OLÍVIA PEREIRA LOPES

ARQUITETURA HIDRÁULICA E DENSIDADE DA MADEIRA DE ÁRVORES DE *Balfourodendron riedelianum*, *Cariniana legalis* E *Handroanthus vellosoi* COM 40 ANOS DE IDADE

Botucatu

2017

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Balfourodendron riedelianum, Cariniana legalis **E** *Handroanthus vellosoi* **COM**
40 ANOS DE IDADE

Tese apresentada à Faculdade de Ciências Agronômicas da Unesp Câmpus de Botucatu, para obtenção do título de Doutor(a) em Ciência Florestal.

Orientador(a): Eduardo Luiz Longui

Botucatu

2017

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Botucatu

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CERTIFICADO DE APROVAÇÃO

TÍTULO DA TESE: ARQUITETURA HIDRÁULICA E DENSIDADE DA MADEIRA DE ÁRVORES DE *Balfourodendron riedelianum*, *Cariniana legalis* E *Handroanthus vellosoi* COM 40 ANOS DE IDADE
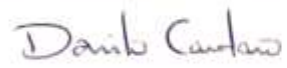
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Botucatu, 14 de dezembro de 2017

AGRADECIMENTOS

Deus, por me guiar todos os dias em minha vida.

Meus pais e irmã, por me apoiarem incondicionalmente, sendo meu alicerce e porto seguro.

UNESP/Faculdade de Ciências Agronômicas (FCA) e todos seus funcionários, pela ajuda ao longo desses anos.

Meu orientador Dr. Eduardo Luiz Longui, pelo apoio e por compartilhar seus conhecimentos e experiências, serei sempre grata.

Aos professores, que acompanharam minha jornada acadêmica e me inspiraram a melhorar como pessoa e profissional.

Aos meus amigos, que tornaram a jornada mais leve e risonha.

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), pela concessão da bolsa.

A todos que de alguma forma contribuíram para esta conquista, muito obrigada!

RESUMO

A movimentação da água no xilema ocorre devido à transpiração foliar, que gera gradientes de pressão hidrostática negativa fazendo com que a água seja absorvida pelas raízes e ascenda em direção às folhas. A heterogeneidade nas características do xilema secundário que ocorre entre espécies, entre indivíduos da mesma espécie, bem como entre diferentes órgãos no mesmo indivíduo influencia diretamente no desempenho hidráulico e físico-mecânico do vegetal. O presente trabalho visou estudar a arquitetura hidráulica e densidade da madeira em três espécies nativas, *Balfourodendron riedelianum, Cariniana legalis e Handroanthus vellosoi*. Foram selecionados seis indivíduos de cada espécie, provenientes de plantio misto de 40 anos da Estação Experimental do Instituto Florestal no município de Luiz Antônio, estado de São Paulo. A condutividade hidráulica a partir do diâmetro e densidade dos vasos (condutividade hidráulica potencial) e a densidade da madeira foram mensuradas ao logo de todo eixo axial dos indivíduos (incluindo raiz e copa), as propriedades hidráulicas (condutividade hidráulica, percentual de perda de condutividade, condutividade específica foliar) foram mensuradas nos ramos nas diferentes posições da copa. Não foi observado um padrão de afunilamento do diâmetro dos vasos ao longo do eixo axial nas espécies estudadas. A densidade da madeira foi maior na raiz e no caule quando comparadas a copa. Não houve um padrão de variação da densidade da madeira ao longo do eixo axial das espécies estudadas, as características dos vasos têm baixa influência na densidade da madeira, mas promovem mudanças significativas na condutividade hidráulica potencial entre as espécies. O percentual de perda de condutividade e diâmetro dos vasos nos ramos não diferiu entre as posições na copa, mas diferiu entre as espécies. Outras propriedades hidráulicas diferiram ao longo da copa, mas não há um padrão de arquitetura hidráulica definido. Apesar de possuírem mesma idade, pertencerem ao mesmo grupo sucessional e estarem inseridas no mesmo local cada espécie possui características intrínsecas que promovem de forma distinta a condutividade hidráulica ao longo do eixo axial.

Palavras-chave: Condutividade; vasos; espécies tropicais.

ABSTRACT

Water movement in secondary xylem occurs due to foliar transpiration, creating negative hydrostatic pressure gradient such that roots assimilate the water and towards to the leaves. Heterogeneous features of secondary xylem between species, individuals in a same species and between root and stem too, affect the hydraulic and physical-mechanic performance of plant. In this study, we examined hydraulic architecture and wood density in three native species, *Balfourodendron riedelianum, Cariniana legalis e Handroanthus vellosoi*, were selected six individuals from each species with the same age (40-year-old) and planted in Luiz Antônio Experimental Station, Luiz Antônio City, São Paulo. The potential hydraulic conductivity and wood density were measured from root to crown in all species, maximum vessel length, specific hydraulic conductivity, percentage loss of conductivity, leaf hydraulic conductivity was measured in different position of the crown. We did not find pattern tapering of vessel diameter along the tree axis. Wood density did not show any evident axial pattern, although presented higher values in root and mean stem when we compare with the crown. There is no difference in percentage loss of conductivity and vessels diameter in crown positions, but were different between species. We did not find a hydraulic pattern for this species. Although species have been cultivated simultaneously, in the same area and belonged to same successional group, they have intrinsic features that promote hydraulic conductivity along tree axial axis.

Keywords: Conductivity; vessels; tropical species.

SUMÁRIO

INTRODUÇÃO GERAL

A importância da água para o desenvolvimento e vida das plantas determina, além de outros fatores, uma arquitetura hidráulica complexa, comandada por princípios físicos ao longo do eixo axial. A ascensão e o transporte de água nas plantas pode ser explicado pela teoria de coesão-tensão, na qual a evaporação de água das folhas propicia a força necessária para a ascensão da água do solo pelas raízes e o transporte pelo xilema secundário até as folhas (RYAN & YODER, 1997).

Entender como o processo de transporte de água ocorre através do xilema secundário é importante para testar hipóteses ecológicas, evolutivas e fisiológicas das espécies arbóreas (PRATT et al., 2007). Devido à transpiração, as folhas são sujeitas a potenciais hidráulicos mais negativos do que as raízes. Embora, todas as plantas apresentem declínio no potencial hidráulico da raiz às folhas, esse é agravado em árvores altas em razão da maior resistência hidráulica devido à estatura da planta (MCCULLOH et al., 2013).

O xilema é o tecido vascular responsável pela translocação de água e nutrientes derivados do solo, as células condutoras e de suporte lignificadas no xilema proporcionam a condução de água de longa distância e o suporte mecânico necessário para que as plantas se fixem em ambiente terrestre (ALONI, 1987).

A arquitetura hidráulica da planta tem efeito direto no transporte de água. Diferentes arquiteturas hidráulicas nas espécies florestais resultam em impactos diversos de acordo com a espécie considerada. O conhecimento dessas diferentes arquiteturas permite compreender as estratégias e o funcionamento das espécies, fornecendo respostas para entender melhor o impacto das mudanças climáticas globais nas florestas (TYREE & EWERS, 1991).

Nas eudicotiledôneas, o transporte de água ocorre pelo lúmen dos elementos de vaso e através das pontoações. Os elementos de vaso são conectados uns aos outros no sentido longitudinal, formando vasos que podem atingir vários metros de comprimento, dependendo da espécie. Devido ao gradiente de tensão, causado pela transpiração, a água passa através das células condutoras das raízes em direção às folhas (FONTI et al., 2010). Em árvores com o xilema secundário já estabelecido, praticamente toda a água que flui em direção á copa passa através dos vasos no alburno, uma vez que os vasos do cerne, em geral, já perderam a capacidade condutora (TYREE & ZIMMERMANN, 2002). Uma das características determinantes do transporte de água é a condutividade hidráulica, que é o volume

de água transportada por unidade de tempo em uma determinada área do xilema, sob um gradiente de pressão (TAIZ & ZEIGER, 2013).

Características que aumentam a eficiência hidráulica, como o diâmetro e a densidade dos vasos, normalmente tendem a diminuir a densidade da madeira e consequentemente a resistência mecânica, uma vez que o lume dos vasos por não contribuir com massa pode tornar a madeira mecanicamente mais fraca (BAAS et al., 2004). Contudo, o equilíbrio mecânico se dá pela contribuição entre as células que compõem a madeira - fibras, vasos e células parenquimáticas.

Há um grande número de espécies nativas utilizadas nas mais diferentes vertentes do setor industrial madeireiro de acordo com as características da madeira, porém mesmo com a ampla utilização, as estratégias de funcionamento e influência das características anatômicas da maioria das espécies tropicais permanecem desconhecidas.

As espécies que foram estudadas no presente trabalho são muito utilizadas na tecnologia da madeira e apresentam as seguintes características gerais:

Cariniana legalis (Mart.) Kuntze pertence a família Lecythidaceae, é conhecida popularmente como jequitibá-rosa, utilizada para restauração ambiental, uso madeireiro geral e confecção de artesanatos (CARVALHO, 2003). A espécie é nativa, endêmica do Brasil, secundária tardia, semidecídua, possui distribuição geográfica no Nordeste (Bahia, Paraíba, Pernambuco), Centro-oeste (Distrito Federal), Sudeste (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo) e Sul (Paraná), no Domínio Fitogeográfico da Mata Atlântica em Área Antrópica e Floresta Ombrófila (= Floresta Pluvial) (LORENZI, 1992; CATENACCI et al., 2018).

Balfourodendron riedelianum (Engl.) Engl. pertence a família Rutaceae, é conhecida popularmente como pau-marfim, tem madeira indicada para fabricação de móveis de luxo, partes internas na construção civil, marcenaria e artefatos decorativos em geral (CARVALHO, 2004). Espécie nativa, não endêmica do Brasil, secundária tardia, semidecídua, possui distribuição geográfica no Centro-oeste (Mato Grosso do Sul), Sudeste (Minas Gerais, São Paulo) e Sul (Paraná, Rio Grande do Sul, Santa Catarina), nos Domínios Fitogeográficos de Cerrado e da Mata Atlântica em Floresta Estacional Semidecidual, Floresta Ombrófila (= Floresta Pluvial) (LORENZI, 1992; PIRANI et al., 2018).

