Trees (2020) 34:497–505
https://doi.org/10.1007/s00468-019-01931-5

ORIGINAL ARTICLE

Traits and trade-offs of wood anatomy between trunks and branches in tropical dry forest species

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Received: 16 April 2019 / Accepted: 13 November 2019 / Published online: 23 November 2019

Abstract

Key message **Differences in wood traits are related to contrasting forces acting over trunks and branches.**

Abstract The wood economic spectrum is one of the most important groups of traits for plant performance due to the multiple functions in mechanical support, water conductivity and water and nutrient storage. Owing to the multiple functions, there are conflicting demands on wood anatomy depending upon environmental and architectural forces that change according to the structure (trunk/branch) in which functional traits are estimated. In this context, we explored how the mean values, variability and correlation patterns of wood anatomy traits varied between trunks and branches. We measured seven wood traits related to hydraulic efficiency and safety and mechanical support in 19 tree species that are widely distributed in tropical dry forests in Colombia. We found higher mechanical support and hydraulic efficiency in trunks than in branches and higher variation in hydraulic traits when compared to mechanical wood traits in both trunks and branches. We also detected higher traits coupling in branches when compared to trunks. Our results showed that contrasting forces acting over trunks and branches result in substantial intra-individual variability. These results are an important contribution when addressing ecological questions relating to the identification of functional strategies, species' response capacity to changing environmental conditions and aboveground biomass estimations.

Keywords Dry forest · Hydraulic traits · Mechanical traits · Wood anatomy traits · Intra-individual variability

Introduction

The cellular structure of xylem is an important ecological spectrum in plants due to its multiple functions in mechanical support, water and nutrient transport and storage (Carlquist 2001; Sperry et al. 2008; Chave et al. 2009; Pratt and Jacobsen 2016), influencing demographic rates and fitness (Poorter et al. 2010; Hietz et al. 2016). The values and variability of wood anatomy traits are the result of multiple ontogenetic, hydraulic, and environmental forces (Zimmermann 1978; Swenson and Enquist 2008; Sarmiento et al. 2011; Rosell et al. 2017) that vary across tree architecture; therefore, we expect to find high trait variability between different parts of a tree. However, intra-individual variation of wood anatomy traits is often ignored despite its importance for our understanding of tree diversity and forest structure in the face of climate change (Malhi et al. 2006), and aboveground biomass estimations (Sarmiento et al. 2011). Here we explore the allometric relationship and variability of seven wood anatomy traits from trunks and branches of

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Communicated by Sano.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00468-019-01931-5) contains supplementary material, which is available to authorized users.

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widely distributed tree species found throughout tropical dry forests (TDF) in Colombia.

Trunks and branches are exposed to contrasting environmental forces. The trunk of trees must support tree static weight and resist higher forces and dynamic loadings from a range of natural factors (Rowe and Speck 2005), and they need to transport water upwards for several meters without breaking the water column across the xylem (Ryan and Yoder 1997). In contrast, branches are subject to mechanical forces acting on a horizontal free hanging structure (Cantilever beam theory, Gere 2004) and, therefore, they need to invest resources to prevent their rupture due to their mass (Sterck et al. 2006). Additionally, branches are exposed to strong environmental filters such as high radiation and wind that create the lowest pressures in the most peripheral parts of the tree resulting in higher cavitation probabilities (Zimmermann 1978), but it is important to recognize that cavitation also can change by aging effects (Sperry et al. 1991; Rodríguez-Zaccaro et al. 2019) and through previous cavitation and refilling cycles (cavitation fatigue phenomenon) (Umebayashi et al. 2019). Environmental conditions play a central role in shaping the distribution and variability of functional traits, and although in the literature there are references related to intra-individual variability (mean and variability) of wood anatomy traits [Swenson and Enquist (2008) and Sarmiento et al. (2011) to wood density (WD), Lachenbruch et al. (2011) to radial variation; Anfodillo et al. (2006) and Olson et al. (2014) to vessel diameter], there are few studies exploring variation in a wide range of wood anatomy traits in tropical species (Jacobsen et al. 2018; Pfautsch et al. 2018).

