). Yet, it is important to note that our findings are based on a small number of species. Therefore, further studies should examine if our results hold true for larger sets of species from different forest types. They may also consider quantifying the effects of axial (i.e., from the base of the trunk to the branch tips) variations in WSG on tree biomass estimations, which seem to be considerable (e.g., Momo et al., 2020).

CONCLUSIONS

In this study, we quantified the effects of radial shifts in WSG on AGB and BGR in a lowland forest from eastern Amazonia. Not considering radial changes in WSG led to substantial errors in AGB and BGR estimations at the species level. In general, using outer WSG values led to over-estimations of AGB in fast-growing species, and under-estimations for slow-growing ones. The use of mean WSG resulted in negative percentage errors in AGB estimations in comparison to outer WSG values. A similar pattern of errors in tree BGR estimations resulted for not considering radial shifts in WSG. In contrast, the effects of radial shifts in WSG on stand AGB and BGR estimations were relatively small, which may be due to the dominance of shade-tolerant species at our site. These findings are important to reduce uncertainties associated to the estimation of AGB and BGR in lowland tropical trees. They may also be useful to increase the accuracy of remote sensing techniques that are increasingly used to estimate forest biomass at large spatial scales.

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APPENDICES

Appendix A. Biomass estimations at the stand level.

We calculated stand-level percentage errors in AGB estimations using census data from both disturbed (plots 2, 7 and 9) and undisturbed forests (plot 25) in Paracou. In order to do it, we started by calculating total stand AGB (AGB_T) as the sum of AGB values of all stems within the plots. AGB per tree was calculated using the function "AGBtree" of the package Biomass (Réjou-Mechain et al., 2017). This function assigns averaged WSG values per tree from global repositories (Chave et al., 2009; Zanne et al., 2009). As wood is typically sampled from the outer part of the stem, we assumed that these WSG values from global repositories correspond to stem outer wood. These WSG values from global datasets differed significantly from WSG_M, WSG_O and WSG_W values of our study species (data not shown).

Then, we fitted linear models predicting percentage errors in species AGB_O and species AGB_M, based on species WSG_O and WSG_M values, respectively. WSG_O predicted AGB_O error while WSG_M was unrelated to AGB_M error (Fig. S1a-b). Using the equation derived from the model predicting AGB_O based on WSG_O (i.e., % error in AGB_O= 23 + (-37*WSG_O)), we assigned percentage errors in AGB estimations per each species within the plots. Then, we recalculated the total corrected AGB (AGB_{TC}), considering the estimated errors in AGB per species, and calculated the stand-level percentage errors in AGB estimations.

Following a similar approach than above, we calculated the stand-level error in BGR estimations using 20-year census data from an undisturbed forest. First, we calculated total stand BGR (BGR_T; see Methods). Then, we ran linear models explaining species BGR_O error and BGR_M error based on WSG_O and WSG_M. WSG_O predicted AGB_O, while WSG_M varied independently from AGB_M (Fig. S1b-c). Based on the equation from the model explaining AGB_O based on WSG_O (i.e., % error in BGR_O= 21 + (-35*WSG_O)), we assigned percentage errors in BGR for each species in the 25-ha plot. Finally, we recalculated total (BGR_{TC}), taking into account the estimated errors in BGR estimations per species, and calculated stand-level percentage error in BGR estimations based on BGR_T and BGR_{TC}.

