



HAL
open science

The links between wood traits and species demography change during tree development in a lowland tropical rainforest

Andrés González-Melo, Juan Manuel Posada, Jacques Beauchêne, Romain Lehnebach, Sébastien Levionnois, Géraldine Derroire, Bruno Clair

► To cite this version:

Andrés González-Melo, Juan Manuel Posada, Jacques Beauchêne, Romain Lehnebach, Sébastien Levionnois, et al.. The links between wood traits and species demography change during tree development in a lowland tropical rainforest. *AoB Plants*, 2024, 16 (1), 10.1093/aobpla/plad090 . hal-04408955

HAL Id: hal-04408955

<https://hal.science/hal-04408955>

Submitted on 22 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

Studies

The links between wood traits and species demography change during tree development in a lowland tropical rainforest

Andrés González-Melo^{1,*}, Juan Manuel Posada¹, Jacques Beauchêne², Romain Lehnebach³, Sébastien Levionnois⁴, Géraldine Derroire² and Bruno Clair^{4,5, }

¹Biology Department, Faculty of Natural Sciences, Universidad del Rosario, Avenida carrera 24 # 63C-69. Bogotá, Colombia

²CIRAD, UMR Ecologie des Forêts de Guyane (EcoFoG), AgroParisTech, CNRS, INRAE, Université des Antilles, Université de Guyane, 97337, France

³CNRS, Laboratory of Botany and Modeling of Plant Architecture and Vegetation (UMR AMAP), 34398 Montpellier, France

⁴CNRS, UMR Ecologie des Forêts de Guyane (EcoFoG), AgroParisTech, CIRAD, INRAE, Université des Antilles, Université de Guyane, Kourou, 97310 France

⁵Laboratoire de Mécanique de Génie Civil (LMGC), CNRS, Université de Montpellier, 34000, France

*Corresponding author's e-mail address: germana.gonzalez@urosario.edu.co

Associate Editor: Juliana Medeiros

Abstract. One foundational assumption of trait-based ecology is that traits can predict 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 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 traits were related to demographic rates in 19 tree species from a lowland forest in eastern Amazonia. We measured 11 wood traits (i.e. structural, anatomical and chemical traits) in sapling, juvenile and adult wood; and related them to growth and mortality rates (MR) at different ontogenetic stages. The links between wood traits and 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, while 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. At the adult stage, RGR scaled 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, wood chemical or anatomical traits may be better predictors of growth and MR 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.

Keywords: Demographic rates; tree size; tropical trees; ontogeny; wood traits.

Introduction

The main goal of trait-based ecology is to understand how 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 (Poorter *et al.* 2010; Wright *et al.* 2010), as well as to improve dynamic global vegetation models (e.g. Worthy and 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; Visser *et al.* 2016), the predictive power of most traits on species demography is generally low (e.g. Visser *et al.* 2016; Yang *et al.* 2018). Two main reasons may explain this pattern. First, research on this topic has focussed largely on a few relatively easy-to-measure traits, which may not fully capture some plant functions (Yang *et al.*

et al. 2018). This leads to the question of whether other traits more mechanistically linked to plant functions, despite being relatively more difficult to measure, can be better predictors of species demographic rates (Poorter *et al.* 2010; Russo *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 and 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 (Chave *et al.* 2009; Poorter *et al.* 2010; Wright *et al.* 2010; Hietz *et al.* 2016; Visser *et al.* 2016). In general, WSG

Received: 7 February 2023; Editorial decision: 14 December 2023; Accepted: 19 December 2023

© The Author(s) 2023. Published by Oxford University Press on behalf of the Annals of Botany Company.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

is negatively related to mortality and diameter growth rates (Poorter *et al.* 2008; Wright *et al.* 2010; but see Russo *et al.* 2010; see Fig. 1). Yet, specific gravity is an emergent property of wood that is affected, in angiosperms, by the fractions and morphologies of fibres, vessels and parenchyma cells (e.g. Ziemska *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 (MR) may be better understood by considering wood anatomy (e.g. Poorter *et al.* 2010; Russo *et al.* 2010; see Fig. 1).

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; Fig. 1). For example, low-WSG species grow fast in part because they generally have lower fibre fractions and/or thinner fibre walls (Ziemska *et al.* 2013), which may reduce stem construction costs (King *et al.* 2006). They also build wider vessels which favour 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; Fig. 1). 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 role in plant metabolism as 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, 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, as 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 MR (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; Fig. 1). This is due to the fact that similar values of WSG can be the product of different wood anatomies (e.g. Ziemska *et al.* 2015) and also, and more importantly because tree mortality can be simultaneously influenced by different processes (Russo *et al.* 2010; Hietz *et al.* 2016; Osazuwa-Peters *et al.* 2017). For instance, the lower MR that characterize high-WSG species may be due to high fibre fractions and thicker fibre walls that may increase structural strength (Poorter *et al.* 2010) and resistance to pathogen attacks (Alvarez-Clare and Kitajima 2007), and/or due to 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; Fig. 1). For instance, a higher allocation to axial (AP) and radial (RP)

