

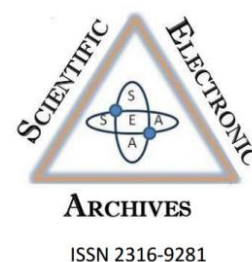
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# Hydraulic structure and wood density from root to the crown in in three native Brazilian tree species

**Olívia Pereira Lopes**

Universidade Estadual Paulista “Júlio Mesquita Filho”

**Bruna Zannato**

Instituto de Pesquisas Ambientais

**Juraci de Andrade Barbosa**

Instituto de Pesquisas Ambientais

**Guillermo Angeles**

Instituto de Ecología, A.C. Red de Ecología Funcional

*Corresponding author*

**Eduardo Luiz Longui**

Instituto de Pesquisas Ambientais

[elongui@sp.gov.br](mailto:elongui@sp.gov.br)

**Abstract.** We study anatomical and hydraulic features of vessels and wood density, and correlations between them, from root to crown in 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosi* trees. We didn't observe gradual tapering of vessel diameter along the tree axis, but hydraulic bottlenecks from stem top to the crown base were noted. Vessel density, did not vary from root to stem, but it was higher in the crown. Vessel features promotes changes in potential hydraulic conductivity, and these changes vary among species, highlighting that the interaction between vessel density and vessel diameter affected potential hydraulic conductivity. Higher values of wood density at trees bases demonstrated an investment in mechanical sustentation. Our results showed a certain synergy between anatomical features and hydraulic conductivity that promotes anatomical adjustments required to meet the hydraulic and mechanical requirements of these tropical trees.

**Keywords:** hydraulic bottlenecks, hydraulic properties, wood axial variation, Brazilian woods

## Introduction

The tapering pattern of conduits from base to tree top is commonly reported (Olson and Rosell, 2013). According to Petit and Anfodillo (2009), conduit tapering is essential to maintain efficiency in water conduction because the water pathway also becomes longer with the increase in age and height of the trees. Thus, if tapering does not occur, an increase in water friction within cell walls will result, leading to a decrease in conductivity. However, the secondary xylem is not a uniform structure along the axial axis of plant and it varies radially from the pith to the bark (juvenile to mature wood) and axially from the root, trunk and branches. This structural heterogeneity results in variation in hydraulic and mechanical performance. Changes in the xylem architecture are often the results of tradeoffs between structure and function, which may vary

according to constraints or adjustments of the architecture and between safety and hydraulic and biomechanical efficiency. Trees usually respond by means of growth in height, increase in trunk diameter and branches, crown size and root distribution and depth during changes in their abiotic and biotic environments.

Schuldt et al. (2013) studied changes in the wood density, wood anatomy and hydraulic properties of the secondary xylem along the root-to-shoot flow path in tropical rainforest trees. Based on their findings, authors of present work confirmed the concept of conduit tapering in trees from humid, or perhumid environments but its validation as a universal rule is still lacking and demands further studies.

The environmental conditions, to which tropical trees species are subjected might offer a

possible explanation for the absence of a classical tapering pattern. According to Schuldt et al. (2013), if compared with temperate or boreal trees, tropical trees, temporarily experience higher atmospheric saturation deficits in the crown, which is not subject to frost. As per these authors such conditions interfere with hydraulic architecture to avoid cavitation and may not represent a crucial competitive advantage in a perhumid climate.

When we analyze only root and crown, we expected to find large diameter vessels with lower vessel density in roots as compared to branches. Other studies have shown that vessels are larger in the root than in stem (Psaras and Sofroniou, 2004). However, analysis of path along the plant, i.e., from root to different positions along trunk to crown, if vessel tapering occurs, vessel density and wood density would either show a gradual increase or decrease from the base to top. As demonstrated by WBE model (West, Brown, Enquist), variations in hydraulic architecture are related to anatomical alterations in the xylem structure, (West et al. 1999), in which conduit diameter tends to decrease with the increase in tree height to maintain hydraulic efficiency and to avoid the disfunctioning of the xylem. Additionally, Murray's law predicts the thickness and ramifications of vessels and holds that an optimum network has a minimum number of wide conduits at the base that feed an increasing number of narrower conduits distally; thus, minimizing the cost of constructing bifurcated structures and conducting fluids. Hydraulically, this configuration is less efficient, but it is more mechanically stable (McCulloh et al., 2004). Since the wood density is negatively correlated with hydraulic conductivity, it was expected that a decrease in wood density towards the crown would be observed during tapering (Baas et al., 2004). This indicates that a balance between hydraulic conduction and mechanical strength would be struck. Considering that vessel dimension and density are directly related to wood density, it is important to investigate wood structure along tree height to understand how trees optimize these competing functions (Gartner and Meinzer, 2005).

In the present study, we examined the axial variation of vessel diameter, vessel density, potential hydraulic conductivity and wood density and it was

correlated among these characteristics, from root to crown in 40-year-old trees of *Balfourodendron riedelianum* (Engl.) Engl., *Cariniana legalis* (Mart.) Kuntze and *Handroanthus vellosi* (Toledo) Mattos trees. We hypothesized that a gradual tapering pattern is not universal in Brazilian native species and these variations in vessel diameter and vessel density. Therefore, potential hydraulic conductivity and wood density depends on combined hydraulic and mechanical requirements.

## Materials and Methods

### Origin of seeds and area of cultivation

Seeds were collected in the state of São Paulo, Brazil, between May and July 1974 by earlier scientists working in the institute. Trees were selected from phenotypic characteristics of interest, such as vigor, form and health. Seedlings of five species (*Balfourodendron riedelianum* (Engl.) Engl., *Cariniana legalis* (Mart.) Kuntze, *Centrolobium tomentosum* Guillemim ex Benth., *Handroanthus vellosi* (Toledo) Mattos and *Peltophorum dubium* (Spreng.) Taub.) were produced and planted at the Luiz Antônio Experimental Station - LA (Cerrado), Luiz Antônio City, São Paulo (21°32'S, 47°42'W, elevation 648 m). The plantation was established in 1975 at a spacing of 3 × 2 m.