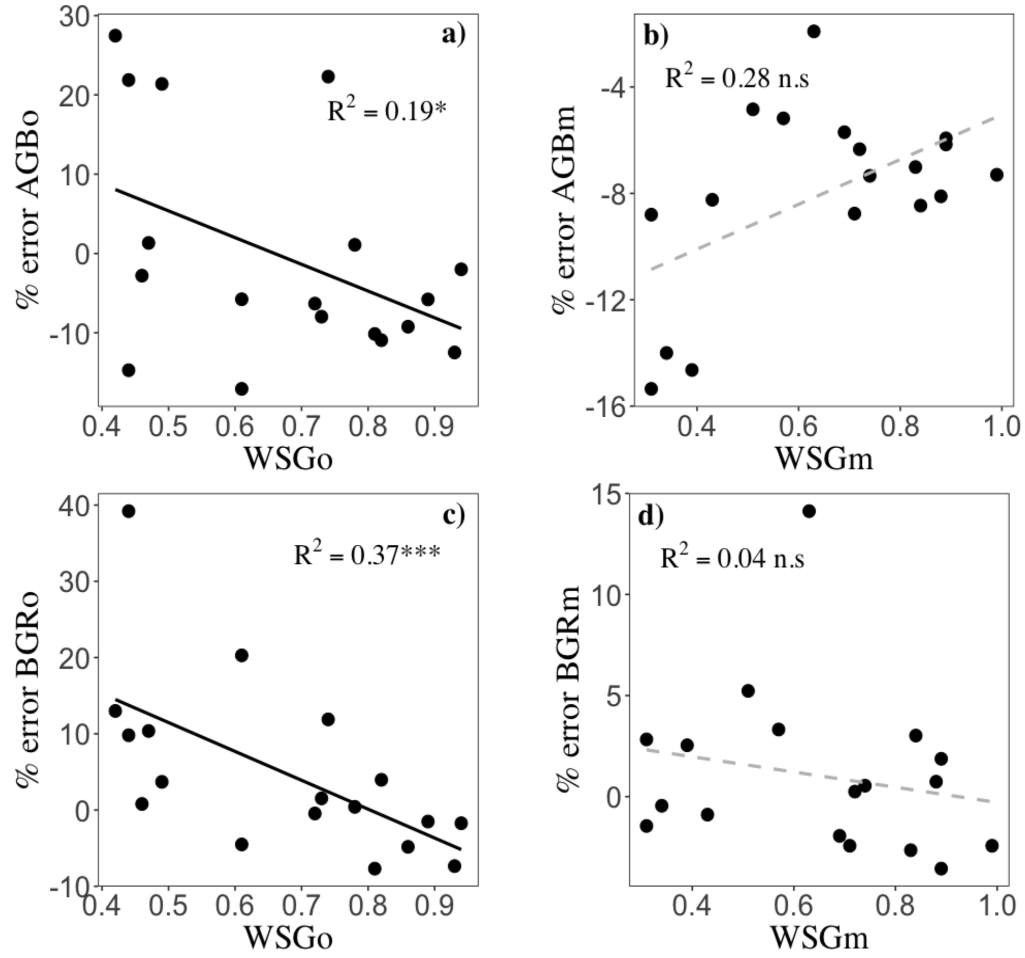
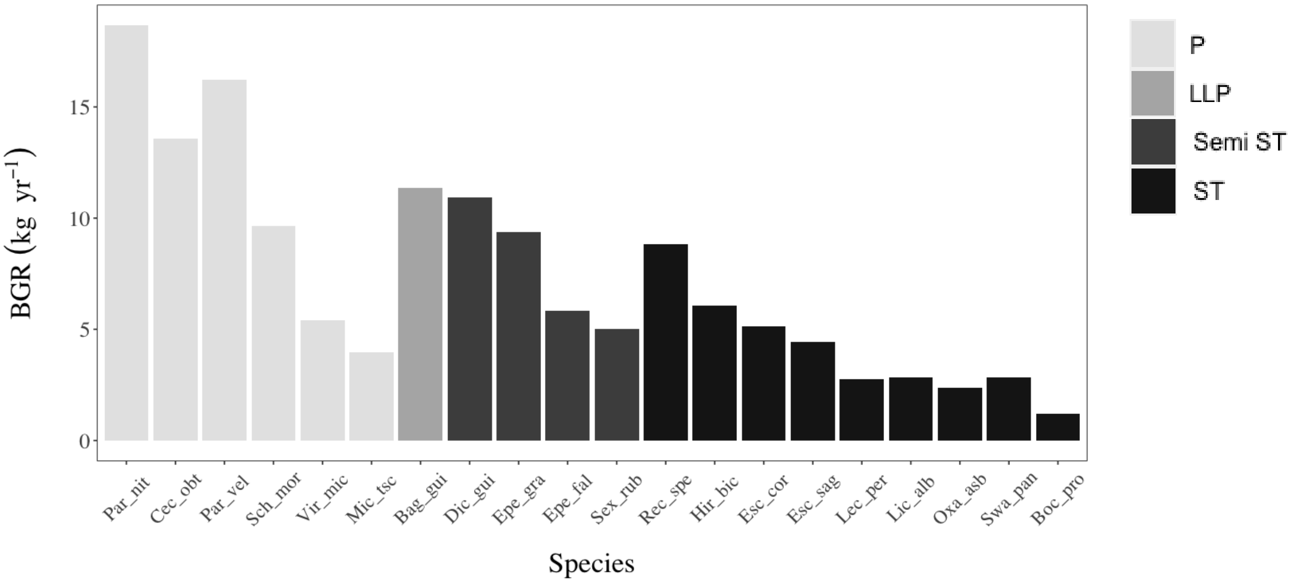


