*Original article*

# Sympatric and phenotypic variation between two representative species of the Atlantic Forest: an analysis of the hydraulic system

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## ABSTRACT

Tropical forests are the most diverse on the planet, and it is essential to understand how plant species adapt to the environmental differences inherent in this environment. This study describes the wood anatomy and hydraulic architecture of *Bathysa cuspidata* and *Bathysa nicholsonii* in two remnants of the Atlantic Forest through a paired analysis of the hydraulic system related to taxonomic and environmental aspects. Samples were collected non-destructively, processed following techniques of wood anatomy. Sympatric species differ taxonomically in *Bathysa cuspidata* showed vessels either solitary or radial multiples of 2 to 4 elements, septate fibre-tracheids with thick walls, and larger rays with sheath cells. At the same time, *B. nicholsonii* has a higher vessel frequency, septate fibre-tracheids with thin walls, narrower rays, vessels with smaller diameters. Although each species' hydraulic system shows acclimatization variations to different sites of occurrence, the structural differences in wood ensure the segregation between the species in each site. Our results corroborate the relevance of the anatomical wood anatomy studies as a subsidy for a better definition of morphologically similar taxa and show structural aspects aimed at survival in the Atlantic Forest. This data combination has often been neglected in understanding biodiversity in the tropics.

**Keywords:** Intraspecific Variation, Wood Anatomy, Anatomical Taxonomy, Wood Ecophysiology, Adaptive Strategies

## Introduction

Atlantic Forest has one of the most significant species diversities related to distinct heterogeneous landscapes throughout its extensive east coast distribution of the South American continent (Oliveira-Filho & Fontes 2000; Scarano 2002). This biome is formed by a complex of ecosystems that offer goods and services to the largest cities in Brazil (Rezende *et al*. 2018; SOSMA & INPE 2019). However, the remnants that still resist must be better understood for their conservation and adoption of measures to restore degraded areas due to reducing their original area. The Atlantic Forest in Bahia and Rio de Janeiro has a high degree of richness and endemism of plant species. Furthermore,

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they have macroclimatic and rainfall differences imposed by spatial separation.

Several researchers seek to understand the different mechanisms by which plants adjust the anatomy of their xylem tissues to meet various macro and microclimatic characteristics (Hacke *et al*. 2006; Zanne *et al*. 2010; Trueba *et al*. 2017; Rosas *et al*. 2019). Tropical forests are the most diverse on the planet, and a wide range of tree strategies have evolved to promote the survival and distribution of these species. Understanding which characteristics contribute to the evolutionary success of plants in such diverse forests is still a challenge (O'Brien 2017). Traits such as vessel length and diameter can clarify the relationship of efficiency and safety in water use (Tyree & Zimmermann, 2002). Thus, the comparative wood anatomy allows a better understanding of the xylem structure-function relationships and hydraulic strategies against environmental variations.

Wood anatomy gathers data of proven relevance for recognizing taxonomic groups and contributes to solving problems about the systematic position of several taxa (ex.: Carlquist & Zona 1988; Baas *et al*. 2004; Lens *et al*. 2007). Thus, the wood anatomy has been used successfully in the botanical identification of species of wood-producing trees and, in particular, commercial material devoid of the vegetative part (Coradin 2002). In addition, ecological wood anatomy includes studying environmental influences on structural variations of species, showing that environmental factors directly influence the anatomical and morphological structure (Baas 1973). The wood anatomy also acts on phenotypic variation and plasticity and, in the long run, performs in the natural selection of species. Wherefore, the relationships between the structure of the wood and the environmental characteristics have been widely studied (Zuidervaart & Anderson 2016). Thus, studies of ecological anatomy that present the hydraulic system's adaptive strategies and the plants responses to the water stress open a new field in the ecological wood anatomy, mainly in the tropical forests (Costa *et al*. 2020; Simioni *et al*. 2020).

The ability of a tree or even a population to undergo morphological or physiological variations in the face of changes in environmental conditions is called phenotypic plasticity (Valladares *et al*. 2006; Gianoli & Valladares, 2012). The phenotypic plasticity is the fastest mechanism for responding to environmental change and plays a key role in the persistence of trees in the face of climate change (Aubin *et al*. 2016). Simultaneously, the gradient of morphological or physiological variation between related individuals resulting from an adaptive process is called phenotypic variability (Gratani, 2014).

