Functional xylem anatomy: intra and interspecific variation in stems of herbaceous and woody species

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Chapter 2

Do woody plants of the Caatinga show a higher degree of xeromorphism than in the Cerrado?

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Abstract

The maintenance and success of plants in different environments is tied to water availability, to the capacities in water transport and to the development of strategies to deal with water deficit. Here, we conducted a study in two seasonally dry Brazilian phytogeographic domains: the cerrado and the caatinga to evaluate whether the adaptive wood anatomy strategies to deal with water deficit would be the same for two species that occur in both domains, and which variables would best explain the variation in wood anatomy variables. Qualitative and quantitative wood anatomy, Student's t-tests, permutational multivariate analyses of variance (PERMANOVA) and pair-contrast analyses were done for 20 specimens of *Tabebuia aurea* and *Tocoyena formosa* from both environments. Our results showed that the species was the strongest variable to explain the variation in the data. But, the environment also appeared as an important variable. Even the caatinga being drier than the Cerrado, this did not result in a higher degree of xeromorphism for both species in the caatinga. Each species, in each environment showed different strategies to deal with the water availability: while vessel diameter and intervessel pit morphology indicate a higher xeromorphic degree for *T. aurea* from the caatinga, vessel grouping index, vessel density, and vessel-ray pit morphology indicate a higher xeromorphic degree of *T. formosa* from the Cerrado. We suggest that the oligotrophic soil and the presence of aluminum in soil may influence the degree of xeromorphism in wood anatomy structure.

Keywords: *Tabebuia aurea*; *Tocoyena formosa*; water availability; wood anatomy strategies; xylem embolism.

Introduction

Water is a primary limiting factor in many terrestrial ecosystems. The plants require water to maintain a variety of physiological process, such as stomatal conductance and CO2 uptake during photosynthesis (Woodruff *et al.* 2016). Inside the plant body, the water is conducted through a complex network of dead cells, and the hydraulic conductance has been linked with transpiration, carbon gain and growth rate (Tyree 2003; Brodribb 2009).

The assumption that water in the xylem is conducted under negative pressure (the Cohesion Tension Theory) was proposed by Dixon in 1914. From that on, studies have shown that the xylem network is prone to become filled with gas (embolism), and its subsequent spread can substantially decrease the hydraulic conductivity, which can result in tissue damage, decreases in gas exchange, and ultimately plant death (Tyree & Zimmermann 2002; Brodersen & McElrone 2013). Thus, hydraulic dysfunction by embolism is a strong selective pressure, and it is imperative for plants to balance the risk of suffering embolism and improving efficiency in water conduction. This balance has led to the development of a variety of hydraulic architecture and mechanisms to maximize efficiency and reduce vulnerability (increasing safety), reflecting differences in species distribution and in ecological and evolutionary aspects (Pockman and Sperry 2000; Sperry 2003; Baas *et al.* 2004).

In this context, there is a general trade-off between safety and efficiency in water conduction taking into account vessels characteristics. Vessels play a key role for angiosperm hydraulic performance. As wider they are, the more efficient conductors of water and more vulnerable to cavitation they will be. On the other hand, as narrower the vessels are the less efficient conductors of water and safer in hydraulic conductance they will be. As a result, safety on water conduction may be adaptive to xeric conditions while efficiency may be adaptive to mesic conditions (Zimmermann 1983; Hacke *et al.* 2006). Although the trade-off safety – efficiency of water transport is true, it is not always observed across species (Tyree *et al.* 1994). For some species, the most common examined wood anatomy traits associated with embolism resistance, for instance vessel diameter, are not correlated with embolism resistance (Schreiber *et al.* 2015). Other species might show both, low efficiency and low safety, which cannot be understood under a trade-off approach (Maherali *et al.* 2004). Furthermore, recent evidences suggest that the vessel diameter – plant size relationship is predictable across species (Olson & Rosell 2013; Olson *et al.* 2013, 2014). The vessel diameter is proportional to stem diameter, and the latter proportional to stem length, suggesting that taper in relation to stem length gives rise to the vessel diameter – stem diameter relationship.