The experimental design consisted of randomized blocks 5 × 6 (5 treatments × 6 blocks) in plots of 15 m × 18 m with 60 plants per plot and two borders. Owing to the high mortality of *C. tomentosum* and *P. dubium* already being studied in another project, we chose to study the other three species mentioned above, and the sampling (Figure 1) was performed in 2015 when trees were 40 years old.

### Collection of samples and their preparations

On the basis of preliminary inventory, samples were collected in 2015, during this survey we measured diameter at breast height, 1.3 m from the ground and the height of some trees of each species, to standardize tree collection, seeking to study trees with the highest lower branches. Six trees were selected for each species. Diameter at breast height (DBH), total height (TH), main stem height (MS) and crown height (CH) of all trees were listed in Table 1.

**Table 1.** Dendrometric data of 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosi* trees.

	<i>Balfourodendron riedelianum</i>				<i>Cariniana legalis</i>				<i>Handroanthus vellosi</i>			
	DBH	TH	MS	CH	DBH	TH	MS	CH	DBH	TH	MS	CH
Tree1	18	21	14.3	6.7	11.5	12.5	8.6	3.9	15	10.4	2.9	7.5
Tree2	21	21.1	7.4	13.6	14	15.1	8.1	7	12	15.9	11.4	4.4
Tree3	13	14.8	5.8	9	14	15.9	9.6	6.3	16	13.6	7.1	6.5
Tree4	16	19.7	11	8.7	12	15.5	10	5.5	15	14.5	3.4	11
Tree5	14	20.9	10.4	10.5	13	13.4	7	6.4	14	13	5.4	7.6
Tree6	16	17.2	6.1	11.1	12	15.9	11.45	4.4	15	11.9	5.2	6.7

DBH = diameter at breast height, 1.3 m from the ground (cm), TH = Total height (m), MS = Main stem (m), CH = Crown height (m).

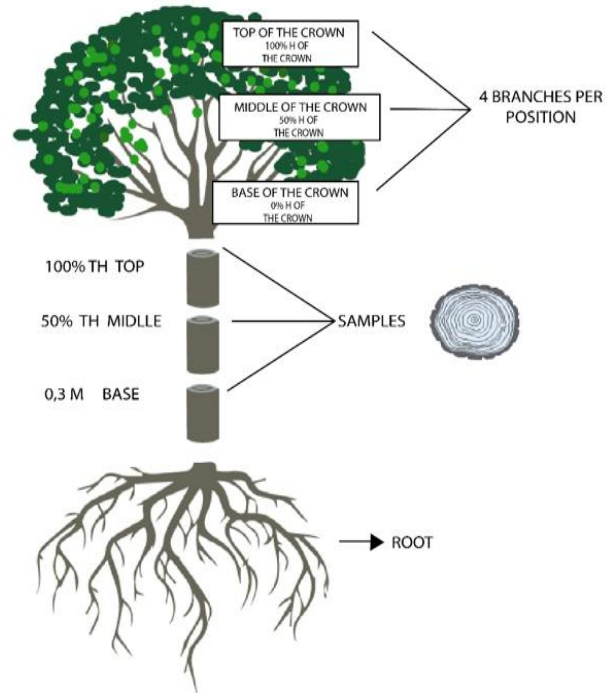
Selected trees were felled, and samples were collected from the root to top of the crown. Root samples were taken from the lateral root about 20 cm from the ground level and only one sample was obtained from the root portion. Stem and crown (branch) samples were obtained at three different heights, *i.e.*, from the base of stem ( $\approx 10$  cm above ground) or crown ( $\approx 10$  cm above main stem bifurcation), middle of the stem or crown and stem ( $\approx 10$  cm below main stem bifurcation) or crown top (Figure 2). In case of stems, the height in meters varied according to stem or crown of individual trees. Because of the difference in sample diameters and to ensure that we were analyzing hydraulically active wood, we studied the wood portion adjacent to the cambium for standardization. Samples of  $1.5 \text{ cm}^3$  were cut from root and stem on each disc, with the exception of branches whose dimensions were less than 1 cm; in the latter, samples consisted of the entire disc.



**Figure 1.** Overview of mixed planting in the Luiz Antônio Experimental Station.

#### Wood anatomy

Samples collected from the root, stem and crown ( $1.5 \text{ cm}^3$  blocks, adjacent to the cambium) were softened in boiling water and glycerin (4:1) for approximately 1h. Transverse sections of 12-15  $\mu\text{m}$  thick were cut using a sliding microtome. Sections were bleached with sodium hypochlorite (60 %) and washed thoroughly in water. We prepared permanent slides, sections were double-stained with aqueous 1% safranin and aqueous 1 % astra blue (1:9). We mounted slides permanently in synthetic resin (Entellan®). Measurements of vessel diameter and vessel density followed the recommendations of the IAWA Committee (1989)



**Figure 2.** Schematic representation of sampling at different tree heights.

#### Potential hydraulic conductivity

From values of vessel diameter and vessel density, we calculated potential hydraulic conductivity (equation 1) by Hagen Poiseuille equation described by Sterck et al. (2008) and Poorter et al. (2010). We used two equations step:

$$K_p = \left( \frac{\pi \rho_w}{128 \eta} \right) \times VD \times D_h^4 \quad \text{Eq.1}$$

where  $K_p$  is potential hydraulic conductivity (in  $\text{kg} \times \text{m} \times \text{MPa}^{-1} \times \text{s}^{-1}$ ),  $\rho_w$  is water density at  $20^\circ\text{C}$  ( $998.2 \text{ kg m}^{-3}$ ),  $\eta$  is the viscosity index of water ( $1.002 \times 10^{-3} \text{ MPa} \times \text{s}^{-1}$  at  $20^\circ\text{C}$ ),  $VD$  is vessel density ( $\text{cells} \times \text{m}^{-2}$ ), and  $D_h$  is vessel hydraulic diameter (m).

