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Plant anatomy: history and future directions

Gelatinous fibretracheids as an escape mechanism for the physiological drought phenomenon

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Abstract

Alchornea sidifolia is a tree species used in the regeneration of degraded forest environments and which grows in both non-flooded and flooded soils. We compared the wood anatomy of trees growing under both conditions in Atlantic Forest remnants in the state of Rio de Janeiro, Brazil, to understand intraspecific aspects of the adaptation of tropical woody species to these conditions. Trees from permanently flooded soils showed wider, shorter, and less frequent vessel elements; wider fibretracheids, with a greater proportion of the gelatinous type; and a lower frequency of radial parenchyma, but with longer strands of axial parenchyma. These results indicate that *A. sidifolia* trees growing in permanently flooded sites do not show water deficit and that the species is capable of maximizing water use in this growth condition. This conclusion may be directly related to the greater proportion of gelatinous fibretracheids in flooded trees and is contrary to what was expected for wood anatomy of trees under physiological drought.

Key words: intraspecific variation, ecological wood anatomy, hydraulic architecture, wetland, Reserva Biológica de Poço das Antas.

Resumo

Alchornea sidifolia é uma espécie arbórea utilizada na regeneração de ambientes florestais degradados e que cresce tanto em solos não alagados quanto alagados. Nós comparamos a anatomia da madeira de árvores crescendo sob ambas as condições em remanescentes de Mata Atlântica no estado do Rio de Janeiro, Brasil, para entender aspectos intraespecíficos da adaptação de espécies lenhosas tropicais a essas condições. As árvores que se desenvolvem em solos permanentemente inundados apresentaram elementos de vasos mais largos, curtos e menos frequentes; fibrotraqueídes mais largas, com maior proporção do tipo gelatinoso; e menor frequência de parênquima radial, mas com séries de parênquima axial mais longas. Esses resultados indicam que as árvores de *A. sidifolia* crescendo em solo permanentemente inundado não apresentam déficit hídrico e que a espécie é capaz de maximizar o uso da água nesta condição de crescimento. Essa conclusão pode estar diretamente relacionada à maior proporção de fibrotraqueídes gelatinosos em árvores de ambientes alagados e contraria o que se esperava para a anatomia do lenho de árvores sob seca fisiológica.

Palavras-chave: variação intraespecífica, anatomia ecológica da madeira, arquitetura hidráulica, zonas úmidas, Reserva Biológica de Poço das Antas.

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Introduction

The Atlantic Forest extends along the entire Brazilian coast, ranging from lowlands close to the ocean to high altitudes towards the central plateau, resulting in a complex of distinct plant communities (Scarano 2002). In this study, we highlight the Alluvial Ombrophilous Dense Forest, a poorly-known phytophysiognomy of the Atlantic Forest lowlands that is severely reduced by anthropic actions.

In general, this phytophysiognomy is composed of a mosaic of microsites with soils free from flooding and soils with temporary or permanent flooding by freshwater. Consequently, its plant community has tree species that vary biogeographically, including species from flood-free forests and from wetlands (*e.g.*, Guedes-Bruni *et al.* 2006; Scarano 2006; Kurtz *et al.* 2013; Lima *et al*. 2006; Chiminazzo *et al.* 2021). However, some species can adjust to different ecological conditions and establish and develop simultaneously in existing microsites. Understanding these aspects has been considered important scientific support for the adoption of actions for the conservation and restoration of the threatened Alluvial Ombrophilous Dense Forest of the Atlantic Forest.

Studies have highlighted the morphological, anatomical, physiological, and biochemical adaptive responses of flood-tolerant and flood-sensitive plants. The main morphological modification is the formation of adventitious roots, while the main anatomical modification is the formation of aerenchyma. This tissue stores air and allows its circulation, contributing to the O_2 stock. The hormones ethylene and gibberellin and the activation of glycolytic and fermentation pathways, which induce the metabolic shift from aerobic to anaerobic, are also crucial for plant adaptations to flooding (*e.g*., Ponnamperuma 1984; Scarano & Crawford 1992; Kozlowski 1997; Davanso-Fabro *et al*. 1998; Lobo & Joly 2000; Parolin & Wittman 2010; Tyagi *et al*. 2023).