Because xylem anatomy is largely responsible for the cavitation resistance (Johnson *et al.* 2012), it is clear that many xylem network traits could contribute to the safety – efficiency trade-off, and that these traits would interact in different ways, and at different multiple scales (Gleason *et al.* 2015). For instance, vessel length and diameter (Loepfe *et al.* 2007) and the degree of vessel grouping (Carlquist 1984; Lens *et al.* 2011) are important determinant components of this trade-off safety – efficiency in angiosperms, influencing the continuity of water flow. In addition, there are general ecological trends in wood anatomy supporting the dominant safety – efficiency trade-off. Species from drier environments tend to have narrow vessels (Carlquist 1966; Bosio *et al.* 2010), short vessel elements (Carlquist 1982), and high values of vessel density and vessel grouping (Baas *et al.* 1983; Carlquist & Hoekman 1985; Sonsin *et al.* 2012). Moreover, these species tend to have low values for vulnerability (V = vessel element diameter/vessel density) and mesomorphy (M = V × vessel element length) indices (Carlquist 1977; Sonsin *et al.* 2012), and show thicker fiber walls (Alves & Angyalossy-Alfonso 2002) necessary to support negative xylem pressures (Hacke & Sperry 2001).

Successful colonization of xeric habitats by both angiosperms and gymnosperms has been linked to xylem highly resistant to embolism formation (Brodribb *et al.* 2012). Different levels of safety and efficiency are expected in different environments because xylem operates at widely different water potentials (Choat *et al.* 2012), and in seasonally dry environments the higher negative pressure in the vessels of plants can increase the risk of cavitation and embolisms (Sperry & Hacke 2002). The cerrado and the caatinga are two examples of seasonally dry environments in Brazil (Pennington *et al.* 2000) with at least five consecutive dry months (Nimer 1972; Silva *et al.* 2008), although climatic conditions are harsher in the latter. The Cerrado, a savanna-like ecosystem, is located in the Brazilian Central Plateau, with annual mean temperatures around 22–23 °C and average annual rainfall around 1,500 mm (Silva *et al.* 2008). Soils are usually deep, nutrient-poor and aluminum-rich, the latter toxic to some plant species (Coutinho 2002). The caatinga is a tropical dry forest ecosystem of the semiarid region of northeast Brazil, with annual mean temperatures around 26–27 °C (Andrade-Lima1981) and average annual rainfall between 300 and 800 mm (Nimer 1972).

In the light of these considerations, we aimed to test if woody species occurring in the cerrado and in the caatinga would show different wood anatomy strategies, and different degree of xeromorphism, to deal with the absence of water during the months of drought. Moreover, we tested the differences between sites and which variables could best explain the variation in the anatomy variables.

Material and Methods

Plant material and study site

We selected two species common to both the Cerrado (Ratter *et al.* 2003) and the caatinga (Moro *et al.* 2014): *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore and *Tocoyena formosa* (Cham. & Schltdl.) K. Schum.

In the Cerrado, we sampled individuals of both species in the "Palmeira da Serra" Private Reserve, in the municipality of Pratânia, in the state of São Paulo (Fig. 1), southeastern Brazil (22° 48′ 35″ S 48° 39′ 57″ W). In the caatinga, we sampled individuals of *Tabebuia aurea* in the municipality of São João do Cariri (7° 23′ 27″ S, 36° 32′ 2″ W) and individuals of *Tocoyena formosa* in the municipality of Serra Branca (7° 29′ 14″ S, 36 ° 39′ 51″ W), both in the state of Paraíba (Fig. 1), northeastern Brazil.

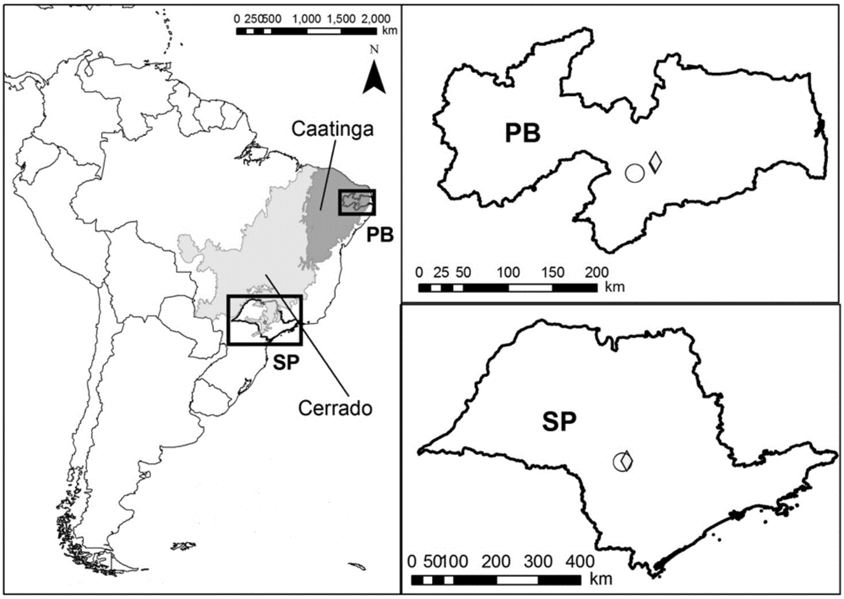

Figure 1 • Study sites in the cerrado and in the caatinga. The circle (O) indicates the study site sampling of *Tocoyena formosa* and the diamond (◊) the study site sampling of *Tabebuia aurea*.