Studies in forest environments about adaptation conditions by trees concerning morphological and functional characteristics enable a better understanding of ecosystem organization (*e.g*., Missio *et al*. 2017). In this sense, the hydraulic system may reflect structural adjustments as means of adaptation by native species to

various phytophysiognomies in the Atlantic Forest (*e.g*., Marques *et al*. 2012; Campbell *et al*. 2016; 2018; Macedo *et al*. 2019). Then, the structure and function of wood, mainly focused on tree hydraulics, is an essential field in biology because it allows a better comprehension of forest ecology and evolutionary analysis of plants (Baldin *et al*. 2016; Hacke 2015).

*Bathysa* C. Presl is widely distributed in the Northeast and Southeast regions of Brazil. This genus is represented by about 15 species, trees that reach 15 m, or shrubs. The species are exclusively Neotropical, occurring in hillside forest formations at 600-800 (-1,100) meters. In Brazil, seven species occur, all exclusive to the Atlantic Forest (Germano-Filho 1999). Some species of this genus are considered relevant by the Importance Value Index (IVI) for studied remnants indicating great representativeness of these species (Guedes-Bruni 1998). This genus has species known as "falsas quinas" that encompass all plants that contain barks with a bitter taste and a red, yellow, or gray color. According to Correa (1984), the bark provides tonics, which are often used in treating anemias, cachexia, fevers, hookworm, convalescent states, and others, in addition, are used as dyes. Although the genus has a high representation in Atlantic Forest remnants, little is known about the ecology of its species.

Considering the environmental variables that occur in a given location throughout the year, as well as the latitude and differences between locations, the present work investigates the hypothesis that the intrinsic environmental variables of different environments, for example, latitude and rainfall, can result in a structural adjustment in the secondary xylem of *Bathysa cuspidata* and *Bathysa nicholsonii* in two different Atlantic Forest remnants. One of the studied remnants is in the Corredor Central of the Atlantic Forest in the Northeast Region of Brazil. The other is in Corredor da Serra do Mar of the Atlantic Forest in the Southeast Region. Therefore, the present work aimed to answer the following questions: (i) Are there anatomical traits that highlight adaptive strategies of the studied species of *Bathysa* in the different studied forest remnants? And, if so, (i) What can be inferred from the hydraulic system of the four analyzed tree groups?

## Materials and methods

Four individuals from *Bathysa cuspidata* (A. St. Hil.) Hook. F. and *Bathysa nicholsonii* K. Schum of approximately the same height and diameter breast height were (DBH) selected from interior areas the Dense Ombrophilous Rainforest in two forest remnants (Tab. 1) Reserva Particular do Patrimônio Natural Serra Bonita, Camacan, Bahia (RPPNSB-BA) and Reserva Biológica do Tinguá, Nova Iguaçu, Rio de Janeiro (REBIO - RJ). Wood samples were obtained non-destructively using a Pressler probe

**Table 1.** Coordinate, climate and precipitation of study sites.

| PARAMETERS | RPPNSB-BA | REBIO-RJ |
|---|---|---|
| Altitude | 200-950m | 100-850m |
| Latitude | 15º 23' S | 22º 39' S |
| Longitude | 39º 33' W | 43º34'W |
| Koppen Type of climate | Af (KÖPPEN, 1936) hot and wet, with no defined dry season | Cwb (wa) (KÖPPEN, 1936) hot and wet, with poorly defined dry season |
| Mean annual precipitation | 1,300 mm | 2,600mm |
| Minimum temperature | 17 ºC | 13 ºC |
| Maximum temperature | 33 ºC | 40 ºC |
| Relative humidity | 80 % | 85 % |
| Soil type | Red-Yellow dystrophic latosol; Red-Yellow dystrophic argisol; Red-Yellow eutrophic argisol and haplic chernosol | Cambisols, latosols and podzols, litolics with rocky outcrops |