Experimental studies of changes in wood anatomical features have been conducted to monitor flood events and climate change through tree-rings (Therrell & Bialecki 2015; Copini *et al*. 2016). There is a large diversity of adaptative responses to conditions of soil humidity among tropical trees, which can vary with the type, duration, and intensity of flooding (*e.g*., Joly 1991; Callado *et al*. 2001a, b; Parolin *et al*. 2002, 2004; Rengifo *et al*. 2005; Cosmo *et al*. 2010; Oliveira & Joly 2010; Granato-Souza *et al*. 2019; Greet *et al.* 2020). Most of these studies deal with plants typical of wetlands with periodic flooding oscillations. However, gaps remain in the understanding of structural differences of plants of woody species simultaneously developing in soils that are always free from flooding and in soils that are always flooded (permanent flooding).

Alchornea sidifolia Müll. Arg. (Euphorbiaceae) is a tree species that occurs naturally in different phytophysiognomies of the Atlantic Forest, under different altitudes and climates from South to Southeast Brazil, and in dry soils or in freshwater flood-prone soils (Inoue *et al*. 1984; Smith *et al*. 1988; Barros *et al*. 2001, 2006; Callado *et al*. 2001a, b). Such growth conditions highlight the potential ability of the taxon to exploit diverse environments. In this study, we compare the wood anatomy of *A. sidifolia* trees under contrasting conditions of soil water regime to investigate structural variation and describe predictive anatomical responses to freshwater flooding.

Material and Methods

The study was conducted in the Reserva Biológica de Poço das Antas (22º30' to 22º33'S, 42º15' to 42º19'W), a reserve which safeguards one of the last remnants of Alluvial Ombrophilous Dense Forest in the state of Rio de Janeiro, Brazil (Guedes-Bruni *et al*. 2006; Lima *et al*. 2006). The remnant possesses a topographic gradient with distinction between natural areas that are not flooded and those that are flooded by freshwater - swamp (Guedes-Bruni *et al*. 2006; Scarano 2006). The local climate is hot and humid, with rains well distributed throughout the year with a dry season from June to August and heavier rains from November to March. During the study period (May 1997 – April 1998), annual precipitation was about 2,200 mm and the mean annual temperature was 25 °C (a detailed description of the local climate is presented in Callado *et al*. 2001b).

Sampling was carried out within an area of 100 m^2 in continuous vegetation with neighbouring non-flooded and permanent flooded patches. Monthly monitoring showed non-flooded areas (Callado *et al*. 2001b), where the groundwater ranged from 2 to 3 m below the soil surface, and permanently flooded areas, where the water table ranged from 4 to 50 cm above the soil surface (Fig. 1a-b). The soil is acidic in both types of areas, but, in the flooded areas, it has less coarse sand; greater quantity of silt; higher Ca, Mg, K, Na and H; lower assimilable P; and higher pH (Guedes-Bruni 1998). Due to the continuum of the evaluated vegetation and the standardization of the size of the *A. sidifolia* trees to be sampled - 9.5 to 12 meters in height and 20 to 28.5 cm in diameter at 1.30 m above the ground (DBH) (Tab. 1) - only three straight-trunk trees, without bifurcations or evident injuries, were selected in each condition (non-flooded / flooded).

Intraspecific variation in wood anatomy was analysed at the same distance from the trunk periphery (between 8 and 10 cm from the bark) and therefore in growth layers formed at the same time. Sampling was non-destructive, being performed with an increment borer at breast height, and wood anatomical analyses were applied to heartwood fragments. Transverse, longitudinal tangential and

Figure 1 – a-b. General view of the soil surface in the two types of studied areas; non-flooded and flooded soil, respectively. c-d. Transverse section of *Alchornea sidifolia* wood in non-flooded and flooded soil, respectively (Scale bar = 200 µm). Arrow indicates growth ring boundaries. White arrow indicates diffuse-in-aggregates apotracheal parenchyma. Details highlight the gelatinous fibretracheids (asterisks) in the *Alchornea sidifolia* wood in non-flooded and flooded soil (Scale bar = 50 µm).

Table 1 – Studied samples with their accession number from the RBw wood collection, size and soil water regime.

Trees	RBw	Height (h)	DBH (cm)	Soil type
1	7506	10.0	20.2	Non-flooded
2	7552	11.7	28.5	Non-flooded
3	7551	12.0	25.7	Non-flooded
4	7507	9.5	24.2	Flooded
5	7546	11.0	28.5	Flooded
6	7656	10.5	25.0	Flooded

DBH = diameter at breast height, approximately 1.30 m above the ground.

radial sections were made with thicknesses between 11 and 20 μm. These histological sections were clarified, dehydrated and stained with 1% aqueous Safranin and 1% Astra Blue (6:4) (Bukatsch 1972). Permanent slides (Johansen 1940) were made with Entellan ® (Merk). Fibretracheids dimensions and vessel element length were measured in macerations by Jeffrey's fluid (Johansen 1940; Dop & Gautié 1909) that were stained with 50% hydroalcoholic Safranin (Sass 1958) and mounted with 50% Glycerol (Strasburger 1924).