A dataset of 12 years (2000 – 2012) was used to estimate the mean monthly rainfall and temperature in that period. The climatic data were provided by the Estação Experimental of the Faculdade de Ciências Agronômicas, Universidade Estadual Paulista (UNESP), Botucatu Campus, for the Cerrado and by the Estação

Experimental of São João do Cariri, for the caatinga. The Cerrado has a milder climate than caatinga, with mean temperature below 25 °C throughout the year. The precipitation in this domain is higher, with maximum monthly rainfall of 350 mm during the wet season. Even though, the Cerrado shows a remarkable dry season from June to September when precipitation reaches less than 50 mm in a month (Fig. 2). The caatinga is a hotter environment, with temperatures above 25 °C throughout the year. This domain also has longer dry season than the Cerrado, extending from July to December, when the precipitation reaches zero. During the rainy season the maximum monthly rainfall does not exceed 100 mm (Fig. 2).

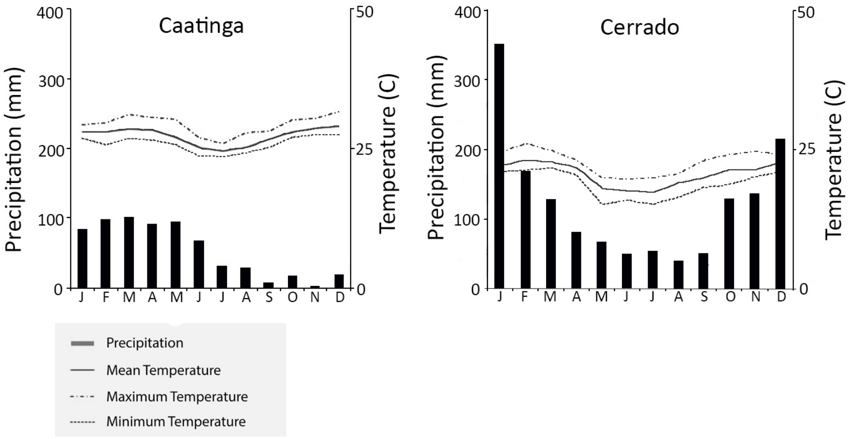

Figure 2 • Climate graphs with mean precipitation and temperature from 2000 to 2012.

Sampling and anatomical study

We standardized the number of individuals studied taking into account the individuals of *Tabebuia aurea* available at the study site in the cerrado area (population size = 5). So, for both species, we collected 5 different individuals, in both areas, amounting 20 individuals studied.

We collected samples from the basal region of the thicker branches of the shrub *Tocoyena formosa* and from the main stem at breast height of the tree *Tabebuia aurea*. In the field we measured the stem circumference at the height at which the samples were taken, and the plant height. The wood samples were fixed in FAA 70% (Formaldehyde 37%, acid acetic, ethanol 70% – 1:1:18) and thereafter stored in 70% alcohol. We cut tangential longitudinal, radial longitudinal and cross sections of 15–20 µm thickness of each sample with a sliding microtome. To prepare permanent histological slides, we followed Johansen (1940) and Sass (1951).

Sections were double-stained with aqueous 1% safranin and aqueous 1% astra blue (1:9). Histological slides were mounted permanently in synthetic resin (Entellan®). For maceration, we followed Franklin's (1945) method modified by Kraus & Arduin (1997). The cells were dissociated in acetic acid and hydrogen peroxide (1:1), stained with aqueous 1% safranin and mounted in a 1:1 glycerin-water solution. The wood anatomy slides were analysed using an Olympus DP70, equipped with Axio Cam MRC and Axiovision software. We followed the suggestions of the International Association of Wood Anatomists Hardwood List (IAWA Committee 1989) to determine the wood anatomy features, and the suggestions of Scholz *et al.* (2013) and Carlquist (1977, 2001) for measurements of the wood anatomy variables. The qualitative data for wood anatomy are given in Supplementary Information.