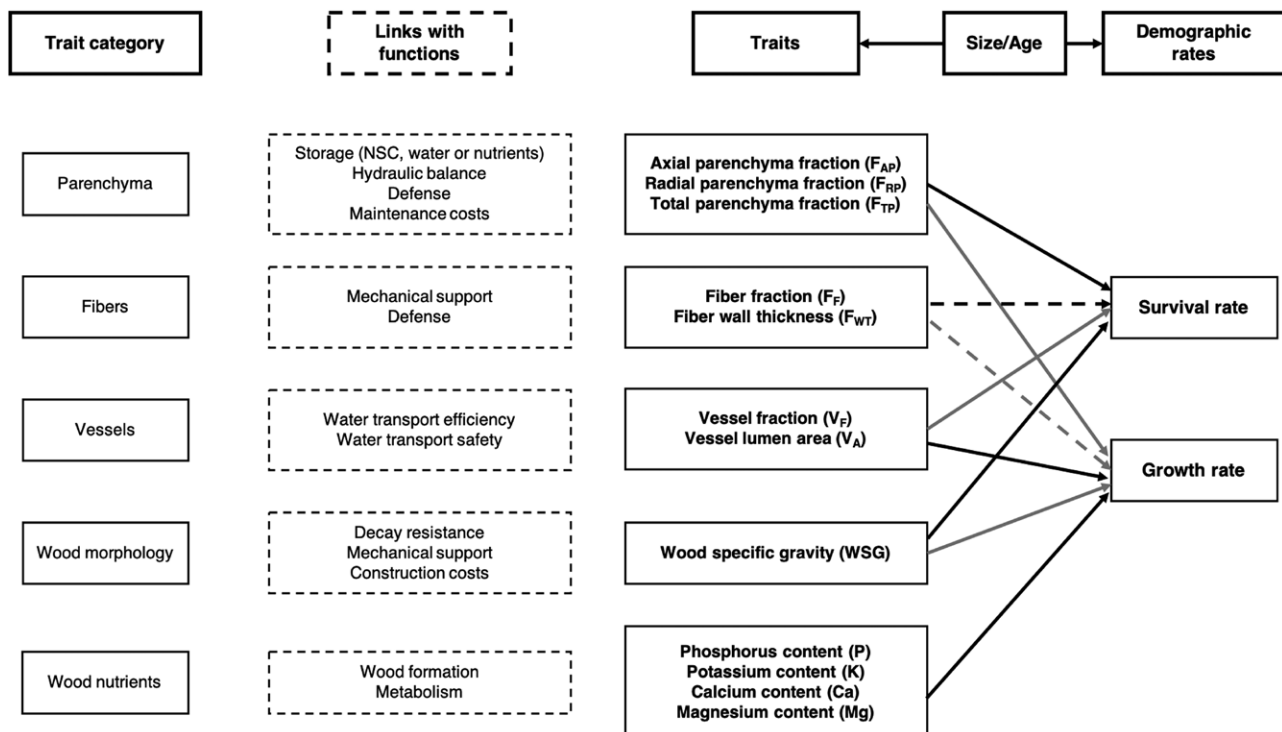


Figure 1. Conceptual framework showing theoretical and realized associations among wood traits and demographic rates. Black and white arrows represent positive and negative associations, respectively. Continuous arrows are theoretical associations supported by our results (see Figs 2, 3 and 4 for details), while dashed arrows are hypothesized, although not realized, links between traits and demographic rates.

parenchyma cells could reduce mortality (Poorter *et al.* 2010), because these cells store non-structural carbohydrates (NSC) and nutrients (Plavcová and Jansen 2015; Kotowska *et al.* 2020), which might enable faster recovery from disturbances (Kitajima and 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 MR 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 (González-Melo *et al.*, unpubl. res.) or RP (Zheng and Martínez-Cabrera 2013) fractions can scale positively with WSG. This suggests that AP and RP cells may have different patterns of associations with WSG and MR. However, very few studies have formally examined the possible links between xylem parenchyma cells and MR across tropical tree species (but see Poorter *et al.* 2010).

As wood traits (e.g. Martin and Thomas 2013; Rungwatanna and 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 trait-demography links may change accordingly (Fig. 1). For instance, seed size and stature are important to predict seedling performance, while WSG seems to be the best predictor of the 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 traits (i.e. WSG, and wood anatomical and chemical traits) are related to growth and MR in 19 tree species from a lowland forest in eastern Amazonia. In particular, we wanted to answer the following questions: (i) How are wood traits related to growth and MR? 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, fibre fraction or fibre wall thickness (F_{WT})). We also predicted that MR will be negatively related to traits linked to stem structural strength (i.e. WSG, fibre fraction and F_{WT}) and either to AP or RP fractions. (ii) Do the links between wood traits and demographic rates vary with tree size? We expected that the traits associated with growth and mortality would change during tree development and that the trait-demography links would be weaker at later ontogenetic stages.

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, the mean annual temperature is 28.4 °C, and annual rainfall averages c. 3000 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.* 2011), and soils are strongly P-limited (Grau *et al.*, 2017).

Species and sampling

We selected 19 tree species that represent a broad gradient of variation in shade tolerance, ranging from pioneers to understorey 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 diameter at breast height (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*, which were collected in nearby secondary forests.

As wood structure is conserved as trees age, ontogenetic shifts in wood structure can be analysed 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 into three radial sections: (i) 1–5 cm, (ii) 5–10 cm and (iii) >10 < 50 cm [see Supporting Information—Fig. S1]. 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).

Trait measurements

Wood specific gravity. In each sapling, juvenile and adult wood section [see Supporting Information—Fig. S1], samples of c. 2 × 2 × 1 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 103 °C to a constant mass for 72 h. WSG per sample was defined as dry mass over fresh volume (Kollman and Coté 1968). Then, mean WSG values for sapling, juvenile and adult wood were calculated by averaging values from the 1-cm samples. As the deposition of wood extractives (WE) in heartwood or sapwood can increase wood dry mass and, thus, alter WSG values (e.g. Lehnbach *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).

Wood anatomy. In sapling and juvenile wood, anatomical analyses were conducted on one wood sample (c.

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.*, (2016).

Species	Family	<i>n</i>	DBH (cm)	Ecological guild	Reference
<i>Bagassa guianensis</i>	Moraceae	5	25.1	Light-demanding/Canopy	Bossu <i>et al.</i> (2016)
<i>Cecropia obtusa</i>	Urticaceae	3	16.1	Light-demanding/Understory	Favrichon (1994)
<i>Dicorynia guianensis</i>	Fabaceae	5	18.2	Semi shade-tolerant/Canopy	Favrichon (1994)
<i>Eperua falcata</i>	Fabaceae	5	19.5	Semis shade-tolerant/Canopy	Favrichon (1994)
<i>Eperua grandiflora</i>	Fabaceae	3	12.4	Semis shade-tolerant/Canopy	Favrichon (1994)
<i>Eschweilera coriacea</i>	Lecythidaceae	3	16.3	Shade-tolerant/Canopy	Favrichon (1994)
<i>Eschweilera sagotiana</i>	Lecythidaceae	2	17.8	Shade-tolerant/Canopy	Favrichon (1994)
<i>Hirtella glandulosa</i>	Chrysobalanaceae	2	15.3	Shade-tolerant/Understory	Favrichon (1994)
<i>Lecythis persistens</i>	Lecythidaceae	5	16.3	Shade-tolerant/Understory	Favrichon (1994)
<i>Licania alba</i>	Chrysobalanaceae	4	14.7	Shade-tolerant/Canopy	Favrichon (1994)
<i>Miconia tschudyoides</i>	Melastomataceae	2	13.2	Light-demanding/Understory	Favrichon (1994)
<i>Oxandra asbeckii</i>	Annonaceae	4	14.6	Shade-tolerant/Understory	Favrichon (1994)
<i>Parkia nitida</i>	Fabaceae	4	18.5	Light-demanding/Canopy	Favrichon (1994)
<i>Parkia velutina</i>	Fabaceae	3	12.4	Light-demanding/Canopy	Favrichon (1994)
<i>Recordoxylon speciosum</i>	Fabaceae	3	12.3	Semi-shade-tolerant/Canopy	Favrichon (1994)
<i>Schefflera morototoni</i>	Araliaceae	3	21.2	Light-demanding/Canopy	Uriarte <i>et al.</i> (2005)
<i>Sextonia rubra</i>	Lauraceae	3	22.4	Semi-shade-tolerant/Canopy	Scotti <i>et al.</i> (2010)
<i>Swartzia panacoco</i>	Fabaceae	3	12.5	Shade-tolerant/Canopy	Favrichon (1994)
<i>Virola michelii</i>	Myristicaceae	3	20.5	Light-demanding/Canopy	Favrichon (1994)

