Brazilian Journal of Botany (2026) 49:8
https://doi.org/10.1007/s40415-026-01132-8

STRUCTURAL BOTANY - ORIGINAL ARTICLE

Ecological trends in the xylem anatomy of *Tapirira guianensis* Aubl. (Anacardiaceae) in mesic and hydromorphic soils in the lowland Atlantic forest

Alessandra Mara Gogosz[1] · Nelson Luiz Cosmo[2] · Paulo César Botosso[3] · Franklin Galvão[2]

Received: 29 July 2025 / Revised: 1 January 2026 / Accepted: 3 January 2026
© The Author(s) 2026

Abstract
This study investigates whether intraspecific variations in the secondary xylem traits of *Tapirira guianensis* occur in response to local edaphic conditions, despite a uniform climate and vegetation type. Wood samples from this species were collected from two soil types—Podzol and Histosol—in the lowland Atlantic Forest along Brazil's southern coastal plain. Histological sections and dissociated material were prepared for qualitative and quantitative anatomical analyses. Principal component analysis and mean comparison tests were used to assess anatomical differences between soil types. The results reveal significant trait variation, with greater vessel grouping, higher vessel density, smaller vessel diameter, and shorter vessel elements in Podzol, a mesic soil, compared to Histosol, an organic and hydromorphic soil. This suggests an investment strategy in xylem that enhances resistance to cavitation in soils with lower water availability, aligning with interspecific and intraspecific trends observed in other studies. Trees in Histosol exhibited a higher percentage of gelatinous fibers, suggesting these cells may help stabilize stem growth in response to substrate instability and/or mitigate the physiological drought effects from prolonged flooding. Allometric patterns were also detected: vessel diameter was negatively correlated with vessel density, and positively correlated with vessel element length and fiber length. Vessel grouping was positively correlated with vessel density. The results indicate that even under homogeneous climatic and vegetational conditions, edaphic gradients can significantly influence xylem anatomy. These findings highlight *T. guianensis*'s xylem plasticity, which may contribute to its resilience to both flooding and drought stress.

Keywords Dense ombrophilous forest · Ecological plasticity · Functional wood anatomy · Peat soil · Swamp forest

1 Introduction

Plants exhibit diverse structural and functional responses to environmental variations, which are crucial for understanding community and ecosystem dynamics (Westoby and Wright 2006). Factors such as geopedological conditions (Cosmo et al. 2024b), soil texture (Sperry and Hacke 2002), humidity, salinity (Ennajeh et al. 2023), soil pH, and toxicity (Dória et al. 2016) influence plant structure and function, driving variation among individuals and species. These responses encompass a range of strategies, including phenological adjustments, variations in rooting depth (Sperry and Hacke 2002), stomatal control (Comstock and Mencuccini 1998), and anatomical responses in leaves, roots, and stems (Ennajeh et al. 2023).

Functional traits of the secondary xylem can provide insights into the efficiency of the conductive system, its vulnerability to cavitation (Carlquist 2001; Hacke and Sperry 2001; Mauseth and Stevenson 2004; Pratt et al. 2012), storage capacity (Plavcová et al. 2023), and biomechanical attributes (Jacobsen et al. 2007; Martínez-Cabrera et al. 2009). Wood anatomical traits exhibit various ecological responses to environmental factors such as latitude, altitude, and water availability (Baas and Wheeler 2011). These responses can be interpreted at different taxonomic levels and scales, ranging from broad floristic patterns

✉ Nelson Luiz Cosmo
ncosmo@ufpr.br

[1] Graduate Program in Ecology and Conservation, Federal University of Paraná, Curitiba, Paraná 81531-980, Brazil

[2] Graduate Program in Forest Engineering, Federal University of Paraná, Curitiba, Paraná 80210-170, Brazil

[3] Brazilian Agricultural Research Corporation - EMBRAPA Forestry, Colombo, Paraná 83411-000, Brazil

Published online: 23 January 2026

(Carlquist 1977; Baas et al. 1983; Segala Alves and Angyalossy-Alfonso 2000; Jacobsen et al. 2007; Martínez-Cabrera et al. 2009; Zanne et al. 2010; Fichtler and Worbes 2012), to genus (Baas 1973; Noshiro and Baas 2000; Choat et al. 2007; Arenas-Navarro et al. 2021; Percolla et al. 2021), to species-specific responses (Liu and Noshiro 2003; Fisher et al. 2007; Silva da Costa et al. 2020; Cosmo et al. 2024a; Cosmo et al. 2024b).

Although high intraspecific variation can occur in response to both broad gradients and microhabitat heterogeneity, this variation in xylem is less understood than interspecific trends. Genetic differences and phenotypic plasticity provide plant species with a greater ecophysiological capacity to respond to highly selective and heterogeneous environments (Ackerly 2000; Westerband et al. 2021). Variation in functional traits that play a key roles in the performance of individuals and populations is crucial for understanding plant-environment interactions, as well as intraspecific and interspecific interactions, and their influence on the structure of communities and ecosystems (Albert et al. 2010; Westerband et al. 2021).

In drier conditions, plants must withstand more negative xylem tensions and develop strategies to minimize cavitation in the xylem, even at the cost of reducing water conduction capacity (Lens et al. 2011). Common anatomical responses in drier environments compared to more moist sites include narrower vessels (Stevenson and Mauseth 2004; Dória et al. 2016), greater vessel density (Castelar et al. 2023; Nery et al. 2023), and increased vessel clustering (Longui et al. 2014). Similar trends can also occur in humid subtropical and tropical climates due to variations in precipitation (Castelar et al. 2022) or soil drainage (Callado et al. 2024; Cosmo et al. 2024b).

Information on xylem variations along mesic-to-hydromorphic gradients is particularly scarce, and the observed trends are less clear (Cosmo 2012; Cosmo 2024a). Some species exhibit responses in flooded soils that are typically expected under conditions of reduced water availability, such as increased vessel density, greater vessel clustering, and/or decreased vessel diameter compared to mesic conditions (Kolb et al. 1998; Bianchini et al. 2000; Luchi 2004; Cosmo et al. 2024b). Other species show trends more similar to those observed when mesic sites are compared to dry environments, such as lower vessel density, wider vessels, and less vessel grouping under flooding compared to mesic sites (Parvin et al. 2018; Bhusal et al. 2020; Callado et al. 2024; Cosmo et al. 2024a). These unclear trends highlight the need for further studies on xylem anatomy in hygrophilous and hydrophilous species.

Species that naturally occur in contrasting conditions or across ecological gradients are particularly useful for investigating such responses. In swamp forests, diversity is directly related to the ecophysiological variability and plasticity of each species (Duarte et al. 2005). Generalist and mesophilic species contribute to increased richness, while species more tolerant to flooding significantly influence forest structure, successional dynamics, and nutrient retention due to their high population density and dominance (Galvão et al. 2002; Marques et al. 2003; Souza and Marques 2010). Among the species that stand out in these environments on the coastal plain of southern Brazil, *Tapirira guianensis* Aubl. (Anacardiaceae) is one of the most common and often exhibits high dominance.

Tapirira guianensis occurs across a wide range of vegetation types and climatic conditions (Miranda et al. 2011; Oliveira et al. 2012; Carvalho et al. 2017; Hollunder et al. 2021). It is particularly prominent in various humid tropical forests and their transitional zones with the Savanna and Caatinga biomes (Ratter et al. 2003; Oliveira-Filho et al. 2005; Chiminazzo et al. 2021). This species often display high density and dominance values across broad altitudinal and latitudinal gradients and plays a crucial role in biomass production within the litter layer (Oliveira et al. 2012; Maçaneiro et al. 2015; Araujo et al. 2019; Hollunder et al. 2021). In lowland forests of the Atlantic Forest biome, it is one of the most important species for nutrient retention and cycling (Protil et al. 2009).

This species is capable of maintaining high water potentials even under conditions of water deficit, due to responses that involve phenological adjustments, water storage in the xylem, and the development of new leaves with greater stomatal control (Miranda et al. 2011). Given its ability to survive and grow in adverse edaphic conditions, including water deficit, soil compaction, and restricted drainage, *T. guianensis* shows potential for the restoration of degraded areas in alluvial environments (Gama et al. 2020) and degraded savanna areas affected by mining processes (Vieira et al. 2022).

Its wide distribution and ability to tolerate contrasting conditions, ranging from water deficit to flooding in swamp forests, make *T. guianensis* a promising species for understanding intraspecific variations in xylem structure. In the coastal plain of southern Brazil, it occurs in both hydromorphic soils and more mesic conditions, with relative importance in both environments (Galvão et al. 2002).

Considering the species' plasticity and existing knowledge on intraspecific variations in plants at the local scale (Sperry and Hacke 2002; Ennajeh et al. 2023; Cosmo et al. 2024a, 2024b), this study aims to address the following questions: i) Does *T. guianensis* exhibit intraspecific variation in its xylem across populations in the same vegetation type, and that experience the same macroclimatic conditions, but grow in different soils? ii) Are the xylem responses of *T. guianensis* to mesic and hydromorphic soils consistent with general trends in xylem responses to water availability, or does flooding induce distinct anatomical variations

compared to the typical contrast between dry and mesic environments?

To test these hypotheses, the anatomical traits of the secondary xylem of *T. guianensis* were analyzed in two soil types: Podzol and Histosol. The microrelief and sandy texture of Podzol create mesic conditions compared to Histosol, an organic and hydromorphic soil. Both sampling locations are in the lowland Atlantic Forest, under a superhumid tropical climate, on the coastal plain of southern Brazil.