We collected soil samples from both regions at a depth of 0–20 cm and of 20–40 cm (ten replicates each), close to the sites of species occurrence. Soil samples were sent to the Departamento de Solos of the Faculdade Ciências Agronômicas, Universidade Estadual Paulista (UNESP), Botucatu, São Paulo state, for physical and chemical analysis. Soil analysis was carried out as per the procedures described by Raij *et al.* (2001). Air-dried soil samples were analyzed for the available contents of phosphorus (P); aluminum (Al); potential acidity (H+Al); the basic cations, including potassium (K), calcium (Ca), and magnesium (Mg); sum of the bases Ca, Mg and K (SB); pH; base saturation (V%); micronutrients boron (B), copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn). The cation exchange capacity (CEC) was analyzed using buffered SMP solution (pH = 7) (Shoemaker *et al.* 1961). The total organic carbon (O.M.) was analyzed using the Colorimetric Method (Walkley & Black 1934, modified).

Statistical analyses

The quantitative analysis was based on 30 individual measurements per specimen to achieve mean values within 90% confidence limits, following Freese (1967) and Eckblad (1991).

To test for differences between sites, we conducted a permutational multivariate analyses of variance (PERMANOVA) with anatomical variables (rank transformed) as dependent variables; the interaction between site and species as independent variable; and plant height and stem diameter as covariates. To avoid collinearity, we selected the variables based on biological knowledge (for variables biologically correlated we choose one of them, e.g. ray height in цm and ray height in number of cells, we selected ray height in цm and deleted ray height in number of cells) , correlation coefficients (values below 0.6), and visual analyses of pairwise scatter-plots (Zuur *et al.* 2010). PERMANOVA was performed using the adonis function in the vegan package (Oksanen *et al.* 2015) in R (R Core Team 2014), based on

Euclidian distances and 999 permutations. To detect specific differences between sites for each species, pair-contrast analyses were done using the contrasts function in the stats package (R Core Team 2014) and the adonis function in the vegan package (Oksanen *et al.* 2015) in R (R Core Team 2014).

To test for anatomical differences within each species between the two sites, we performed Student's t-test for each wood anatomical variable with normal distribution (fiber length, fiber lumen diameter, ray width in µm and in number of cells, ray frequency, intervessel pit diameter and aperture, vessel-ray pit diameter and aperture). Because vessel element length, vessel diameter, vessel density, vessel grouping, fiber diameter, fiber wall thickness, ray height in µm and in number of cells, vulnerability and mesomophy indexes did not present normal distribution (graphical tools analyses as proposed by Zuur *et al.* 2010), we performed Kruskal-Wallis Rank Sum test.

Results

Wood anatomy differences

The wood anatomy description of *Tabebuia aurea* and *Tocoyena formosa* is given in Supplementary Information (Fig. S1, Fig. S2).

To avoid collinearity, we selected five wood anatomy variables, out of 19, to be tested in the permutational multivariate analyses. The five variables selected were: vessel element length, vessel grouping index, fiber lumen diameter, ray width in цm, and intervessel pit diameter (Table 1). The covariates plant height and stem diameter were not included in the final model because they were not significant. According to PERMANOVA results (Table 1), site, species and the interaction site × species explained 50% of the variation in the group of anatomical variables analyzed. Species was the strongest explanatory variable (28%). The contrast analysis testing the differences between sites within each species showed significant differences only for *T. aurea*.

Tabebuia aurea from caatinga differed from those of the Cerrado in eight out 19 wood anatomy features analyzed, which were: vessel diameter, fiber wall thickness, ray height in цm, ray width in цm and in number of cells, ray frequency, intervessel pit diameter, vessel-ray pit diameter (Table 2). Narrower vessels, narrower intervessel pits diameter and vessel-ray pits diameter, thinner fiber wall thickness, shorter and narrower rays, and higher frequency of rays were observed in individuals from caatinga.

Table 1: Summary of PERMANOVA, results based on 999 permutations, with anatomical variables (rank transformed) as dependent variables; the interaction between site and species as independent variable; and plant height and stem diameter as covariates.

Parameters	***df***	**SS**	**MS**	***F* Model**	R^2	***P*(>*F*)**
Site	1	0.965	0.965	4.249	0.132	0.005
Species	1	2.066	2.066	9.098	0.282	0.001
Site : species	1	0.654	0.654	2.878	0.089	0.031
Plant height	---	---	---	---	---	---
Stem diameter	---	---	---	---	---	---
Residuals	16	3.634	0.227		0.497	
TOTAL	19	7.319			1.000	
Contrast analysis						
T. aurea in the caatinga and in the cerrado	1	1.407	1.407	4.196	0.192	0.008
T. formosa in the caatinga and in the cerrado	1	0.212	0.212	0.632	0.029	0.620
Residuals	17	5.700	0.335		0.779	
TOTAL	19	7.319			1.000	

SS, sum-of-squares; MS, mean squares; and *P*(>*F*) are *P*-values. ---: non-significant. We used Euclidian distance to measure dissimilarity between samples.