Since vessels are not exactly circular, we calculate vessel hydraulic diameter from equation 2, from diameter of each vessel as the mean of the minimum and maximum diameters. The average  $D_h$  was calculated as Sterck et al. (2008) and Poorter et al. (2010).

$$D_h = \left[ \left( \frac{1}{n} \right) \sum_{i=1}^n d^4 \right]^{1/4} \quad \text{Eq.2}$$

where  $n$  is the number of vessels, and  $d$  is vessel diameter.

#### Density

Density ( $\rho_{12}$ ) was determined at equilibrium moisture content (EMC-12%) condition and calculated based on the relationship between mass and volume at the same moisture content. Volume was evaluated by the volume of water displaced

during immersion of the specimens (Glass and Zelinka, 2010), as

$$\rho_{12} = \frac{M}{V} \quad \text{Eq.3}$$

where  $\rho_{12}$  is density ( $\text{kg.m}^{-3}$ ),  $M$  is wood mass at 12 % moisture content (kg), and  $V$  is wood volume at 12 % moisture content ( $\text{m}^3$ ).

#### Statistical analyses

We initially undertook a parametric analysis of variance (one-way analysis of variance, ANOVA) was performed. When a significant difference was observed, Tukey's test was used to identify pairs of significantly different means, and results were presented in Box Plot graphics, except to potential hydraulic conductivity, since it is not possible to perform statistical analyses, because we are left with only one value per tree; in this case were showed graphics with values in each point distance from the tip of trees. Pearson's product-moment correlation coefficients between variables were also performed.

#### Results and discussion

We found variations among the studied characteristics. Larger vessels occurred in the stem of all three species, but with differences among them. For example, in *B. riedelianum*, larger vessels were found at all three stem positions, while in *C. legalis*, larger vessels were found at the stem top, and in *H. vellosi*, they were found in the middle and top of stem (Figure 3).

In general, vessel density was higher in the crown. In *B. riedelianum*, higher vessel density occurred in the middle and top of the crown, in *C. legalis* only at the top of the crown, and in *H. vellosi*, at the base and middle of the crown (Figure 4). We found denser wood at root and stem base in *B. riedelianum*, and denser wood in root of *C. legalis*, and at stem base in *H. vellosi* (Figure 5). Potential hydraulic conductivity ( $K_p$ ) showed different patterns among species. Higher values occur in stem middle (*B. riedelianum*), stem top (*C. legalis*), and root (*H. vellosi*), and lower values occur in crown top (*B. riedelianum*), and stem base (*C. legalis* and *H. vellosi*) (Figure 6).

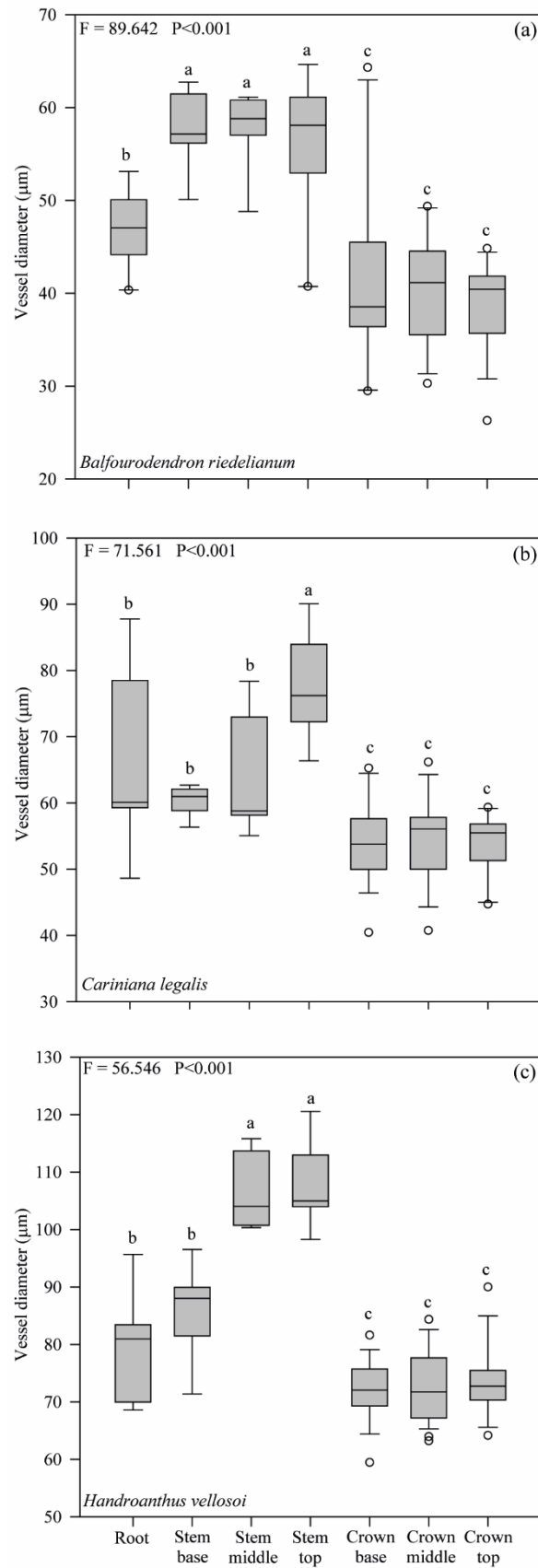
In transverse sections, the most notable differences are the presence of larger vessels in the root and stem compared to the branches, which in turn had higher vessel density. *Balfourodendron riedelianum* had scarce paratracheal axial parenchyma, or it appeared in thin and discontinuous lines or bands. *Cariniana legalis* presented apotracheal axial parenchyma in wavy lines or strands, and *H. vellosi* had paratracheal axial parenchyma, vasicentric,

aliform, confluent, with the tendency to form long confluences that resembled wide bands (Figure 7).