2 Material and methods

Collection sites – Trees of *Tapirira guianensis* were sampled in areas of the Atlantic Forest on the coastal plain of the state of Paraná, Brazil. In the Palmito State Forest (Paranaguá municipality), six trees were sampled in Podzol. In the municipality of Matinhos, five trees were sampled in Histosol. The two locations are approximately 20 km apart and both are situated in recent marine sediments of coastal plains, dating from the Quaternary-Holocene (Mineropar 2001). The climate is Super Humid Tropical, without a dry season and free from frost, Köeppen Af type, with an average annual temperature between 19 and 21 °C, average maximum temperatures between 26 and 27 °C and minimum temperatures between 17 and 18 °C. The average temperature of the coldest month varies from 15 to 17 °C and that of the hottest month, from 23 to 26 °C. The annual precipitation in the region varies from 2000 to 2600 mm (IDR 2019).

Podzol primarily develops from quartzose sands in high-moisture conditions within tropical and subtropical climates, typically on flat terrain and in depressions. However, in the sampled area, local topographic variations can create variable hydromorphic conditions, with sandbars characteristic of the Quaternary plain (Scarano 2002). The Podzol in this area is very sandy (over 75%), acidic (pH < 4), and of low fertility (Sereda et al. 2016), and is occupied by the lowland Atlantic Forest, where *T. guianensis* often stands out as a dominant canopy species (Roderjan et al. 2002). The sandy texture and microrelief positions (mainly on the tops of sandbars) frequently create more mesic conditions compared to Histosol.

The sampled area in Histosol is located in a broad and deep floodplain, characterized by a shallow water table and continuous flooding. These conditions lead to the formation of hydromorphic soils with a thick acidic organic layer overlying a sandy substrate, containing more than 2 m of dystrophic organic fibric-woody material (Rachwal and Curcio 2001; Galvão et al. 2002). The accumulation of plant residues in varying stages of decomposition is due to anaerobic conditions, which restrict organic matter mineralization and soil development (EMBRAPA 2018). These features drive the occurrence of herbaceous and arboreal pioneer formations with fluvio-lacustrine influence in the region, locally known as caxetal. During the successional process, these formations can evolve into more complex and biodiverse ecosystems, classified as Lowland Atlantic Forest. This is the case in the sampled area, which is dominated by hydrophilic specialists such as *Tabebuia cassinoides* (Lam.) DC. and *Calophyllum brasiliense* Cambess., along with more than 30 other tree species, including *T. guianensis* (Galvão et al. 2002).

Collection and preparation of samples – In both locations, adult, dominant trees with straight bole were selected, with an average height of 12 m and an average trunk diameter of 25 cm. Wood samples were collected from the trunk at 1.30 m height, with a depth of 20 mm, using an increment borer (Pressler, 12 mm in diameter). The samples were stored in 70% ethanol. For microscopic analyses, they were sectioned using a sliding microtome in transverse, radial, and tangential planes. The sections were stained in an alcoholic solution (30%) with Astra blue (1%) and Safranin (1%) in a ratio of 9:1, dehydrated in an ethylic series, and mounted on permanent slides. The samples were also subjected to maceration in a solution of glacial acetic acid and hydrogen peroxide (1:1) (Franklin 1945). The macerated material was stained with Safranin solution (1%), dehydrated in an alcoholic series, and prepared on permanent slides. Both the sections and macerated material were mounted between a slide and coverslip using the synthetic resin Entellan.

Anatomical study – The anatomical description was carried out based on the classification proposed by the International Association of Wood Anatomists (IAWA Committee 1989).

The histological sections were photographed under an optical microscope at high resolution (2592 × 1944 pixels), to quantify the vessel density/mm^2 (VD) and mean vessel lumen diameter (MVD). Six fields per sample were considered, measured with an average of 60 vessels per sample. All vessel elements in each field were automatically measured and counted, using the Sigma Scan-Pro 5.0 software. This procedure also made it possible to measure the vessel lumen area and the total vessel area per field (TVA), which was used to estimate the vessel lumen fraction (VLF), in percentage, dividing TVA by the field area (FA):

$$\mathrm{VLF} = \mathrm{TVA/FA} \times 100$$

During the tabulation of data, vessels were categorized by classifying them as solitary (1) or multiple (2, 3, 4, 5…), using the average of these values as the vessel grouping index (VG). The vessel element length (VEL) was also recorded; fiber diameter (FD); fiber length (FL); fiber wall thickness (FWT); ray height (RH), in nº of cells and in µm; ray width, in µm (RW). All these measurements were

performed using an eyepiece with a graduated optical microscope scale, with 30 measurements taken per tree.

To estimate the percentage of fibers with gelatinous layer were taken photographs of 20 fields per sample, each measuring 100 × 80 microns. The fields were systematically distributed across the sample, avoiding areas that included vessels. In each field, the total number of fibers (NF) and the number of gelatinous fibers (NGF) were counted, and the fraction of gelatinous fibers (FGF) was calculated using the formula:

$$FGF = NFG/NF.100$$

Additionally, vulnerability indices (V = MVD/VD) and mesomorphy indices (M = (MVD × VEL)/VD) were estimated, following the method described by Carlquist (2001).

For all the variables analyzed were calculated the Relative Distance Plasticity Index (RDPI) and Phenotypic Plasticity Index (PPI), were both ranging from 0 (no plasticity) to 1 (maximal plasticity), according to Valladares et al. (2006):

$$RDPI = \Sigma(dij \rightarrow i\prime j\prime/(xi\prime j\prime + xij))/n$$

where "d" is the pairwise distance among trait values between individuals (j) of different soils (i), which are computed and divided by the sum of the corresponding pair of trait values to obtain relative distances. The total number of distances (n) divides the sum of these relative distances.

The Phenotypic Plasticity Index (PPI) was calculated based on the maximum (Max) and minimum (Min) means for each trait:

$$PPI = (Max - Min)/Max$$

These indices were applied primarily to assess the range of intraspecific variation in the studied species and to compare them with others, rather than to evaluate actual phenotypic plasticity, which requires a specific design that distinguishes between genetic and environmental influences.

Data analysis – For the data analysis and graph development, the software R (R Core Team 2022), version 4.2.2 (2022–10-31 ucrt), and RStudio Desktop were used. The Bartlett test (bartlett.test()) was applied to verify the homogeneity of variances, and means were compared using the t-test (t.test()), both implemented in the stats package, considering a significance level of $\alpha = 0.05$. Principal Component Analysis (PCA) was conducted to evaluate the data structure and identify the attributes that contributed most to the variation, using the function prcomp() from the same package. Prior to the analysis, the data were standardized with the function decostand() from the vegan package (Oksanen et al. 2022).

3 Results

Tapirira guianensis wood is diffuse-porous, with vessels arranged in diagonal and/or radial patterns (Fig. 1a, b), occurring singly or in multiples of 2 to 4. Vessel density ranges from 13.0—25.6—41.9 vessels/mm^2, with tangential diameter of 76.0—57.2—93.2 µm and vessel element lengths of 67.4—90.6—110.8 µm, often showing short tails at one or both ends. Vessel outlines are circular to oval, with simple perforation plates (Fig. 1c, d). Septate fibers measure 805—1117—1364 µm in length, with thin to thick walls (3.9—4.2—4.7 µm). Gelatinous fibers are present (Fig. 1e, f), identifiable by a bright blue layer in double-stained sections, and appear dispersed in the fiber matrix, in small clusters, or, in some samples, as continuous bands, particularly in earlywood. Axial parenchyma is scanty paratracheal. Rays are composed of procumbent body cells, and one or two rows of upright or square marginal cells (Fig. 1g), 2–3 cells wide (26.1—30.7—42.2 µm) and 15—32—48 cells high (306—369—468 µm). Rays with secretory canals are present (Fig. 1h, i). Idioblasts containing rhombohedral crystals are found at the ray margins, and silica bodies are present in procumbent cells (Fig. 1j). Vessel-ray pits have highly reduced borders to a nearly simple form, with rounded outlines (Fig. 1k, l), while intervessel bordered pits are alternate and polygonal (Fig. 1m–o).

The first two principal axes of the PCA account for approximately 65% of the variance in the data, while the first three axes account for about 75%. The traits are shown in Fig. 2a in descending order of relevance on the first axis of variation, based on the eigenvectors. The first component (Fig. 2b) is mainly associated with vessel traits: vessel density per mm^2 (VD), mean vessel diameter (MVD), vessel grouping index (VG), vessel element length (VEL), and gelatinous fiber fraction (GF). The second axis is primarily characterized by fiber diameter (FD), fiber length (FL), and ray height (RH). Vessel lumen fraction (VLF) and ray height (RH) are the variables most correlated with the third axis (Fig. 2c). The remaining traits contribute less to the overall variance in the data.

The Relative Distance Plasticity Index (RDPI) ranged from 0.04 to 0.54, while the Phenotypic Plasticity Index (PPI) varied from 0.02 to 0.58. Factors such as the fraction of gelatinous fibers, vessel grouping, vessel density, mesomorphy, and vulnerability exhibited the highest plasticity indices. In trees grown in Podzol, there is a higher vessel grouping index (VG), smaller mean vessel diameter (MVD), and higher vessel density (VD) compared to those grown in Histosol. The vessel lumen fraction (VLF) is greater in trees from Podzol, with a significance level of 0.07. In contrast, the vessel element length (VEL) is greater in trees from Histosol, with a significance level of 0.08 (Table 1).