As trunks and branches are exposed to contrasting abiotic conditions, and have different roles in plant functioning, we expect differences in variability and coupling of traits in those structures of plant. The trunk is the only pathway that enables to transport water and solutes from roots to branches and leaves (Meinzer et al. 2001), it is responsible for support of the tree itself (Niklas 2000) and is important to propagation and growth of tree, thus should be subject to robust selection. Meanwhile, branches frequently have one of the lowest priorities for carbon allocation within plant and can be replaced in face of physiologically or mechanically failure (Hinckley and Schulte 1995). For example, it has been proposed that hydraulic constraints enable the plant to sacrifice organs of lesser importance such as branches and twigs and invest to save organs that are critical for long-term survival and propagation as trunks (Zimmermann 1983; Tyree and Ewers 1991). This hydraulic segmentation hypothesis could involve other biochemical, morphological and developmental responses following injury (Hinckley and Schulte 1995). Therefore, we can expect lower variability but higher coupling of traits in trunks since a coordinated phenotype can respond to environmental variation more efficiently (Schlichting 1989; Waitt and Levin 1993; Gianoli 2004). Several studies have shown that WD integrates many xylem traits relating to water stress tolerance (Hacke et al. 2001; Jacobsen et al. 2005, 2007; Pratt et al. 2007). However, studies related to variation in traits coupling between trunks and branches are scarce in angiosperms (Sarmiento et al. 2011; Jacobsen et al. 2018).

In this study, we address the following predictions: (1) as branches and trunks are subject to different environmental, hydraulic and mechanical forces, we expect differences in wood anatomy traits between them. Particularly, we expect trunks to have trait values related to higher hydraulic efficiency [wider vessel and intervessel pit diameter (PDi) and lower vessel density (VD)] to reduce hydraulic resistance imposed by increased gravitational forces and path length. Additionally, we expect higher investment in structures providing mechanical support in trunks [fiber and vessel cell thickness and fiber length (Fl)] than branches. (2) We expect lower coefficient of variation (CV) in hydraulic than in mechanical traits, both in trunks and branches, because those traits are related to reduce embolism vulnerability and, therefore, mortality, under dry environments. Finally, (3) we expect higher trait coupling in trunks than in branches, because trunks are subject to greater static and dynamic forces, and their damage is more serious to plant survival than damage to peripheral parts such as stems or leaves that are expendable organs.

Materials and methods

Study area

The study was conducted in a TDF in the upper basin of the Magdalena River, in Cundinamarca department, Colombia. The study area is located at an elevation of 340 m above the sea level, with a mean annual rainfall of 1400 mm with two dry periods between May and September and December and March and a mean annual temperature of 27 °C (Mendoza 1999). We selected 19 species, which represent most of the dominant species in the study area (Table 1). These species are widely distributed across TDF in Colombia (González et al. 2018). Furthermore, the species span the range from acquisitive to conservative strategies with both leaf phenologies ranging from evergreen to deciduous. The trees provide evidence of all wood anatomy combinations in TDFs (Online resource 1).

Wood anatomy traits

Five individuals were sampled for each species, and we measured seven wood anatomy traits per individual in both a trunk and a branch (Table 2). It is recognized that xylem

Table 1 Species list by family

Species	Family
Anacardium excelsum (Bertero ex Kunth) Skeels	Anacardiaceae
Astronium graveolens Jacq.	Anacardiaceae
Brosimum alicastrum Sw.	Moraceae
Casearia corymbosa Kunth	Salicaceae
Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae
Cupania cinerea Poepp.	Sapindaceae
Curatella americana L.	Dilleniaceae
Guazuma ulmifolia Lam.	Malvaceae
Handroanthus ochraceus (Cham.) Mattos	Bignoniaceae
Machaerium capote Dugand	Fabaceae
Myrcianthes sp.	Myrtaceae
Nectandra turbacensis (Kunth) Nees	Lauraceae
Piper reticulatum L.	Piperaceae
Piptocoma cf niceforoi (Cuatrec.) Pruski	Asteraceae
Quadrella indica (L.) Iltis & Cornejo	Capparaceae
Swartzia amplifolia Harms	Fabaceae
Tabernaemontana grandiflora Jacq.	Apocynaceae
Triplaris americana L.	Polygonaceae
Zanthoxylum rigidum Humb. & Bonpl. ex Willd.	Rutaceae

Table 2 Abbreviations, units and number of measurements per species per trait in trunks and branches