Handroanthus vellosoi (Toledo) Mattos pertence a família Bignoniaceae, é conhecida popularmente como ipê-amarelo e sua madeira tem sido usada na

construção, principalmente na forma de piso, também é utilizada para fabricação de dormentes, postes e vigas (CARVALHO, 2003). Espécie nativa, endêmica do Brasil, secundária inicial, decídua, possui distribuição geográfica no Sudeste (Minas Gerais, Rio de Janeiro, São Paulo), Sul (Paraná), nos Domínios Fitogeográficos do Cerrado e da Mata Atlântica em Floresta Estacional Perenefólia, Floresta Ombrófila (LORENZI, 1992; LOHMANN, 2015).

Nesta tese estudamos características dos vasos, propriedades hidráulicas e a densidade da madeira ao longo do eixo axial, da raiz ao topo da copa, das três espécies destacadas acima. O objetivo desse estudo foi conhecer os possíveis padrões hidráulicos estabelecidos por espécies tropicais.

No capítulo 1, investigamos a variação no diâmetro e densidade de vasos, condutividade hidráulica potencial e densidade da madeira, e as correlações entre essas variáveis. As amostras de madeira foram retiradas em sete diferentes posições: raiz, base, meio e topo do caule e base, meio e topo da copa. Nossa hipótese é que o afunilamento dos vasos em direção da copa não é um padrão universal nas espécies nativas brasileiras e que a variação no diâmetro e densidade de vasos, consequentemente na condutividade hidráulica e densidade da madeira depende de uma combinação dos requerimentos hidráulicos e mecânicos. Com os resultados esperamos contribuir para o entendimento da arquitetura hidráulica ao longo das árvores dessas espécies e sua relação com a densidade da madeira.

No capítulo 2, estudamos o comprimento máximo de vasos, condutividade hidráulica específica, porcentagem de perda de condutividade, condutividade hidráulica foliar, diâmetro e densidade de vasos, condutividade hidráulica potencial e densidade da madeira. Hipotetizamos que existem diferenças anatômicas, hidráulicas e na densidade da madeira entre as posições da copa, no sentido de que as características de condutividade e também a densidade da madeira apresentem valores mais baixos em posições mais altas da copa. Também esperamos encontrar diferenças nas propriedades hidráulicas e densidade da madeira entre as espécies, pois apesar de elas crescerem no local com as mesmas condições ambientais e serem do mesmo grupo sucessional (secundárias), as espécies são de famílias diferentes com diferentes padrões anatômicos.

CAPÍTULO I -There is no gradual decrease in hydraulic characteristics and wood density in axial axis in three native Brazilian tree species

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Abstract

In this study, we examined axial variation of vessel diameter, vessel density, potential hydraulic conductivity and wood density, as well as correlations among these characteristics, from root to crown in 40-year-old *Balfourodendron riedelianum* (Engl.) Engl., *Cariniana legalis* (Mart.) Kuntze and *Handroanthus vellosoi* (Toledo) Mattos trees. While we did not find gradual tapering of vessel diameter along the tree axis, hydraulic bottlenecks from root to stem base and from main trunk to the crown base were noted. These hydraulic constrictions may reduce the occurrence of embolism. Vessel density, in general, did not vary from root to stem, but it was higher in the crown. A combination of 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 in the three-studied species. Although c, higher values at tree bases demonstrated an investment in mechanical sustentation. Vessel features had little influence on wood density. Collectively, 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.

Introduction

In this study, we examined the axial variation of vessel diameter, vessel density, potential hydraulic conductivity and wood density, as well as correlations among these characteristics, from root to crown in 40-year-old *Balfourodendron riedelianum* (Engl.) Engl., *Cariniana legalis* (Mart.) Kuntze and *Handroanthus vellosoi* (Toledo) Mattos trees.

Previous studies have reported a tapering pattern of the conduits from base to treetop (Olson and Rosell, 2013; Petit and Crivellaro, 2014). Schuldt et al. (2013) studied changes in wood density, wood anatomy and hydraulic properties of xylem along the root-to-shoot flow path in tropical rainforest trees. Based on their findings, these authors confirmed the concept of conduit tapering in trees from humid, or perhumid, environments, but its validation as a universal rule is still lacking. In fact, while Longui et al. (2017) studied vessel features of *Anadenanthera peregrina*, *Copaifera langsdorffii*, *Handroanthus ochraceus*, *Ocotea corymbosa* and *Xylopia aromatica*, which not represent such tapering pattern, their study (2012) of *Eriotheca gracilipes* did find such characteristic. Similarly, although Longui et al. (2017) observed the presence of hydraulic bottlenecks, or hydraulic constrictions, in the

transition from root to stem, no such transition was observed from stem to branch in four of the five species studied. Thus, in these five species, the authors concluded that wood of the stem base must exercise some mechanism as a safeguard against air embolism by producing narrower vessels to protect the main stem from constant loss of conductivity.

The environmental conditions to which tropical tree species are subjected might offer a possible explanation for the absence of a classical tapering pattern. According to Schuldt et al. (2013), tropical trees, compared with temperate or boreal trees, temporarily experience higher atmospheric saturation deficits in the crown, which is not subject to frost. They found that such conditions interfere with hydraulic architecture such that cavitation avoiding mechanisms may not represent a crucial competitive advantage in a perhumid climate.

When we analyze only root and crown, we can expect to find larger vessels with lower vessel density at the root compared to branches. Other studies have shown that vessels are larger in the root than in stem (Machado et al., 1997; Martínez-Vilalta et al., 2002; Psaras and Sofroniou, 2004). However, if we analyze the path along the plant, i.e., root anatomy and different positions along trunk to crown, we asked if vessel tapering, vessel density, and wood density would show either a gradual increase or decrease from base to top. Some authors have proposed that variations in hydraulic architecture are related to anatomy, as demonstrated by the West, Brown, Enquist (WBE) model (West et al., 1999), in which conduit diameter tends to decrease with the increase in tree height, thus maintaining hydraulic efficiency and avoiding dysfunction in 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. This configuration is less efficient hydraulically, but it is more mechanically stable (McCulloh et al., 2003, 2004). In addition, since wood density is negatively correlated with hydraulic conductivity (Baas et al., 2004), it is expected that a decrease in wood density towards the crown would be observed during tapering. This means 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).

We hypothesized that a gradual tapering pattern is not universal in Brazilian native species and that variations in vessel diameter and vessel density and, hence, potential hydraulic conductivity and wood density, depend on combined hydraulic and mechanical

requirements. We tested this hypothesis with the goal of understanding hydraulic architecture in the context of wood density of three native Brazilian tree species: *B. riedelianum*, *C. legalis* and *H. vellosoi*.

Material and Methods

Origin of seeds and area of cultivation

Seeds were collected in the state of São Paulo, Brazil, between May and July 1974. Although no exact collection sites were recorded, trees were selected from phenotypic characteristics of interest, such as vigor, form and health. Seedlings of five species (*Balfourodendron riedelianum, Cariniana legalis*, *Centrolobium tomentosum*, *Handroanthus vellosoi* and *Peltophorum dubium*) 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 x 6 (5 treatments x 6 blocks) in plots of 15 m x 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. The data from precipitation, hydric deficit (def-1), hydric excedent (exc), and mean temperature can be observed in Figure 2.

Figure 1. Overview of mixed planting in the Luiz Antônio Experimental Station.
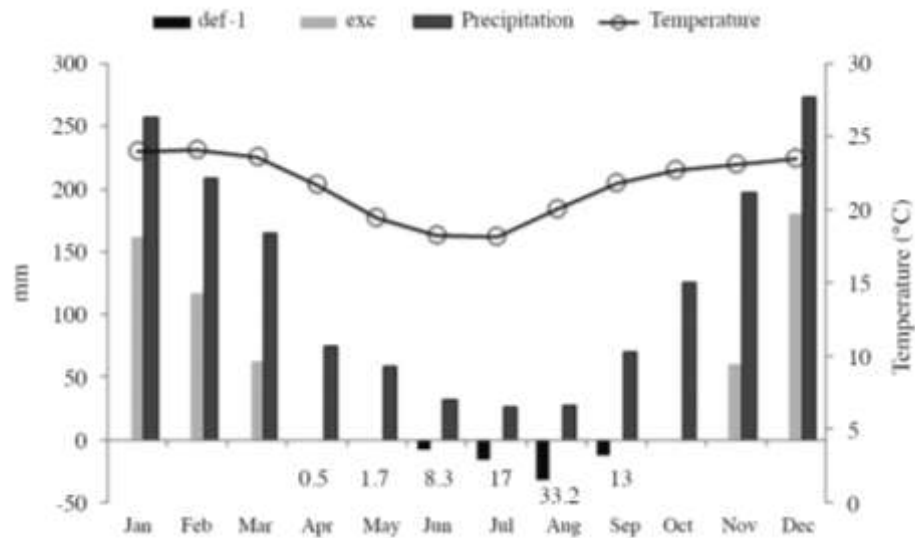
Figure 2. Average monthly sum of precipitation, hydric deficit (def-1), hydric excedent (exc), and mean temperature (lines) at Luiz Antônio City – 1961-1990 (Centro de Pesquisas Meteorológicas e Climáticas Aplicadas à Agricultura (CEPAGRI), 2017).

Collection and preparation

The collection during the year of 2015, from a preliminary inventory, 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. We selected six trees from 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.