Barros et al. (2001, 2006) described the wood structure of A. sidifolia at the study site using wood samples from both flooded (periodic or permanent) and non-flooded sites to obtain an average wood anatomy of the population. Here, we compare the descriptions, measurements and counts of wood cells of trees from non-flooded and permanently flooded sites following the standard recommendations of the IAWA Committee (Wheeler *et al*. 1989). Percentages of cell types were calculated according to Luchi (2004). Measurements were taken with Image Pro Plus 4.1 software for Windows, using a Q Color R3 camera attached to an Olympus BX41-BF-I-20 microscope or a Coolsnap camera attached to an Olympus BX50 microscope. Indexes of vulnerability, mesomorphy and conductivity were calculated with the formulas of Carlquist (1977, 2001). Theoretical hydraulic conductivity was estimated by the equation of Zimmermann (1983), as modified by Fahn *et al*. (1986).

Twenty-one anatomical features were statistically tested between trees of non-flooded and flooded areas. Shapiro-Wilk's W and Levene's tests were used to test, respectively, the normality and homoscedasticity of the data. Student's t and Mann-Whitney t tests were used to evaluate the significance of differences of wood features between the types of areas (Zar 1996). All statistical tests were performed in Statistica 7 software.

Results

Wood anatomical features were similar in trees of *Alchornea sidifolia* from the two sampling areas: distinct growth ring boundaries, marked by radial flattening of fibretracheids (gelatinous and non-gelatinous) and greater thickening of their walls in latewood; diffuse porosity (Fig. 1c-d); vessel elements solitary or in radial multiples of 2–5 (Fig. 1c-d), rarely 6; perforation plates simple; intervessel pits alternate and polygonal; vessel-ray and vessel parenchyma pits circular and minutely bordered or simple; sclerotic tyloses present; gelatinous fibretracheids present (Fig. 1c-d); rays uniseriate (rarely biseriate), > 1 mm in height, composed of square or upright cells; laticifers radial; ray cells perforated; and prismatic crystals in ray cells.

Twelve of the 21 studied quantitative anatomical features differed significantly between non-flooded and flooded areas: proportion of total fibretracheids and proportion of gelatinous and non-gelatinous fibretracheids; vessel element frequency, length and tangential diameter; fibretracheid total diameter and lumen diameter; axial parenchyma strand length; ray frequency; and vulnerability and mesomorphy indexes (Tab. 2).

Vessel elements of non-flooded trees were longer, narrower and more numerous than in flooded trees, but intervessel and vessel-ray pit diameter were similar (Tab. 2). Arrangement and proportion of gelatinous fibretracheids differed according to conditions of soil flooding (Tab. 2). Non-flooded trees had few gelatinous fibretracheids that were located mainly in the latewood, while flooded trees had them in large quantities and arranged throughout the entire growth ring (Fig.

Table 2 – Quantitative analysis of wood anatomical features of *Alchornea sidifolia* trees in non-flooded and flooded soils. Anatomical features that are significantly different according to Student's *t* test or Mann-Whitney U test ($p < 0.05$) are marked by bold and *.