Trait	Abbreviation	Units	Measurements
Wood density	WD	g/cm^3	5
Vessel diameter	VDi	µm	125
Intervessel pit diameter	PDi	µm	125
Vessel density	VD	#/mm^2	50
Fiber cell wall thickness	FCT	µm	125
Vessel element length	Vl	µm	125
Fiber length	Fl	µm	125

conduits of trunks and branches are connected shaping a continuous way to transport water, and studies have reported changes in functional traits along it (Anfodillo et al. 2006; Olson et al. 2014). In this study, we only sampled trunks and branches because they represent the two extremes of the transport continuum and are exposed to contrasting environmental, hydraulic and architectural forces. Additionally, these structures are commonly sampled in ecological studies. All individuals showed diameter at breast height > 10 cm and canopy height between 14 and 18 m, with exception for understory species such as *Curatella americana* L. *Myrcianthes* sp, and *Piper reticulatum* L. that showed height between 4 and 8 m. The samples were collected between January and May 2015. For the trunks, a 5-mm-diameter core sample was used to extract recent sapwood at 1.3 m above ground level. Core lengths varied between 8 and 13 cm, depending on the hardness of the sampled wood. The samples were placed in a plastic tube with holes and immersed in water with formalin (1%) to avoid fungi proliferation. Branches were cut down using a tree pole clipper from the same five individuals per species. We selected secondary branches located between 5 and 7 m above ground with a radius of approximately 1–2 cm in diameter. Branches with this radius are usually used to estimate WD in tropical forest plots (Swenson and Enquist 2008; Baraloto et al. 2010; Sarmiento et al. 2011). Care was taken to sample branches that had similar length (between 120 and 150 cm), as stem length explains large proportion of variation in hydraulic traits across the tree (Olson et al. 2014). All bark was removed from the branch wood section in the field, and branch segments were immersed in water with 1% formalin in plastic bags with a zipper seal to conserve and prevent decomposition. Cores and branch segments were transported to the wood laboratory in Universidad Distrital Francisco Jose de Caldas in Bogotá. Trunk and branch wood densities were calculated as the dry mass per fresh volume of each sample. Samples were saturated with water and fresh volume was estimated using water displacement. After fresh volume was measured, samples were dried at 70 °C for 72 h, and dry mass was determined. The trunk and branch of hardwoods (density > 0.65 gr cm^{-3}) were immersed in a mixture of glycerine–water and heated to soften the samples (Jansen et al. 1998). Samples of active xylem were taken, and sapwood was measured in trunks, while in branches, samples were obtained along the radius. Longitudinal and transverse sections were cut with a sliding microtome (Leica RM 2255), and sections with a thickness between 12 and 40 µm were obtained to determine the diameter of vessel lumen (excluding cell wall thickness) and density (10×), intervessel PDi (100×; horizontal pit border diameter) and fiber cell wall thickness (FCT) (40× to 100×). The tissues were then cut, bleached, stained, and dehydrated, before mounting them on slides following Jansen et al. (1998). Vessel elements and Fls were estimated by maceration of the wood slivers (Jansen et al. 1998). Tissue slices were photographed with a digital camera mounted on a microscope Primo Start (5× to 100×) and the images were processed using the imaging software ImageJ (http://imagej.nih.gov/ij/). The measurement of xylem anatomy was done according to Richter and Dallwitz (2000).

Statistical analysis

Overall multivariate relations and trait differences among species were explored using a principal component analysis (PCA). To compare trait values between trunks and branches, four traits were log-transformed to improve normality: VDi, Vl, VD and Fl, and *T* tests were used. The non-parametric Wilcoxon tests were used when data did not meet the assumption of normality such as WD, intervessel PDi and FCT. To evaluate the relationship between trunk and branch traits, we used linear models (lm) in the R package ‘lme4’ (Bates et al. 2018), using trunk traits as independent variables and branch traits as dependent variables. To test significant differences between 1:1 slope and the slopes estimated from the linear models, we used the linear hypothesis test (LHT) in the ‘car’ package. To compare the variability of wood anatomy traits, we determined the CV for each trait in the trunks and the branches. Additionally, we performed Pearson correlation with Bonferroni correction for multiple comparisons. All analyses were carried out using R statistical program (R Development Core Team 2005, version 3.2.2).