Selected trees were felled, and samples were taken from root to top of the crown. Root samples were taken about 20 cm deep from lateral root. Stem and crown (branch) samples were obtained at three different heights, i.e., from the base of stem (≈10 cm above ground) or crown (≈10 cm above main stem bifurcation), middle of the stem or crown and stem (≈10 cm below main stem bifurcation) or crown top (Figure 3). While samples from the roots were obtained from only one location, i.e., 20 cm deep from the ground level, the height in meters varied according to stem or crown. 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 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.

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

	Balfourodendron riedelianum				*Cariniana legalis*				*Handroanthus vellosoi*			
	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

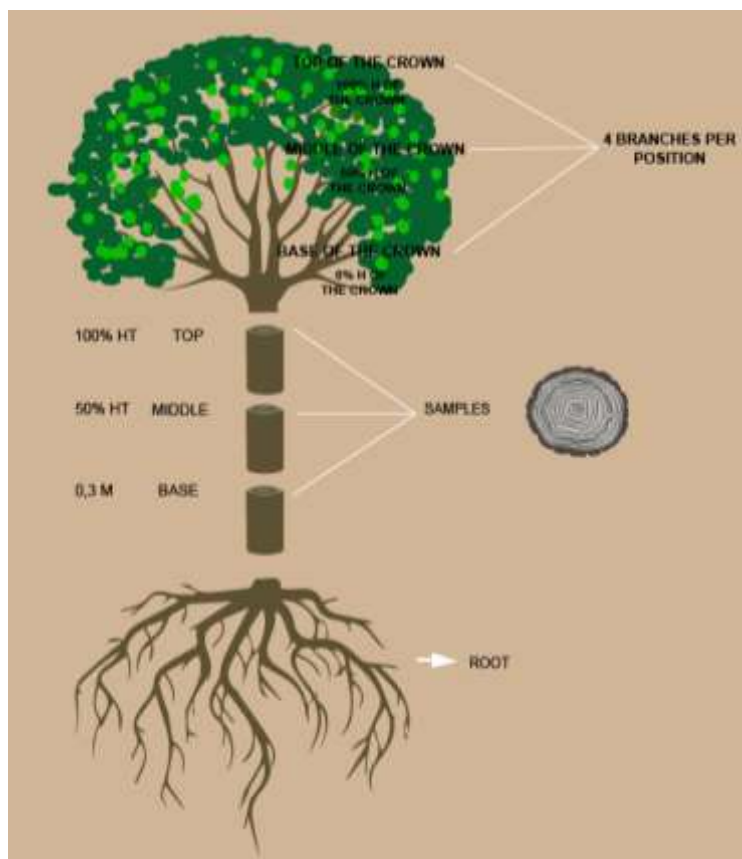DBH = diameter at breast height, 1.3 m from the ground (cm), Th = Total height (m), Ms = Main stem (m), Ch = Crown height (m).

Figure 3. Schematic representation of sampling at different tree heights.

Wood anatomy

Samples from root, stem and crown (1.5 cm^3 blocks, adjacent to the cambium) were softened in boiling water and glycerin (4:1) for approximately 1h. Transverse sections 12-15

μm thick were cut using a sliding microtome. Sections were bleached with sodium hypochlorite (60%) and washed thoroughly in water. We prepared permanent slides according to Johansen (1940) and Sass (1951). Sections were double-stained with aqueous 1% safranin (Bukatsch, 1972) and aqueous 1% astra blue (1:9) (Roeser, 1972). We mounted slides permanently in synthetic resin (Entellan®). Measurements of vessel diameter and vessel density followed the recommendations of the IAWA Committee (1989).

Potential hydraulic conductivity

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

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

where K_p is potential hydraulic conductivity (in kg x m x MPa^{-1} x s^{-1}), ρ_w is water density at 20°C (998.2 kg.m^{-3}), η is the viscosity index of water (1.002 x 10^{-3} MPa x s^{-1} at 20°C), VD is vessel density (cells x m^{-2}), and D_h is vessel hydraulic diameter (m). Since vessels are not exactly circular, we calculated vessel hydraulic diameter from Equation 2, as

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

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

Density

Density (ρ_{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

$$\rho_{12} = M/V \qquad Eq.\,3,$$

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

Statistical analyses

We initially undertook descriptive statistical analysis and used Box Plot graphics to detect outliers. Thus, values 1.5 times higher than the 3rd quartile and 1.5 times lower than the 1st quartile were excluded from the analysis. Normality tests were performed to check the distribution of data, and when a normal distribution was not observed, data were square root-transformed. Then, 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. Pearson's product-moment correlation coefficients between variables were also performed.

Results

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 in the middle and top of stem, while in *C. legalis*, larger vessels were found at the stem top, and in *H. vellosoi*, they were found at all three stem positions (Figure 4a). 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. vellosoi*, at the base and middle of the crown (Figure 4b). 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. *B. riedelianum* had scarce paratracheal axial parenchyma, or it appeared in thin and discontinuous lines or bands. *C. legalis* presented apotracheal axial parenchyma in wavy lines or strands, and *H. vellosoi* had paratracheal axial parenchyma, vasicentric, aliform, confluent, with the tendency to form long confluences that resembled wide bands (Figure 5).

Potential hydraulic conductivity (K_p) showed different patterns among species. In *B. riedelianum*, higher K_p values occurred at base and middle of stem, whereas in *C. legalis* , higher K_p occurred at crown top, while in, *H. vellosoi*, it occurred at the base and middle of crown (Figure 4c). We found denser wood at root and stem base in *B. riedelianum*, but denser wood in root of *C. legalis* and at stem base in *H. vellosoi* (Figure 4d).
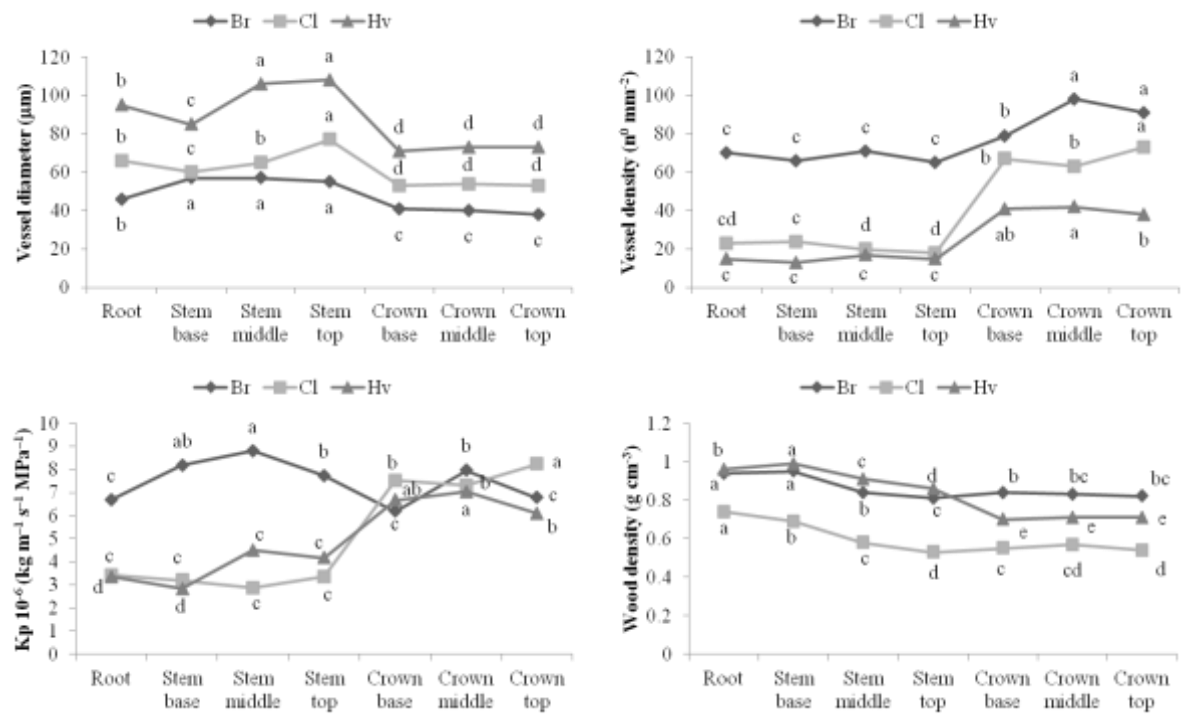
Figure 4. Vessel diameter, vessel density, potential hydraulic conductivity and wood density from 40-year-old *Balfourodendron riedelianum* (Br), *Cariniana legalis* (Cl) and *Handroanthus vellosoi* (Hv) from root to the crown top. Statistical difference among axial positions from root to crown top is represented by distinct letters (P < 0.05) by Tukey's test.

Figure 5. 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 *Handroanthhus vellosoi* wood. O. Crown top. P. Crown middle. Q. Crown base. R. Stem top. S. Stem middle. T. Stem base. U. Root. Scale bars = 200 µm.

In *B. riedelianum*, we found a positive correlation between axial position and vessel density, but 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, axial position and potential hydraulic conductivity and vessel density and potential hydraulic conductivity. Negative correlations were observed between axial position and wood density, vessel diameter and vessel density and vessel diameter and potential hydraulic conductivity (Table 2). In *H. vellosoi*, we found positive correlations between axial position and vessel density, axial position and potential hydraulic conductivity, and between vessel density and potential hydraulic conductivity. Negative correlations were found between axial position and wood density, vessel diameter and vessel density, vessel density and wood density, and between potential hydraulic conductivity and wood density (Table 2).

Table 2. Pearson correlation coefficient (*r*) in the first row and significance level (*p*) in the second row among axial position (Ap, from root to crown top), vessel diameter (Vdi, μm), vessel density (Vde, n^0 mm^{-2}), potential hydraulic conductivity (K_p, 10^{-6}, kg m^{-1} s^{-1} MPa^{-1}) and wood density (ρ_{12}, g.cm^{-3}) from 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosoi*. The significant correlations are highlighted by an asterisk.