Table 2. Summary characteristics of wood 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
Fibre 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
Fibre 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
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	<i>P</i>	$\mu\text{g g}^{-1}$							65.1	31.3	20.6–153.7
Wood calcium	<i>Ca</i>	$\mu\text{g g}^{-1}$							2152	2059	281–7239
Wood potassium	<i>Mg</i>	$\mu\text{g g}^{-1}$							162.5	164.2	19.4–643.5
Wood magnesium	<i>K</i>	$\mu\text{g g}^{-1}$							359.2	306.0	63.2–1269
Relative growth rate	RGR	$\text{mm}\cdot\text{mm yr}^{-1}$	0.83	1.04	0.01–3.71	0.98	0.59	0.39–2.57	0.26	0.17	0.07–0.70
Mortality rate	MR	$\% \text{ yr}^{-1}$	3.62	6.14	0.61–23.7	2.10	2.09	0.23–7.29	0.82	1.66	0.1–7.27

2 × 2 × 1 cm); whereas in adult wood, anatomy was analysed every 1.5 cm until reaching the bark, and an averaged value was calculated [see Supporting Information—Fig. S1]. 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. Photographs were taken at 5–10 × objective lenses using a reflected light (episcopic) microscope (BFMX, Olympus, Tokyo, Japan), equipped with a digital camera (Canon EOS T6i; Canon Inc., Tokyo, Japan). For each wood sample, between 10 and 20 partially focussed 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 fibres (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 coloured using Photoshop (Adobe Systems Incorporated, USA), and traits were calculated automatically using the batch function in the software ImageJ (<https://imagej.nih.gov/ij/>). F_{WT} (μm) was measured by taking photographs at 50–100 × objective lenses using a laser microscope (VK 8850, Keyence). To do so, each anatomical image was

divided into 4 equal sections, and 8 pairs of fibres were randomly selected in each section, for a total of 32 pairs of fibres 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).

Wood nutrient concentrations. We measured wood nutrient concentrations in both sapling and adult wood [see Supporting Information—Fig. S1]. Yet, as wood nutrients tend to be reabsorbed from inner to outer wood, during heartwood formation, in several of our study species (A. González-Melo, *et al.*, unpub. res.), 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 ground and dry-ashed at 550 °C for 1 h, and then the ash was dissolved in HNO_3 (1 M). 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 DBH; see Supporting Information—Fig. S1) 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 5 years in the 25-ha plot, and every 2 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; see Supporting Information—Fig. S1) and juvenile (5–10 cm DBH; see Supporting Information—Fig. S1) demographic rates, we used 2 datasets: the first dataset belongs to the Guyafor network and is based on *c.* 750 8-m radii circular subplots established in 12 6.25-ha permanent plots to monitor forest regeneration dynamics in Paracou. Diameter increments and MR 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 20 × 250 m transects established in Paracou in 1994 by Molino and Sabatier (2001). In these transects, inventories of diameter growth and MR of saplings and juveniles were conducted for a 7-year period (1995–2002).

Diameter relative growth rates (RGR, $\text{mm}\cdot\text{mm}^{-1}\cdot\text{y}^{-1}$) were calculated as $\ln(\text{DBH}_f/\text{DBH}_i)/\Delta t$, 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. MR ($\% \text{y}^{-1}$) were calculated as $100 \times (1 - (N_f/N_i)) \times 1/t$, 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 and 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 Supporting Information—Table S1.

Statistical analyses

Trait–demography relationships, for each ontogenetic stage, were examined using pairwise Pearson’s correlations (*stats* library (version 4.4.0), *cor* function), with species as data points. We also used Pearson’s correlations to evaluate trait–trait associations, as well as the effects of WE on WSG–demography associations (see above). Growth–mortality, for each ontogenetic stage, was examined using linear regressions (*lme4* library (version 1.1-34), *lm* function). All statistical analyses were conducted in R version 4.3.0 (R Development Core Team, 2019).

Results

Overall, there was substantial variation in mean trait values both among species and ontogenetic stages. Most species mean trait values were higher in adults than in juveniles or sapling wood, except for fibre 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 saplings than for adult or juvenile wood. Species mean RGR was higher for juveniles, while MR was higher for saplings (Table 2).

Relationships between wood traits and MR

Sapling and juvenile MR were significantly related to different wood traits (Table 3). In contrast, adult MR was unrelated to wood traits (Table 3). Sapling MR decreased with radial parenchyma fractions (F_{RP} ; Fig. 2c; $r = -0.59$, $P < 0.05$), but increased with vessel lumen area (V_A ; Fig. 2d; $r = 0.53$, $P < 0.05$); while juvenile MR decreased with both WSG (Fig. 3a; $r = -0.71$, $P < 0.05$) and axial parenchyma fractions (A_{PF} ; Fig. 3b; $r = -0.59$, $P < 0.05$).

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 (Table 3). Sapling RGR were negatively related to both WSG (Fig. 2a; $r = -0.63$, $P < 0.05$) and total parenchyma fractions (F_{TP} ; Fig. 2b; $r = -0.56$, $P < 0.05$), while adult RGR scaled positively with V_A (Fig. 4a; $r = 0.46$, $P < 0.05$) and wood K concentrations (Fig. 4b; $r = 0.47$, $P < 0.05$).