Figure A1. Linear models showing the relationships of wood specific gravity (WSG) with the percentage errors in above-ground biomass (AGB) and biomass growth rates (BGR) estimations, across 18 tree species from Eastern Amazonia. a) outer WSG (WSG_O) and outer AGB (AGB_O), b) mean WSG (WSG_M) and mean (AGB_M), c) WSG_O and outer BGR (BGR_O), and d) WSG_M and mean BGR (BGR_M). Coefficients of determination (R^2) and significance levels (n.s: $P > 0.05$; *: $P < 0.05$; ***: $P < 0.001$) are provided.

Appendix B. Species biomass growth rates.

Fig. B2. Adult (i.e., 10-50 cm DBH) biomass growth rates (BGR) for 18 tree species belonging to four ecological guilds: Pioneers (P), long-lived pioneers (LLP), semi shade-tolerants (Semi ST) and shade-tolerants (ST). BGR were calculated using weighted WSG (WSG_W) values per species. See Table 1 for species codes.



Chapter 6

General discussion

DISCUSSION

In this thesis, I studied different aspects of radial variations in wood functional traits for multiple trees species, and the links between stem traits, demography and above-ground biomass estimations. The aim was to expand our knowledge on wood strategies among trees from a tropical humid forest in French Guiana. Here, I discuss how the main findings of this study contribute to this aim, and how they might lead to new research.

Radial variations in wood functional traits— One of the main results of this thesis is that positive radial gradients in wood specific gravity (WSG), that are frequent among fast-growing species, were underpinned by different wood anatomies, particularly by fiber and parenchyma traits. This finding expands previous knowledge from a few studies conducted on forest trees from humid (Mc Donald et al., 1995) and dry forests (Rungwattana & Hietz, 2017). Interestingly, I found that fast-growing species may increase WSG radially either by two alternative ways: (i) increasing both fiber fractions and wall thickness, or (ii) increasing fiber wall thickness. These different solutions are in line with Zieminska et al., (2015), who showed that similar values of twig WSG, especially low and medium ones, can be driven by different variations in wood anatomical traits. The finding outlined above suggests that coexisting tree species with similar shade-tolerance and radial trends in WSG may have different wood anatomies.

I also found that, in most of the study species, vessel fraction (F_V) represents an axis of variation in wood structure that is independent from WSG as trees grow. This independence between WSG and F_V has been reported previously among species (Zanne et al., 2010; Zheng & Martínez-Cabrera, 2013) and radially within stems of dry forest trees (Rungwattana & Hietz, 2017). Yet, as far as I know, it has not been studied in humid tropical forest trees. The fact that these traits tend to be orthogonal when analyzed radially within stems suggests that hydraulic and mechanical functions can be decoupled during tree development as well. This, in turn, may have important implications for understanding wood allocation patterns in high-diversity forests. For instance, 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.