	Balfourodendron riedelianum				*Cariniana legalis*				*Handroanthus vellosoi*			
	Vdi	Vde	K_p	ρ_{12}	Vdi	Vde	K_p	ρ_{12}	Vdi	Vde	K_p	ρ_{12}
Ap	-0.68	0.81	-0.23	-0.80	-0.55	0.85	0.87	-0.820	-0.610	0.850	0.88	-0.93
	0.0952	0.0270*	0.616	0.0322*	0.204	0.0162*	0.0105*	0.0232*	0.149	0.0145*	0.00961*	0.00238*
Vdi	-----	-0.84	0.71	0.31	-----	-0.86	-0.80	0.120	-----	-0.840	-0.67000	0.69
		0.0188*	0.0734	0.504		0.0143*	0.0302*	0.807		0.0176*	0.097	0.0862
Vde	-----	-----	-0.22	-0.46	-----	-----	0.99	-0.48	-----	-----	0.96	-0.96
			0.641	0.299			0.00000335*	0.275			0.000463*	0.000765*
K_p	-----	-----	-----	0.003	-----	-----	-----	-0.52	-----	-----	-----	-0.97
				0.993				0.233				0.000257*

Discussion

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 and planted in the same area. We found no gradual tapering of vessel toward the crown. Instead, vessel density and wood density decreased toward the crown. Potential hydraulic conductivity showed a similar pattern in *Cariniana legalis* and *Handroanthus vellosoi* 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.

The tapering pattern of conduits from base to tree top is commonly reported (Lintunen and Kalliokoski, 2010; Olson and Rosell, 2013 and Petit and Crivellaro, 2014). According to Petit and Anfodillo (2009) and Sperry et al. (2006), conduit tapering is essential to maintain efficiency in water conduction because as trees grow, the water pathway also becomes longer. Thus, if tapering does not occur, an increase in water friction within cell walls will result, leading to a decrease in conductivity. However, xylem is not a uniform structure along the axial axis of plant and varies radially from the pith to the bark and axially from the root, trunk and branches. This structural heterogeneity results in variation in hydraulic and mechanical performance (Gartner, 1995). Changes in xylem architecture are often the result 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, trunk diameter and branches, crown size and root distribution and depth during changes in their abiotic and biotic environments (Hinckley et al., 2011).

We did not observe a gradual tapering, and axial variation of vessel diameter was not equal among the three species. Similar to studies of Schuldt et al. (2013) and Kotowska et al. (2015), vessel diameter distribution in the three species 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, Fig. 2), and we did not study the depth of roots from cut trees. However,

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.

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*, *Copaifera langsdorffii*, *Handroanthus ochraceus*, *Ocotea corymbosa* and *Xylopia aromatica*. 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, as hypothesized, and 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 ≈ 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. Additionally, Petit et al. (2007) studied *Acer pseudoplatanus* trees and reported that conduit tapering is more substantial in shorter trees than in taller trees, indicating that tapering is more related to height than to tree age. In our study, we did not observe any relationship between tree height and tapering.

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 the three-studied species, we noted hydraulic bottlenecks in the transition from main stem to crown base. In the transition from root (lateral roots) to stem base, only *B. riedelianum* showed no decrease in vessel diameter. Longui et al. (2017) reported no hydraulic bottlenecks from 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, deep roots have access to water, even in the dry season, in the Luiz Antônio region. 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 compared to the stem (Martinez-Vilalta et al., 2002; Pratt et al. 2007 and 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., 2012 and 2017).

Different from vessel diameter, whose values oscillated in the stem, vessel density presented little variation in the stem, but it did increase to 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, whereas in older tissues, i.e., stem base or wood near the bark, we see wider vessels with less density. Our results show negative correlations between vessel diameter and vessel density in the three-studied species. The same pattern is mentioned by Baas et al. (2004), Fan et al. (2012), and Longui et al. (2012) in *Eriotheca gracilipes*, another native Brazilian tree, as well as Schuldt et al. (2013). Studying hydraulic efficiency, Tyree et al. (1994) reported that one vessel 40μm in diameter is as conductive as 16 vessels 20μm in diameter or 256 vessels 10μm in diameter. In general, studies associate 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, more numerous vessels are associated with higher hydraulic safety (Baas et al., 2004).

Potential hydraulic conductivity, as calculated from vessel diameter and vessel density, showed a similar pattern in *C. legalis* and *H. vellosoi* with increase towards the crown. A different result was observed in *B. riedelianum* that shows a hump-shaped pattern in stem and crown. Higher conductivity in the crown, with narrower vessels, compared with the stem, is not an expected result since the paradigm points out that higher conductivity is associated with larger vessels (Tyree and Zimmermann, 2002). 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. However, based on potential hydraulic conductivity, we obtained results not commonly found. Specifically, vessel density correlated positively with conductivity in *C. legalis* and *H. vellosoi*. Although vessel features were used in the calculation of potential hydraulic conductivity, we emphasize that they did not present

correlations in *B. riedelianum*. In *C. legalis*, conductivity was related to both vessel features, and in *H. vellosoi*, only with vessel density (Table 2). Longui et al. (2017) found positive correlation between hydraulic conductivity and vessel diameter and negative correlation with vessel density, just the opposite *C. legalis* in the present study, revealing the complexity involved in assigning the participation weight of vessel diameter or vessel density to conductivity.

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), π value and viscosity of liquid (n), or ($r^4 \pi/8n$).

Among the three tree species in this study, potential hydraulic conductivity was higher in *C. legalis*, but the numerical values were still close between species, even though they were from different families. However, Gerolamo and Angyalossy (2017) found very 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.

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, presented lower values in the crown in the three species (Figure 4 and Table 2). Only in *H. vellosoi* was a correlation with vessel features identified, i.e., negative correlation with vessel density (Table 2). For the other two species (*B. riedelianum* and *C. 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* 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 of 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., 2012; 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 (Jacobsen et al., 2007; Zanne et al., 2010 and 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 (Telewski et al., 1996 and Niklas, 2000).

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, whereas in the transition from root to stem, only *B. riedelianum* did not show hydraulic bottlenecks.

Vessel density shows the same pattern in all three species, with practically no variation between root and stem, but higher density in the crown. These results interfere in the potential hydraulic conductivity that showed a similar pattern in *C. legalis* and *H. vellosoi* with increase towards the crown. A different result was observed in *B. riedelianum* that showed a hump-shaped pattern in stem and crown.

Correlations show that vessel diameter and vessel density promote changes in potential hydraulic conductivity and does so differently in different species. Vessel diameter was negatively correlated with conductivity in *C. legalis*, whereas vessel density was positively correlated with conductivity in *C. legalis* and *H. vellosoi*. In *B. riedelianum*, no correlation was observed. These results show the effect of interaction between vessel diameter and vessel density on potential hydraulic conductivity of the three studied species.

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 *H. vellosoi*.

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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CAPÍTULO II - Hydraulic properties differs in crown gradients in three native Brazilian species

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Abstract

Hydraulic limitation hypothesis postulates increase in water conduction resistance as trees become higher. We hypothesized there are anatomical, hence hydraulic properties and wood density differences between crown positions, we also expect to find differences in hydraulic properties and wood density among species cultivated simultaneously. Based on these statements, we hypothesized that hydraulic efficiency decreases toward the crown top in *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosoi* trees. We also expected to found differences in hydraulic properties and wood density among species cultivated simultaneously, in the same area and belonged to same successional group (secondary). We examined the maximum vessel length, specific hydraulic conductivity, percentage loss of conductivity, leaf hydraulic conductivity, vessel diameter, vessel density and wood density. We did not observe variations in percentage of conductivity loss, vessel diameter and wood density along the crown. All of characteristics analyzed varied among the species, except foliar conductivity. Our results indicate that each species has different strategy for conducting water in the crown and the observed patterns differ from the established by hydraulic limitation hypothesis among species with different average height of crown.

Keywords: axial crown variation, Brazilian woods, hydraulic conductivity, vessel features, wood density.

Introduction

Hydraulic architecture should share an important relationship with crown architecture. Vertical position of crown interferes in morphological and physiological acclimation for light absorption and hydraulic conductivity. The uppermost branch within the crown has a longer hydraulic pathway for sap flow than lower branches, which causes decrease in hydraulic conductivity (Yoshimura 2011). Additionally, the absolute value of tree conductance will be highly influenced by the terminal branches and leaves (Sperry et al. 2007).

The Hydraulic limitation hypothesis (HLH) tries to explain tree limitation in height and decrease of photosynthesis as the trees become higher. Basically, it describes that stomatal closure in tall trees results from an increase in resistance to sap flow promoted by longer hydraulic path, higher gravitational potential for rising of water in high trees and maintenance of a minimum water potential in leaves (Yoder et al. 1994; Ryan and Yoder 1997). However, the evaluation of branches of *Sequoia sempervirens* showed slightly increased of sapwood-specific hydraulic conductivities (K_s) and high increase of leaf-specific hydraulic

conductivities according the plants' height (Burgess et al. 2006). The authors reported that results are probably adaptive responses to the increased transport requirements of leaves growing in the upper crown where evaporative demand is greater.

Ryan et al. (2006) revisited HLH and report that this hypothesis has stimulated several studies in trees of different heights and ages and it has encouraged the understanding of how trees overcome the challenge of moving water, nutrients and sugars to different plant parts. The authors describe that high trees differ physiologically from shorter individuals, since stomatal conductance, photosynthesis and leaf-specific hydraulic conductance are often, but not always, lower in high trees. Additionally, leaf mass per area is often greater in high trees. Then, how do hydraulic properties vary along the crown of trees?