Results

Mean and coefficient of variation

All measured traits in the branches and trunks were strongly positively correlated (Fig. 1). Although the relationships were positive and strong, substantial variation remained unexplained (15–61%). All the relationships between branch and trunk were significantly different from the 1:1 relationship, with the exception of intervessel PDi (Fig. 1). All traits showed higher values in the trunks than in branches with the exception of VD (Fig. 2, Online resource 2).

Related to variability, traits associated with hydraulic conductivity such as VDi (CV trunk: 125.81% and CV branch: 76.61%), intervessel PDi (CV trunks: 51.82% and CV branches: 38.89%) and VD (CV trunks: 46.44% and CV branches: 36.30%) showed the highest CV in both trunks and branches. WD showed the lowest variation (CV trunks: 17.48% and CV branches: 18.88%) followed by traits related to mechanical support, such as FCT (CV trunks: 26.17% and CV branches: 28.99%) and Fl (CV trunks: 29.19% and CV branches: 24.17%).

Trait coupling between trunks and branches

Trait coupling was higher in branches than in trunks with more significant relationships in branches (Table 3). In both structures, hydraulic traits were more related among them than mechanical traits. However, in trunks both kinds of traits were decoupled themselves (Table 3). There were no correlations between FCT and VDi ($r = 0.06$, $p = 0.54$), nor between VD ($r = 0.06$, $p = 0.59$), and Vl to VDi ($r = 0.12$, $p = 0.25$), VD ($r = -0.08$, $p = 0.44$) and intervessel PDi ($r = 0.06$, $p = 0.53$) (Table 3). Interestingly, WD was related to almost all traits, but it was not correlated with FCT even in trunks and branches.

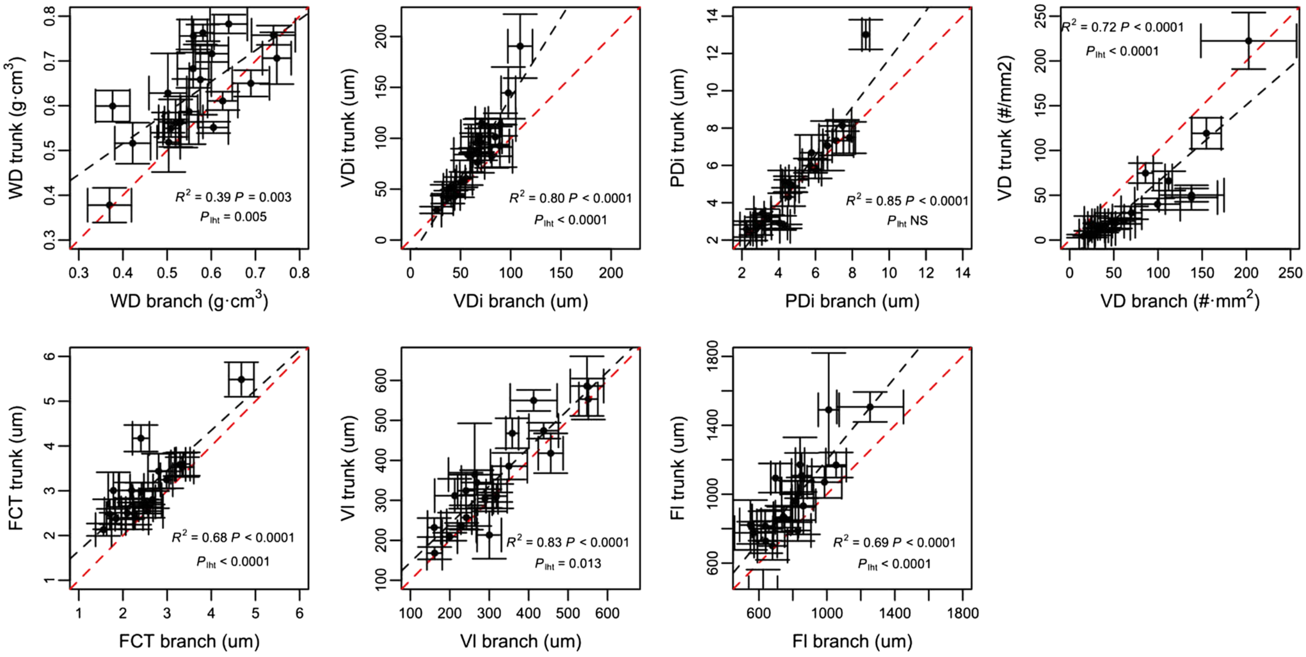

Fig. 1 Linear models (lm) between wood trait anatomies among 19 Colombian tropical dry forest tree species. Points represent species mean; bars are standard deviation. The black line represents lm for community level, and the red line represents the expected 1:1 relationship between traits. Trait abbreviations as in Table 2. Plht represents *P* value of linear hypothesis test