(Increment Borer, SUUNTO, USA) at approximately 1.30 m above the ground (DBH). For arboreous individuals, samples were taken using a Pressler probe at approximately 1.30 m above the ground, whereas for shrubby individuals, samples were taken as stem disks using a machete. Part of the wood samples and permanent slides were deposited and registered in the wood collection of the Universidade Estadual do Norte Fluminense (HUENFw), whereas the remainder was used for anatomical identification and exsiccates were deposited at the Herbarium of Universidade Estadual do Norte Fluminense (HUENF). Wood samples were obtained from the sapwood, according to Coradin & Muniz (1992). The samples were sectioned with a sliding microtome (SM2010 R, Leica, Germany) in transverse and longitudinal (radial and tangential) planes, at an average thickness of 20 μm. Sectioned material was dehydrated in ethanol and stained with Astra Blue and hydro-alcoholic Safranin (Burger & Richter 1991). Wood fragments were subjected to dissociation by Franklin solution (1945), washed and stained with 1 % aqueous safranin. Anatomical measurements were performed using a light microscope (Axioplan Zeiss, Oberkochen, Germany); measurement techniques and terminology followed IAWA guidelines (IAWA committee 1989). To establish the relationship between the environment and the wood characters, vulnerability (VI = tangential diameter of vessels/vessel frequency) and mesomorphy (MI = VI x length of vessels) indices were calculated, following Carlquist (2001).
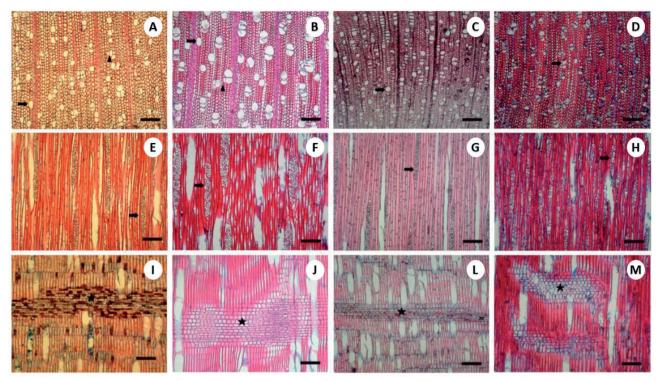
Samples for scanning electron microscopy were subjected to critical point drying with $CO_2$ (CPD 030, Baltec, Heerbrugg, Switzerland), adhered to stubs using carbon adhesive tape and covered with a layer of approximately 20 nm of gold (SCD 050, Baltec, Heerbrugg, Switzerland). Images were obtained using a ZEISS-DSEM 962 scanning electron microscope (Oberkochen, Germany) at a voltage of 25 kV.

Quantitative data were subjected to the Kolmogorov-Smirnov normality test (Hollander & Wolfe 1973). Nonparametric tests were used to verify the significance of the differences between species in the two forest remnants in Bahia and Rio de Janeiro, respectively, through multiple comparisons using the Kruskal-Wallis test (Kruskal & Wallis 1952). Analyses were performed with Statistica 7 software. The principal component analysis (PCA) was performed with the PC-ORD version 6.0 software, using a matrix with anatomical characteristics in columns and sampling units (individuals / species) in rows, to verify a possible pattern within plant traits describing plant strategies in the different environments.
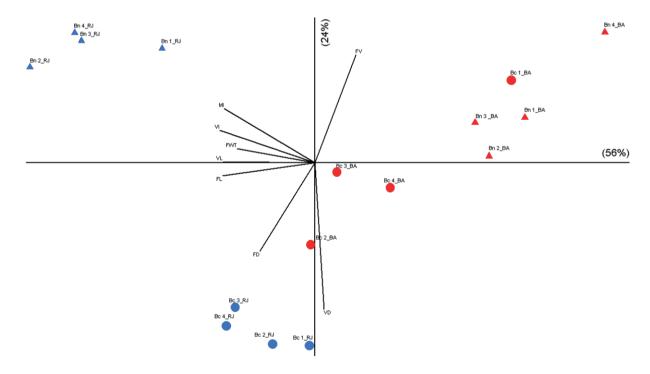
## Results

Anatomical traits of both *Bathysa cuspidata* and *B. nicholsonii* are shown in Table 2 according to sampling site, REBIO-RJ, and RPPNSB-BA. In general, the qualitative wood anatomy traits proved to be similar in both species regardless of the studied sites, showing: diffuse porosity; solitary vessels or in multiple radial arrangements of 2 to 4 elements; vessels with simple perforation plates located on inclined end walls and, sometimes, on side walls, and with alternate and ornamented intervessel pits; septate fibre-tracheids; axial parenchyma absent or extremely rare; and heterogeneous uniseriate and/or multiseriate rays formed by procumbent, upright and square cells (Fig. 1). The distinct traits for *B. cuspidata* (Figs. S1, S3) are indistinct or absent growth rings; lower vessel frequency; fibre-tracheids with thick walls; and multiseriate rays of 3 to 4 cells wide. The distinct traits for *B. nicholsonii* (Figs. S2, S4) are presence of poorly distinct growth rings, marked by the greater thickening and radial flattening of the fibres of the latewood; higher vessel frequency; uniseriate, biseriate and triseriate rays, sometimes fused; and the presence of tyloses.