Studies on hydraulic properties reported different patterns of responses. Despite an apparent universal rule to explain values of hydraulic properties along the crown of trees, it appears that each species, plant group or vegetation presents anatomical and/or physiological peculiarities in the sense of balancing efficiency and safety in water conduction. According to Koch et al. (2004) growth can be limited as consequence of limitation of leaf expansion and photosynthetic rate promoted by the increase of water stress due to gravity and resistance to water conduction. This process can occur even with wide water availability in soil. Sellin et al. (2008) reported no trend to specific conductivity in lower, middle and upper crown of *Betula pendula*, but acropetal decrease of leaf specific conductivity. Yoshimura (2011) based on morphological, anatomical and hydraulic characteristics reported higher specific hydraulic conductivity in upper than lower crown in *Quercus crispula*. This author concluded that morphological and physiological characteristics in the upper crown reduce hydraulic stress, and those in the lower crown reduce shade stress. Mokany et al. (2003) studied interaction between sapwood and foliar area in *Eucalyptus delegatensis* trees of different heights and observed that leaf specific conductivity increased with total tree height.

In addition to hydraulic properties, wood density has a remarkable relation with anatomical features, such as vessel diameter and density (Fan et al. 2012). Thus, wood density, mechanical properties and water transport efficiency are correlated because they are properties determined by amount of empty spaces occupied by water conductive cells (Pratt et al. 2007).

Our goal was to investigate whether there are variations in the hydraulic properties and wood density in the crown of three native Brazilian tree species, *Balfourodendron riedelianum* (Engl.) Engl., *Cariniana legalis* (Mart.) Kuntze and *Handroanthus vellosoi* (Toledo) Mattos. We examined the maximum vessel length, specific hydraulic conductivity,

percentage loss of conductivity, leaf hydraulic conductivity, vessel diameter, vessel density and wood density. We hypothesized there are anatomical, hence hydraulic properties and wood density differences between crown positions, i.e., hydraulic properties and wood density have lower values at higher crown positions. We also expect to find differences in hydraulic properties and wood density among species cultivated simultaneously, in the same area and belonged to same successional group (secondary).

Material and Methods

Origin of seeds and area of cultivation

The seeds were collected in the state of São Paulo, Brazil between May and July 1974. Although no exact collection sites were recorded, trees were selected from phenotypic characteristics of interest such as high vigor, form and sanity. Seedlings of five species (*Balfourodendron riedelianum, Cariniana legalis*, *Centrolobium tomentosum*, *Handroanthus vellosoi* e *Peltophorum dubium*) were produced and planted at the Luiz Antônio Experimental Station - LA (Cerrado), Luiz Antônio City, São Paulo state (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 used was randomized blocks 5 x 6 (5 treatments x 6 blocks) in plots of 15 m x 18 m with 60 plants per plot, two borders. Due to the high mortality of *C. tomentosum* and *P. dubium* already being studied in another research, we chose to study the other three species (mentioned above), and the sampling (detailed below) was performed in 2015, when the trees had 40 years.

Selection of trees

We selected six trees from each species. Information such as diameter at breast height (DBH) (1.3 m above the ground) and tree height (Th) of all trees were listed in Table 1.

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

	Balfourodendron riedelianum				*Cariniana legalis*				*Handroanthus vellosoi*			
	DBH	TH	MS	CH	DBH	TH	MS	CH	DBH	TH	MS	CH

Tree1	18.0	21.0	14.3	6.7	11.5	12.5	8.6	3.9	15.0	10.4	2.9	7.5
Tree2	21.0	21.1	7.4	13.6	14.0	15.1	8.1	7.0	12.0	15.9	11.4	4.4
Tree3	13.0	14.8	5.8	9.0	14.0	15.9	9.6	6.3	16.0	13.6	7.1	6.5
Tree4	16.0	19.7	11	8.7	12.0	15.5	10	5.5	15.0	14.5	3.4	11
Tree5	14.0	20.9	10.4	10.5	13.0	13.4	7.0	6.4	14.0	13.0	5.4	7.6
Tree6	16.0	17.2	6.1	11.1	12.0	15.9	11.50	4.4	15.0	11.9	5.2	6.7
mean	16.3	19.1	9.2	9.9	12.8	14.7	9.1	5.6	14.5	13.2	5.9	7.3

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

Initial procedure

Immediately after tree was felled we cut the branches using a Jameson Big Mouth Pruner. We removed four branches per tree from three different positions: base, middle and top of crown (total of 12 branches per tree). Three branches of each position were immersed in a water container made with a PVC tube 15 cm wide and 100 cm long, sealed tightly at its bottom, and transported to the laboratory to determine hydraulic conductivity, leaf hydraulic conductivity (extracting all the leaves to determine the area and mass), percentage of embolized vessels, vessel diameter, vessel density, potential hydraulic conductivity and wood density at 12% moisture content. One branch of each position was not immersed in water in order to measure vessel length, the fourth branch (each position). In total, we studied 18 trees (six of each species) and 216 branches. We emphasize samples came from young branches without presence of heartwood, which in this species presents vessels obstructed by tyloses.

Maximum vessel length (MVL)

The technique described by Ewers and Fisher (1989) was used to measure MVL. It is important to determine MVL to make certain that the segments used to measure hydraulic conductivity have, at least, one vessel end. We assumed vessel end distribution is hazardly distributed inside the branches (Tyree and Zimmermann 2013). Once leaves were removed, both ends of each branch were cut with the aid of prunning scissors. Posteriorly shaving was made using new razor blades to remove debris.

One branch end was debarked for a length of 2 cm to allow connection to an air compressor using high pressure-resistant (up to 50 KPa) plastic tubing, aided with connectors and fasteners. The opposite branch end was kept immersed in water. Once the system was

perfectly mounted with no air leaks, air was blown into the branch, carefully checking for the presence of bubbles coming out of the branch end immersed in water. If no bubbles were present, a segment 2-cm long was removed from the distal end and reimmersed in water. The procedure was repeated as many times as needed, until the first bubble was observed coming from the open vessels (Figure 1). After this procedure, the branch segment remaining was measured with a measuring tape, adding 1 cm to compensate for the uncertainty of the last cut (length of segment removed each time, divided by two). This measurement provides a good approximation of MVL.

Specific hydraulic conductivity (K_s)

Once the MVL was known, segments shorter (15 cm) than MVL were obtained from a different branch, keeping the branch under water to avoid introducing air into the exposed vessels. Both ends of these new segments were trimmed with a cutter and retrimmed with new razor blades (Sperry et al. 1988, Tyree and Ewers 1991, Davis et al. 2009) to keep vessels open.

One end of each segment was connected to a set of multiple connectors (a manifold), using plastic fasteners to seal the connection. If the branch was too thick for the hose, a band of bark 2-cm wide was removed, as necessary. If, on the contrary, the branch was thinner than the hose, a band 2-cm wide of a thinner hose was inserted in one branch end and then the branch and hose were inserted into the manifold (Figure 1).

To measure hydraulic conductance, a solution of 1% acetic acid in distilled water was prepared, to avoid fungal and bacterial growth during measurements. This solution was kept under refrigeration until use. Just before use, this solution was subjected to vacuum for 24 hours to eliminate air dissolved in the solution, to avoid introducing air into the vessels. To measure the flux of solution through each branch segment in the manifold, a container (a bag originally used for intravenous infiltration) filled with the degassed acetic acid solution, as described above, was kept at a height of 60 cm from the working surface. The valve connecting the container to the manifold was opened, while the valves connecting each branch segment were kept closed. After confirming that the system was air-free, the valve connected to the first branch segment was opened, allowing the solution to flow through that branch segment. At the other end of the branch, the solution coming out the branch segment was collected in a glass vial that was previously weighed. The vial was tagged to identify it as belonging to that particular branch segment. Then, the vial with the collected solution was weighed using an electronic balance with a precision of 0.001 mg (Figure 1). The amount of

water collected in 1 minute was calculated by subtracting the weight of the vial from the weight of the vial with the collected solution. The same procedure was repeated 10 times to obtain the amount of water flowing through each branch segment during one minute in response to the pressure differential created by the water head at 0.6 m, i.e., 60×10^{-3} MPa. After this, the valve leading to that branch segment was closed, and the next one was opened to repeat the procedure.

Hydraulic conductance for each segment was calculated by multiplying the water flux times the quotient of pressure gradient (dp = 0.006 MPa), divided by the branch segment (dl):

$$K_h = Flux \; \frac{d_p}{d_l} \qquad \left[\frac{kg \times MPa}{sec \times m} \right] \qquad eqn.\,1$$

This represents hydraulic conductance before removing embolisms. To remove embolisms from the system, the solution container was elevated to 7 m, using a support with a pulley placed on the outside of the laboratory building to connect to the manifold. At this step, passage of this solution was forced through all the segments at the same time for 20 minutes, to remove embolisms. After this, the system was again brought up to the original height of 0.6 m, and the K_h was calculated again for each branch segment to obtain maximum K_{hi}. To make sure all embolisms had been removed, the system was subjected again to high pressure for 20 minutes, and K_{hf} was calculated, as described. In all cases, no significant differences were observed between K_{hf} and $K_{hi.}$ Therefore, it was assumed that one removal of embolisms was enough to allow for accurate calculation of the maximum K_h.