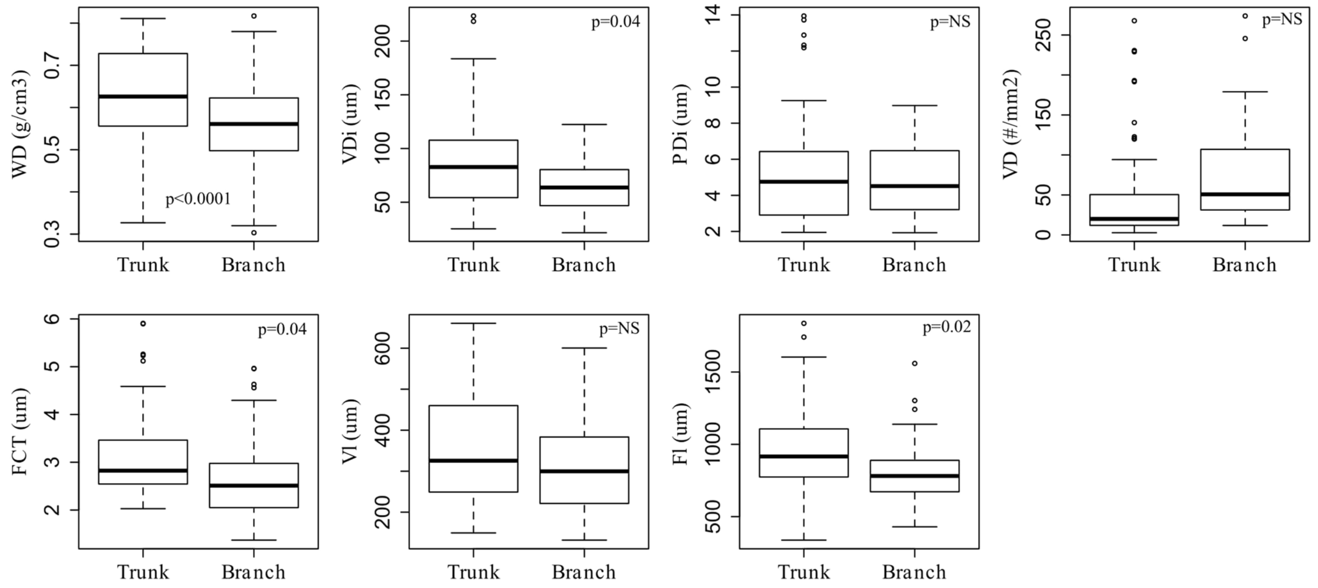

Fig. 2 Differences in wood trait anatomy among 19 Colombian tropical dry forest tree species. Trait abbreviations as in Table 2

Table 3 Pearson correlation coefficients and Bonferroni corrections between seven anatomy wood traits of 19 Colombian tropical dry forest tree species

	WD	VDi	PDi	VD	FCT	Vl	Fl
WD		−0.50***	−0.30	0.28	−0.08	−0.44***	−0.41***
VDi	−0.64***		0.68***	−0.63***	0.06	0.12	0.39***
PDi	−0.40***	0.48***		−0.40***	−0.29	0.06	0.18
VD	0.55***	−0.81***	−0.49***		0.06	−0.08	−0.44***
FCT	0.07	−0.22*	−0.40***	0.28**		0.30	0.35**
Vl	−015	−0.21*	−0.23*	0.20*	0.42***		0.48***
Fl	−0.55***	0.28***	0.02	−0.29***	0.20*	0.45***	

Trunks are at the top of the table and branches are at the bottom of the table. *$p < 0.05$, **$p < 0.01$, ***$p < 0.0001$. Trait abbreviations as in Table 2

Discussion

Our results showed considerable variation in wood anatomy traits between trunks and branches produced by contrasting environmental and architectural forces. Notably, trunks showed higher mechanical support and hydraulic efficiency than branches and hydraulic traits showed higher coefficients of variation than mechanical traits in both trunks and branches. In contrast to trunks, branches showed higher coupling among traits which could be related to higher environmental variability such as radiation, temperature and water deficit. To our knowledge, this is the first study exploring changes in distribution, variability, and coupling of seven of the most important wood anatomy traits between trunks and branches in TDFs.