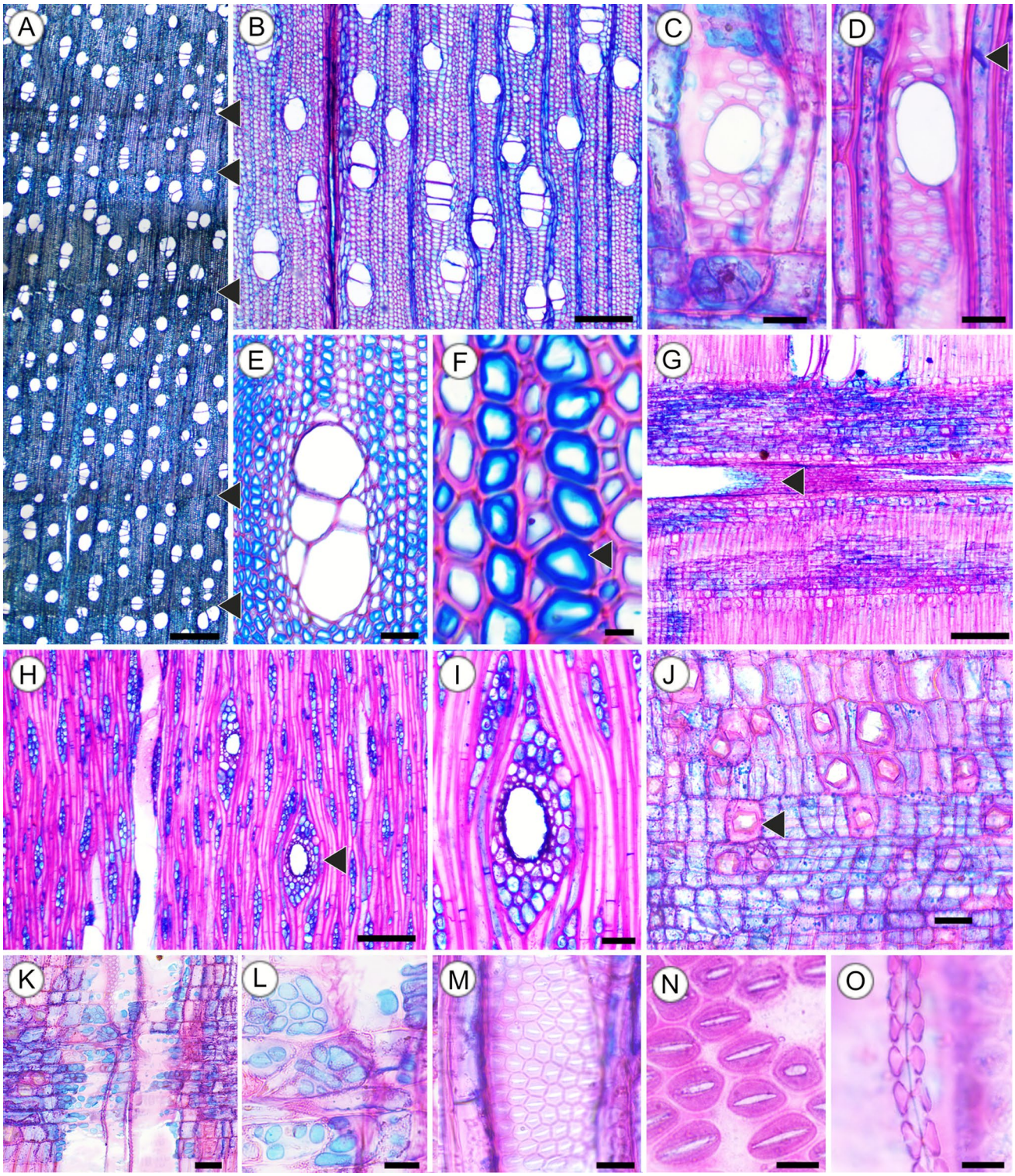


Fig. 1 Xylem anatomical traits of *Tapirira guianensis* Aubl.: **A**: cross-section showing poorly distinct growth rings, demarcated by flattening of the fibers and/or greater thickness of their walls in the latewood; **B**: Difuse porosity with solitary and multiples vessels, in cross-section; **C**, **D** simple perforated plate in radial and tangential sections, respectively (arrow point to fiber sept); **E**, **F**: gelatinous fibers in cross-section (arrow in G-layer); **G**: radial section with the secretory channel; **H**: tangential section; **I**: detail of the secretory channel, in tangential section; **J**: radial section, with prismatic crystals (arrow); **K**, **L** vessel to rays pits in radial section; **M**–**O**: intervessel pits. Scale bars: A = 500 µm; B = 200 µm; C, D = 200 µm; E = 50 µm; F = 10 µm; G, H = 50 µm; I, J = 20 µm; K = 50 µm; L, M = 20 µm; N, O = 10 µm

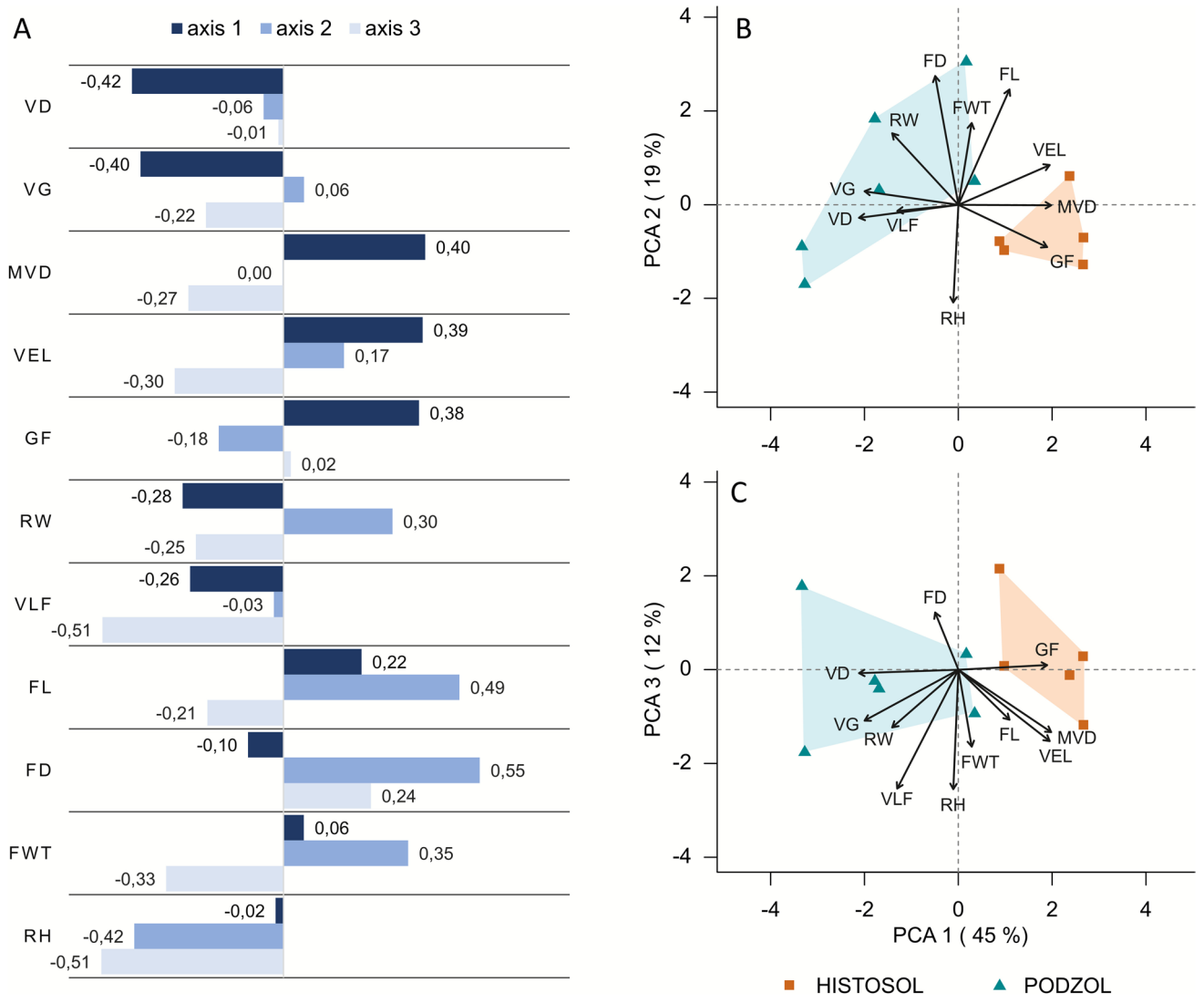


Fig. 2 Principal Component Analysis from xylem anatomical features of *Tapirira guianensis*, in two soil types (Histosol and Podzol), in a coastal plain, in southern Brazil. **A**: Traits in descending order of relevance for the first axis of variation, based on the eigenvectors. **B**: axis 1 and 2 of PCA, **C**: axis 1 and 3 plot. Vessel lumen fraction (VLF), vessel grouping index (VG), mean vessel diameter (MVD), vessel density (VD), vessel element length (VEL), gelatinous fiber fraction (GF), fiber length (FL), fiber diameter (FD), fiber wall thickness (FWT), ray height (RH), ray width (RW)

Although gelatinous fibers were observed in all samples, they were more conspicuous in Histosol (Fig. 3), occupying up to approximately 70% of the fiber matrix in some samples. Additionally, a statistically significant difference was found in ray width (RW and RC), which was greater in Podzol. However, no significant differences were observed in other ray and fiber characteristics between the two soil conditions. Furthermore, vulnerability and mesomorphy values were higher in Histosol than in Podzol.

Vessel diameter and vessel density are negatively correlated in the studied species (Fig. 4a). Although with a weaker correlation, a similar trend was observed between vessel lumen fraction and vessel density (Fig. 4b). However, there is no significant correlation between vessel diameter and the fraction of area occupied by vessels (Fig. 4c). The vessel grouping level is directly correlated with vessel density (Fig. 4d), while vessel element length is positively correlated with both vessel diameter and fiber length (Fig. 4e-f).