Anatomical features	Non-flooded trees	Flooded trees	Student's *t* test		Mann-Whitney U test	
	Average (± standard deviation)	Average (± standard deviation)	*t*	*P*	U	*p*
Total percentage of vessels (%)	6.9 (±3.6)	5.6 (±3.9)			111.5000	0.966915
Total percentage of fibretracheids (%)*	**52.4 (±13.5)**	**56.1 (±9.3)**			**92.0000**	**0.395159**
Percentage of non-gelatinous fibretracheids (%)*	**41.3 (±19.5)**	**19.3 (±22.5)**			**48.5000**	**0.007941**
Percentage of gelatinous fibretracheids (%)*	**11.1 (±17.9)**	**36.9 (±27.0)**			**62.5000**	**0.038089**
Percentage of axial parenchyma (%)	11.3 (±7.2)	11.3 ±(7.5)			110.0000	0.917411
Percentage of radial parenchyma (%)	29.4 (±14.8)	27.0 (±8.7)			104.5000	0.740022
Vessel frequency (mm^2)*	**4.20 (±2.57)**	**1.97 (±1.54)**			**231.5000**	**0.001236**
Vessel element length (µm)*	**830.7 (±173.3)**	**709.9 (±130.0)**	**4.79644**	**0.000004**		
Vessel diameter (µm)*	**149.6 (± 14.9)**	**185.9 (±26.7)**			**1505.500**	**0,000001**
Intervessel pit diameter (µm)	10.7 (±3.7)	11.6 (±3.3)			392.0000	0.391171
Vessel-ray pit diameter (µm)	12.8 (±3.2)	13.7 (±2.8)			349.0000	0.135379
Fibretracheid length (µm)	1.258,9 (±181.8)	1.287.6 (±225.4)			2775.000	0.887908
Fibretracheid total diameter (µm)*	**32.4 (±5.7)**	**36.4 (±6.4)**	**-4.07311**	**0.000075**		
Fibretracheid lumen diameter (µm)*	**24.2 (±5.6)**	**27.8 (±6.1)**	**-3.73000**	**0,000272**		
Fibretracheid wall thickness (µm)	4.1 (±0.9)	4.3 (±0.9)			2358.000	0.087574
Axial parenchyma strand height (µm)*	**707.4 (±175.3)**	**769.6 (±163.2)**	**-2.23118**	**0.027173**		
Axial parenchyma strand height (number of cells)	5.6 (±1,5)	5.9 (±1.7)			2451.500	0.174814
Rays per mm*	**16.8 (±3.3)**	**14.0 (±3.0)**			**963.000**	**0.000011**
Hydraulic conductivity (vessel radius^4/vessel per mm^2)	144379 (±17511363)	78473407 (±167299887)			162.0000	0.000021
Vulnerability (vessel diameter / vessel per mm^2)*	**46 (±36)**	**103 (±76)**			**161.5000**	**0.000020**
Mesomorphy (vulnerability x vessel element length)*	**36652 (±27704)**	**74541 (±56634)**			**241.0000**	**0.002002**

1c-d). Flooded trees had a higher proportion of total fibretracheids and higher values for their diameters (Tab. 2). A strong inversion in relative proportions of gelatinous and non-gelatinous fibretracheids was observed between conditions (Tab. 2), with non-flooded trees having more non-gelatinous fibretracheids (41.3% of total) and flooded trees having more gelatinous fibretracheids (36.9% of total) (Tab. 2).

The type of axial parenchyma differed between conditions. Non-flooded trees presented scanty paratracheal and diffuse apotracheal parenchyma, while flooded trees had scanty paratracheal and diffuse-in-aggregates apotracheal parenchyma, but with a tendency to form lines and bands (Fig. 1d). In addition to this qualitative feature, the only statistically significant difference regarding axial parenchyma was parenchyma strand length, which was greater in flooded trees. The only significant difference between conditions regarding rays was their frequency (Tab. 2).

Trees of both conditions had a Vulnerability Index above 1 and a Mesomorphy index above 200, qualifying the wood of *A. sidifolia* trees in both sites as mesomorphic. However, flooded trees had higher values for Mesomorphy and Vulnerability. Although theoretical hydraulic conductivity did not differ significantly between conditions, it was higher for trees under flooding.

Discussion

There are few reports about correlations between swamp conditions and wood anatomical structure or hydraulic architecture of tropical angiosperm stems (Sidiyasa & Baas 1998; Luchi 2004). However, physiological studies suggest that root permeability is reduced in flooded soils due to the alteration of many physical, chemical and biological soil processes. Reduced root permeability increases resistance to water flow in the cortex and, therefore, reduces water absorption. Such conditions cause water deficit in above-ground organs, resulting in a similar response to drought called physiological drought (Ponnamperuma 1984; Worbes 1985, 1995, 1997; Kozlowski 1997; Scarano & Crawford 1992; Sidiyasa & Baas 1998; Lobo & Joly 2000; Parolin & Wittman 2010; Tyagi *et al*. 2023).

Species that occur in sites with less available water tend to decrease vessel diameter, yet increase vessel frequency to maximize water transport (Baas *et al.* 1983; Carlquist 2001). This trade-off guarantees maximum efficiency and minimizes cavitation risk (Fichtler & Worbes 2012). Furthermore, there is a tendency for plants growing under lower water availability to show increased vessel grouping and decreased vessel length and intervessel pit diameter, usually accompanied by decreased fibre length and increased thickness of their cell walls (Baas 1973; Zimmermann 1983; Wheeler & Baas 1991; Sperry & Saliendra 1994; Noshiro & Baas 2000; Carlquist 2001, 2012; Liu & Noshiro 2003; Lens *et al.* 2004; Beeckman 2016).

Although wood structural features of *A. sidifolia* trees growing in flooded soil can be expected to express a state of physiological drought, only vessel element length is congruent with that condition. The other analysed anatomical traits are inconsistent with the hypothesis of physiological drought since *A. sidifolia* trees growing in flooded areas had lower vessel frequency, greater vessel diameter, greater fibretracheid diameter and length, and wider intervessel pits, although these latter two features were not statistically significant.