Effect of WE on WSG–demography associations

The concentration (i.e. % wood dry mass) of 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 Pearson correlations that included WSG_{REC} (see ‘Materials and Methods’ section) did not differ, in terms of the correlation coefficients or level of significance, from the Pearson correlation that included WSG (data not shown).

Table 3. Pairwise Pearson correlations between wood traits and demographic rates for sapling, juvenile and adult wood. See Table 2 for trait abbreviations. Significant correlations ($P < 0.05$) are shown in bold.

Traits	Sapling wood		Juvenile wood		Adult wood	
	RGR	MR	RGR	MR	RGR	MR
WSG	-0.63	-0.41	-0.51	-0.71	-0.43	-0.15
F_F	0.48	0.39	0.52	0.35	0.35	0.08
F_{TP}	-0.56	-0.29	-0.48	-0.46	-0.28	-0.08
F_{AP}	-0.39	-0.02	-0.25	-0.59	-0.07	-0.05
F_{RP}	-0.32	-0.59	-0.43	0.19	-0.34	-0.06
F_V	0.17	-0.31	0.29	0.4	-0.13	0.1
V_A	0.49	0.53	0.38	-0.01	0.46	0.32
F_{WT}	-0.26	-0.41	-0.12	-0.43	-0.27	0.17
P					-0.12	0.11
Ca					0.13	0.3
K					0.47	0.23
Mg					0.20	0.25

Note: Multiple comparisons corrections were not accounted for.

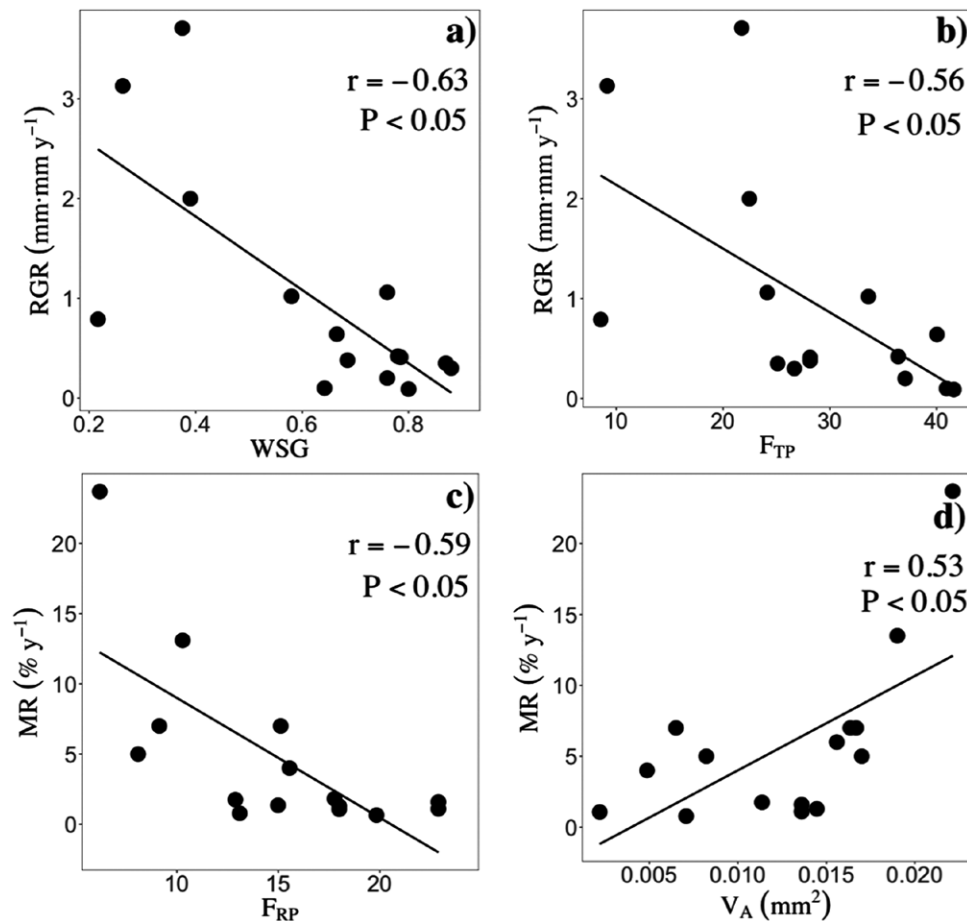


Figure 2. Significant pairwise relationships between demographic rates and wood traits at the sapling stage. A) WSG, B) total parenchyma fractions, C) radial parenchyma fractions and D) vessel lumen area. Points represent species means. Black and solid lines represent significant ($P < 0.05$) relationships. P values and Pearson correlation coefficients (r) are shown for each pairwise relationship.

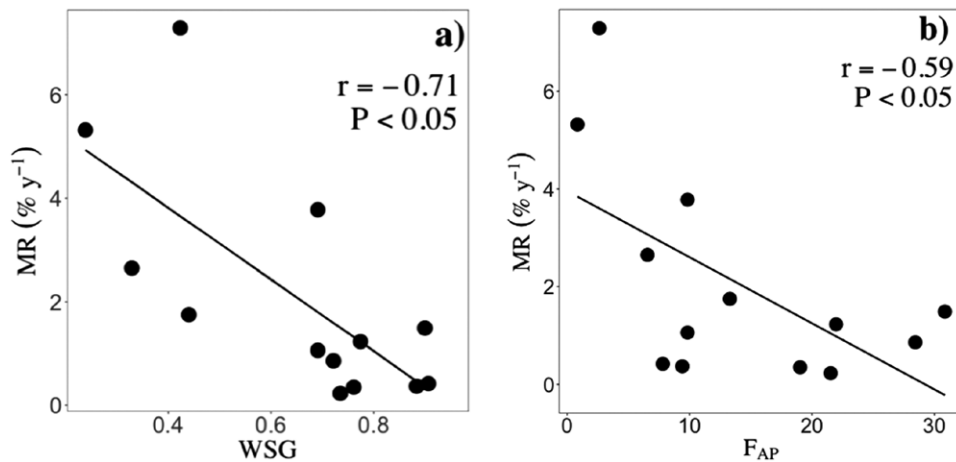


Figure 3. Significant pairwise relationships between MR and wood traits at the juvenile stage. A) WSG, and B) A_{PF} . Black and solid lines represent significant ($P < 0.05$) relationships. Points represent species means. P values and Pearson correlation coefficients (r) are shown for each pairwise relationship.