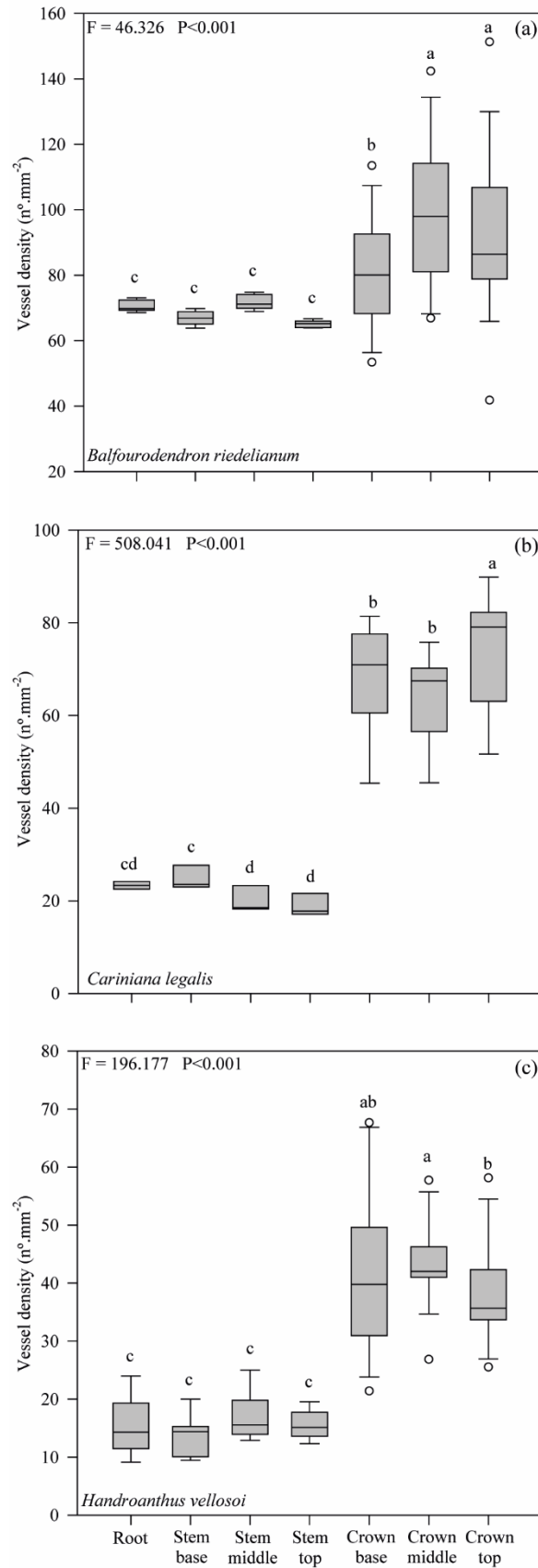
In *B. riedelianum*, we found a positive correlation between axial position and vessel density, positive correlation between axial position and potential hydraulic conductivity (from the crown top to the root), negative correlations between axial position and wood density and between vessel diameter and vessel density (Table 2). In *C. legalis*, we found positive correlations between axial position and vessel density, and negative correlations were observed between axial position and wood density, and vessel diameter and vessel density and vessel diameter (Table 2). In *H. vellosi*, we found positive correlations between axial position and vessel density. Negative correlations were found between axial position and wood density, vessel diameter and vessel density, vessel density and wood density (Table 2).

In this study, we examined the axial variation of vessel diameter, vessel density, potential hydraulic conductivity and wood density in three Brazilian tree species of the same age that were growing under same microclimatic conditions. No gradual tapering of the vessel was observed from the root towards crown. Instead, vessel density and wood density decreased toward the crown. Potential hydraulic conductivity showed a similar pattern in *Cariniana legalis* and *Handroanthus vellosi* with increase towards the crown. A different result was observed in *Balfourodendron riedelianum* with higher values in the stem. These results showed that these three species have differences in terms of hydraulic adjustments and strength (based on wood density) relative to their respective anatomy.