Tocoyena formosa from caatinga differed from those of the Cerrado in five out 19 wood anatomy features analyzed, which were: vessel density, vessel grouping index, vessel-ray pit diameter, vulnerability index and mesomorphy index (Table 2). Lower density of vessels and vessel group index, and higher values for mesomorphy and vulnerability indexes were observed in the individuals from caatinga. Moreover, as well as *T. aurea*, narrower vessel-ray pit diameter were observed for *T. formosa* in caatinga.

Soil characterization

The soils in both domains were sandy (Table 3). The cerrado soils were more acid, with higher aluminum and H saturation of soil cation exchange capacity (Table 3) and lower concentration of macronutrients (P, K, Ca, Mg) and micronutrients, such as manganese (Table 3). In addition, the cerrado soils showed a higher proportion of copper and iron than the caatinga soils (Table 3).

Discussion

In this study we investigated whether two species occurring both in the caatinga and in the cerrado, two seasonally dry environments in Brazil, would show different wood anatomy strategies to deal with the drought period. We also tested if the sites would be differentiated by the wood anatomy variables and which variables, such as the species-specific characteristics, and the environmental influence could explain the variation in the wood anatomy data variables.

The plant height and the stem diameter were not significant to explain the variation in the wood anatomical data using the PERMANOVA model (Table 1). Rather than plant height and stem diameter, site, species and site × species interaction explained half of the variation (Table 1). Most of the variation was explained by the variable species, emphasizing the importance of the phylogenetic traits. However, the site also appeared as an important source of variation, but not as a universal trend, because the site did not explain the variation for *Tocoyena formosa* (contrast analyses Table 1). Nevertheless, the influence of the site is supported by the differences in the Students t-test, which showed nine different anatomical variables for *Tabebuia aurea* and five different variables for *T. formosa* (Table 2). These results seem to point out *T. aurea* as more sensitive to the environmental conditions (higher phenotypic plasticity) than *T. formosa*. The differences in wood anatomy variables within species in different environments, can be seen as different wood anatomical strategies in drought resistance for each species in both environments.

Worldwide, forest species operate with narrow margins of hydraulic safety (Choat *et al.* 2012), frequently leading to embolism formation. Therefore, strategies to prevent or reverse embolisms are required to increase plant survival. Plants in drier sites frequently present narrower vessels than plants in moister sites (Carlquist 1966; Carlquist & Hoekman 1985; Alves & Angyalossy-Alfonso 2000; Lens *et al.* 2004; Bosio *et al.* 2010). Indeed, we found narrower vessels in *T. aurea* from caatinga that is a drier environment than cerrado. This characteristic could be explained in terms of increased safety on sap flow. Based on the Hagen–Poiseuille law the diameter scales to the fourth power of the conductance, so, a narrow vessel is associated with lower hydraulic efficiency (or high hydraulic resistance) (Ewers *et al.* 1990), being less vulnerable to the impact of drought induced cavitation than wider conduits (Lens *et al.* 2004; Schreiber *et al.* 2015). In addition to narrower vessels, we also found narrower intervessel pit diameter in *T. aurea* from caatinga. A decrease in the membrane area of the intervessel pit is correlated with an increase in resistance to drought-induced cavitation (Hacke *et al.* 2006). Vessel and intervessel pits diameter directly influence the resistance in hydraulic conductivity, each accounting for about half of the total resistance (Sperry *et al.* 2005). Our data

Table 2: Quantitative wood anatomy characters of *Tabebuia aurea* and *Tocoyena formosa* from the cerrado and the caatinga. t-test was performed for variables with normal distribution, and the others with Kruskal-Wallis Rank Sum test. The values are means with the corresponding standard error.