Then, the initial (without embolism removal) and final or maximum (after embolism removal) specific hydraulic conductivities (K_s) were calculated by multiplying the conductance by sample length and dividing by the xylem cross-sectional area of samples.

$$Ksi = khi \; x \frac{L}{CSA} \qquad eqn.\,2$$

$$Ksf = khf \; x \frac{L}{CSA} \qquad eqn.\,3$$

where K_s = specific hydraulic conductivity (in kg m*MPa^{-1}*s^{-1}), K_{hi} = hydraulic conductance initial, K_{hf} = hydraulic conductance final, L= sample length (m), CSA = cross sectional area of

sample (m^2). K_{si} = initial specific hydraulic conductivity and K_{sf} = final specific hydraulic conductivity.
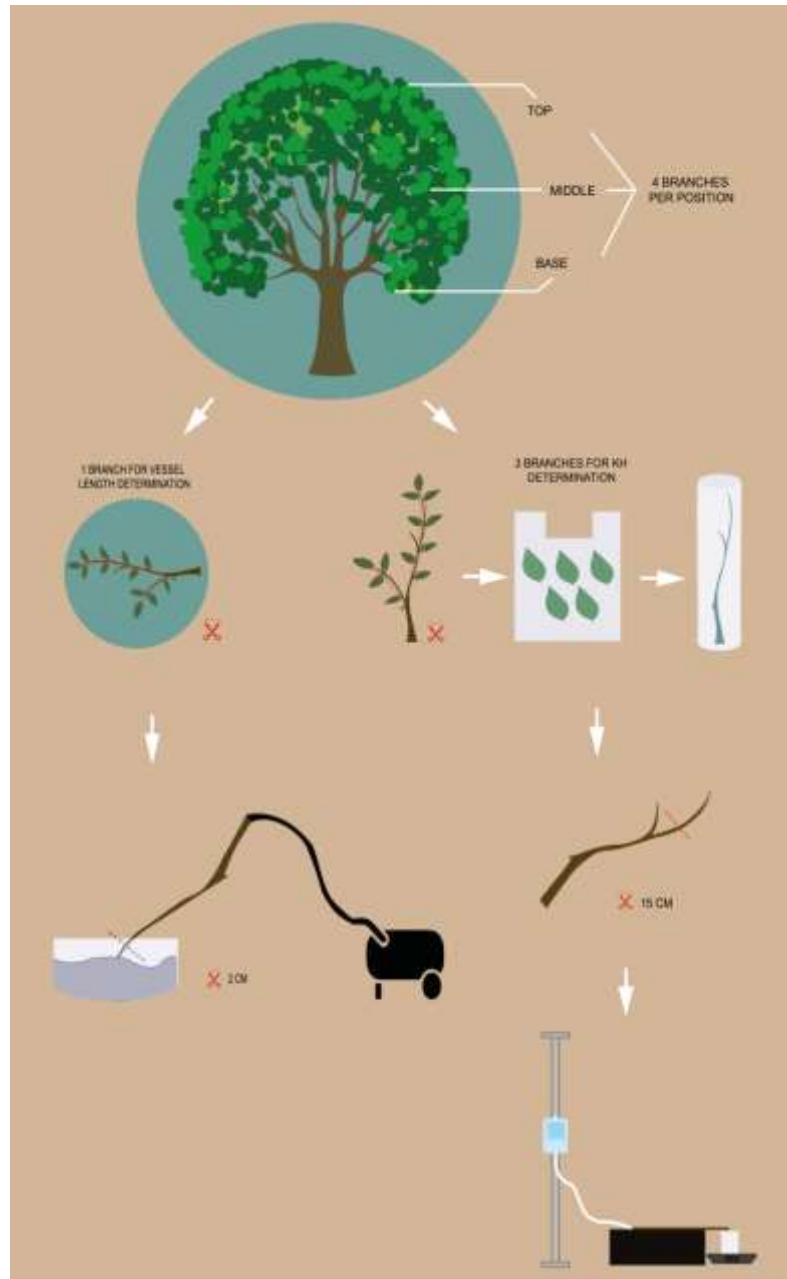

Figure 1. Schematic representation for maximum vessel length (MVL) and hydraulic conductance (K_h) determination.

Percentage loss of conductivity (PLC)

The difference between maximum and minimum K_h gives the percentage loss of conductivity (PLC), the degree of embolism in the branch at the time of its collection. Percentage loss of conductivity (PLC) was determined according to Cochard et al. (2013), when PLC=0%, then maximum K_h= minimum K_h and none of the conduits were embolized, however, when PLC=100%, maximum K_h= 0 and all the conduits were embolized.

$$PLC \left(\frac{maximum\ Kh - minimum\ Kh}{maximum\ Kh} \right) x\ 100 \qquad eqn.4$$

Leaf hydraulic conductivity (branch conductance per unit leaf area, K_l)

The procedure for measuring the leaf area was performed based on Nicotra (2017). For this analysis we considered all the leaves from branches in which we measured hydraulic conductivity. We carefully removed the leaves from the petioles and stored them in paper envelopes, then separated 20 leaves per crown position (base, middle and top, 60 leaves per tree). The leaves were pressed, to prevent shrinkage and contortion of them, and dried in laboratory kiln for three days. Subsequently, we weighed all the leaves individually to determine their masses (g), and their individual areas were measured using LI-3100C Area Meter.

The leaves left in the paper envelopes were taken to laboratory oven at 60-70°C to dry for three days. After this period, we obtained the total weight of leaves. For calculation of total area, a regression was elaborated with values of area and mass from each 60 leaves.

Leaf conductivity (K_l) was calculated by dividing the maximum hydraulic conductance (K_h) of branch segment by corresponding leaf area.

Wood anatomy

Samples from base, middle and top of crown ($\approx$ 1 cm^3 blocks) were softened in boiling water and glycerin (4:1) for approximately 1h. Transverse sections 12-15 µm thick were cut using a sliding microtome. We prepare permanent slides according to Johansen (1940) and Sass (1951). Sections were double-stained with aqueous 1% safranin (Bukatsch 1972) and aqueous 1% astra blue (1:9) (Roeser 1972). We mounted slides permanently in synthetic resin (Entellan®). Measurements of vessel diameter and vessel density followed the recommendations of the IAWA Committee (1989).

Potential hydraulic conductivity (K_p)

From values of vessel diameter and vessel density, we calculate the potential hydraulic conductivity (equation 1) according to the Hagen-Poiseuille law described by Sterck et al. (2008) and Poorter et al. (2010). We used two equations in this step:

$$K_p = \left(\frac{\pi \rho_w}{128\eta}\right) \times VD \times D_h^4 \qquad eqn.5$$

where K_p = potential hydraulic conductivity (in kg x m x MPa^{-1}x s^{-1}), ρ_w = water density at 20°C (998.2 kg.m^{-3}), η is the viscosity index of water (1.002 x 10^{-3} MPa x s^{-1} at 20°C), VD = vessel density (cells x m^{-2}) and D_h = vessel hydraulic diameter (m). Since vessels are not exactly circular, we calculate vessel hydraulic diameter from equation 2.

$$D_h = \left[\left(\frac{1}{n}\right) \sum_{i=n}^{n} d^4\right]^{1/4} \qquad eqn.6$$

where n = number of vessels and d = vessel diameter.

Density (ρ_12)

In this step, we analyzed six samples ($\approx$ 2 cm in length) in each branch, 36 in each crown position, totaling 108 samples per species. After removing the bark of samples, density (ρ_{12}) was determined at equilibrium moisture content (EMC-12%) and calculated by the relation 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).

$$\rho_{12} = M/V \qquad eqn.7$$

where ρ_{12} = density (kg.m^{-3}); M = wood mass at 12% moisture content (kg); and V = wood volume at 12% moisture content (m^3).

Statistical analyses

We initially undertook descriptive statistical analysis and used Box Plot graphics to detect outliers. Thus, values 1.5 times higher than the 3rd quartile and values 1.5 times lower than the 1st quartile were excluded from the analysis. Normality tests were performed to check the distribution of data, and when a normal distribution was not observed, data were

square root-transformed. Then, 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. We analyzed the axial variation within the same species and also three axial positions in crown together comparing the species. We also performed linear regression analyzes between the vessel features (MVL, diameter and density) and hydraulic features (K_p, K_{si}, K_{sf}, K_l, PLC) and wood density; in these analyzes we used mean values of three crown position from six trees each species.

Results

The maximum vessel length (MVL) gradually decreased from base to crown top in *B. riedelianum*. *Cariniana legalis* presented longer vessels in the middle portion of crown. In *H. vellosoi* longer vessels occurred at base and middle of crown. *Handroanthus vellosoi* presented longer vessels compared to other two species (Table 2).

The specific hydraulic conductivity initial (K_{si}) did not differ among crown positions in *B. riedelianum* and *C. legalis*, whereas in *H. vellosoi* the K_{si} at the base and crown middle was lower than crown top. *Cariniana legalis* presented the highest K_{si}, followed by *H. vellosoi* and *B. riedelianum* (Table 2). The final specific hydraulic conductivity (K_{sf}) was measured after removing the embolisms by increasing the height of solution container. In *B. riedelianum* K_{sf} was lower at the crown top; in *C. legalis* there was no difference between crown positions, while in *H. vellosoi*, the highest K_{sf} values were observed at the top and base of crown, the latter not differing from middle of crown. Higher K_{sf} values were observed in *B. riedelianum* and *C. legalis* (Table 2).

The percentage loss of conductivity (PLC) did not differ among crown positions from three species. *Balfourodendron riedelianum* presented a higher PLC when compared to *C. legalis* and *H. vellosoi* (Table 2).

Vessel diameter (Vdi) did not differ between crown positions in the three species. Among the species, *H. vellosoi* presented wider vessels and *B. riedelianum* narrower ones (Table 2 and Figure 2). Vessel density (Vde) in *B. riedelianum* was higher in the middle and top of crown, in the middle of crown in *C. legalis*, and in *H. vellosoi* there was no difference between positions. Among the species, *B. riedelianum* presented higher vessel density and *H. vellosoi* lower (Table 2 and Figure 2).

Leaf hydraulic conductivity (K_l) did not differ between crown positions in *B. riedelianum* and *C. legalis*. For *H. vellosoi* the highest K_l values were observed at the top and base of

crown, the latter not differing from middle of crown. The K_l did not differ between species (Table 2).

The potential hydraulic conductivity (K_p) was higher in the middle of crown in *B. riedelianum*, at the base and crown top in *C. legalis* and at the base and crown middle in *H. vellosoi*. *Cariniana legalis* showed the highest potential hydraulic conductivity among three species (Table 2).

Wood density did not differ between crown heights in the three species. Higher density was observed in *B. riedelianum* and lower in *C. legalis* (Table 2).

Table 2. Anatomical, hydraulic properties and wood density of 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosoi* for three crown heights.