4 Discussion

The qualitative xylem attributes of *T. guianensis* in the sampled areas are similar to those observed for the species in the Amazon Forest (Ferreira et al. 2020) and in the Atlantic Forest, both in coastal restinga and mountain forests (Castelar

Table 1 Xylem anatomical traits of *Tapirira guianensis* Aubl., in two soil types (Histosol and Podzol), in a coastal plain in southern Brazil

	Podzol	Histosol		RDPI	PPI
	mean ± s	mean ± s	mean		
Vessel grouping	2.39 ± 0.44 a	1.55 ± 0.09 b	1,97	0.21	0.35
Vessel lumen fraction (%)	12.15 ± 2.02 a**	9.83 ± 1.88 b**	10,99	0.13	0.19
Mean vessel diameter (µm)	68.74 ± 7.99 b	83.34 ± 11.24 a	76,04	0.11	0.18
Vessel density.mm^{-2}	32.50 ± 8.55 a	18.61 ± 4.64 b	25,55	0.28	0.43
Vessel element length (µm)	486 ± 71.62 b*	562 ± 48.02 a*	524,1	0.09	0.14
Fiber length (µm)	1097 ± 183 a	1137 ± 112 a	1117	0.07	0.03
Fiber diameter (µm)	20.45 ± 2.06 a	18.82 ± 0.78 a	19,64	0.05	0.08
Fiber wall thickness (µm)	4.33 ± 0.28 a	4.16 ± 0.33 a	4,24	0.04	0.04
Gelatinous fibers fraction (%)	19.00 ± 14.62 b	58.20 ± 15.29 a	36,82	0.54	0,67
Ray Height (µm)	365 ± 55.79 a	372 ± 66.48 a	369,1	0.09	0.02
Ray Width (µm)	34.45 ± 4.94 a	27.03 ± 0.73 b	30,74	0.12	0.22
Ray Height (nº of cells)	31.21 ± 12.52 a	32.97 ± 10.32 a	32,01	0.20	0.05
Ray Width (nº of cells)	2.68 ± 0.26 a	2.32 ± 0.27 b	2,52	0.08	0.14
V: vulnerability	2.33 ± 1.01 b	4.83 ± 1.81 a	3,58	0.35	0.52
M: mesomorphy	1173 ± 625 b	2762 ± 1159 a	1968	0.41	0.58

s—Standard deviation. PPI—Phenotypic Plasticity Index (PPI). RDPI—Relative Distance Plasticity Index. Means followed by the same letter do not differ statistically by the t-test, at the probability of 0.05, *0.07, **0.08

et al. 2023). The poorly distinct growth rings in this species (dos Santos Silva et al. 2017) appear to be a genetic trait characteristic of humid tropical and equatorial environments, and genus as a whole (Terrazas and Wendt 1995). However, the lack of data on this feature in other biomes and more seasonal climates hinders generalization across the species' broader distribution, which includes forests and savannas (Ratter et al. 2003; Oliveira-Filho et al. 2005; Chiminazzo et al. 2021).

The presence of gelatinous fibers is also a common feature in the genus *Tapirira* (Terrazas and Wendt 1995). These cells have a thick, non-lignified inner wall made of highly crystalline cellulose (G-layer), in which the microfibrils are oriented approximately parallel to the fiber axis (Du and Yamamoto 2007). These features of the G-layer alter the micromechanical properties of the wood and may result in higher elastic modulus and hardness compared to the other wall layers (Liang et al. 2021).

Although typical of tension wood in eudicots, in inclined stems (Cutter 1971), gelatinous fibers can also occur more extensively in some species, not necessarily linked with reaction wood. The higher percentage of gelatinous fibers in trees from Histosol supports the hypothesis raised by Cosmo et al. (2010) that gelatinous fibers may be important in hydromorphic soils, helping trees adjust stem growth in response to substrate instability. The thick organic layer and shallow water table in Histosol result in a very unstable support for the growth of tree species (Rachwal and Curcio 2001). Although the distribution patterns of gelatinous fibers in response to water conditions vary among species (Callado et al. 2001; Luchi 2004; Cosmo et al. 2024a, b), Callado et al. (2024) suggest that this type of cell may also contribute to overcoming the physiological drought effects caused by flooding.

The presence of septate living fibers also has functional implications. This type of cell can serve both biomechanical and storage functions (e.g., starch and water storage). Additionally, they contribute to the axial connectivity of the xylem in species lacking axial parenchyma or where it is scarce (Plavcová et al. 2023). The combination of this type of cell with the conspicuous presence of rays, as seen in *T. guianensis*, may provide the species with a high water capacity and assimilate storage, which can contribute to growth and stress tolerance. The accumulation of starch, for example, may be important for plants subjected to flooding in maintaining high levels of anaerobic metabolism (Lobo and Joly 1998). There is also evidence that both gelatinous fibers and living fibers may serve a function in aluminum immobilization (Sonsin et al. 2012). *T. guianensis* is highly tolerant to excess aluminum, which frequently occurs in the environments where the species grows, such as in the nutrient-poor, acidic soils of tropical plains and the cerrado. This tolerance is likely associated with physiological mechanisms that neutralize its toxicity (De Britez et al. 2002). Future investigations into the functions of living and gelatinous fibers could provide valuable insights into the species' responses to stress factors it encounters.

The predominance of vessel and fiber attributes in explaining data variation, as indicated by the first two principal axes of the PCA, highlights the functional importance

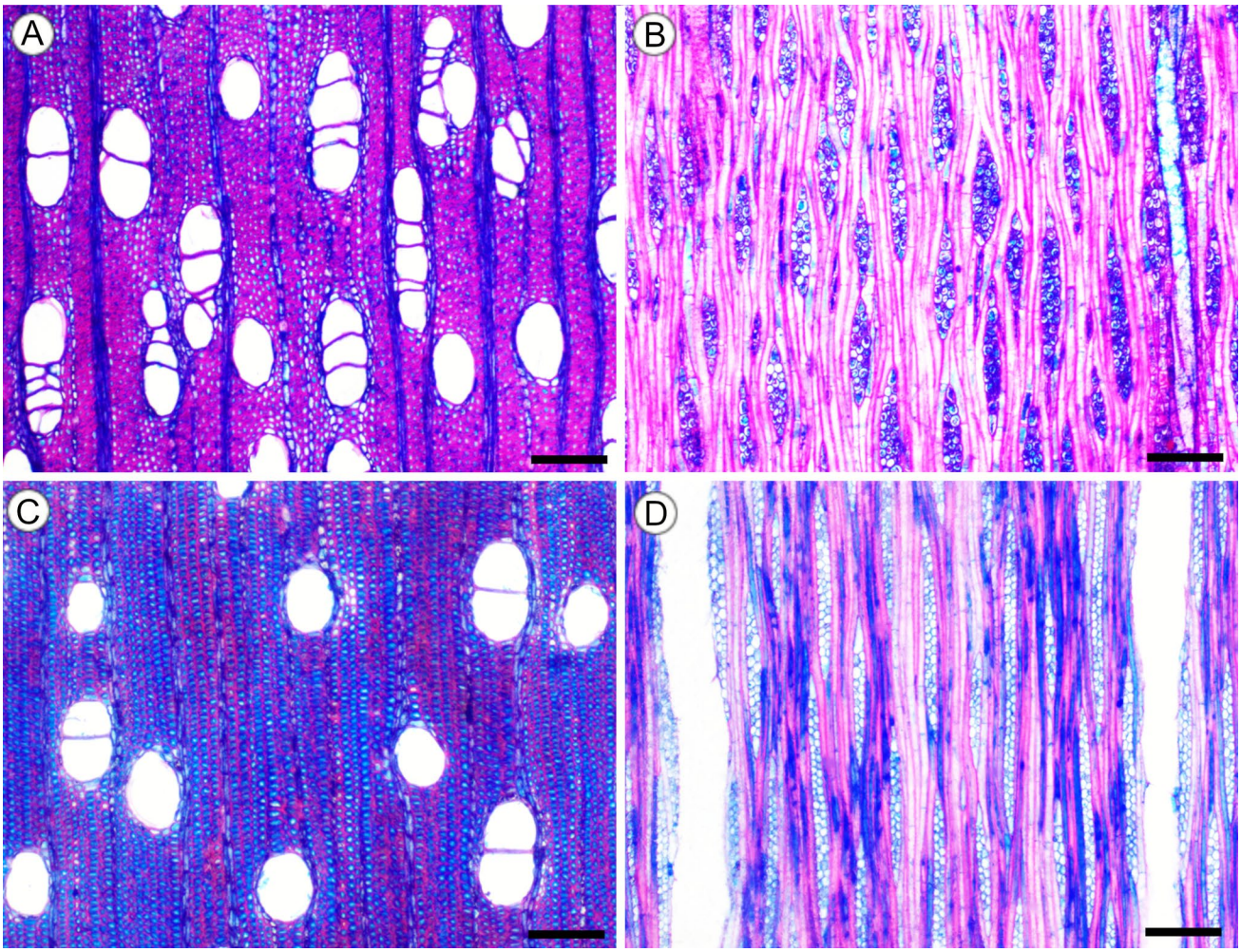


Fig. 3 Intraspecific variation on secondary xylem traits of *Tapirira guianensis* Aubl.: **A**: Cross-section, showing several multiples vessels in tree sampled in Podzol; **B**: tangential section on tree sampled in Podzol, showing predominance of rays with three cells in with; **C**: Cross-section showing predominance of solitary vessels, in tree sampled in Histosol; **D**: tangential section on tree sampled in Histosol, showing rays predominantly two cells in with. Scale bars: A–D = 200 µm

of biomechanical and hydraulic traits. Comparable patterns have been reported in species from subtropical ecosystems in southern Brazil (Cosmo 2012), South Africa (Jacobsen et al. 2007), subtropical shrubs in North and South America (Martínez-Cabrera et al. 2009), as well as in *Bathysa spp*. (Castelar et al. 2022) and intraspecific variation in *Gymnanthes klotzschiana* Müll.Arg. (Cosmo et al. 2024b).