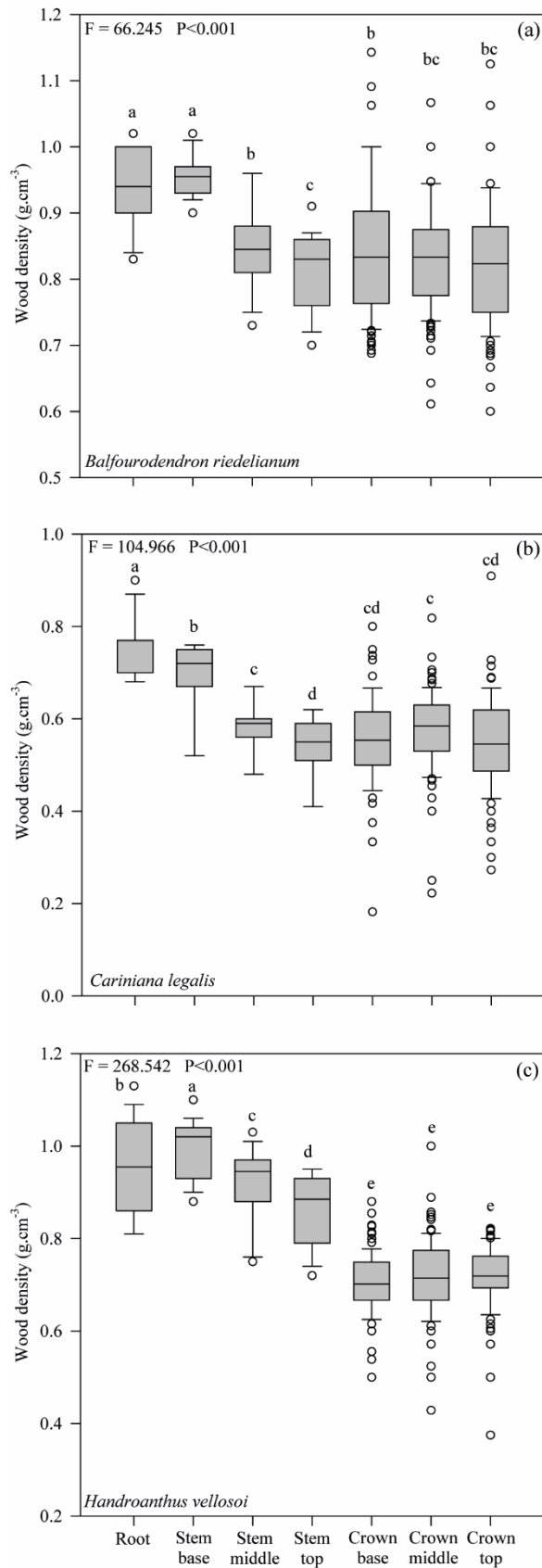
We did not observe a gradual tapering, and axial variation of vessel diameter was not equal among all these three species. Present study is in agreement to those of Schuldt et al. (2013) and Kotowska et al. (2015), where vessel diameter distribution in all the species investigated followed a hump-shaped pattern, with higher values at different stem positions, depending on the species (figure 3A). According to Kotowska et al. (2015), a hump-shaped pattern could represent the tree's response to permanent water availability and lower evaporative demand in a humid region where trees without severe drought limitation might have developed roots with relatively larger lumen area and less structural tissue. Luiz Antônio has a 6-month period of water deficit (April-September, figure 2). According to Sarmiento et al. (1985), who studied adaptive strategies of woody species in neotropical savannas, it is possible that the trees had longer roots for access to a deep-water table in dry periods.



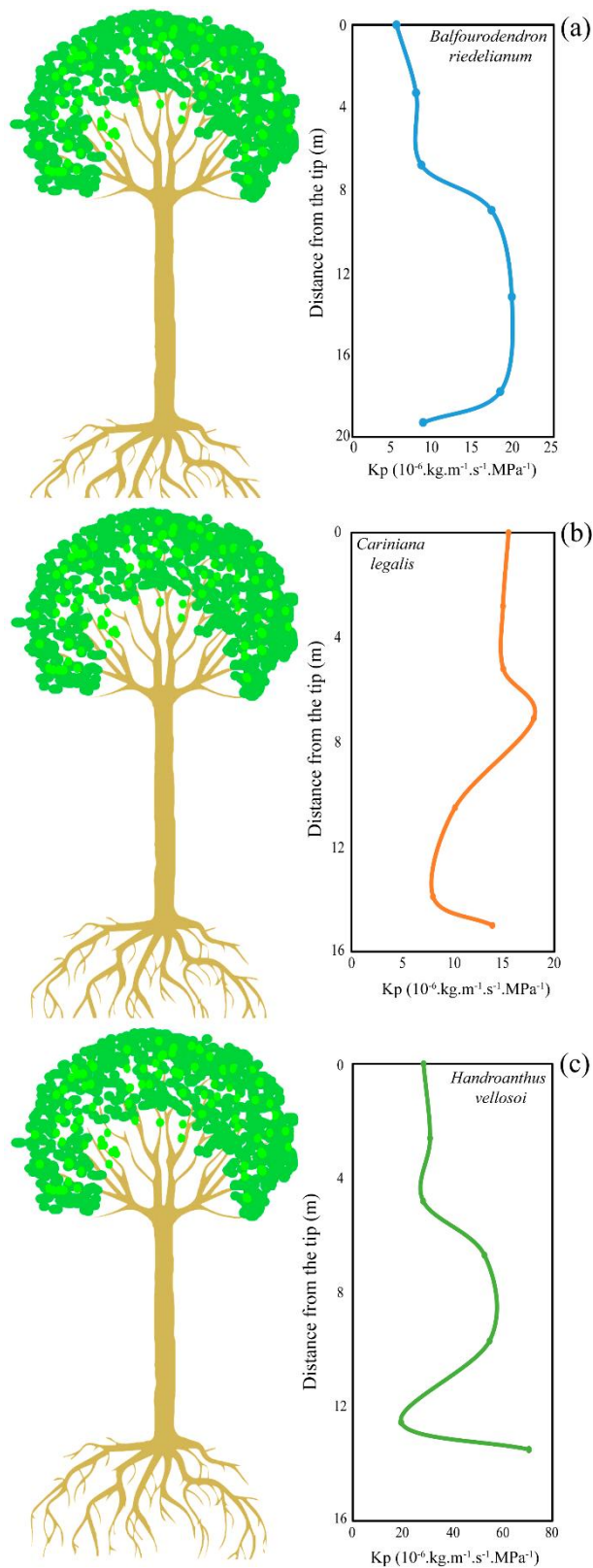
**Figure 3.** Vessel diameter from 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis*, and *Handroanthus vellosi* from root to the crown top. Statistical difference among axial positions from root to crown top is represented by distinct letters by Tukey's test.