Quantitative comparative analysis of wood anatomy in relation to the study areas (Tab. 2) revealed that vessel frequency and vessel wall thickness are greater in RPPNSB-BA for both species, however, tangential diameter of vessels and ray width did not differ between sampling areas for both species. In addition, both species had lower values for the vulnerability index, longer vessels and fibres, and larger intervessel pits at REBIO-RJ. The principal component analysis of the quantitative data explained 80% of the total variation in wood anatomical traits (Fig. 2) and ordered the four analyzed species separately. Axis 1 explained 56 % of

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**Figure 1.** Comparison of wood anatomy of co-occurring species at RPPNSB-BA and REBIO-RJ. **A, E, I**: sections in three planes of *Bathysa cuspidata* RPPNSB-BA, note smaller diameter and greater frequency of vessels (arrow, triangle). **B, F, J**: sections in three planes of *Bathysa cuspidata* at REBIO-RJ, note greater diameter and lesser density of vessels (arrow, star). **C, G, L**: sections in three planes of *Bathysa nicholsonii* at RPPNSB-BA, note greater vessel density and smaller width of rays (arrow, star). **D, H, M**: sections in three planes of *Bathysa nicholsonii* at REBIO-RJ, note lower vessel density and greater width of rays (arrow, star). Scale A-M = 100 μm.



**Figure 2.** Principal component analysis (PCA) with variables secondary xylem anatomical of *Bathysa cuspidata* RPPNSB-BA (Bc_BA, red circles), *Bathysa nicholsonii* at RPPNSB-BA (Bn_BA, red triangles) and *Bathysa cuspidata* at REBIO-RJ (Bc_RJ, blue circles), *Bathysa nicholsonii* at REBIO-RJ (Bn_RJ, blue triangles). FV=Frequency vessel, VL=Vessel length, VD=Vessel diameter, FD=Fiber diameter, FL=Fiber length, FWD=Fiber wall thickness, VI=Vulnerability index, MI=Mesomorphy index.

**Table 2.** Average and standard deviation of the quantitative parameters of the wood of the four Bathysa species studied.

| Parameters | Bathysa cuspidata (BA) | | | Bathysa cuspidata (RJ) | | | Bathysa nicholsonii (BA) | | | Bathysa nicholsonii (RJ) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Vessels** | | | | | | | | | | | | |
| Frequency (vessels/mm²) | 37.8 | ± | 10.1 | 29.0 | ± | 2.8 | 87.7 | ± | 16.7 | 60.0 | ± | 5.0 |
| Length (µm) | 1078.7 | ± | 171.9 | 1186.3 | ± | 231.0 | 908.1 | ± | 181.2 | 1335.9 | ± | 272.2 |
| Diameter tangential (µm) | 61.5 | ± | 9.0 | 85.6 | ± | 11.0 | 59.3 | ± | 8.6 | 48.8 | ± | 6.4 |
| Diameter radial (µm) | 69.7 | ± | 8.1 | 86.3 | ± | 15.2 | 60.5 | ± | 9.3 | 47.1 | ± | 6.9 |
| Vessel lumina area (µm²) | 4307.1 | ± | 912.0 | 6432.2 | ± | 1371.4 | 3666.6 | ± | 648.1 | 2458.9 | ± | 443.2 |
| Wall thickness (µm) | 4.62 | ± | 0.89 | 3.80 | ± | 0.50 | 3.72 | ± | 0.50 | 3.69 | ± | 0.50 |
| Intervessel pits (µm) | 3.04 | ± | 0.44 | 3.16 | ± | 0.36 | 2.66 | ± | 0.42 | 2.83 | ± | 0.32 |
| Vessel-ray pits (µm) | 3.08 | ± | 0.42 | 3.41 | ± | 0.38 | 2.65 | ± | 0.44 | 3.04 | ± | 0.35 |
| **Fibres** | | | | | | | | | | | | |
| Diameter (µm) | 30.7 | ± | 9.2 | 39.4 | ± | 6.7 | 32.3 | ± | 6.0 | 35.3 | ± | 5.2 |
| Lumina (µm) | 19.3 | ± | 6.9 | 23.9 | ± | 5.5 | 18.3 | ± | 4.3 | 16.5 | ± | 4.0 |
| Length (µm) | 1700.1 | ± | 160.6 | 1803.8 | ± | 143.6 | 1563.8 | ± | 163.5 | 1881.7 | ± | 126.6 |
| Wall thickness (µm) | 5.67 | ± | 1.42 | 7.81 | ± | 1.43 | 6.98 | ± | 1.55 | 9.37 | ± | 1.66 |
| Pits (µm) | 5.00 | ± | 2.18 | 7.34 | ± | 1.70 | 8.79 | ± | 1.87 | 120.24 | ± | 1.56 |
| **Radial parenchyma** | | | | | | | | | | | | |
| Frequency (Rays/mm) | 6.42 | ± | 1.46 | 4.96 | ± | 1.02 | 8.14 | ± | 2.29 | 11.71 | ± | 1.57 |
| Length (µm) | 684.4 | ± | 125.6 | 817.3 | ± | 119.2 | 656.1 | ± | 179.9 | 521.5 | ± | 68.1 |
| Width (µm) | 67.2 | ± | 14.0 | 81.1 | ± | 12.1 | 47.8 | ± | 11.2 | 46.1 | ± | 7.1 |
| Vulnerability Index | 1.76 | ± | 0.60 | 1.99 | ± | 0.47 | 0.70 | ± | 0.16 | 3.75 | ± | 0.64 |
| Mesomorphy Index | 188.3 | ± | 674.7 | 1681.9 | ± | 463.7 | 640.6 | ± | 200.1 | 4290.0 | ± | 1116.2 |