Wood anatomy features	***T. aurea* caatinga**	***T. aurea* cerrado**	**t test (p value)**	**Kruskal-Wallis Rank Sum test**	***T. formosa* caatinga**	***T. formosa* cerrado**	**t test (p value)**	**Kruskal-Wallis Rank Sum test**
Vessel element length (µm)	259.0 ± 3.4	271.0 ± 14.7		0.6015	557.7 ± 48.7	466.1 ± 25.8		0.1745
Vessel diameter (µm)	89.6± 4.1	106.9 ± 5.7		0.0472	48.4 ± 0.9	44.4 ± 1.5		0.0758
Vessel density (nº mm^{-2})	8.9 ± 1.4	10.9 ± 1.3		0.6015	52.6 ± 4.3	81.3 ± 7.7		0.0163
Vessel grouping index (nº of vessels per group)	1.5 ± 0.0	1.9 ± 0.2		0.1172	1.2 ± 0.0	1.5 ± 0.0		0.0090
Fiber length (µm)	799.8 ± 33.9	839.9 ± 32.3	0.4160		1146.9 ± 56.0	1052.6 ± 39.2	0.2092	
Fiber diameter (µm)	16.3 ± 0.2	17.2 ± 0.5		0.2506	21.4 ± 0.9	22.3 ± 0.3		0.6015
Fiber lumen diameter (µm)	8.5 ± 0.2	8.4 ± 0.5	0.8863		7.9 ± 0.4	8.3 ± 0.5	0.5755	
Fiber wall thickness (µm)	3.9 ± 0.1	4.4 ± 0.2		0.0090	6.7 ± 0.3	7.0 ± 0.1		0.4647
Ray height (µm)	139.7 ± 7.2	200.3 ± 12.6		0.0090	549.9 ± 29.0	575.0 ± 6.8		0.1745
Ray height (number of cells)	6.8 ± 0.3	7.9 ± 0.7		0.1745	11.8 ± 0.7	13.0 ± 0.8		0.2506
Ray width (µm)	20.6 ± 2.9	29.8 ± 1.8	0.0326		22.9 ± 1.2	23.5 ± 3.6	0.8933	
Ray width (number of cells)	1.4 ± 0.1	1.7 ± 0.1	0.0215		1.3 ± 0.0	1.5 ± 0.1	0.1212	
Ray frequency (nº mm^{-1})	13.9 ± 0.9	10.3 ± 0.5	0.0092		19.4 ± 0.6	17.8 ± 0.3	0.0741	
Intervessel pit diameter (µm)	4.6 ± 0.2	5.9 ± 0.2	0.0035		4.5 ± 0.3	4.5 ± 0.1	0.9464	
Intervessel pit aperture (µm)	2.4 ± 0.1	2.6 ± 0.1	0.3668		1.7 ± 0.1	1.5 ± 0.1	0.2252	
Vessel-ray pit diameter (µm)	4.0 ± 0.1	4.5 ± 0.1	0.0155		4.1 ± 0.1	4.4 ± 0.0	0.0169	
Vessel-ray pit aperture (µm)	2.5 ± 0.1	2.9 ± 0.2	0.0765		1.6 ± 0.0	1.8 ± 0.1	0.1104	
Vulnerability index	12.1 ± 3.4	10.3 ± 1.3		0.9168	0.9 ± 0.1	0.6 ± 0.1		0.0163
Mesomorphy index	3124.8 ± 865.6	2809.9 ± 430.7		0.9168	528.7 ± 63.6	259.9 ± 19.1		0.0090

Table 3: Soil analysis of collection sites, from the Private Cerrado Reserve “Palmeira da Serra” in the cerrado and from the municipality of Serra Branca, in the caatinga.

Physical analyses

Domains	Sandy					
	Coarse	Fine	Total	Clay	Silt	Texture
	g/kg					
cerrado	----	----	861	99	40	sandy
caatinga	----	----	921	36	43	sandy

Micronutrients

Domains	Boron	Copper	Iron	Manganese	Zinc
	mg/dm^3				
cerrado	0.21	0.7	115	1.2	0.2
caatinga	0.13	0.2	65	8.0	0.3

Fertility

Domains	pH CaCl$_2$	O.M.	P$_{resin}$	H + Al	K	Ca	Mg	SB	CEC	V%	S
		g/dm^3	mg/dm^3	mmol/dm^3							
cerrado	4.0	6.0	2.0	36.0	0.3	1.0	0	2.0	38.0	5.0	---
caatinga	4.7	8.0	5.0	15.0	1.1	7.0	3.0	11.0	26.0	42.0	5.0

pH CaCl$_2$ = hydrogen ion concentration; O.M. = organic matter; P$_{resin}$= phosphor; H+Al = potential acidity; K = potassium; Mg = magnesium; SB = sum of basis; CEC = cation exchange capacity; V% = saturation/base; S = sulfur; CaCl$_2$ = calcium chloride; g/dm^3 = gram/decimeter cubic; mg/dm^3 = miligram/decimeter cubic; mmol/dm^3 = milimoles charge/decimeter cubic; g/kg = gram/kilogram.

on vessel and intervessel pit morphology in *T. aurea* indicate a higher xeromorphic degree of plants in the caatinga. A similar relationship has been observed in other Brazilian species from dryer environments (Marcati *et al.* 2001; Sonsin *et al.* 2012), confirming its significance for hydraulic safety on this species.