**Figure 4.** Vessel density from 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis*, and *Handroanthus vellosi* from root to the crown top. Statistical difference among axial positions from root to crown top is represented by distinct letters by Tukey's test

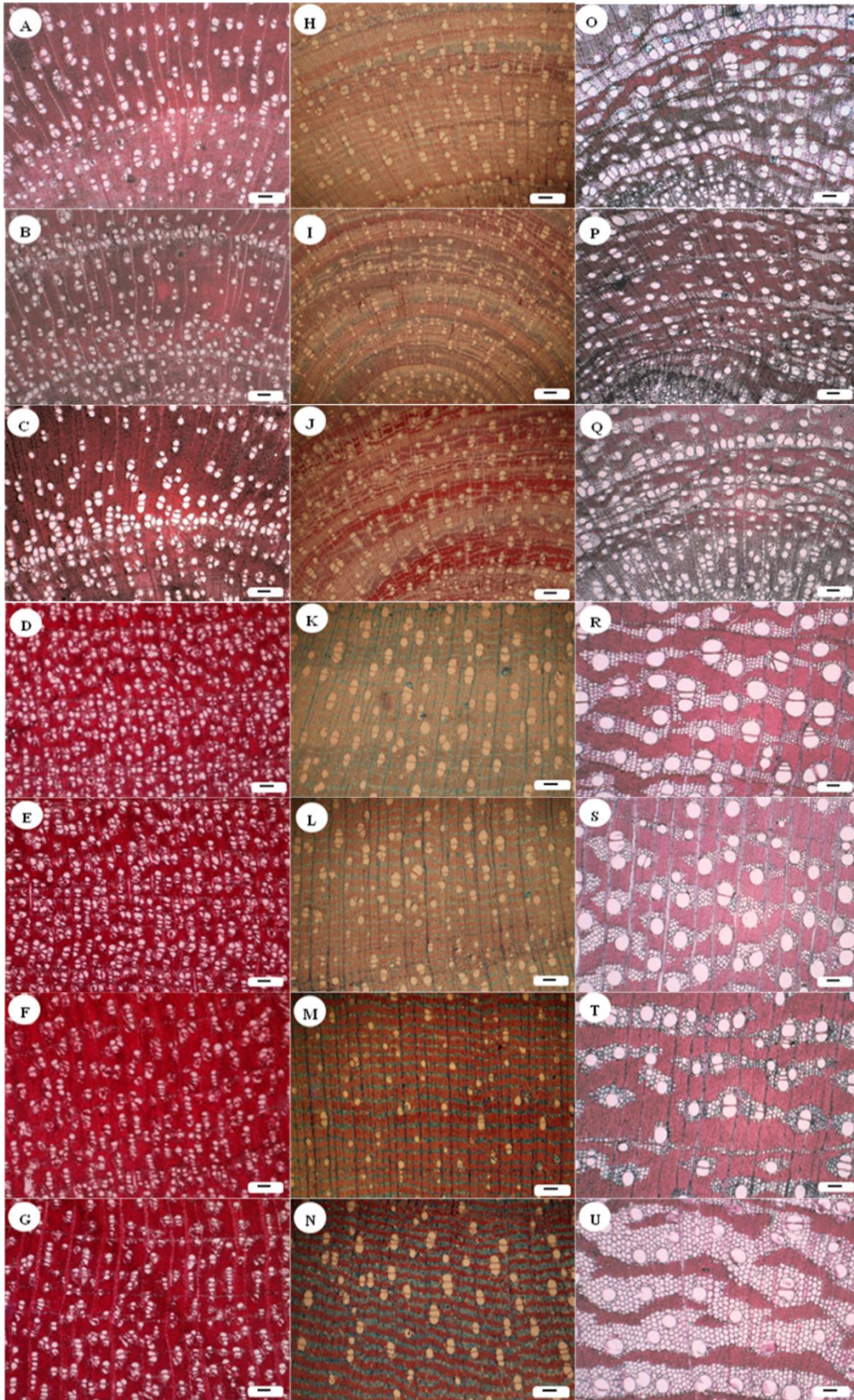


**Figure 5.** Wood density from 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis*, and *Handroanthus vellosi* from root to the crown top. Statistical difference among axial positions from root to crown top is represented by distinct letters by Tukey's test.



**Figure 6.** Potential hydraulic conductivity from 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis*, and *Handroanthus vellosi* from root to the crown top.





**Figure 7.** Transverse sections of *Balfourodendron riedelianum* wood. A. Crown top. B. Crown middle. C. Crown base. D. Stem top. E. Stem middle. F. Stem base. G. Root; Transverse sections of *Cariniana legalis* wood. H. Crown top. I. Crown middle. J. Crown base. K. Stem top. L. Stem middle. M. Stem base. N. Root; Transverse sections of *Handroanthus vellosi* wood. O. Crown top. P. Crown middle. Q. Crown base. R. Stem top. S. Stem middle. T. Stem base. U. Root. Scale bars = 200  $\mu$ m.

**Table 2.** Pearson correlation coefficient ( $r$ ) in the first row and significance level ( $p$ ) in the second row among axial position from 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosi*.

	<i>Balfourodendron riedelianum</i>				<i>Cariniana legalis</i>				<i>Handroanthus vellosi</i>			
	Vdi	Vde	$K_p$	$\rho_{12}$	Vdi	Vde	$K_p$	$\rho_{12}$	Vdi	Vde	$K_p$	$\rho_{12}$
Ap	-0.68	0.81	-0.55	-0.80	-0.55	0.85	0.53	-0.82	-0.61	0.85	-0.54	-0.93
	0.095	0.027*	0.203	0.032*	0.204	0.016*	0.220	0.023*	0.149	0.014*	0.213	0.002*
Vdi	-----	-0.84	0.98	0.31	-----	-0.86	0.16	0.120	-----	-0.84	0.74	0.69
		0.018*	0.00001*	0.504		0.014*	0.739	0.807		0.017*	0.0608	0.086
Vde	-----	-----	-0.75	-0.46	-----	-----	0.36	-0.48	-----	-----	-0.52	-0.96
			0.052	0.299			0.423	0.275			0.228	0.0007*
$K_p$	-----	-----	-----	0.17	-----	-----	-----	-0.55	-----	-----	-----	0.44
				0.721				0.197				0.322