the total variation and ordered the RPPNSB-BA samples on the positive side of the axis and the REBIO-RJ samples on the negative side, regardless of species. The traits that most influenced this segregation were vessel frequency and diameter. Axis 2 explained 24 % of the variation and ordered the two species separately, with *B. cuspidata* negatively positioned on this axis and *B. nicholsonii* (RJ) positively positioned. The traits that most influenced this separation were fibre diameter and vessel length.

## Discussion

*Bathysa cuspidata* and *B. nicholsonii* wood was described and compared structurally for two different areas of the Atlantic Forest (Rio de Janeiro and Bahia), with traits being identified with value for the systematics of the genus and for species ecology in the forest environment. Our results suggest that some traits that can be considered taxonomically useful at the level of the genus for *Bathysa*, such as diffuse porosity or pores in multiple radials, simple perforation plate, absent axial parenchyma and septate fibre-tracheids with simple pits, which agree with the wood characteristics of Group II, according to Jansen *et al.* (2002).

Wood anatomical traits are essential in studies of ecological structural variation due to microclimatic changes (*e.g.*, Carlquist 1977; Campbell *et al.* 2018). In the present study, the wood anatomical traits showed different strategies of the species in the different remnants. At REBIO-RJ species showed lower frequency, higher vessel length, and vessel diameter; longer fiber and ticker fibre-tracheids walls;

and higher levels of vulnerability. In contrast, species from RPPNSB-BA showed higher frequency, and lower length, and diameter of vessels; lower length and thickness of walls of fibre-tracheids; and lower levels of vulnerability. Such traits may be associated with microclimate differences between the areas, resulting in adaptations to the hydraulic system of both species. These findings corroborate other studies of intraspecific variation in wood involving morphological, anatomical, and physiological traits. For example, Lens *et al.* (2004) analyzed ecological trends in tropical forests and described the importance of the amount of precipitation in influencing the continuous traits of wood. Melo Júnior *et al.* (2018) analyzed species under different climate and soil types and found differences in xylem structure favoring safety and water conduction efficiency, showing how hydraulic processes can influence plants.

Qualitatively, the studied species were very similar. Quantitatively, however, the species showed differences related to the distinct environmental pressures of the two analyzed sites, although not characterized as a set of convergent responses. Both species had larger vessel diameters and lower vessel frequencies in REBIO-RJ compared to RPPNSB-BA. These traits reflect a tradeoff between efficiency and safety in water transport, corroborating to Carlquist (2001); Melo Junior *et al.* (2018) and Simioni *et al.* (2020).

The environmental variables occur at a given location throughout the year, latitude, and between sites. For example, annual rainfall is greater in REBIO RJ. Individuals in the REBIO-RJ have greater vessel length and diameter, slightly larger intervascular pits than individuals in RPPNSB-

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BA, suggesting that the vessels have smaller diameters and lengths in drier environments (Luchi 2004; Lima *et al.* 2009). Furthermore, longer vessels offer less resistance in the cell wall, favoring higher resistance and greater conductive efficiency (Sperry *et al.* 2005).

At RPPNSB-BA, both species had a majority of relatively long vessels, ranging from 1335.9 µm to 846.71 µm. They both also had higher vessel frequencies and smaller vessel diameters, shorter vessel lengths, lower vulnerability indices, and greater thickness of fibre-tracheids, which together represent a strategy that provides greater safety in water conduction. These differences in anatomical wood traits can be attributed to the structural adjustments of individuals in the different areas (Lens *et al.* 2004; Melo Júnior *et al.* 2018; Costa *et al.* 2020).