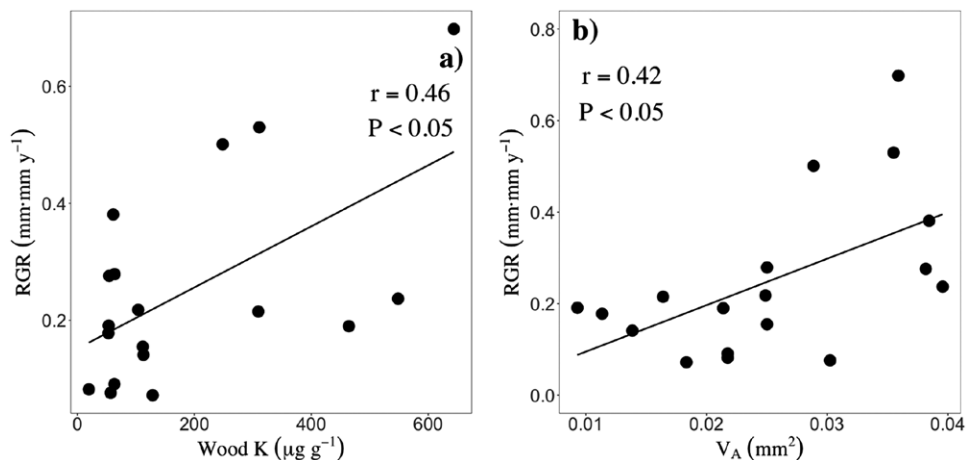


Figure 4. Significant pairwise relationships between growth rates and wood traits at the adult stage. A) wood potassium concentrations and B) vessel lumen area. Black and solid lines represent significant ($P < 0.05$) relationships. Points represent species means. P values and Pearson correlation coefficients (r) are shown for each pairwise relationship.

Discussion

Relationships between wood traits and MR

We hypothesized that MR will decrease with stem traits related to wood strength (i.e. WSG, fibre fractions or FWT) 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. 3a; $r = -0.71$, $P < 0.05$). This agrees 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; Phillipson *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 favour denser tissues that increase survival due to reduced mechanical damages from falling debris or lower risk of pathogen attacks (Alvarez-Clare and Kitajima 2007; Kitajima *et al.* 2012; Reich 2014). For instance, stem tissue density was strongly correlated with the modulus of elasticity and toughness of stems, and was the best predictor of species MR in saplings of eight lowland tropical

tree species (Alvarez-Clare and Kitajima 2007). Second, high-WSG species may have lower MR 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). Third, as both F_{WT} and T_{PF} scale with WSG at the juvenile stage [Supporting Information—Fig. S3b], it is possible that these traits might mediate the negative association between WSG and juvenile MR, as thicker fibres increase stem strength and living parenchyma cells can provide an active response against pathogens (Morris *et al.* 2016b). Further studies could examine the mediating effects of wood anatomical traits on the links between WSG and plant performance.

We also found a significant and positive relationship between vessel lumen area (V_A) and sapling MR (Fig. 2d; $r = 0.53$, $P < 0.05$). 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 for this result should be that species with wider conduits have a higher risk of drought-induced xylem embolisms, which may eventually cause mortality. Yet, we ruled out this possibility, as at our study site vessel lumen size was found to be independent from pit traits, and is weakly associated with xylem cavitation (Levionnois *et al.*, 2020). 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 favour water transport and ultimately growth (e.g. Santiago *et al.* 2004; Russo *et al.* 2010; Hietz *et al.* 2016). Yet, at the same time, species that grow faster tend to have higher MR (e.g. Poorter *et al.* 2008; Russo *et al.*, 2020). For instance, among our study species, growth rates were traded-off against MR at the sapling stage [Supporting Information—Fig. S2a]. Evidence suggests that saplings of fast-growing species have higher MR because they tend to have poorly defended tissues (Alvarez-Clare and Kitajima 2007; Kitajima *et al.* 2012). It is likely, then, that saplings with wider conduits (i.e. fast-growing saplings) die more often because they are more susceptible to pathogens or herbivores (e.g. Alvarez-Clare and Kitajima 2007; Zhu *et al.* 2018), 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. 2c; $r = -0.59$, $P < 0.05$) and axial (F_{AP} ; Fig. 3a; $r = -0.59$, $P < 0.05$) parenchyma fractions, respectively. Storage of nutrients and 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.* 2016a). 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 favour a faster recovery from periods of drought, defoliation or shading (Poorter and Kitajima 2007; Herrera-Ramírez *et al.*, 2021). An alternative, but not mutually exclusive, explanation is that radial and axial parenchyma cells increase survival, as 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 with 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 and Martínez-Cabrera 2013). Thus, future studies should consider measuring the spatial arrangements and classify parenchyma cells into more specific categories.

Relationships between wood traits and RGR

As expected, adult RGR scaled positively with wood K (Fig. 4a, $r = 0.47$, $P < 0.05$). This result is in line with fertilization experiments in lowland tropical forests showing that tree growth is strongly limited by soil K availability, although differed from those of Heineman *et al.* (2016), which 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.*, 2009; 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). As 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 was positively associated with adult RGR (Fig. 4b; $r = 0.46$, $P < 0.05$). 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 species with wider vessels grow faster. As xylem-specific hydraulic conductivity (K_s) increases exponentially with vessel lumen area, but only linearly with V_N (Tyree and Zimmermann 2002), K_s is expected to be significantly higher in species that build large conduits. In turn, K_s tends to be positively related to stomatal conductance and leaf maximum photosynthetic carbon gain (Santiago *et al.* 2004), which ultimately favours 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. 2a; $r = -0.63$, $P < 0.05$), which agrees 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 fibre walls (Supporting Information—Fig. S3a), representing higher stem construction costs.

Total parenchyma fractions (F_{TP}) were negatively related to sapling RGR (Fig. 2b; $r = -0.56$, $P < 0.05$). 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-fibres (Carlquist 2015). Living parenchyma cells, and, in particular, contact cells (i.e. cells having functional connections with vessels), are metabolically highly active (Spicer and 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. 4, Table 3).