The xylem vessel diameter and density in *T. guianensis* are comparable to those of other tropical and subtropical hygrophilous species, such as *Luehea divaricata* Mart., *Matayba elaeagnoides* Radlk., *Vitex megapotamica* (Spreng.) Moldenke, *Didymopanax morototoni* (Aubl.) Decne. and Planch, and *Gymnanthes klotzschiana*. Hydrophilic specialists, including, *Calophyllum brasiliense* Cambess., *Erythrina crista-galli* L., and *Tabebuia cassinoides* (Lam.) DC., tend to have even wider vessels and lower densities (Cosmo 2012). Large vessel diameters and low vessel density are characteristic of species in humid tropical forests. In contrast, narrow, highly numerous vessels increase the safety of the conductive system by enhancing resistance to cavitation (Tyree and Zimmermann 2002), a typical feature of xerophytic species (Carlquist 2001). While wider vessels have greater conductance—proportional to the fourth power of the vessel radius—they are more susceptible to cavitation caused by water deficits, frost, or mechanical damage (Tyree and Zimmermann 2002; Sperry 2003; Mauseth and Stevenson 2004). This trade-off between efficiency and safety influences the distribution of woody species in tropical forests, as it reflects variable responses to differences in water availability (Zhu et al. 2017).

Although the humid climate of the Atlantic Forest favors species with high water conduction capacity, geopedological variations and substrate texture may result in different levels of water availability, even at a local scale. In Podzol

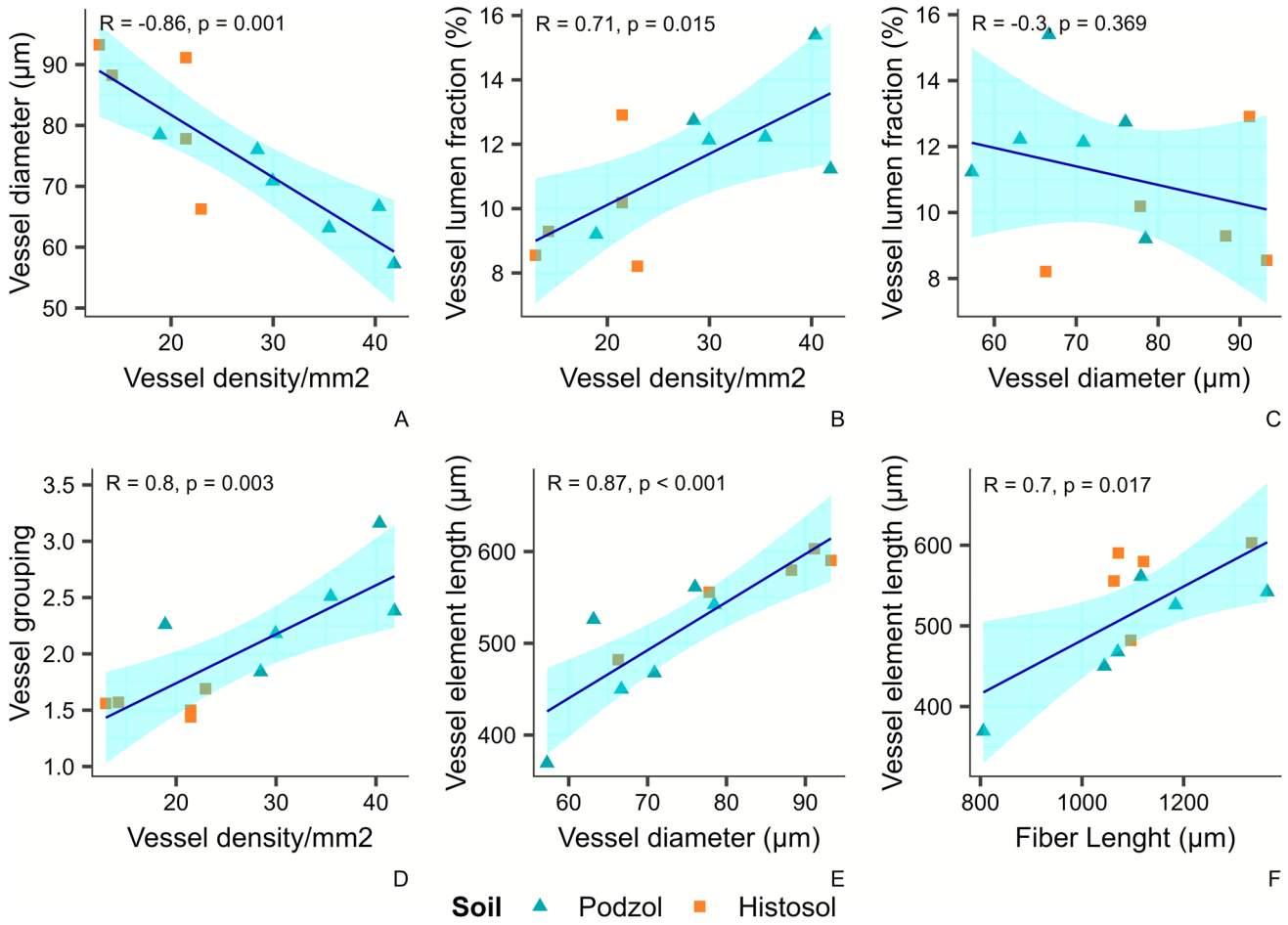


Fig. 4 Allometric correlations between anatomical attributes of the wood of *Tapirira guianensis*, in two pedological units, in a coastal plain on Southern Brazil

soil, the sandy texture and microrelief—particularly at sandbar summits—often result in drier conditions and a deeper water table compared to Histosol. Such variations in water availability likely drive intraspecific differences in xylem traits associated with conduction function. Increased vessel grouping and density, narrower vessels, and shorter vessel elements observed in Podzol compared to Histosol reflect strategies of *T. guianensis* to these changes in water availability. These traits represent an investment in a safer conduction system to mitigate cavitation under greater drainage conditions typical of Podzol soils.

A higher number of vessels, along with greater connectivity within vessel groupings, increases the redundancy of the conduction system and, beyond a certain threshold, enhances safety against cavitation. When embolism occurs, a greater number of alternative pathways increases the likelihood that some vessels will remain functional, allowing flow to be maintained through the non-embolized vessels (Baas et al. 1983; Tyree and Zimmermann 2002; Ewers et al. 2007). In *T. guianensis*, Castelar et al. (2023) found that increased resistance to embolism (P50) is associated with a higher vessel grouping index (IVG), with intraspecific variation observed across different phytophysiognomies and soil types. In the genus Acer, Lens et al. (2011) reported a strong correlation between greater vessel grouping, more negative mean cavitation pressure, and lower hydraulic conductivity. However, increased redundancy through greater vessel connectivity and grouping can occur without necessarily reducing hydraulic conductivity (Mrad et al. 2021).

Similar to *T. guianensis*, *Calophyllum brasiliense* shows higher vessel density in trees growing in Podzol soils compared to those in Histosol, within the same sampled areas of this study (Cosmo et al. 2024a). An increase in the number of vessels under drier conditions, compared to flooded soils, has also been observed in *Annona glabra* L. (Yáñez-Espinosa and Terrazas 2001), *Corchorus capsularis* L. (Parvin et al. 2018), and *Malus* x *domestica* Borkh (Bhusal et al. 2020). In *Alchornea sidifolia* Müll.Arg. trees, those from non-flooded soils exhibited narrower and more numerous vessel elements compared to those from flooded

soils (Callado et al. 2024). In *Hevea brasiliensis* (Willd. ex A.Juss.) Müll. Arg., an increase in vessel density occurs as water availability is reduced (Nery et al. 2023). In *Croton urucurana* Baill., Luchi (2004) observed higher vessel density under mesic conditions compared to both dry and flooded soils. Cacti respond to water deficit by increasing the frequency of smaller-diameter vessels and decreasing the number of larger-diameter vessels (Stevenson and Mauseth 2004).

The observed variations in *T. guianensis* in terms of vessel diameter, density, and grouping indicate an investment in a more secure conductive system to resist cavitation in better-drained soils (Podzol). This pattern of intraspecific response aligns with expectations for interspecific variations in xylem anatomy. Levionnois et al. (2021), evaluating the correlation between anatomical traits and embolism susceptibility (P50) in 25 neotropical tree species, found that larger vessel diameters are associated with greater susceptibility, while higher vessel density and grouping are linked to lower susceptibility.

The allometric relationships among xylem traits generally reveal functional trade-offs along the plant economic spectrum (Alvarado and Terrazas 2023). A negative correlation between vessel diameter (VD) and mean vessel diameter (MVD), as observed in *T. guianensis* (Fig. 4a), is commonly found both at the interspecific level in broad floras (Carlquist 2001; Martínez-Cabrera et al. 2009; Zanne et al. 2010; Martínez-Cabrera et al. 2011; Fichtler and Worbes 2012; Olson et al. 2020; Olson 2023) and within specific taxonomic groups (Lens et al. 2003). This phenomenon is attributed to the trade-off between xylem efficiency and safety (Gleason et al. 2016), which shapes species distribution in response to water availability (Zhu et al. 2017).

The length of vessel elements exhibited a similar trend to vessel diameter, with which it was positively correlated (Fig. 4e). A positive relationship between vessel element length and vulnerability to cavitation has been observed (Olson 2023). Shorter vessel element length (VEL) is thought to help isolate air bubbles during cavitation and resist higher negative pressures, although the underlying mechanisms remain unclear (Carlquist 2001; Ewers et al. 2023). Another hypothesis suggests that vessel element length may influence vulnerability to cavitation only insofar as it affects vessel length, a trait that has a stronger correlation with embolism (Lens et al. 2011). Regardless, VEL is an important trait for understanding the functional responses of xylem, and, unlike vessel length, it is relatively easy to measure. This trait was also positively correlated with fiber length, highlighting the convergence of trends in these two characteristics.

In response to anoxia or hypoxia, some species exhibit trends in waterlogged soils similar to those seen under conditions of reduced water availability: an increase in vessel density, greater vessel clustering, and/or a decrease in vessel diameter in waterlogged soils compared to mesic conditions (Kolb et al. 1998; Bianchini et al. 2000; Luchi 2004; Cosmo et al. 2024b). However, the xylem responses of *Tapirira guianensis* between Podzol and Histosol soils resemble the general trends observed in both inter- and intraspecific studies, with greater vessel grouping, smaller vessel diameter, higher vessel frequency, and shorter vessel elements in environmental conditions with lower water availability.