Crown position	MVl	K_{si}	K_{sf}	PLC	Vdi	Vde	K_l	K_p	ρ_{12}
Balfourodendron riedelianum									
Base	104a	0.265a	1.095a	77a	41a	79b	1.885a	6.18b	0.84a
Middle	94ab	0.210a	1.025a	81a	40a	98a	1.987a	7.95a	0.83a
Top	88b	0.224a	0.711b	68a	38a	91a	1.420a	6.77b	0.82a
Mean	**96B**	**0.233C**	**0.940A**	**76A**	**40C**	**89A**	**1.763A**	**6.98B**	**0.83A**
Cariniana legalis									
Base	84b	0.982a	0.928a	27a	53a	67b	2.476a	7.51ab	0.55a
Middle	99a	0.889a	0.986a	34a	54a	63b	2.450a	7.30b	0.57a
Top	84b	1.081a	0.812a	38a	53a	73a	2.192a	8.22a	0.54a
Mean	**90B**	**0.982A**	**0.913A**	**33B**	**53B**	**68B**	**2.377A**	**7.68A**	**0.55C**
Handroanthus vellosoi									
Base	117a	0.462b	0.649ab	24a	71a	41a	2.381ab	6.66ab	0.70a
Middle	112a	0.519b	0.514b	30a	73a	42a	2.065b	7.03a	0.71a
Top	95b	0.832a	0.917a	28a	73a	38a	2.977a	6.10b	0.71a
Mean	**109A**	**0.601B**	**0.697B**	**27B**	**72A**	**40C**	**2.477A**	**6.61B**	**0.71B**

MVL = maximum vessel length (cm), K_{si} = specific hydraulic conductivity initial (K_{si}, 10^{-6}, kg m^{-1} s^{-1} MPa^{-1}), K_{sf} = specific hydraulic conductivity final (K_{sf}, 10^{-6}, kg m^{-1} s^{-1} MPa^{-1}), PLC = percentage loss of conductivity (%), Vdi = vessel diameter (µm), Vde = vessel density (cells.mm^{-2}), K_l = leaf hydraulic conductivity (K_l, 10^{-6}, kg m^{-1} s^{-1} MPa^{-1}), K_p = potential hydraulic conductivity (K_p, 10^{-6}, kg m^{-1} s^{-1} MPa^{-1}), ρ_{12} = wood density at 12% moisture content (g.cm^{-3}). The difference among axial positions in crown is represented by lowercase letters, while the comparison among species is represented by uppercase letters. Distinct letters differ statistically (P < 0.05) by Tukey's test.

We observed different positive relation between vessel features (diameter and density) and specific hydraulic conductivity final and potential hydraulic conductivity; and negative relations between hydraulic properties and wood density in *C. legalis*, and positive relation in *H. vellosoi* (Table 3).

Table 3. Regression equations showing the correlation between vessel diameter (Vdi) and vessel density (Vde) and specific hydraulic conductivity final (K_{sf}), potential hydraulic conductivity (K_p) and wood density (ρ_{12}) of 40-year-old *Balfourodendron riedelianum*, *Cariniana legalis* and *Handroanthus vellosoi* trees.

Species	Equation	F	P	R^2
Balfourodendron riedelianum	K_{sf} = -0.00369 + (0.000106*Vdi)	16.795	0.020	0.85
	K_p = 0.00000256 + (0.0000000503*Vde)	6.994	0.050	0.64
Cariniana legalis	K_p = -0.00000275 + (0.000000154*Vde)	9.482	0.030	0.70
	K_{si} = 0.00413 - (0.00665* ρ_{12})	50.168	0.002	0.93
	K_{sf} = 0.00356 - (0.00539* ρ_{12})	21.587	0.010	0.84
	K_l = 0.0141 - (0.00223* ρ_{12})	23.981	0.008	0.86
Handroanthus vellosoi	K_p = -0.0000124 + (0.000000262*Vdi)	14.644	0.010	0.79
	K_p = -0.00000326 + (0.000000244*Vde)	32.153	0.005	0.89
	K_{sf} = -0.00778 + (0.0114* ρ_{12})	110.855	<0.001	0.97

Anatomically we have highlighted the differences in axial parenchyma types between species. We observed that *B. riedelianum* has scarce paratracheal axial parenchyma or in thin and discontinuous lines or bands, *C. legalis* present apotracheal axial parenchyma in wavy lines or strands, and *H. vellosoi* has paratracheal axial parenchyma, vasicentric, aliform, confluent, with the tendency to form long confluences that resemble wide bands (Figure 2).
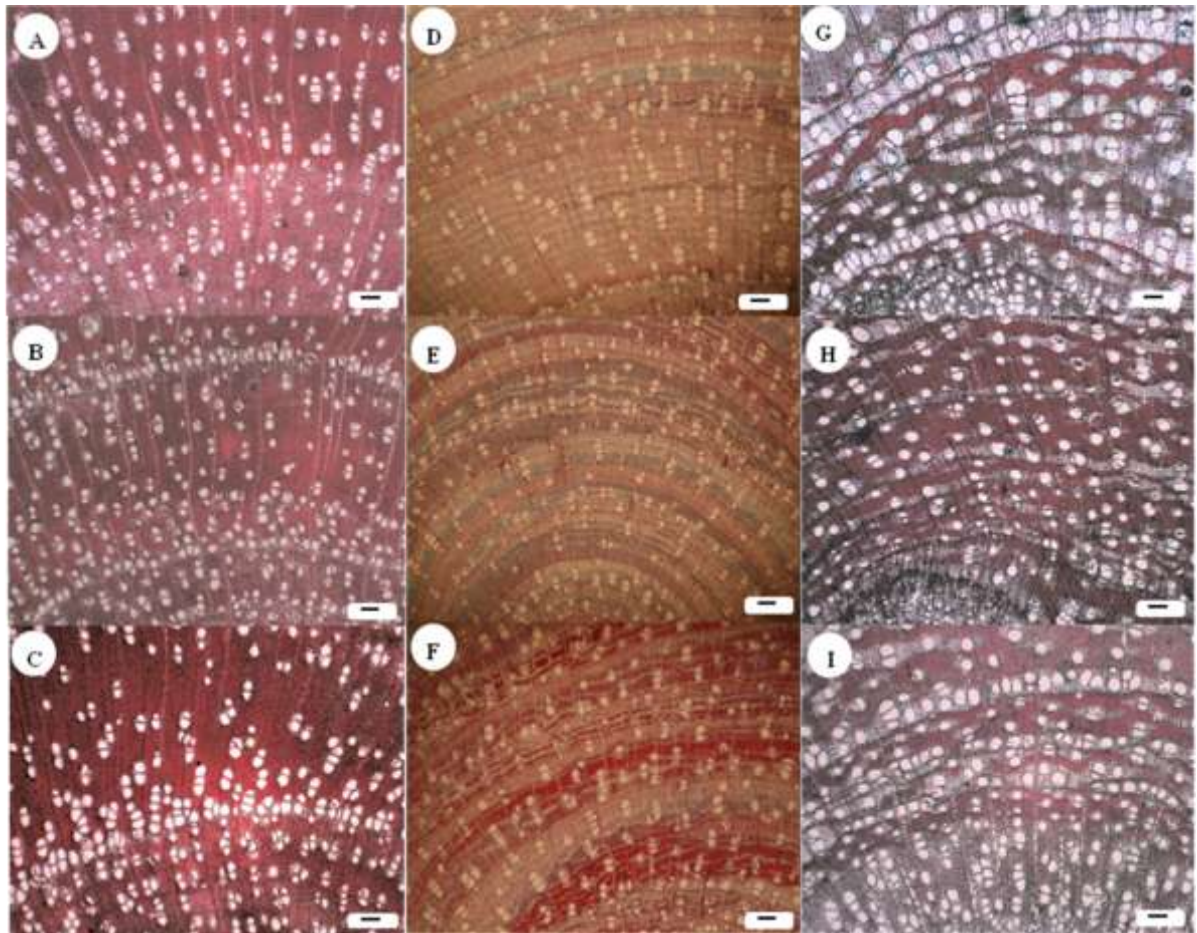

Figure 2. Transverse sections from branches of top, middle and base crown, respectively. a-c. *Balfourodendron riedelianum*. d-f. *Cariniana legalis*. g-i. *Handroanthus vellosoi*. Scale bars = 200 μm.

Discussion

We did not found variations in percentage loss of conductivity, vessel diameter and wood density among the three crown positions. The other studied characteristics showed variation, but we were not able to establish a same pattern for three species. Thus, our first hypothesis of finding lower values of wood conductivity and density properties in higher crown positions

was not confirmed. Even with variation of average crown height among species, in *B. riedelianum* it was 9.9m, in *C. legalis* it was 5.6m and in *H. vellosoi* 7.3m. However, when comparing the species, with exception of foliar conductivity, all the other characteristics studied presented variation, and this hypothesis was confirmed, since the species present differences, although they grow under the same environmental conditions and are of the same successional group. These results show that each species has different strategies of water conduction in the crown.

The reason why we expect lower values of conductivity in higher crown positions was based on understanding of height limitation of trees, according to hydraulic limitation hypothesis (HLH), proposed by Yoder et al. (1994) and Ryan and Yoder (1997). However, our results showed that HLH does not apply to trees we studied, because of relatively short stature compared to large trees as proposed by Burgess et al. (2006). It is possible leaves of trees that we studied have adaptations or there are other anatomical and/or physiological adjustments in trees not investigated in this study that could explain hydraulic and wood density variations.

In our study, specific hydraulic conductivity, leaf conductivity and potential conductivity, although showing some variations in different heights of crown, did not show a pattern between species nor an association with tree heights. Ryan et al. (2006) reported that leaf-specific hydraulic conductance is often, but not always, lower in higher trees. Other studies describe different results for hydraulic properties between species. Sellin et al. (2008) reported no trend to specific conductivity in lower, middle and upper crown of *Betula pendula*, but acropetal decrease of leaf specific conductivity. Yoshimura (2011) reported that specific hydraulic conductivity was higher in upper than lower crown in *Quercus crispula*. Mokany et al. (2003) observed leaf specific conductivity increased with total tree height in *Eucalyptus delegatensis*. As seen there are many variations in results of specific hydraulic conductivity and leaf conductivity among different species, and what seems to us is that each species in its water conditions and luminous intensity adopt anatomical structures that allow them to meet their hydraulic and mechanical demands.