Although fibres or fibre-tracheids vary in length and width in the wood, the sampling of the present study was standardized for the same collection time, tree diameter, and the distance from bark (sapwood), allowing comparisons to be made of the length of these cells between the four groups. In this sense, fibre-tracheids were shown to be longer and wider at REBIO-RJ, corroborating previous studies that related greater fibre length to environments with greater precipitation (Carlquist 1975; Barajas-Morales 1985; Noshiro & Baas 2000). Mesomorphy indices above 200 indicate species from mesic environments, while values below 200 indicate plants from xeric environments (Carlquist 1977). In the present study, both species showed mesomorphy indices well above 200, corroborating with other results obtained for Rubiaceae in mesic environments of the Atlantic Forest (*e.g.*, Callado *et al.* 2003; Marques *et al.* 2015; Campbell *et al.* 2016; Melo Júnior *et al.* 2017).

Based on the ecological anatomy of Carlquist, Olson (2020) established the vulnerability index by relating vessel frequency to vessel diameter because they are traits that demonstrate the risk of embolism. That is, the lower the index, the safer the conductive element and, consequently, the lower its hydraulic conductivity. In the present study, the vulnerability indices were near 1, and only lower for *B. nicholsonii* at RPPNSB-BA, which may reflect an adjustment to the local climatic conditions with less annual rainfall. This adjustment characterizes greater safety in the hydraulic system by reducing the risk of embolism and cavitation and corroborates other studies with species from different environments (Longui *et al.* 2009; Campbell *et al.* 2018, Melo Junior *et al.* 2018).

The differences in microclimatic conditions between the two areas favored structural adjustments to hydraulic traits, such as vessel frequency, length, and diameter. These traits were also shown to be greater in REBIO-RJ, representing a strategy that favors transport efficiency. This improved efficiency is due to the lumen having a greater volume and capacity for water transport, which contrasts with the conservative strategy of the species at RPPNSB-BA, with higher density, smaller diameter, and shorter length

for the vessels. These are traits that provide safe transport and less risk of cavitation and have been shown to be wood anatomical traits that are influenced by the environment (Baas *et al.* 2004; Poorter *et al.* 2010; Marques *et al.* 2015; Campbell *et al.* 2016, 2018; Melo Junior *et al.* 2018; Costa *et al.* 2020; Vasconcelos & Callado 2020).

Both studied areas varied in precipitation, but the REBIO-RJ shows higher rainfall, although geographically distant. As a result, higher frequency, shorter length, and smaller vessel diameter providing both species greater safety in transport at RPPNSB-BA. In contrast, at REBIO-RJ, both species have vessels with larger diameters and longer lengths, which is more efficient for transport. Thus, the traits found confer different strategies for the same species in different environments, suggesting responses to different macro- and micro-environmental pressures.

Although each species hydraulic system shows acclimatization variations to different sites of occurrence, the structural differences in wood ensured the structural adjustments between the species studied in each of these sites. These results corroborate the relevance of the wood anatomy studies as a subsidy for a better definition of morphologically similar taxa and show structural aspects aimed at survival in the Atlantic Forest. The combination of anatomical and environmental traits is often neglected. Here we showed that this combination could be an essential tool to understanding tropical biodiversity.

## Acknowledgments

## References

Aubin I, Munson AD, Cardou F, et al. 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. Environmental Reviews. 24: 164-186.

Baas P. 1973. The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea: Biodiversity, Evolution and Biogeography of Plants 21: 193-260.

Baas P, Ewers FW, Davis SD, Wheeler EA. 2004. Evolution of xylem physiology. In: Helmsley AR, Poole I (eds.), The Evolution of Plant Physiology. London, Elsevier Academic Press. p. 273-295.

Baldin T, Sielgloch AM, Marquiori JNC, Denardi L. 2016. Análise comparativa da anatomia da madeira de 41 espécies de Rubiaceae sob enfoque taxonômico. Boletin de la Sociedad Argentina de Botanica 51: 623-634.

Barajas-Morales J. 1985. Wood structural differences between trees of two tropical forests in Mexico. IAWA Bulletin 6: 355-364.

Burger LM, Richter HG. 1991. Anatomia de madeira. São Paulo, Nobel.

Callado CH, Silva Neto SJ. 2003. Anatomia do lenho de três espécies do gênero *Simira* Aubl. (Rubiaceae) da Floresta Atlântica no Estado do Rio de Janeiro. Rodriguésia 54: 23-53.