Tabebuia aurea from the cerrado seems to have a different strategy to avoid air-seeding and embolism formation. Our data showed taller and wider rays for these individuals, which could be interpreted as an evidence of drought resistance mechanism played by the parenchyma tissue (Brodersen *et al.* 2010; Nardini *et al.* 2011). The parenchyma cells have already been shown to be correlated with drought mechanisms such as xylem capacitance and refilling of embolised vessels (Trifiló *et al.* 2014). It has been speculated that this tissue not only stores water, but could also provide symplastic connections with bark and pith, both important water reservoirs (Scholz *et al.* 2007). Additionally, it has been suggested that vessel-associated radial and axial parenchyma may be involved in the embolism refilling process by releasing sugars and water into embolised vessels (Salleo *et al.* 2008; Brodersen & McElrone 2013). The rays work, in this case, as an efficient radial pathway from the phloem carrying water, needed to raise the water potential for refilling. Moreover, the rays could also play the role of carrying ions (being the phloem as the source), to be loaded into xylem, responsible to create the osmotic force to the refilling process (Metzner *et al.* 2010; Nardini *et al.* 2011).

The large diameter of vessel-ray pits in the two cerrado species indicates an investment in a more efficient sugar transport into embolized vessels. The vessel-ray pits are effective in the transport of osmotically active sugar (from starch hydrolysis; Bucci *et al.* 2003) from these parenchyma cells into embolized vessels, providing an osmotic mechanism for embolism reversal (Salleo *et al.* 2006, 2008; Nardini *et al.* 2011). A higher concentration of solutes and, therefore, a lower osmotic potential in the embolized vessels, increases the water transport into these vessels reestablishing the flow with a possible reversal mechanism of embolisms (Hacke & Sperry 2003). A decrease in starch concentration in parenchyma cells would turn these cells into sinks for the phloem. As a response, the phloem would unload sugars and water into these cells, via their rays, generating the necessary driving force for refilling the xylem, and potentially reversing embolism (Salleo *et al.* 2009; Nardini *et al.* 2011).

Different from *T. aurea*, the higher values for the vessel density and vessel grouping index, and lower values for vulnerability and mesomorphy indices of *T. formosa* seem to be good predictors of strategies to deal with water deficit of this species from the cerrado. The relationship of these predictors with hydraulic safety and conductivity has already been reported (Carlquist 2001, 2012; Bosio *et al.* 2010; Sonsin *et al.* 2012;) . A higher vessel grouping index allows the continuity of water transport if one or several vessels in a group are incapacitated by air embolisms (Carlquist 1984, 2012), therefore improving the hydraulic efficiency.

In spite of the remarkable dry season, the cerrado is not considered a xerophytic vegetation type as the caatinga is (Oliveira & Marquis 2002). For instance, most of cerrado ‘s plants develop large green leaves in the body plant throughout the year (Morretes & Ferri 1959). Moreover, some plants also flourish during the dry period (Rivera *et al.* 2002), and develop deep root system enabling plants to access water stored deeply in the soil during the periods of drought, maintaining transpiration and carbon fixation (Oliveira *et al.* 2005). Taking these general characteristics of cerrado plants into account, we believe that the drought resistance adaptations discussed here for both cerrado species are not an adaptive response to water availability. We suggest that this can be a response for the chronic low availability of edaphic mineral nutrients (oligotrophism) and the high aluminum concentration (aluminum toxicity) in the cerrado soils (Table 3). The oligotrophic and aluminum toxic soils have been reported as the main cause of xeromorphic features in the cerrado plants, such as sclerophylly in leaves (Coutinho 1983; Salatino 1993), being conceptualizedas the theory of Oligotrophic Scleromorphism (Arens 1958; Arens *et al.* 1958; described in English in Salatino 1993), or peinomorphism (sensu Walter 1973). In the same way, by the higher sclerophylly commonly found in the leaves of the cerrado species (Oliveira *et al.* 2003; Souza *et al.* 2015), we would expect higher sclerophylly for wood characters as well, which was shown by the thicker fiber walls found in individuals of *T. aurea* from the cerrado. Moreover, the individuals of *T. formosa* from the cerrado are shorter (Table S1, Supplementary Information) than those from the caatinga. This reduced size can also be explained by the higher aluminum concentration (Table 3) as well as the lower concentration of essential micronutrients, such as manganese (Table 3) in the cerrado soils. Aluminum is a strong plant growth reducing element in acid soils (Kochian 1995), and the deficiency of any essential micronutrient can cause disorders in physiological and biochemical processes, resulting in reduced plant growth (Kozlowski *et al.* 1991). These results point to mention that the Oligotrophic Scleromorphism Theory can also be applied to wood anatomical features in this particular case, supporting our hypotheses of high aluminum concentration and oligotrophism as a cause of the presence of xeromorphic features in wood of *T. formosa* from the cerrado.