Wood nutrient concentrations— Wood nutrients are hypothesized to covary along the wood economics spectrum (Martin et al., 2014), yet evidence supporting this hypothesis has been scarce and non-conclusive (e.g., Becker et al., 2012; Martin et al., 2014; Heineman et al., 2016). This thesis extends previous research on this topic by showing that wood nutrients (i.e., phosphorus, potassium, magnesium and calcium) may have different patterns of associations with WSG, and that these associations can be size-dependent because they change between inner and outer wood. To better understand interspecific variations in wood nutrients, I asked if wood nutrients covary with xylem parenchyma fractions. With the exception of a positive link between axial parenchyma fractions and phosphorous contents in outer wood, wood nutrients were unrelated, or negatively related, to parenchyma fractions across our study species. This suggests that an important fraction of wood nutrients may be allocated to other xylem cells or can be stored in the bark, which highlight a potentially interesting research direction.

I also examined nutrient resorption within stems. While leaf nutrient resorption has been documented previously in forests of the Guiana Shield (Hammond, 2005; Urbina et al., 2021), to the best of my knowledge this is the first study to analyze wood nutrient resorption in a Guianan forest. One important finding on this regard is that wood nutrient resorption rates did not vary among functional groups. The fact that the resorption of wood nutrients is unrelated to species life-history strategies (i.e., functional groups) suggest that nutrient resorption may be species-specific in the forest of Paracou. Thus, future studies should examine the possible role of species growing conditions on nutrient resorption rates.

Size-related relationships between wood traits and demographic rates—The findings of this study indicate that the relationships of wood traits in explaining species demography change during tree development. Recent studies on leaf traits (Iida et al., 2014; Gibert et al., 2016) and WSG (Visser et al., 2016) have reported similar results for tropical forests, yet I am aware of only one published study of this type on wood anatomical traits of humid tropical trees (Osazuwa-Peters et al., 2017). One important difference between this study and the study by Osazuwa-Peters *et al*. is that here I examined the independent effects of axial and radial parenchyma fractions on tree demography. I found that radial and total parenchyma fractions were negatively related to sapling mortality rates and adult growth rates, respectively (see details in chapter 4). A previous study reported positive associations between parenchyma fractions and demographic rates of trees from a tropical dry forest (Herrera-Ramirez et al., 2021). However, as far as I am concern, this is the first report of significant relationships between parenchyma fractions and species demography in a humid tropical forest. Yet, it is likely that other parenchyma traits, such as parenchyma spatial arrangement and morphology, may have important effects on tree functioning as well. For instance, one question that could be asked is: Do the spatial arrangement (i.e., banded parenchyma) and morphology (i.e., uni- or multiseriate rays) of parenchyma cells can be related to tree mortality?

Wood specific gravity is one of the most widely measured of all plant functional traits (Kattge et al., 2011), and is assumed to be a good indicator of species demographic rates (Chave et al., 2009; Visser et al., 2016; but see Russo et al., 2010). The results of this study show, however, that the relationship between WSG and demography can be more complex than expected, because the importance of WSG in explaining species demography vary depending on the size of the trees and the demographic rate considered. For example, in this study WSG was unrelated to adult demography, but it was significantly and negatively related to sapling growth rates and juvenile mortality rates. These insights may help to reinterpret the functional significance of WSG, and its role in shaping species ecological strategies.