In hydromorphic soils of humid tropical forests in the Amazon biome, Ferreira et al. (2020) observed average vessel diameters of up to 135 µm in *T. guianensis*, much larger than the average value observed in Histosol (83 µm) and lower vessel density in trees from the Amazon. A range of vessel diameters similar to that observed in the present study was noted by Sonsin et al. (2012) in savanna and gallery forest in the Cerrado biome (70 and 90 µm, respectively). Although differences in tree size and age among the samples in these studies may influence quantitative variations, the hypothesis that these variations reflect functional differences between the distinct biomes cannot be ruled out, considering the climatic differences, such as higher precipitation and temperature in the Amazon biome compared to the Atlantic Forest in southern Brazil and the Savanna.

The values of RDPI and PPI show that species exhibits considerable intraspecific variation in several of the evaluated traits, with values higher than those observed in *C. brasiliense* at the same locations for most traits (Cosmo et al. 2024a), reflecting the different levels of plasticity between the two species. While *C. brasiliense* is a hydrophilic specialist, with low tolerance to water deficit, *T. guianensis* is a generalist that, in addition to tolerating flooding, occurs in a wider range of environments and has greater tolerance to water deficit. Castelar et al. (2023) also observed considerable intraspecific variation in *T. guianensis*, when comparing populations from two phytophysiognomies (restinga and montane Atlantic Forest).

Even under water deficit conditions, *T. guianensis* can maintain a positive water status during dry periods, due to its ability to store water in the xylem and develop new leaves with greater stomatal control during droughts (Miranda et al. 2011). The species' xylem also responds to water stress and hormonal imbalances caused by the parasitic plant *Phoradendron crassifolium* (Pohl ex DC.) Eichler. Parasitized branches exhibit more numerous, more clustered, and narrower vessels compared to non-parasitized branches (Teixeira-Costa et al. 2015).

Empirical indices of vulnerability and mesomorphy, established by Carlquist, provide an alternative method for evaluating cavitation vulnerability using anatomical xylem traits, which are relatively easy to obtain (Carlquist 2001). These indices are generally consistent with current knowledge of water transport physiology in xylem (Ewers et al.

2023). Xerophilic species tend to exhibit low values of V and M, as they have numerous, narrow vessels with short elements. In species from mesic environments, the trend is the opposite (Carlquist 2001). Studies on these attributes in hydrophilic species are scarce, but they appear to follow the general trend, with V and M values even higher than those of mesophilic species (Cosmo 2012a).

In tropical trees, the safety margins of the conductive system against embolism are narrow, impacting species productivity and survival, especially under conditions of increasing drought and reduced groundwater availability (Choat et al. 2012; Trueba et al. 2017) driven by climate change (IPCC 2022). Xylem traits are important indicators of this vulnerability (Sperry et al. 2006) and are especially useful for predicting ecosystem-level impacts (Zhu et al. 2017; Anfodillo and Olson 2021; Olson et al. 2023). Intraspecific variation provides insights into adaptive strategies and help understand the effects of these changes (Moran et al. 2016), including identifying current and future environmental refugia (Ramirez et al. 2020). Understanding species' responses to both permanent and temporary flooding is also crucial for preserving and managing ecosystems under changing pressures (Parolin and Wittmann 2010), as well as for identifying species that are valuable for ecosystem restoration (Cosmo et al. 2024b).

The efficiency of plants in overcoming the effects of flooding is typically associated with morpho-functional and physiological adaptations (Kolb et al. 1998; Lobo and Joly 1998; Barddal et al. 2016). The structure and functioning of hydrophilic forests are strongly influenced by the eco-physiological diversity of the communities and the plasticity of each species (Duarte et al. 2005). Tree species most tolerant to flooding significantly influence the structure, dynamics, and nutrient retention within these communities (Galvão et al. 2002; Marques et al. 2003). The anatomical structure of the secondary xylem in these species enables high water conduction capacity, although they generally exhibit high vulnerability to embolism. Changes in the hydrological regime of soils can lead to significant alterations at the ecosystem level, particularly in Histosols, where the organic layer is extremely fragile and prone to degradation due to subsidence when drained (Rachwal and Curcio 2001). In this context, identifying species that are tolerant to flooding yet plastic enough to withstand some degree of water deficit, as shown to be the case with *T. guianensis*, may be highly relevant for the conservation and restoration of these environments.

Consistent with this perspective, the present study reveals significant variation in the secondary xylem of *Tapirira guianensis* across different soil types within the same vegetation type and climate. The observed trends suggest a strategy of investing in xylem that is more resistant to cavitation in soils with lower water availability, compared to Histosol, where flooding is a permanent condition. This variation—characterized by greater vessel grouping, higher vessel density, smaller vessel diameters, and shorter vessel elements in soils with lower water availability—aligns with patterns observed in other inter- and intraspecific studies. These findings highlight *T. guianensis*'s xylem plasticity, which may contribute to its resilience to both flooding and drought.

Acknowledgements Not applicable.

Author contributions All authors contributed to the conception and design of the study. AMG and NLC prepared the samples, analyzed the data, and drafted the manuscript. PCB and FG selected the collection sites, revised the manuscript, and contributed to the discussion of the results.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Data availability The data sets generated and analyzed in this study are available from the corresponding author upon reasonable request.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

Consent for publication Consent for publication has been obtained from all authors.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE et al (2000) The evolution of plant ecophysiological traits: recent advances and future directions. Bioscience 50:979–995. https://doi.org/10.1641/0006-3568(2000)050[0979:TEOPET]2.0.CO;2

Albert CH, Thuiller W, Yoccoz NG, Douzet R, Aubert S, Lavorel S (2010) A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Funct Ecol 24:1192–1201. https://doi.org/10.1111/j.1365-2435.2010.01727.x

Alvarado MV, Terrazas T (2023) Tree species differ in plant economic spectrum traits in the tropical dry forest of Mexico. PLoS ONE 18:1–23. https://doi.org/10.1371/journal.pone.0293430

Anfodillo T, Olson ME (2021) Tree mortality: testing the link between drought, embolism vulnerability, and xylem conduit diameter remains a priority. Front for Glob Change 4:704670. https://doi.org/10.3389/ffgc.2021.704670

Araujo TG, Queiroz AB, Lopes SF (2019) Plant communities in a brejo de altitude of the Brazilian semiarid: change of dominant species along the elevation gradient. Cienc Florest 29:779–794. https://doi.org/10.5902/1980509821231

Arenas-Navarro M, Oyama K, García-Oliva F, Torres-Miranda A, De La Riva EG, Terrazas T (2021) The role of wood anatomical traits in the coexistence of oak species along an environmental gradient. AoB Plants 13:1–14. https://doi.org/10.1093/aobpla/plab066

Baas P (1973) The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea 21:193–260

Baas P, Wheeler EA (2011) Wood anatomy and climate change. In: Hodkinson TR, Jones MB, Waldren S, Parnell JAN (eds) Climate change, ecology and systematics. Cambridge University Press, Cambridge, pp 141–155. https://doi.org/10.1017/CBO9780511974540.007

Baas P, Werker E, Fahn A (1983) Some ecological trends in vessel characters. IAWA J 4:141–159. https://doi.org/10.1163/22941932-90000407

Barddal ML, Curcio GR, Bonnete A (2016) Relationship between soil moisture and distribution of trees of the Iguaçu River: the importance of relief, soil type and water saturation in the dynamics of tree occupation of river banks. Verlag, London

Bhusal N, Kim HS, Han SG, Yoon TM (2020) Photosynthetic traits and plant–water relations of two apple cultivars grown as bi-leader trees under long-term waterlogging conditions. Environ Exp Bot 17:1–13. https://doi.org/10.1016/j.envexpbot.2020.104111

Bianchini E, Medri ME, Pimenta JA, Giloni CPP, Kolb RM, Correa GT (2000) Anatomical alterations in plants of *Chorisia speciosa* A. St.-Hil. submitted to flooding. Interciencia 25:436–441

Callado CH, da Silva Neto SJ, Scarano FR, Barros CF, Costa CG (2001) Anatomical features of growth rings in flood-prone trees of the Atlantic rain forest in Rio de Janeiro, Brazil. IAWA J 22:29–42. https://doi.org/10.1163/22941932-90000266

Callado CH, dos Santos GUCA, Barros CE, Scarano FR, Costa CG (2024) Gelatinous fibre-tracheids as an escape mechanism for the physiological drought phenomenon. Rodriguésia 75:1–10. https://doi.org/10.1590/2175-7860202475029

Carlquist S (1977) Ecological factors in wood evolution: a floristic approach. Am J Bot 64:887–896. https://doi.org/10.2307/2442382

Carlquist S (2001) Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer-Verlag, New York, p 446

Carvalho MC, Gomide LR, dos Santos RM, Scolforo JRS, de Carvalho LMT, de Mello JM (2017) Modeling ecological niche of tree species in Brazilian tropical area. Cerne 23:147–157. https://doi.org/10.1590/01047760201723022308

Castelar JVS, Mangabeira PA, Campbell G, Callado CH, Da Cunha M (2022) Sympatric and phenotypic variation between two representative species of the Atlantic Forest: an analysis of the hydraulic system. Acta Bot Bras 36:1–12. https://doi.org/10.1590/0102-33062021abb0195

Castelar JVS, Da Cunha M, Simioni PF, Castilhori MF, Lira-Martins D, Giles AL, Costa WS, Alexandrino CR, Callado CH (2023) Functional traits and water-transport strategies of woody species in an insular environment in a tropical forest. Am J Bot 110:1–15. https://doi.org/10.1002/ajb2.16214

Chiminazzo MA, Andrade RS, Knopczyk RMG, Vieira LP, Ferreira-Júnior WG (2021) Swamp vegetations in Brazilian hotspots: threats, phytogeographical patterns and influences of climate. Aquat Bot 168:1–7. https://doi.org/10.1016/j.aquabot.2020.103293