Changes in trait-demography relationships during tree development

A number of studies have shown that both traits (Hietz *et al.* 2016; Rungwattana and 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 was negatively associated with MR only at the juvenile stage (Fig. 2d; $r = -0.71$, $P < 0.05$). 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.* 2018), and is also strongly associated with soil topography and drainage, with higher treefall rates in bottomlands with waterlogged soils where root anchorage is limited (Ferry *et al.* 2011). 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 (Table 3; Figs 2 and 3). This, together with the fact that adult MR were unrelated to wood traits, suggests that wood traits tended to be 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 possible 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 favoured the detection of stronger relationships between traits and demographic rates 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, for many tree species in Paracou, growth rates are lower at larger than at intermediate stem diameters (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 MR (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 was negatively related to RGR, but unrelated to sapling MR; while the opposite trend was found at the juvenile stage. These findings add to recent studies showing that demographic rates may be better explained in some cases 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 these 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 (Ziemińska *et al.* 2015).

Finally, it is important to note that while our study species reflect a wide spectrum of ecological strategies and wood structures, the number of species we sampled is relatively low, which might limit the generalizability of our findings. 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, demographic rates of saplings, juveniles and adults were associated with different wood traits. We also showed that the strength of the trait–demography associations tended to decrease at later ontogenetic stages. Overall, our results support the growing evidence that the effects of 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 traits such as wood chemical or anatomical traits are considered. These findings also support the general expectation that traits can be strongly 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.

Supporting Information

The following additional information is available in the online version of this article –

Table S1. RGR and MR for saplings, juveniles and adults of 19 tree species from a lowland forest in eastern Amazonia.

Figure S1. Schematic representation of trait and demographic sampling.

Figure S2. Relationships between relative growth and MR for tree species in a lowland forest in eastern Amazonia.

Figure S3. Correlation matrices, using Pearson correlation coefficients, among wood traits.

Acknowledgments

We are grateful to Jonathan Prunier for laboratory and field support, to Pascal Petronelli for his help with botanical identification, and to Daniel Sabatier, Jean-Françoise Molino, Jérôme Chave and Stéphane Traissac for providing data on tree demography. We would like to thank Soepe Koesse for his help collecting and preparing the wood samples, as well as Katherine Rivera, Camila Monje and Laura Baldion who assisted in processing anatomical images. Finally, we thank Beatriz Salgado-Negret, Adriana Sánchez and Jennifer Powers for insightful comments on a previous version of this manuscript. This study was funded by a student grant awarded to A.G.M. by COLCIENCIAS (Colombian Agency for Science and Technology. Grant 476), a short-term fellowship by the

Smithsonian Tropical Research Institute, and a field grant from the University of Guyane.

Author Contributions

The study was designed by A.G.M., J.M.P., B.C. and J.B. Most wood samples were collected by R.L. and A.G.M. Additional samples were provided by B.C., J.B. and S.L. Functional traits were calculated by A.G.M. Demographic data of adult trees were provided by G.D. Data analyses were performed by A.G.M. with contributions from J.M.P. The first draft of the manuscript was written by A.G.M. with inputs from J.M.P. All authors contributed equally to the writing and interpretation of advanced versions of the manuscript.

Conflict of Interest Statement

None declared.

Data Availability

The data that support the findings of this study are openly available in Figshare.com at: 10.6084/m9.figshare.22015805.