(Ap, from root to crown top), vessel diameter (Vdi,  $\mu\text{m}$ ), vessel density (Vde,  $\text{n}^0.\text{mm}^{-2}$ ), potential hydraulic conductivity, ( $K_p$ ,  $10^{-6}.\text{kg}.\text{m}^{-1}.\text{s}^{-1}.\text{MPa}^{-1}$ ) and wood density ( $\rho_{12}$ ,  $\text{g}.\text{cm}^{-3}$ ) from 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosi*. The significant correlations are highlighted by an asterisk

Longui et al. (2017) studied the axial variation of vessel features from the main root to branch and also found no gradual tapering in five other Brazilian native trees, including *Anadenanthera peregrina* (Benth.) Altschul, *Copaifera langsdorffii* Desf., *Handroanthus ochraceus* (Cham.) Mattos, *Ocotea corymbosa* (Meisn.) Mez and *Xylopia aromatica* (Lam.) Mart. Based on the present study and investigations of Kotowska et al. (2015) and Longui et al. (2017), we suggest that gradual vessel tapering along trees axis does not occur in all species universally. It is hypothesized that each species, or individual, can develop vessel diameter variations to meet the particular, abiotic-driven hydraulic requirements associated with mechanical requirements for tree support. We emphasize that Kotowska et al. (2015) studied different species in a cacao agroforestry system with 25-year-old. Longui et al. (2017) studied different tree species, as noted above, but only  $\approx 5$  to 10 years of age, and in the present study, the trees were cut at 40 years of age. This shows that tapering pattern is not related to age, but rather to the hydraulic-mechanical strategy adapted by the species in order to assistant physiological and anatomical needs of the species.

Petit et al. (2008) studied *Acer pseudoplatanus* L. trees and reported that conduit tapering is more substantial in shorter trees as compared to that of taller trees, indicating that tapering is more related to height than the tree age. In our study, we did not observe any such relationship between tree height and tapering.

Also according to Petit et al. (2008) vessel tapering almost eliminates the increase in hydraulic resistance in relation to tree increase, and changes related to size in tapering and in apical vessel diameter may be explained by the combined need to reduce the accumulation of hydraulic resistance, minimizing the carbon costs of building vessel walls. Petit et al. (2010) reported that vessel tapering is one of main adaptations in *Eucalyptus regnans* wood, favoring that this species has very tall trees.

Rosell et al. (2017) argue that a more or less constant rate among vessel tapering between species, from the tip of crown to the tree base, associated with the assumption that larger vessels are more vulnerable to embolism, suggests how the

climate should limit the maximum height of vegetation. These two factors together (tapering and climate) influence the maximum average vessel diameter permitted by temperature and availability of water in a location and, therefore, maximum tree height. Among species we studied, *H. vellosi*, was the one that on average has wider vessels, especially in stem middle and stem top positions, so the most susceptible positions to embolisms, the same applies to all stem positions in *B. riedelianum*, and stem top in *C. legalis*, positions with wider vessels.

Pfautsch et al. (2018) studied traits and trade-offs in whole-tree hydraulic architecture along the vertical axis of *Eucalyptus grandis*. The authors found that strong apical dominance of water transport resulted in an increase in the volumetric water supply per unit of leaf area with tree height. This was due to continuous tapering (from 250 to 20  $\mu\text{m}$ ) and an exponential increase in frequency (from 600 to 13,000  $\text{cm}^{-2}$ ) of vessels towards the treetops, and they found wider vessels about 4 m above the stem base. In our study, we found wider vessels, with no statistical difference, in all stem positions in *B. riedelianum*, which gives a wide variation in height and does not fit the pattern described by Pfautsch et al. (2018) for *Eucalyptus grandis*. However, in *C. legalis*, wider vessels occurred around 6-8m, and in *H. vellosi*, between 6-10m, results closer to those found in *Eucalyptus grandis*.

The occurrence of hydraulic bottlenecks, or hydraulic constrictions, *i.e.*, a sharp drop in vessel diameter just above the branch junctions (Tyree and Zimmermann 2002), did seem to represent a clear pattern observable at the transition from root to stem base. In all the species investigated, we noted hydraulic bottlenecks in the transition from stem top to crown base. In the transition from root to stem base no hydraulic bottlenecks were observed. Longui et al. (2017) reported no hydraulic bottlenecks from the stem top to branch. However, they mention the occurrence of hydraulic bottlenecks from root (main sinker root) to stem base in other tropical species *Anadenanthera peregrina*, *Copaifera langsdorffii*, *Ocotea corymbosa* and *Xylopia aromatica*. Narrower vessels in the stem base, compared to root vessels, according to Tyree and Zimmermann (2002), are in accordance with the

segmentation hypothesis, which holds that a decrease of vessels in the stem base functions in a manner similar to that when narrower vessels are present at nodal regions to restrict embolism because the main stem represents the highest investment of the tree and should not, under any circumstances, be lost. According to Longui et al. (2017), bottlenecks from root to stem base could impose a difficult flow to the stem base, which would be important in drought periods or in plants subjected to longer dry periods after wet seasons. As mentioned above, in the Luiz Antônio region deep roots have access to water, even in the dry season. Therefore, the occurrence of bottlenecks may be another mechanism to balance the efficiency and safety of water transport. Studies with trees of temperate or Mediterranean climates have reported larger vessels in the root as compared to that of stems (Pratt et al., 2007; Domec et al., 2009). However, our studies with tropical species have shown that this may not be the case for all Brazilian trees (Longui et al., 2017). Emphasizing that in the present study, hydraulic bottlenecks were only noted in the transition from stem top to crown base.