Choat B, Sack L, Holbrook NM (2007) Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. New Phytol 175:686–698. https://doi.org/10.1111/j.1469-8137.2007.02137.x

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG et al (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–755. https://doi.org/10.1038/nature11688

Committee IAWA (1989) IAWA list of microscopic features for hardwood identification. IAWA Bull 10:219–332

Comstock J, Mencuccini M (1998) Control of stomatal conductance by leaf water potential in *Hymenoclea salsola* (Torr. & A. Gray), a desert subshrub. Plant Cell Environ 21:1029–1038. https://doi.org/10.1046/j.1365-3040.1998.00353.x

Cosmo NL, Kuniyoshi YS, Botosso PC (2010) Wood anatomy of *Sebastiania commersoniana* (Baill.) Smith & Downs (Euphorbiaceae): functional and ecological aspects. Acta Bot Bras 24:747–755. https://doi.org/10.1590/S0102-33062010000300018

Cosmo NL, Gogosz AM, Botosso PC, Galvão F (2024a) Soil moisture influence on the xylem anatomy of *Calophyllum brasiliense* Cambess. (Calophyllaceae) in a coastal plain in southern Brazil. S Afr J Bot 174:258–268. https://doi.org/10.1016/j.sajb.2024.09.014

Cosmo NL, Gogosz AM, Botosso PC, Kuniyoshi YS, Curcio GR (2024b) Geopedological influence on the wood anatomy of *Gymnanthes klotzschiana* (Euphorbiaceae) in a subtropical riparian forest in southern Brazil. Plant Biosyst 158:511–522. https://doi.org/10.1080/11263504.2024.2329460

Cosmo NL (2012) Wood ecology of 19 native species of the State of Paraná. PhD thesis, Federal University of Paraná, Curitiba. Accessed 15 December 2024

Cutter EG (1971) Plant anatomy: experiment and interpretation. Addison-Wesley Publishing Company, Reading

da Silva Costa W, da Cunha M, Pena Rodrigues JF, Iguatemy MA, Valladares F, Barros CF (2020) Intraspecific variation in functional wood anatomy of tropical trees caused by effects of forest edge. For Ecol Manage 473:1–13. https://doi.org/10.1016/j.foreco.2020.118305

De Britez RM, Reissmann CB, Watanabe T, Osaki M (2002) Effect of aluminum on the development and nutrition of *Tapirira guianensis* Aublet in hydroponic solution. Floresta 32:171–187. https://doi.org/10.5380/rf.v32i2.2282

Dória LC, Podadera DS, Batalha MA, Lima RS, Marcati CR (2016) Do woody plants of the Caatinga show a higher degree of xeromorphism than in the Cerrado? Flora 224:244–251. https://doi.org/10.1016/j.flora.2016.09.002

dos Santos Silva M, de Assis Ribeiro Santos dos F, Callado CH, Barros CF, da Silva LB (2017) Growth rings in woody species of Ombrophilous Dense Forest: occurrence, anatomical features and ecological considerations. Braz J Bot 40:281–290. https://doi.org/10.1007/s40415-016-0313-8

Du S, Yamamoto F (2007) An overview of biology of reaction wood formation. J Integr Plant Biol 49:131–143. https://doi.org/10.1111/j.1744-7909.2007.00427.x

Duarte HM, Gessler A, Scarano FR, Franco AC, de Mattos EA, Nahm M, Rennenberg H, Pena Rodrigues PJF, Zaluar HLT, Lüttge U (2005) Ecophysiology of six selected shrub species in different plant communities at the periphery of the Atlantic Forest of SE Brazil. Flora 200:456–476. https://doi.org/10.1016/j.flora.2005.02.004

EMBRAPA (2018) Brazilian soil classification system. 5th edn. Brazilian Agricultural Research Corporation, Brasília, 626 pp. Accessed 15 December 2024

Ennajeh M, Coleman M, Fickle JC, Castro V, Pratt RB, Jacobsen AL (2023) Xylem structure and function of two saltbush shrub species (*Atriplex*) from differing microhabitats. J Plant Ecol 16:1–16. https://doi.org/10.1093/jpe/rtad022

Ewers FW, Ewers JM, Jacobsen AL, López-Portillo J (2007) Vessel redundancy: modeling safety in numbers. IAWA J 28:373–388. https://doi.org/10.1163/22941932-90001650

Ewers FW, Jacobsen AL, López-Portillo J (2023) Carlquist's indices for vulnerability and mesomorphy of wood: are they relevant today? IAWA J 44:1–13. https://doi.org/10.1163/22941932-bja10113

Ferreira CA, Ribeiro ADO, Urbinati CV, Duarte PJ, Mori FA, Moglio BV (2020) Comparative wood anatomy of two tropical species. Sci Agrar Parana 19:43–51. https://doi.org/10.18188/sap.v19i1.22640

Fichtler E, Worbes M (2012) Wood anatomical variables in tropical trees and their relation to site conditions and individual tree morphology. IAWA J 33:119–140. https://doi.org/10.1163/22941932-90000084

Fisher JB, Goldstein G, Jones TJ, Cordell S (2007) Wood vessel diameter is related to elevation and genotype in the Hawaiian tree *Metrosideros polymorpha* (Myrtaceae). Am J Bot 94:709–715. https://doi.org/10.3732/ajb.94.5.709

Franklin GL (1945) Preparation of thin sections of synthetic resins and wood-resin composites, and a new macerating method for wood. Nature 155:51. https://doi.org/10.1038/155051a0

Galvão F, Roderjan CV, Kuniyoshi YS, Ziller SR (2002) Floristic composition and phytosociology of caxetais from the coast of Paraná State. Floresta 32:115–128. https://doi.org/10.5380/rf.v32i1.2347

Gama DC, Ferreira RA, Jesus JB (2020) Establishment of native forest species in riparian recovery forest in the Piauitinga River, Sergipe, Brazil. Floresta 50:1325–1334. https://doi.org/10.5380/rf.v50i2.62987

Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, Bhaskar R, Brodribb TJ, Bucci SJ, Cao KF et al (2016) Weak trade-off between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. New Phytol 209:123–136. https://doi.org/10.1111/nph.13646

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. Perspect Plant Ecol Evol Syst 4:97–115. https://doi.org/10.1078/1433-8319-00017

Hollunder RK, Mariotte P, Carrijo TT, Holmgren M, Luber J, Stein-Soares B, Guidoni Martins KG, Ferreira-Santos K, Scarano FR, Garbin ML (2021) Topography and vegetation structure mediate drought impacts on the understory of the South American Atlantic Forest. Sci Total Environ 766:144234. https://doi.org/10.1016/j.scitotenv.2020.144234

IDR (2019) Climatic atlas of the State of Paraná. Institute of Rural Development of Paraná, Curitiba. Accessed 10 December 2024

IPCC (2022) Climate change 2022: impacts, adaptation and vulnerability. Summary for policymakers. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. United Nations Environment Programme, Geneva. https://doi.org/10.1017/9781009325844

Jacobsen AL, Agenbag L, Esler KJ, Pratt RB, Ewers FW, Davis SD (2007) Xylem density, biomechanics and anatomical traits correlate with water stress in 17 evergreen shrub species of the Mediterranean-type climate region of South Africa. J Ecol 95:71–83. https://doi.org/10.1111/j.1365-2745.2006.01186.x

Kolb RM, Medri ME, Bianchini E, Pimenta JA, Giloni PC, Correa GT (1998) Ecological anatomy of *Sebastiania commersoniana* (Baill.) Smith & Downs (Euphorbiaceae) submitted to flooding. Rev Bras Bot 21:305–312

Lens F, Gasson P, Smets E, Jansen S (2003) Comparative wood anatomy of epacrids (Styphelioideae, Ericaceae s.l.). Ann Bot 91:835–856. https://doi.org/10.1093/aob/mcg089

Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S (2011) Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. New Phytol 190:709–723. https://doi.org/10.1111/j.1469-8137.2010.03518.x

Levionnois S, Jansen S, Wandji RT, Beauchêne J, Ziegler C, Coste S, Stahl C, Delzon S, Authier L, Heuret P (2021) Linking drought-induced xylem embolism resistance to wood anatomical traits in Neotropical trees. New Phytol 229:1453–1466. https://doi.org/10.1111/nph.16942

Liang R, Zhu YH, Yang X, Gao JS, Zhang YL, Cai LP (2021) Study on the ultrastructure and properties of gelatinous layer in poplar. J Mater Sci 56:415–427. https://doi.org/10.1007/s10853-020-05226-w

Liu J, Noshiro S (2003) Lack of latitudinal trends in wood anatomy of *Dodonaea viscosa* (Sapindaceae), a species with a worldwide distribution. Am J Bot 90:532–539. https://doi.org/10.3732/ajb.90.4.532

Lobo PC, Joly CA (1998) Tolerance to hypoxia and anoxia in Neotropical tree species. In: Scarano FR, Franco AC (Eds) Ecophysiological strategies of xerophytic and amphibious plants in the Neotropics, Oecol Bras 4:137–156

Longui EL, Costa NO, Cielo-Filho R, Marcati CR, Romeiro D, Rajput KS, Lima IL, Florsheim SMB (2014) Wood and leaf anatomy of *Copaifera langsdorffii* dwarf trees. IAWA J 35:170–185. https://doi.org/10.1163/22941932-00000058

Luchi AE (2004) Wood anatomy of *Croton urucurana* Baill. (Euphorbiaceae) from soils with different moisture levels. Rev Bras Bot 27:271–280. https://doi.org/10.1590/S0100-84042004000200007

Maçaneiro JP, Seubert RC, Schorn LA (2015) Phytosociology of a primary subtropical rain forest in southern Brazil. Floresta 45:555–566. https://doi.org/10.5380/rf.v45i3.38157