Literature Cited

- Ache P, Fromm J, Hedrich R. 2009. Potassium-dependent wood formation in poplar: seasonal aspects and environmental limitations. *Plant Biology* 12:259–267.
- Ache P, Fromm J, Hedrich R. 2010. Potassium-dependent wood formation in poplar: seasonal aspects and environmental limitations. *Plant biology (Stuttgart, Germany)* 12:259–267.
- Alvarez-Clare S, Kitajima K. 2007. Physical defence traits enhance seedling survival of Neotropical tree species. *Functional Ecology* 21:1044–1054.
- Amusant N, Nigg M, Thibaut B, Beauchene J. 2014. Diversity of decay resistance strategies of durable tropical woods species: *Bocopa prouacensis* Aublet, *Voucapoua americana* Aublet, *Inga alba* (Sw) Wild. *International Biodeterioration and Biodegradation* 94:103–108.
- Aritsara, Amy Ny Aina, Razakandraibe, Vonjisoa M., Ramanantoandro, Tahiana, Gleason, Sean M., Cao, Kun-Fang. Increasing axial parenchyma fraction in the Malagasy Magnoliids facilitated the co-optimisation of hydraulic efficiency and safety. *New Phytologist* 2020;229 (3):1467–1480.
- Aubry-Kientz M, Rossi V, Wagner F, Hérault B. 2015. Identifying climatic drivers of tropical forests dynamics. *Biogeosciences* 12:5583–5596.
- Baraloto C, Forget PM, Goldberg D. 2005. Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology* 93:1156–1166.
- Bossu J, Beauchêne J, Estevez Y, Duplais C, Clair B. 2016. New insights on wood dimensionality stability influenced by secondary metabolites: the case of a fast-growing tropical species *Bagassa guianensis* Aubl. *PLoS One* 11:e0150777–e0150717.
- Carlquist S. 2001. *Comparative wood anatomy: systematic, ecological and evolutionary aspects of dicotyledon wood*. Berlin: Springer.
- Carlquist S. 2015. Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function. *Botanical Journal of the Linnean Society* 177:291–321.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zane A. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Fan ZX, Zhang SB, Hao GY, Ferry JW, Cao KF. 2012. Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density. *Journal of Ecology* 100:732–741.
- Favrichon V. 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. *Revue d'Ecologie Terre et Vie* 49:379–403.
- Ferry B, Morneau F, Bontemps JD, Blanc L, Freycon V. 2011. Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology* 98:106–116.
- Fortunel C, Ruelle J, Beauchene J, Fine PVA, Baraloto C. 2013. Wood specific gravity and anatomy of branches and roots in 113 Amazonian rainforest tree species across environmental gradients. *New Phytologist* 202:79–94.
- Fromm J. 2010. Wood formation of trees in relation to potassium and calcium nutrition. *Tree Physiology* 30:1147.
- Godfrey, Jessie M., Riggio, Jason, Orozco, Jessica, Guzmán-Delgado, Paula, Chin, Alana R. O., Zwieniecki, Maciej A.. Ray fractions and carbohydrate dynamics of tree species along a 2750 m elevation gradient indicate climate response, not spatial storage limitation. *New Phytologist* 2019;225 (6):2314–2330.
- Grau, Oriol, Peñuelas, Josep, Ferry, Bruno, Freycon, Vincent, Blanc, Lilian, Desprez, Mathilde, Baraloto, Christopher, Chave, Jérôme, Descroix, Laurent, Dourdain, Aurélie, et al Nutrient-cycling mechanisms other than the direct absorption from soil may control forest structure and dynamics in poor Amazonian soils. *Scientific Reports* 2017;7 (1):45017
- Heineman KD, Turner BL, Dalling WJ. 2016. Variation in wood nutrients along a tropical soil fertility gradient. *New Phytologist* 211:440–454.
- Hérault B, Bachelot B, Poorter L, Rossi V, Bongers F, Chave J, Paine CET, Wagner F, Baraloto C. 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology* 99:1431–1440.
- Herrera-Ramírez, David, Sierra, Carlos A., Römermann, Christine, Muhr, Jan, Trumbore, Susan, Silvério, Divino, Brando, Paulo M., Hartmann, Henrik. 2021. Starch and lipid storage strategies in tropical trees relate to growth and mortality. *New Phytologist* 230 (1):139–154.
- Hietz P, Ronser S, Hietz-Seifert U, Wrigh SJ. 2016. Wood traits related to size and life history of trees in a Panamanian rainforest. *New Phytologist* 213:170–180.
- Jiang M, Caldaranu S, Zaehle S, Ellsworth D, Medlyn B. 2019. Towards a more physiological representation of vegetation phosphorus processes in land surface models. *New Phytologist* 222:1223–1229.
- King DA, Davies SJ, Tan S, Noor NS. 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology* 94:670–680.
- Kitajima K, Poorter L. 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology* 88:1000–1011.
- Kitajima K, Llorens AM, Stefanescu C, Timochenko M, Lucas P, Wright SJ. 2012. How cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of shade-tolerant species. *New Phytologist* 195:640–652.
- Kollman F, Coté WA. 1968. *Principles of wood science technology. I. Solid wood*. New York: Springer-Verlag.
- Kotowska M, Wright I, Westoby M. 2020. Parenchyma abundance in wood of evergreen trees varies independently of nutrients. *Frontiers in Plant Science* 11:86.
- Langer K, Ache P, Geiger D, Stinzing A, Arend M, Wind C, Regan S, Fromm J, Hedrich R. 2002. Poplar potassium transporters capable of controlling K⁺ homeostasis and K⁺-dependent xylogenesis. *Plant Journal* 32:997–1009.
- Laurans M, Martin O, Nicolini E, Vincent G. 2012. Functional traits and their plasticity predict tropical tree regeneration niche even among species with intermediate light requirements. *Journal of Ecology* 100:1440–1452.
- Lehnbach R, Bossu J, Va S, Morel H, Amusant N, Nicolini E, Beauchêne J. 2019. Wood density variations of legume trees in French Guiana