Different from vessel diameter, whose values oscillated in the stem, vessel density presented little variation in the stem, but it did increase in relation to the crown. In general, the stem presents an increase in vessel diameter and decrease of vessel density toward the bark. Thus, in younger tissues (pith or branches), we see smaller vessels with higher vessel density. In contrast, in older tissues, i.e., stem base or wood portion adjacent to the bark, wider vessels with less density. Our results show negative correlations between vessel diameter and vessel density in all the species investigated. The same pattern is also reported by Baas et al. (2004) and Fan et al. (2012), as well as Schuldt et al. (2013). Studying hydraulic efficiency, Tyree et al. (1994) reported that one vessel 40 $\mu$ m in diameter is as conductive as 16 vessels 20 $\mu$ m in diameter or 256 vessels 10 $\mu$ m in diameter. In general, studies associated hydraulic efficiency with vessel diameter. Since vessel lumen strongly affects hydraulic efficiency with the fourth power of its diameter by the Hagen-Poiseuille equation (Tyree and Zimmermann, 2002). Meanwhile, smaller and more numerous vessels are associated with higher hydraulic safety (Baas et al., 2004).

As mentioned above,  $K_p$  showed different patterns among species, higher values occur in stem middle (*B. riedelianum*), stem top (*C. legalis*), and root (*H. vellosi*), and lower values occur in crown top (*B. riedelianum*), and stem base (*C. legalis* and *H. vellosi*). As calculated from vessel diameter and vessel density, potential hydraulic conductivity, especially vessel diameter, i.e., according to Tyree and Zimmermann (2002) higher conductivity is associated with larger vessels. Results of present study corroborate the findings by Schuldt et al. (2013) and Kotowska et al. (2015), followed a hump-shaped pattern, with higher values at different stem positions. This can be explained by the increased

efficiency of wider conduits over narrower ones and comparatively speaking, a wood with narrower vessels would need to allocate higher construction costs to attain the same hydraulic efficiency as wood with larger vessels. Longui et al. (2017) found positive correlation between hydraulic conductivity and vessel diameter and negative correlation with vessel density. In our study, we observed positive correlation between vessel diameter and hydraulic conductivity just in *B. riedelianum*, and no relationship between vessel density and conductivity was observed.

In general, studies that calculate potential conductivity collect samples from one region of the tree, especially the main stem. Our study collected samples at seven different heights and obtained results that do not fully fit the currently accepted paradigm since it is generally expected that vessel tapering from tree base to crown is accompanied by a decrease in conductivity based on the close relationship between vessel diameter and efficient water conduction. Considering these results, we question whether potential conductivity is a reasonable indicator when studying samples at different plant heights, whether vessel diameter determination alone can give an estimate of conductivity, or whether conductivity should be assessed by formulas using only vessel diameter, e.g., the equation proposed by Zimmermann (1983), using vessel radius ( $r$ ),  $\pi$  value and viscosity of liquid ( $n$ ), or ( $r^4 \pi / 8n$ ).

Among the species investigated in this study, potential hydraulic conductivity was higher in *Handroanthus vellosi*. The values were similar to Gerolamo and Angyalossy (2017), who found different values between *Handroanthus heptaphyllus* and *Handroanthus ochraceus*, respectively 62.2 and 16.7  $K_p$ ,  $10^{-6}$  kg.m.MPa $^{-1}$ .s $^{-1}$ , highlighting that these values can vary widely, even among species of the same genus, and on the same plant depending on height.

Wood density is related to hydraulic conductivity since trees seek to balance mechanical and hydraulic demands by means of variations in the dimensions, quantity and wall thickness of cells. In our study, wood density did not show an evident pattern of variation, but in general it showed lower values in the crown portion of all three species (figure 4 and table 2). Only in *Handroanthus vellosi* was a correlation with vessel features identified, i.e., negative correlation with vessel density (table 2). For the other two species (*Balfourodendron riedelianum* and *Cariniana legalis*), density may have been influenced by other characteristics. Another unusual result was the occurrence of higher wood density in the roots of *B. riedelianum* and *C. legalis*. However, a similar result was reported by Schuldt et al. (2013) for *Cryptocarya laevigata* Blume when comparing wood of strong roots (> 50 mm), trunks, branches and twigs in five Indonesian species. Wood anatomists know that roots do not need a strong mechanical investment since they are supported by the soil. Accordingly, roots tend to have larger

vessels, a higher percentage of parenchyma cells, a lower proportion of fibers and fibers with thinner walls. However, we have noticed in other studies of our group (Longui et al., 2017) that this pattern may present variations, depending on the hydraulic x mechanical tradeoff.

It should be noted that wood density is given by a complex relationship among the values of vessel diameter and vessel density, as well as features of fibers and parenchyma cells (Zanne et al., 2010; Badel et al., 2015). In spite of values found in the root, stem base also showed denser wood when compared to other stem positions and branches. This result is related to mechanical requirements of the trees because trees are tall, self-supporting plants that need to resist static loads, lateral wind forces, or their own weight.

### Conclusions

The gradual tapering of vessel diameter along the tree axis does not occur in the species we studied, but hydraulic bottlenecks were seen in the transition from the main trunk to the crown base.

Vessel density shows the same pattern in all three species, with practically no variation between root and stem, but higher density in the crown.

Wood density does not show any evident pattern of axial variation, but, in general, presents lower values in the crown in the three species and higher values in trees bases, demonstrating an investment in mechanical sustentation. Vessel features appear to have minimal influence on wood density since a negative correlation between wood density and vessel density was only observed in *Handroanthus vellosi*.

Correlations show that vessel diameter and vessel density promote changes in potential hydraulic conductivity and does so differently in different species. Vessel diameter was positively correlated with conductivity in *Balfourodendron riedelianum*, and no relationship between vessel density and conductivity was observed. These results show the effect of interaction between vessel diameter and vessel density on potential hydraulic conductivity of the three studied species.

The variations highlighted in this work show a synergy that promotes anatomical adjustments that, in turn, meet the hydraulic and mechanical requirements of these tropical trees.

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