Campbell G, Rabelo GM, Da Cunha M. 2016. Ecological significance of wood anatomy of *Alseis pickelii* Pilg. & Schmale (Rubiaceae) in a Tropical Dry Forest. Acta Botanica Brasilica 30: 124-130.

Campbell G, Mielke MS, Rabelo GM, Da Cunha M. 2018. Key anatomical attributes for occurrence of *Psychotria schlechtendaliana* (Müll.Arg.) (Rubiaceae) in difference successional stages of a tropical moist forest. Flora 246-247: 33-41.

Carlquist S. 1977. Ecological factors in wood anatomy: a floristic approach. American Journal of Botany 64: 887-896.

Carlquist S. 1975. Ecological strategies of xylem evolution. Berkeley, University of California Press.

Carlquist S, Zona S. 1988. Wood anatomy of Papaveraceae, with comments on vessel restriction patterns. IAWA journal 9: 253-267.

Carlquist S. 2001. Comparative wood anatomy. Systematic, ecological and evolutionary aspects of dicotyledonous wood. 2 ed. Berlin, Springer Science & Business Media.

Coradin VTR, Muniz GI. 1992. Norma e procedimentos em estudos de anatomia da madeira: Angiospermae II-Gimnospermae. Série Técnica 15. IBAMA. DRPED.LPF. Brasília. p. 17.

Coradin VTR, Camargo JAA. 2002. A Estrutura Anatômica da Madeira e Princípios para a sua identificação. Brasília: IBAMA, LPF.

Costa WS, Da Cunha M, Rodrigues PJFP, Iguatemy MA, Valladares F, Barros CF. 2020. Intraspecific variation in functional wood anatomy of tropical trees caused by effects of forest edge. Forest Ecology and Management 473: 118305.

Franklin GL. 1945. Preparation of thin sections of synthetic resins and wood-resin composites, and a new macerating method for wood. Nature 155: 51.

Germano-Filho P. 1999. Estudos taxonômicos do gênero *Bathysa* C. Presl (Rubiaceae, Rondoletiae) no Brasil. Rodriguésia 50: 49-75.

Gianoli E, Valladares F. 2012. Studying phenotypic plasticity: the advantages of a broad approach. Biological Journal of the Linnean Society 105: 1-7.

Guedes-Bruni RR. 1998. Composição, estrutura e similaridade florística de dossel em seis unidades fisionômicas de Mata Atlântica no Rio de Janeiro. PhD Thesis, Universidade de São Paulo, São Paulo.

Gratani L. 2014. Plant phenotypic plasticity in response to environmental factors. Advances in Botany 2014: 1-17.

Hacke UG, Sperry JS, Wheeler JK, Castro L. 2006. Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiology. 54: 689-701.

Hacke UG, Lachenbruch B, Pittermann J, Mayr S, Domec JC, Shulte PJ. 2015. The hydraulic architecture of conifers. In: Hacke U (eds). Functional and Ecological Xylem Anatomy. Switzerland, Springer. p. 39-75.

Hollander M, Wolfe DA. 1973. Nonparametric statistical methods. New York, John Wiley & sons.

IAWA Committee. 1989. IAWA list of microscopic features for hardwood identification. IAWA Bull 10: 218-359.

Jansen S, Robbrecht E, Beeckman H, Smets E. 2002. A survey of the systematic wood of the Rubiaceae. IAWA Journal 23: 1-67.

Kruskal WH, Wallis WA. 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47: 583-621.

Lens F, Luteyn JL, Smets E, Jansen S. 2004. Ecological trends in the wood anatomy of Vaccinioideae (Ericaceae s.l.). Flora 199: 309-319.

Lens F, Baas P, Jansen S, Smets E. 2007. A search for phylogenetically informative wood characters within Lecythidaceae sl. American Journal of Botany 94: 483-502.

Lima RS, Oliveira P, Rodrigues LR. 2009. Anatomia do lenho de *Enterolobium contortisiliquum* (Vell.) Morong (Leguminosae-Mimosoideae) ocorrente em dois ambientes. Revista Brasileira de Botânica 32: 361-374.

Longui EL, Bufolo A, Aguiar OT, Lima IL, Florshein SMB. 2009. Anatomia comparada do lenho de *Piptadenia gonoacantha* (Mart.) J.F. Macbr em dois tipos de vegetação. Hoehnea 36: 715-724.

Luchi AE. 2004. Anatomia do lenho de *Croton urucurana* Baill. (Euphorbiaceae) de solos com diferentes níveis de umidade. Revista Brasileira de Botânica 27: 271-280.