Radial trends in WSG and their effect on biomass estimations—Since WSG is an important predictor of above-ground biomass (AGB, Chave et al., 2014) and biomass growth rates (BGR), radial trends in WSG are expected to affect AGB and BGR estimations at the species and stand level (e.g., Plourde et al., 2015). The effects of radial shifts in WSG on AGB and BGR estimations have been examined before in different tropical forests (e.g. Hietz et al., 2013; Bastin et al., 2015; Plourde et al., 2015), but to my knowledge not in forests from eastern Amazonia. I showed that these radial changes in WSG can have important implications on AGB and BGR estimations at the species level. In particular, not taking into account radial trends in WSG led to over-estimations of both AGB and BGR in the case of light-demanding species, and to under-estimations in shade-tolerant species. These effects in AGB and BGR estimations were larger for fast-growing species as they tend to show more pronounced radial trends in WSG, in comparison with shade-tolerant species. I found that the estimated effects on AGB an BGR at the stand level were negative (i.e., under-estimations) and relatively small, as our study site is dominated by shade-tolerant species that generally have modest and negative (i.e., decreases in WSG from pith to bark) radial trends in WSG.

LIMITATIONS AND FUTURE STUDIES

Wood anatomical quantification is a time-consuming and laborious process. Unfortunately, in this study the time constraints related to anatomical characterization imposed limitations on the number of species sampled, the replicates per species, as well as the type of anatomical traits measured. Although the set of species studied here reflects a broad gradient of variation in wood traits and shade-tolerance, it is small and not fully representative of the floristic composition of Paracou. For instance, Lecythidaceae and Chrysobalanaceae are two representative families at our study site, but they are poorly represented in our sampling, while Sapotaceae, another dominant family, is absent. Furthermore, the number of trees sampled per species is in some cases low (< 5), which may limit the strength of the inferences that can be drawn from this study.

I focused on the quantification of wood anatomical fractions because they are important drivers of WSG variations and are considered good indicators of wood functions. Yet, there are other wood anatomical traits that might be informative of species performance. For example, the spatial arrangement and morphology of parenchyma cells are thought to play an important role in tree defense and survival. Furthermore, other anatomical traits related to the structure of pits may also be potentially important to understand tree hydraulics and demography.

Due to constraints in the field, for many of the study species I was not able to sample large-diameter trees. This had evident implications in the analyses of size-related variations in wood traits, and may limit my interpretations about the magnitude and ecological significance of these radial gradients in wood structure.

As parenchyma cells are thought to play a central role in storage, I focused on the links between wood nutrients and parenchyma fractions. However, wood nutrients can also be allocated to vessels, fiber walls or bark tissues. In this sense, the use secondary ion mass spectrometry coupled with scanning electron microscopy may be useful to have a better understanding of nutrient allocations within stems.

THESIS CONTEXT AND SIGNIFICANCE

The wood economics spectrum (WES, Chave et al., 2009) has given us an important context to understand interspecific variations in wood traits. However, and despite recent insightful studies on wood traits, there are still many knowledge gaps on our understanding of wood strategies such as: size-related variation of wood traits, covariation of wood nutrients along the WES, and the effect of wood traits on species demography. In that sense, my dissertation has contributed to our understanding of the WES by:

- Illustrating that positive radial gradients in WSG can be underpinned by different combinations of wood anatomical traits, particularly fiber and parenchyma traits.

- Showing that vessel fractions generally vary independently from WSG during tree development.

- Indicating that wood nutrients may have different patterns of associations with other wood economics traits (i.e., WSG and parenchyma fractions), and to show that these associations may be different between inner and outer wood.

- Providing evidence on wood nutrients contents and resorption rates at the species and ecological guild level.

- Showing that the relative importance of wood traits in explaining species demography change as trees grow.

- Illustrating the extent to which radial trends in WSG can influence above-ground biomass and biomass growth rates estimations at both the species and stand level.

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From a biological perspective, French Guiana is part of the Guiana Shield, a landscape covering much of the north-east corner of South America. The Guiana Shield is one of the most ancient and least populated regions of the world. It is also known as a land of old rocks, much water, extensive forests and high biological diversity. As a forest ecologist, I feel fortunate that I had the chance to work in such a unique and inspiring place.

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