Marques MCM, Silva SM, Salino A (2003) Floristics and structure of the shrub and tree layer of a swamp forest in the Jacaré-Pepira River, southeastern Brazil. Acta Bot Bras 17:495–506. https://doi.org/10.1590/S0102-33062003000400002

Martínez-Cabrera HI, Cynthia SJ, Espino S, Schenk HJ (2009) Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. Am J Bot 96:1388–1398. https://doi.org/10.3732/ajb.0800237

Martínez-Cabrera HI, Schenk HJ, Cevallos-Ferriz SRS, Jones CS (2011) Integration of vessel traits, wood density, and height in angiosperm shrubs and trees. Am J Bot 98:915–922. https://doi.org/10.3732/ajb.1000335

Mauseth JD, Stevenson JF (2004) Theoretical considerations of vessel diameter and conductive safety in populations of vessels. Int J Plant Sci 165:359–368. https://doi.org/10.1086/382808

MINEROPAR (2001) Atlas geológico do Estado do Paraná. Minerais do Paraná S.A., Curitiba. Accessed 15 July 2024

Miranda LAP, Vitória AP, Funch LS (2011) Leaf phenology and water potential of five arboreal species in gallery and montane forests in the Chapada Diamantina, Bahia, Brazil. Environ Exp Bot 70:143–150. https://doi.org/10.1016/j.envexpbot.2010.08.011

Moran EV, Hartig F, Bell DM (2016) Intraspecific trait variation across scales: implications for understanding global change responses. Glob Change Biol 22:137–150. https://doi.org/10.1111/gcb.13000

Mrad A, Johnson DM, Love DM, Domec JC (2021) The roles of conduit redundancy and connectivity in xylem hydraulic functions. New Phytol 231:996–1007. https://doi.org/10.1111/nph.17429

Nery IRAM, Vergilio PCB, Viégas LB, da Silva MR, Resende RT, Chagas MP, Pace MR, Marcati CR (2023) Water availability influences both wood anatomy and laticifer density in rubber

tree saplings. Flora 304:1–11. https://doi.org/10.1016/j.flora.2023.152301
Noshiro S, Baas P (2000) Latitudinal trends in wood anatomy within species and genera: case study in *Cornus* s.l. (Cornaceae). Am J Bot 87:1495–1506. https://doi.org/10.2307/2656876
Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, et al. (2022) Vegan: community ecology package. R package version 2.6–4
Oliveira LSB, Marangon LC, Feliciano ALP, Cardoso MO, Lima AS, Santos WB, Silva VF (2012) Structure of the woody component of an Atlantic forest fragment, Moreno, Pernambuco. Semina Cienc Agrar 33:203–212. https://doi.org/10.5433/1679-0359.2012v33n1p203
Oliveira-Filho AT, Tameirão-Neto E, Carvalho WAC, Werneck M, Brina AE, Vidal CV, Rezende SC, Pereira JAA (2005) Floristic analysis of the tree component of Atlantic Forest areas in central eastern Brazil. Rodriguésia 56:129–146. https://doi.org/10.1590/2175-78602005568715
Olson ME (2023) A skeptic's guide to Sherwin Carlquist's inferences of xylem function. IAWA J 44:287–303. https://doi.org/10.1163/22941932-bja10109
Olson ME, Rosell JA, Martínez-Pérez C, León-Gómez C, Fajardo A, Isnard S, Cervantes-Alcayde MA, Echeverría A, Figueroa-Abundiz VA, Segovia-Rivas A et al (2020) Xylem vessel-diameter–shoot-length scaling: ecological significance of porosity types and other traits. Ecol Monogr 90:1–32. https://doi.org/10.1002/ecm.1410
Parolin P, Wittmann F (2010) Struggle in the flood: tree responses to flooding stress in four tropical floodplain systems. AoB Plants 3:1–19. https://doi.org/10.1093/aobpla/plq003
Parvin D, Rashid P, Karmoker J (2018) Anatomical responses of jute (*Corchorus capsularis* L. cv. D-154) to waterlogging. Dhaka Univ J Biol Sci 27:213–219. https://doi.org/10.3329/dujbs.v27i2.46470
Percolla MI, Fickle JC, Rodríguez-Zaccaro FD, Pratt RB, Jacobsen AL (2021) Hydraulic function and conduit structure in the xylem of five oak species. IAWA J 42:279–298. https://doi.org/10.1163/22941932-bja10059
Plavcová L, Olson ME, Jandová V, Doležal J (2023) Parenchyma is not the sole site of storage: storage in living fibres. IAWA J 44:465–476. https://doi.org/10.1163/22941932-bja10112
Pratt RB, Jacobsen AL, Jacobs SM, Esler KJ (2012) Xylem transport safety and efficiency differ among fynbos shrub life-history types and between two sites differing in mean rainfall. Int J Plant Sci 173:474–483. https://doi.org/10.1086/665267
Protil CZ, Marques R, Protil RM (2009) Seasonal variation and redistribution of nutrients in four tree species in three forest typologies of the Atlantic Forest in Paraná State, Brazil. Floresta 39:699–717. https://doi.org/10.5380/rf.v39i3.15371
R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Rachwal MFG, Curcio GR (2001) Pedological attributes and occurrence of caixeta in the coastal region of Paraná. For Sci 59:153–163
Ramírez AR, De Guzman ME, Dawson TE, Ackerly DD (2020) Plant hydraulic traits reveal islands as refugia from worsening drought. Conserv Physiol 8:1–16. https://doi.org/10.1093/conphys/coz115
Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian cerrado vegetation III: comparison of the woody vegetation of 376 areas. Edinb J Bot 60:57–109. https://doi.org/10.1017/S0960428603000064
Roderjan CV, Galvão F, Kuniyoshi YS, Hatschbach G (2002) The phytogeographic units of the State of Paraná. Cienc Ambient 13:75–92
Scarano FR (2002) Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Ann Bot 90:517–524. https://doi.org/10.1093/aob/mcf189
Segala Alves ES, Angyalossy-Alfonso V (2000) Ecological trends in the wood anatomy of some Brazilian species. 1. Growth rings and vessels. IAWA J 21:3–30. https://doi.org/10.1163/22941932-90000233
Sereda F, Reissmann CB, Boeger MR, Marques R (2016) Foliar content and esclerophylly of *Calophyllum brasiliense* Cambess. (Clusiaceae) and their edaphic relationships in coast of Paraná State, Brazil. Hoehnea 43:583–590. https://doi.org/10.1590/2236-8906-87/2015
Sonsin JO, Gasson PE, Barros CF, Marcati CR (2012) A comparison of the wood anatomy of 11 species from two cerrado habitats (cerrado s.s. and adjacent gallery forest). Bot J Linn Soc 170:257–276. https://doi.org/10.1111/j.1095-8339.2012.01282.x
Souza LC, Marques R (2010) Nutrient fluxes in Lowland Dense Ombrophylous Forest in the coast of Paraná. Floresta 40:125–136. https://doi.org/10.5380/rf.v40i1.17104
Sperry JS (2003) Evolution of water transport and xylem structure. Int J Plant Sci 164:115–127. https://doi.org/10.1086/368398
Sperry JS, Hacke UG (2002) Desert shrub water relations with respect to soil characteristics and plant functional type. Funct Ecol 16:367–378. https://doi.org/10.1046/j.1365-2435.2002.00628.x
Sperry JS, Hacke UG, Pittermann J (2006) Size and function in conifer tracheids and angiosperm vessels. Am J Bot 93:1490–1500. https://doi.org/10.3732/ajb.93.10.1490
Stevenson JF, Mauseth JD (2004) Effects of environment on vessel characters in cactus wood. Int J Plant Sci 165:347–357. https://doi.org/10.1086/382807
Teixeira-Costa L, Ceccantini G (2015) Embolism increase and anatomical modifications caused by a parasitic plant: *Phoradendron crassifolium* (Santalaceae) on *Tapirira guianensis* (Anacardiaceae). IAWA J 36:138–151. https://doi.org/10.1163/22941932-00000091
Terrazas T, Wendt T (1995) Systematic wood anatomy of the genus *Tapirira* Aublet (Anacardiaceae): a numerical approach. Brittonia 47:109–129. https://doi.org/10.2307/2806951
Trueba S, Pouteau R, Lens F, Feild TS, Isnard S, Olson ME, Delzon S (2017) Vulnerability to xylem embolism as a major correlate of the environmental distribution of rain forest species on a tropical island. Plant Cell Environ 40:277–289. https://doi.org/10.1111/pce.12859
Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap, 2nd edn. Springer-Verlag, Berlin, p 284
Valladares F, Sanchez-Gomez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. J Ecol 94:1103–1116. https://doi.org/10.1111/j.1365-2745.2006.01176.x
Vieira DA, Martins TO, Miranda Matias RA, Fernandes Silva PH, Valadão MBX, Barbosa PVG et al (2022) Relationships between soil properties and species establishment in the restoration of mined soils in the Cerrado biome. PLoS ONE 17:0277193. https://doi.org/10.1371/journal.pone.0277193
Westerband A, Funk J, Barton K (2021) Intraspecific trait variation in plants: a renewed focus on its role in ecological processes. Ann Bot 127:397–410. https://doi.org/10.1093/aob/mcab011
Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. Trends Ecol Evol 21:261–268. https://doi.org/10.1016/j.tree.2006.02.004
Yáñez-Espinosa L, Terrazas T (2001) Wood and bark anatomy of *Annona glabra* L. under flooding. Agrociencia 35:51–63
Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SEJ, Coomes DA (2010) Angiosperm wood structure: global

patterns in vessel anatomy and their relation to wood density and potential conductivity. Am J Bot 97:207–215. https://doi.org/10.3732/ajb.0900178

Zhu SD, Chen YJ, Fu PL, Cao KF (2017) Different hydraulic traits of woody plants from tropical forests with contrasting soil water availability. Tree Physiol 37:1469–1477. https://doi.org/10.1093/treephys/tpx094

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.