Among the wood anatomical features compared by Sidiyasa & Baas (1998) for species of section *Alstonia* (Apocynaceae) and by Luchi (2004) for *Croton urucurana* Baill. (Euphorbiaceae), growing under flooded soil, only variation in vessel element length was similar among all species and *A. sidifolia* in the present study. Although vessel diameter and fibretracheid total diameter, lumen diameter and length were statistically different in *C. urucurana* and *A. sidifolia*, in opposition of what Luchi (2004) noted, *A. sidifolia* had lower vessel frequency, higher relative proportion of fibretracheid and thicker fibretracheid walls in trees growing in flooded sites. Copini *et al*. (2016) compared plants over different flood durations (2, 4, and 6 weeks) using stems of four-year-old *Quercus robur* L. (Fagaceae) and found a reduction of vessel area in earlywood and an increase of vessel frequency in all treatments.

Flooding generally stimulates an increase the proportion of parenchyma in secondary xylem and phloem, for both angiosperms and gymnosperms, mainly by increasing ray frequency or the size of their cells (Yamamoto *et al*. 1987; Kozlowski *et al*. 1991; Koszlowski 1997). Sidiyasa & Baas (1998) analysed the influence of flooding on wood anatomy and noted significant differences in ray height. Increasing the differentiation of ray cells could be an alternative for increasing the lateral transport of oxygen and its transport to intercellular spaces (Yamamoto & Kozlowski 1987; Koszlowski *et al*. 1991; Lev-Yadun &

Aloni 1995; Koszlowski 1997; Tyagi *et al*. 2023). *Alchornea sidifolia* showed uniseriate rays under both growth conditions; however, there was a significant reduction in ray frequency for trees growing in flooded soil. On the other hand, there was an increase in axial parenchyma strand height, which may somehow compensate for the reduction of radial parenchyma.

Worbes *et al*. (1992) suggested that species that grow in both non-flooded and flooded sites are not primarily adapted to flooding, but generally tolerant to these growing conditions. Callado *et al*. (2001b) corroborated this opinion pointing to a conservative growth rhythm for *A. sidifolia* trees growing in flooded area. This is because these last authors observed a typical non-flooded tree growth pattern in flooded trees, with leaf-fall and cambial dormancy in the driest period of the year. In present study, the wood structure of *A. sidifolia* trees showed features that favour the transport of a greater amount of water in the trees under flooding, with wider vessels at lower density. This set of features results in higher indexes of mesomorphy and vulnerability, as well as higher theoretical hydraulic conductivity.

The formation of gelatinous fibres is what characterizes tension wood in angiosperms (*e.g.*, Fahn 1974). According to Fang *et al*. (2008), their presence could be a response to different gravitational stimuli that trees experience during development in flooded soil, which are unstable. Yáñez-Espinosa *et al*. (2004) also noted differences in the proportion of gelatinous fibres in trees of *Laguncularia racemosa* (L.) C.F. Gaertn. in mangroves of Mexico. These differences were related to soil composition and structure, and to the levels of flooding typical of the areas where the trees grow, suggesting that other environmental variables, or variables intrinsic of the species, could be involved in the development of tension wood in *L. racemosa* trees. While studying the underground system of plants in the Brazilian Cerrado, Paviani (1978) demonstrated the importance of gelatinous fibres in adverse hydric conditions, indicating that they probably play a role in water storage. This hypothesis was also accepted by Chalk (1989), who stated that the walls of these fibres are composed of highly hygroscopic cellulose, which results in high water storage ability. Thus, our observations corroborate the hypothesis that trees respond to the different gravitational stimuli caused by development in flooded soil with the formation of a greater number of gelatinous fibretracheids in *A. sidifolia* trees that grow in flooded areas. However, we also support the hypothesis that these cells can play a fundamental role in guaranteeing and maximizing the transport of water under these conditions. Therefore, the increase in gelatinous fibretracheids may be, in part, responsible for the conservative growth rate, as described by Callado *et al.* (2021b), and the greater efficiency of water transport of *A. sidifolia* growing under permanent flooding. It is also worth mentioning that escape from the physiological drought phenomenon is also supported by the absence of morphological features associated with flooding in *A. sidifolia* (field observations), such as the formation of adventitious roots, hypertrophic stem lenticels (Kozlowski 1997; Shimamura *et al.* 2010; Somavilla & Graciano-Ribeiro 2012) and stem cracks (Davanso-Fabro *et al*. 1998; Medri *et al*. 2011).

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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