- along the shade tolerance continuum: heartwood effects on radial patterns and gradients. *Forests* 10:1–22.
- Levionnois, Sébastien, Jansen, Steven, Wandji, Ruth T chana, Beauchêne, Jacques, Ziegler, Camille, Coste, Sabrina, Stahl, Clément, Delzon, Sylvain, Authier, Louise, Heuret. Patrick. 2020. Linking drought-induced xylem embolism resistance to wood anatomical traits in Neotropical trees. *New Phytologist* 229 (3):1453–1466.
- Lida Y, Kohyama T, Swenson N, Su S, Chen C, Chiang J, Sun I. 2014. Linking functional traits and demographic rates in a subtropical tree community: the importance of size-dependency. *Journal of Ecology* 102:641–650.
- Martin A, Thomas S. 2013. Size-dependent changes in leaf and wood chemical traits in two Caribbean rainforest trees. *Tree Physiology* 33:1338–1353.
- Martin A, Erickson DL, Kress WJ, Thomas C. 2014. Wood nitrogen concentrations in tropical trees: phylogenetic patterns and ecological correlates. *New Phytologist* 204:484–495.
- Molino JF, Sabatier D. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294:1702.
- Morris H, Plavcová L, Cvecko P, Fichtler E, Gillingham MA, Martínez-Cabrera H, McGlenn DJ, Wheeler E, Zheng J, Zieminska K, et al. 2016a. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. *New Phytologist* 209:1553–1565.
- Morris H, Brodersen C, Schwarze F, Jansen S. 2016b. The parenchyma of secondary xylem and its critical role in tree defense against fungal decay in relation to the CODIT model. *Frontiers in Plant Science* 7:1665.
- Morris H, Gillingham MA, Plavcová L, Gleason S, Olson M, Coomes D, Fichtler E, Klepsch M, Martínez-Cabrera H, McGlenn D, et al. 2017. Vessel diameter is related to amount and spatial arrangement of axial parenchyma in woody angiosperms. *Plant Cell Environment* 41:245–260.
- Morris H, Hietala AM, Jansen S, Ribera J, Rosner S, Salmeia KA, Schwarze F. 2019. Using the CODIT model to explain secondary metabolites of xylem in defence systems of temperate trees against decay fungi. *Annals of Botany* 125:701–720.
- Osazuwa-Peters, O, Wright SJ, Zanne A. 2017. Linking wood traits to vital rates in tropical rainforests trees: insights from comparing sapling and adult wood. *American Journal of Botany* 104:1464–1473.
- Pfautsch S, Renard J, Tjoelker M, Salih A. 2015. Phloem as Capacitor: radial transfer of water into xylem of tree stems occurs via symplastic transport in ray parenchyma. *Plant Physiology* 167:963–971.
- Phillipson C, Dent D, O'Brien M, Chamagne J, Dzulkifli D, Nilus R, Reynolds G, Saner P, Hector A. 2014. A trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific relative growth rates. *Ecology and Evolution* 18:3675–3688.
- Pillet M, Joetzier E, Belmin C, Chave J, Ciais P, Dourdain A, Evans M, Hérault B, Luysaert S, Benjamin P. 2018. Disentangling competitive vs climatic drivers of tropical forest mortality. *Journal of Ecology* 106:1165–1179.
- Placvová L, Jansen S. 2015. The role of xylem parenchyma in the storage and utilization of nonstructural carbohydrates. In U. Hacke, ed. *Functional and ecological xylem anatomy*. Switzerland: Springer International Publishing Switzerland.
- Poorter L, Wright SJ, Paz H, Ackerly DD, Condit R, Ibarra-Martínez G, Harms KE, Licona JC, Martínez-Ramos M, Mazer SJ, et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 98:1908–1920.
- Poorter L, McDonald I, Alarcon A, Fichtler E, Licona JC, Peña-Claros M, Sterck F, Villegas Z, Sass-Klaassen U. 2010. The importance of Wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *The New Phytologist* 185:481–492.
- R Development Core Team. 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Reich P. 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* 102:275–301.
- Rodrigues AMS. 2010. *Análise e valorização bioinspirada dos metabólitos secundários responsáveis pela durabilidade natural de madeiras exploradas na Guiana Francesa*. PhD Thesis, University of Brasília, Brazil.
- Rungwattana K, Hietz P. 2017. Radial variation of wood functional traits reflects size-related adaptations of tree mechanics and hydraulics. *Functional Ecology* 32:260–272.
- Russo S, Jenkins KL, Wiser SK, Uriarte M, Duncan R, Coomes D. 2010. Interspecific relationships among growth, mortality and xylem traits of woody species from New Zeland. *Functional Ecology* 24:253–262.
- Russo, Sabrina E., McMahon, Sean M., Detto, Matteo, Ledder, Glenn, Wright, S. Joseph, Condit, Richard S., Davies, Stuart J., Ashton, Peter S., Bunyavejchewin, Sarayudh, Chang-Yang, Chia-Hao, et al The interspecific growth–mortality trade-off is not a general framework for tropical forest community structure. *Nature Ecology & Evolution* 2020;5 (2):174–183.
- Santiago L, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T. 2004. Leaf photosynthetic traits with hydraulic conductivity and wood density in Panamanian forest canopy traits. *Oecologia* 140:550.
- Santiago L, De Guzman M, Baraloto C, Vogenberg J, Brodie M, Hérault B, Fortunel C, Bonal D. 2018. Coordination and trade-offs among hydraulic safety, efficiency and drought avoidance traits in Amazonian rainforest canopy tree species. *New Phytologist* 218:1015–1024.
- Scotti I, Calvo-Viale L, Scotti-Saintagne C, Citterio M, Degen B, Bonal D. 2010. Genetic variation for growth, morphological, and physiological traits in a wild population of the Neotropical shade-tolerant rainforest tree *Sextonia rubra* (Mez) van der Werff (Lauraceae). *Tree Genetics & Genomes* 6:319–329.
- Sheil D, May RM. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84:91–100.
- Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin D, Reich P. 2016. Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* 180:923–931.
- Spicer R, Holbrook NM. 2007. Parenchyma cell respiration and survival in secondary xylem: does metabolic activity decline with cell age? *Plant, Cell and Environment* 30:934–943.
- Sylvie Gourlet-Fleury, Jean-Marc J.-M. Guehl, Olivier Laroussinie. Ecology and management of a neotropical rainforest. Lessons drawn from Paracou, a long-term experimental research site in French Guiana. *Elsevier*, 350 p., 2004, 2-84299-455-8
- Thomas SC. 1996. Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *Oikos* 76:145–154.
- Turner B, Brenes-Arguedas T, Condit R. 2018. Pervasive phosphorous limitation of tree species but not communities in tropical forests. *Nature* 555:367–370.
- Tyree MT, Zimmermann MH. 2002. *Xylem structure and the ascent of sap*. Berlin: Springer.
- Uriarte M, Canham CD, Thompson J, Ziemmerman J, Brokaw N. 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density dependence and the spatial distribution of parent trees. *Journal of Ecology* 93:291–304.
- Visser MD, Bruijning M, Wright SJ, Muller-Landau H, Jongejans E, Comita LS, Kroon H. 2016. Functional traits as predictor of vital rates across the life cycle of tropical trees. *Functional Ecology* 30:168–180.
- Vitousek PM. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–298.
- Wagner F, Hérault B, Stahl C, Bonal D, Rossi V. 2011. Modeling water availability for trees in tropical forests. *Agricultural and Forest Meteorology* 151:1202–1213.
- Wheeler JK, Sperry JS, Hacke UG, Hoang N. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment* 28:800–812.

- Worthy S, Swenson N. 2019. Functional perspectives on tropical tree demography and forest dynamics. *Ecological Processes* 8:1–11.
- Wright S, Joseph, Yavitt, Joseph B., Wurzbarger, Nina, Turner, Benjamin L., Tanner, Edmund V. J., Sayer, Emma J., Santiago, Louis S., Kaspari, Michael, Hedin, Lars O., Harms, Kyle E., et al. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* 92 (8):1616–1625.
- Wright SJ, Jaramillo A, Pavon J, Condit R, Hubbell SP, Foster R. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* 21:307–315.
- Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Diaz S, et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* 91:3664–3674.
- Wright SJ, Turner BL, Yavitt SB, Harms K, Kaspari M, Tanner EV, Bujan J, Griffin EA, Mayor JR, Pasquini S, et al. 2018. Plant responses to fertilization experiments in lowland, species-rich, tropical forests. *Ecology* 99:1129–1138.
- Yang J, Cao M, Swenson N. 2018. Why functional traits do not predict tree demographic rates. *Trends in Ecology and Evolution* 33:326–336.
- Zheng J, Martinez-Cabrera H. 2013. Wood anatomical correlates with theoretical conductivity and wood density across China: evolutionary evidence of the functional differentiation of axial and radial parenchyma. *Annals of Botany* 112:927–935.
- Zhu Y, Queenborough SA, Condit R, Hubbell SP, Ma KP, Comita LS. 2018. Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecology Letters* 21:506–515.
- Ziemska K, Butler DW, Gleason SM, Wright I, Westoby M. 2013. Fiber wall lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB PLANTS* 5:1–14.
- Ziemska K, Westoby M, Wright IJ. 2015. Broad anatomical variation within a narrow wood density range—A study of twig Wood across 69 Australian Angiosperms. *PLoS One* 10:e0139496–e0139425.