One of anatomical features that could theoretically influence the conductivity is maximum vessel length. The expected result would be a positive relation between vessel length and conductivity, since there would be less efficiency loss in conduction with longer vessels with less oscillations of water flow in the connection between vessels. We observed decrease in MVL toward the crown top in *B. riedelianum* and *H. vellosoi*, however we found no relation between MVL and hydraulic properties. In general, for three species, we observed

vessels about 1m long, values similar to those reported by Jacobsen et al. (2012) for some tree species, although this value shows great variation depending on the species. Zimmermann and Jeje (1981) and Ewers and Fisher (1989) report vessel influences hydraulic efficiency and safety, and it may be positively related to vessel diameter. Among species we studied, longer vessels of *H. vellosoi* could contribute to higher conductivity, compared to *B. riedelianum* and *C. legalis*, since water flow would be more efficient than in shorter vessels, but *H. vellosoi* did not show highest conductivities. Gartner and Meinzer (2005) reported that perforations between vessel elements contribute less to flow resistance than do pits, and differences in cells length between mature and juvenile wood has a negligible effect on K_s. Thus, we assume that differences found for maximum vessel length between the different crown positions, and even between species did not significantly influence hydraulic conductivity. Additionally, we found no correlation between vessel diameter or vessel density with maximum vessel length. The same result was reported by Wheeler et al. (2005) for vessel diameter and length. Whereas Sperry et al. (2007) reported a significant relationship between these two vessel features and their lengths.

Vessel length may also be related to occurrence of embolism. According to Comstock and Sperry (2000), longer and wider vessels increase the chances of cavitation. However, if we analyze based on percentage loss of conductivity (PLC), we did not observe significant relations between MVL and PLC in our samples. We observed longer and wider vessels in *H. vellosoi*, while higher PLC values were observed in *B. riedelianum* with narrower vessels among three species we studied. It is possible that differences in vessel length and diameter were not sufficient to observe a significant effect in the presence of embolism or other physiological aspects not studied by us are involved. Lemoine et al. (2002) studied the susceptibility to cavitation in different branches of crown in *Fagus sylvatica*, sun-exposed branches and shaded ones. The authors noted that shade branches are more vulnerable to cavitation than sun-exposed branches and that stomatal control is involved in this response. The results of Lemoine et al. (2002) do not explain our study, since PLC values did not vary in three heights of crown of the three species, even in *C. legalis*, in which the crown is more closed and the leaves in lower crown receive less light, comparing with *B. riedelianum* and *H. vellosoi*.

Brodersen et al. (2010) and Brodersen and McElrone (2013) reported that plants have many strategies to prevent or restore hydraulic conductivity through cavitation resistance with specialized anatomy or metabolically active embolism repair mechanism, and metabolically active cells (parenchyma) surrounding the xylem conduits in some, but not all, species can

restore hydraulic conductivity. Among the species we studied, Mainieri et al. (1983) describe that *B. riedelianum* has axial parenchyma in thin lines or bands, sometimes discontinuous. *C. legalis* has axial parenchyma in very thin wavy lines. While *Handroanthus* spp. has axial parenchyma vasicentric, aliform, confluent, grouping several vessels in oblique arrangements. In general, the types of axial parenchyma that we found corroborate those reported by Mainieri et al. (1983), described from main stem. However there are some differences in our samples, possibly because they are branches, the axial parenchyma differences were : scarce parenchyma in *B. riedelianum*, wide bands in *C. legalis* and *H. vellosoi*, in this last one due to the confluences. If we analyze the participation of parenchyma cells, especially the axial parenchyma, we note that *B. riedelianum* has the least favorable anatomical structure for embolisms recovery via secretion of solutes from surrounding parenchymatic cells into the vessels. Thus the tree can establish an osmotic gradient that reestablishes the water into the vessel. We asked whether K_{sf} value in *B. riedelianum*, which increased most in relation to K_{si} in the three species, may in fact represent the capacity of *B. riedelianum* to recover embolisms or the increase between K_{si} to K_{sf} only occurs in a "forced" manner as in the executed methodology for specific hydraulic conductivity? The fact is that *B. riedelianum* trees were higher and wider than the two-other species we studied, with high or low capacity for embolism recovery, *B. riedelianum* was efficient in growth and also has the highest density value.

Hoeber et al. (2014) studied hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate, and founded that fast-growing tree species with light wood possessed a more efficient hydraulic system. In our study, although *C. legalis* showed a higher conductivity, and is a species whose trees reach high stature (Batista et al. 2014), being among the highest in Brazil, in the studied trees, on average, *B. riedelianum* showed higher trees with wider trunks compared other two species at 40 years (Table 1). As mentioned above, after embolism removal, hydraulic conductivity of *B. riedelianum* did not differ from that of *C. legalis*. According to Fan et al. (2012), stem xylem features have a great impact on growth and adult stature of trees because of their role in water transport, mechanical support and carbon allocation. Despite that narrower vessels comparing with the other two species, *B. riedelianum* has a higher vessel density which may have contributed to making water conduction efficient in order to positively impact tree growth.

Due we did not find clear patterns of variation in crowns of three species, we developed regression analyzes with the mean values of each tree (metting three crown positions) and the results showed that, in general, vessel diameter and vessel density were positively related to

hydraulic properties. The positive relation between vessel diameter and hydraulic conductivity is widely reported in many studies (Ewers et al. 1991, Tyree and Zimmermann 2002, Baas et al. 2004, Poorter et al. 2010). Poorter et al (2010) reported a negative relation between vessel density and hydraulic conductivity. We emphasize that in our study, effective vessel density contribution for hydraulic conductivity, since positive relations occurred in three species, reinforcing the synergy between vessel diameter and density in the hydraulic efficiency. Similarly, Barotto et al. (2017) in a study of wood density and anatomy of three *Eucalyptus* species and implications for hydraulic conductivity reported despite the importance of vessel diameter in K_s determination, total vessel lumen area has a greater relative influence on K_s.

Other observed relationships were among hydraulic properties with wood density. Noting that according to Zanne et al. (2010) this physical property is a good predictor of stem mechanical strength. However, we observed totally different results among the species, and other studies cited below also found different results. In *B. riedelianum* there are no significant relationships, same result of Poorter et al. (2010) reported for the relation between potential hydraulic conductance and wood density in 42 rainforest tree species, Fan et al. (2012) between potential hydraulic conductivity and wood density in 40 Asian tropical tree species, and Schuldt et al. (2013) between hydraulic parameters and wood density in five species from an Indonesia tropical rainforest. In *C. legalis*, three hydraulic properties (K_{si}, K_{sf} and K_l) were negatively correlated with wood density. Zheng and Martínez-Cabrera (2013) also observed K_s negatively associated with wood density in approximately 800 tree species from China; Santiago et al. (2004) reported a negative relationship between leaf-specific hydraulic conductivity and branch wood density in study with Panamanian forest canopy trees. While *H. vellosoi* trees in our study, K_{sf} was positively related to wood density, a result that is not common in the tradeoff between hydraulic efficiency and wood resistance (based on wood density). Whereas Longui et al. (2017) observed a negative relation between potential conductivity and wood density in other *H. vellosoi* trees. This result shows that even the same species (*H. vellosoi*) may present different results, but we can not find an explanation for this difference.

Despite variations presented by three species we could not determine a pattern in hydraulic properties. It is possible that lack of variations in vessel diameter and wood density is because, despite the variation in height, samples of terminal branches practically do not differ in diameter and are from equally young regions.

Conclusions

In this study we tested two hypotheses: i) hydraulic efficiency decreases toward the canopy top in in three Brazilian species, and potential hydraulic conductivity variations would be associated with anatomical changes, and these in turn interfere on wood density; ii) there are differences in the hydraulic properties and wood density among species, even trees belonged to same successional group (secondary) growing simultaneous and in the same planting. Our first hypothesis was not confirmed because we did not found variations in percentage loss of conductivity, vessel diameter and wood density along the crown, other studied features showed variation, however we did not establish a same pattern for three species. Thus, the species did not follow hydraulic limitation hypothesis, even with variations in average height of crown among species. Our results indicate that each species has different strategies for conducting water in the crown. The second hypothesis was confirmed, since except for foliar conductivity, all other characteristics analysed showed variation among the species, but without a universal pattern. These results indicated each species has its anatomical, hydraulic and mechanical (density) adjustments, even growing in homogeneous plantation.

Acknowledgement

Conflict of interest

None declared.

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CONSIDERAÇÕES FINAIS

As espécies estudadas não apresentaram um padrão de afunilamento no sentido raiz- topo da copa. A diminuição gradual do diâmetro do vaso ao longo do eixo da árvore não ocorre nas espécies que estudamos. A densidade do vaso apresentou o mesmo padrão nas três espécies, com praticamente nenhuma variação entre raiz e caule, e maior densidade nas posições da copa. As correlações evidenciam que o diâmetro e a densidade de vasos promovem mudanças na condutividade hidráulica potencial entre as espécies.

Com exceção da condutividade específica foliar, todas as outras características analisadas apresentaram variação entre as espécies, mas sem padrão definido.

A densidade da madeira não mostra nenhum padrão evidente de variação axial, mas, em geral, apresenta valores mais baixos na copa quando comparados à raiz e posições do caule principal. As características dos vasos aparentam ter influência mínima na densidade da madeira, uma vez que correlação negativa entre a densidade da madeira e a densidade do vaso só foi observada em *H. vellosoi.* Os resultados indicam que cada espécie tem seus ajustes anatômicos, hidráulicos e mecânicos (densidade), mesmo crescendo em plantios homogêneos.

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