Higher mechanical support and hydraulic efficiency in trunks than branches

As we predicted, we found higher mechanical support for trunks rather than branches, probably due to a greater proportion of mature wood and higher secondary compound concentration in the trees (Wilson and Archer 1977; Patiño et al. 2009) and the necessity to resist the force of wind on the entire crown (Niklas 2000). Higher WD, vessel and Fl and fiber cell content in trunks as compared to branches represent an advantage for mechanical stability (Niklas 1997) that could be necessary for species with different functional strategies. For example, canopy species such as S*wartzia amplifolia* have high WD and FCT because it needs to support its huge weight, while *C. americana* L. exhibits a mixture between thick and long fibers enabling it to tolerate strong winds under full solar exposure (Van Gelder et al. 2006). Additionally, branches might have other strategies to lead with environmental forces such as align their leaves and sway in the wind (Ennos 1997). It is important to recognize that variation between trunk and branch traits might be related to other variables that we did not include in our study such as branch inclination (King et al. 2006; Sterck et al. 2006) or branch thickness and slenderness (Huang et al. 2010; Eloy 2011).

Vessel diameters varied between trunks and branches because selection favors tapering, with narrower apical vessels in twigs buffering path length-imposed resistance (Anfodillo et al. 2006; Olson et al. 2014). Additionally, smaller vessels on branches represent higher hydraulic safety in places with more negative pressures (Zimmermann 1978) and they ensure a comparable supply of resources to all leaves, regardless of plant height (West et al. 1999). Following these ideas, we may suppose that vessel tapering is particularly important in seasonal ecosystems limited by water, where strong dry seasons result in very low pressures on the most peripheral parts of the tree with lethal consequences for branches and twigs. However, there is no evidence about it. Additionally, the tapering of diameters helps to reduce the differences in conductance to leaves throughout the crown and buffer hydraulic resistance of height growth (Becker et al. 2000). Our results agree with previous studies that have reported higher WD (Swenson and Enquist 2008; Sarmiento et al. 2011) and wider vessels (Anfodillo et al. 2006) in trunks than branches.

Contrary to our predictions, intervessel PDi did not vary between trunks and branches. Embolisms within the xylem are thought to result from air seeding at pit membranes (Zimmermann 1983); therefore, we expected lower intervessel PDi in branches than in trunks due to higher drought and cavitation pressures on branches. However, the absence of variability could be related to what other traits are more important for determining embolism resistance. For example, traits related to membrane porosity such as the spatial density and three-dimensional arrangement of cellulose microfibrils (Li et al. 2016), the quality and quantity of intervessel pit membranes (Wheeler et al. 2005), or pit membrane thickness, that show strong correlations with P_{50} (Lens et al. 2011; Li et al. 2016). Functional interpretations of the structural and chemical composition of pit membranes remain poorly understood in relation to embolism resistance in seasonal ecosystems limited by water.

Higher variation in hydraulic than mechanical wood traits

Contrary to our predictions, hydraulic traits showed higher coefficients of variation than do mechanical traits in both trunks and branches. This finding could be the result of different environmental and architectural forces acting in different ways on these two structures. Since wood space is limited and needs to be divided between tissues with different functions (parenchyma to storage, vessels to hydraulic conductivity, and fibers to mechanical support), there are conflicting forces on how to distribute space between these tissues. Probably, tissues that have a mechanical function in trunks (static weight) and branches (cantilever) are the most determinant, and thereby subject to important selection, resulting in low trait variability. It is important to mention that several angiosperms from water-limited environments (Mediterranean ecosystems) have evolved cells with different functions, such as tracheids that are structurally and functionally intermediate fiber and vessels providing mechanical support and water transport at the same time (Pratt and Jacobsen 2016), or their lumens that can act as a compartment for water storage that can be released when they undergo cavitation (Lo and Salleo 1992). However, in our species, we only find tracheids in three species: *C. americana, Cupania cinerea* and *Myrcianthes* sp. Another not excluding explanation to higher variability of hydraulic traits could be related to the high seasonality of TDFs. TDFs are subject to extreme changes in water availability due to the alternation between wet and dry seasons, with dry seasons with 6 months or more of 100 mm rainfall or less (Allen et al. 2017). Species with high variability in hydraulic traits or bimodal distribution of the traits could have a greater ability to cope with drought (Salgado-Negret et al. 2013) because in wetter seasons their wide vessels are more efficient for water transport, while in the drier season when wider vessels are more prone to cavitation, plants can use the narrower vessels to maintain water transport. This idea could be applied to other hydraulic traits such as intervessel PDi. Conversely, mechanical traits are dependent on architectural aspects like height or branch inclination, which are relatively constant through the years.