Macedo TM, Lima HC, De Souza ND, et al. 2019. Intraspecific variation of *Paubrasilia echinata* (Fabaceae) wood along a latitudinal gradient in Brazil. Flora 258 :151437.

Marques JBC, Callado CH, Rabelo GR, Silva Neto SJS, Da Cunha M. 2015. Comparative wood anatomy of species of *Psychotria* L. (Rubiaceae) in Atlantic Rainforest remnants of Rio de Janeiro State, Brazil. Acta Botanica Brasilica 29: 433-444.

Marques PA, Callado CH, Barros CF, Costa CG. 2012. Variação intraespecífica do lenho de *Eugenia uniflora* L. Floresta e Ambiente 19: 423-496.

Melo Júnior JCF, Amorim MW, Oliveira GB, Vieira CV. 2017. Wood functional anatomy of Chiococca alba hitch. (Rubiaceae) from cerrado. Acta Biológica Santa Catarina 4: 52-61.

Melo Júnior JCF, Amorim MW, Soffiatti P. 2018. Comparative wood anatomy of *Ficus cestrifolia* (Moraceae) in two distinct soil conditions. Rodriguésia 69: 2109-2118.

Missio FF, Silva AC, Higuchi P, et al. 2017. Functional traits of tree species in a fragment of Araucaria Forest in Lages, Santa Catarina State. Ciência Florestal 27: 215-224.

Noshiro S, Baas P. 2000. Latitudinal trends in wood anatomy within species and genera: case study in *Cornus* s.L. (Cornaceae). American Journal of Botany 87: 1495-1506.

O'Brien MJ, Engelbrecht BMJ, Joswig J, et al. 2017. A synthesis of tree functional traits related to drought-induced mortality in forests across climatic-zones. J Appl Ecol 54:1669-1686

Oliveira-Filho AT, Fontes MAL. 2000. Patterns of floristic among Atlantic Forests in southern Brazil and the influence of climate. Biotropica 32: 793-810.

Olson ME. 2020. From Carlquist's ecological wood anatomy to Carlquist's Law: why comparative anatomy is crucial for functional xylem biology. American Journal of Botany 107: 1328-1341.

Pio Correa, M. 1984. Dicionário das plantas úteis do Brasil e das exóticas cultivadas. Rio de Janeiro, Instituto Brasileiro de Desenvolvimento Florestal.

Poorter L, McDonald I, Alarcón A, et al. 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforests tree species. New Phytologist 185: 481-492.

Rezende CL, Scarano FR, Assad ED, et al. 2018. From hotspot to hopespot: Na opportunity for the Brazilian Atlantic Forest. Perspective in Ecology and Conservation 16: 208-214.

Rosas T, Mencuccini M, Barba J, Cochard H, Saura-Mas S, Martínez-Vilalta J. 2019. Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient. New Phytologist 223: 632-646.

Scarano FR. 2002. Structure, function and floristic relationships of plants communities in stressful habitats marginal to Brazilian Atlantic Rainforest. Annals of Botany 90: 517-524.

Simioni P, Campbell G, Pinto VD, et al. 2020. Do anatomical wood traits suggest adjustments in the hydraulics architecture of dominant species in Amazonian savannah? Plant Biosystems 154: 1-20.

SOS Mata Atlântica & INPE. 2019. Atlas dos remanescentes florestais da Mata Atlântica. São Paulo, SOS Mata Atlântica and INPE.

Sperry JS, Hacke UG, Wheeler JK. 2005. Comparative analysis of end wall resistance in xylem conduits. Plant, Cell and Environment 28: 456-465.

Trueba S, Pouteau R, Lens F, et al. 2017. Vulnerability to xylem embolism as a major correlate of the environmental distribution of rain forest species on a tropical island. Plant, Cell & Environment, 40: 277-289.

Tyree MT, Zimmermann MH. 2002. Hydraulic Architecture of Whole Plants and Plant Performance. In: Xylem structure and the ascent of sap. Berlin, Springer. p. 175-214.

Valladares F, Sanchez-Gomez D, Zavalat MA. 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. Journal of Ecology 94: 1103-1116

Vasconcelos TJ, Callado CH. 2020. Wood anatomy of *Ceiba speciosa* (A. St.-Hil.) Ravenna under urban pollution. IAWA Journal 41: 30-47.

Zanne AE, Westoby M, Falster DS, et al. 2010. Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. American Journal of Botany. 97: 207-215.

Zuidervaart HJ, Anderson D. 2016. Antony van Leeuwenhoek's microscopes and other scientific instruments: new information from the Delft archives. Annals of Science 73: 257-288.