Higher trait coupling in branches than trunks

Contrary to our expectations, we found more significant trait correlations in branches than trunks. Additionally, we found high coupling among hydraulic traits with two strategies related to water economy in both trunks and branches. At one extreme, acquisitive strategy is characterized by low WD, few and wide vessels, long fibers and wide intervessel pits that favor hydraulic efficiency and storage capacity due to their greater lumen per unit of volume (Poorter et al. 2010). At the other extreme, conservative strategy showed contrasting traits, favoring safe conduction and reduced cavitation risk (Méndez-Alonzo et al. 2012). In branches, in contrast to trunks, we found a higher coupling between hydraulic and mechanical traits with significant correlations between FCT and Vl while VDi and

VD and intervessel PDi could be related to stronger and highly variable environmental conditions such as water deficit, radiation, and temperature. Other studies of trait coordination also show greater correlation values in heterogeneous environments, but the functional benefits or constraints on this pattern for plants have not been clearly established (Gianoli 2004; Matesanz et al. 2010).

Wood density is unrelated to fiber cell wall thickness but it is connected to hydraulic traits. Previous studies have reported that WD is strongly affected by abundance and characteristics of wall fibers (Jacobsen et al. 2007; Chave et al. 2009; Ziemińska et al. 2015). Low density wood can be the result of a different combination of tissue and cell distribution, for example, by reducing fiber lumen while increasing storage capacity through increased axial parenchyma, increasing the fiber wall fraction with high fiber lumen and low fiber walls (Ziemińska et al. 2015), or reducing abundance of fibers (Jacobsen et al. 2005). In addition to cell characteristics, factors such as chemical deposits within and between the cells can create high WD, especially unusual deposits of resins around the ring shake (Zobel and Van Buijtenen 1989) or increase the proportion of ray tissue due its configuration with the absence of large internal cell voids and few intercellular spaces giving it a high specific gravity of rays (Taylor 1969). We also reported negative relationships between WD and vessel diameter, a finding that has already been reported by other studies (Preston et al. 2006; McCulloh et al. 2011). The nature of this relationship is that vessel lumens do not contribute to dry mass; therefore, WD can be partitioned into the proportion of stem that is not vessel lumen (Zanne et al. 2010). Additionally, we also reported a negative relationship between WD and intervessel PDi, strengthening the link between WD and hydraulic traits, but the nature of those relationships remains poorly understood.

In conclusion, we demonstrated high intra-individual variability of wood anatomy traits produced by contrasting ontogenetic, hydraulic, architectural, and environmental forces. This is important in ecological studies because identification of functional strategies and the response capacity to changing environmental conditions may vary according to the structure (trunk/branch) in which functional or physiological traits are estimated. Additionally, this variation is important to avoid underestimation of carbon stocks that traditionally estimate WD based on branches. It is important to recognize that we sampled one branch per individual excluding variability between branches of different sizes. However, we used secondary branches with the radius usually used to estimate wood traits, ecological strategies and biomass in tropical forest plots and we controlled for height and position of branches between individuals and species, so that these results highlight the importance of including intra-individual variability for addressing ecological questions.

Author contribution statement EPR, RLC and BSN conceived and designed the research. EPR, JT and EV conducted fieldwork. EPR, RLC and BSN analyzed the data. EPR and BS wrote the manuscript and EPR, RLC, JT, EV and BSN approved the final version.

Acknowledgements The authors thank two anonymous reviewers and the editor for comments that improved the manuscript. We are grateful to Elkin Tenorio for his statistical support and to Roy Gonzalez, Natalia Norden and Nicolás Urbina for useful discussions and comments on the manuscript. We express acknowledgements to Reserve Mana Dulce and especially to Constanza Mendoza for their help in the field.

Compliance with ethical standards

Conflict of interest The authors declare that we have no conflict of interest.

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