When we compare in general the anatomical adaptation of the two species, on each environment, we notice particular adaptations for each species. In other words, each species has its own trade-off to deal with the environment adversities both in the cerrado and in the caatinga. For instance, while *T. aurea* ranged on vessel diameter (wider in the cerrado), and *T. formosa* ranged in the vessel density and vessel index grouping (both higher in the cerrado), maintaining relatively steady the vessel diameter. Moreover, *T. aurea* showed a huge variation in the rays (wider and higher in the cerrado), while the same did not occurr for *T. formosa*, which preserved constant size of the rays. This constancy in ray size could be probably compensated by the higher number of vessels/mm² in *T. formosa* compared with *T. aurea*. It seems that the lower number of vessels/mm² in *T. aurea* can be offset by the variation in ray size, which in some way, interact with the sparse vessels via the vessel-ray pits connections.

In summary, the environment has a noteworthy influence in wood anatomy characters, even if it is not a universal key to explain the variation. Its influence is noticed on the particular adaptation within species for each environment. Woody plants of the caatinga did not necessarily show a higher degree of xeromorphism than in the cerrado. Despite the fact that both environments show a period of water deficit, the difference in the rainfall is different for each environment. In the caatinga the irregularity in the rainfall is remarkable during the years and the mean precipitation is less and concentrated in three months. In the cerrado the rainy and drought period is well-defined during the years, but, on the other hand, the plants have to deal with the edaphic adversities. These particular characteristics of both environments is reflected in the particular wood anatomy strategies within species in both environments. It is important to point that the drought adaptation strategies are not restricted to the xylem. The characteristics of leaves (density of stomata, stomatal conductance, epicuticular waxes), rooting depth, and physiological processes (photosynthetic capacity, deciduousness), are also variables that could influence plant responses to water deficit.

Supplementary information

Wood anatomy descriptions

Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S. Moore

Growth rings: delimited by axial parenchyma in marginal lines or bands (Fig. 1 A–D) in the wood of individuals from both environments. Vessels: wood diffuse-porous (Fig. 1 A–D); 49% of solitary vessels (Fig. 1 C) in individuals from the cerrado and 54% (Fig. 1 D) in individuals from the caatinga; clusters rare (Fig. 1 C) in both environments, but more frequent in individuals from the cerrado; simple perforation plates (Fig. 1 E) predominant, and foraminate (Fig. 1 E) in a few vessel elements; vessel element tails present; intervessel pits alternate; vessel-ray pits with distinct borders, similar to intervessel pits in size and shape throughout the ray cell. Fibers: simple to minutely bordered pits in both radial and tangential walls. Axial parenchyma: in marginal lines or bands, paratracheal confluent forming irregular bands often, and lozenge-aliform (Fig. 1 A–D); 2–4 cells per parenchyma strand; amount of 63% of axial parenchyma in both environments; storage starch in axial parenchyma. Rays: 2-seriate (Fig. 1 G) rays predominantly in individuals from the cerrado and uniseriate (Fig. 1 H) predominantly in individuals from the caatinga; all ray cells procumbent (Fig. 1 I–J); storage starch in rays. Storied structure: rays irregularly storied (Fig. 1 G) in individuals from the cerrado and rays, axial parenchyma and vessel elements storied (Fig. 1 H) in individuals from the caatinga. Chrome Azurol-S test: positive.

Tocoyena formosa (Cham. & Schltdl.) K. Schum.

Growth rings: delimited by thick-walled and radially flattened latewood fibers (Fig. 2 A–D) in the wood of individuals from both environments. Vessels: wood diffuse-porous (Fig. 2 A–D); 61% of solitary vessels in individuals from the cerrado and 85% in individuals from the caatinga; simple perforation plates (Fig. 2 E, G, I); vessel elements tails present, conspicuous (Fig. 2 E); intervessel pits alternate, vestured (Fig. 2 F); vessel-ray pits with distinct borders, similar to intervessel pits in size and shape throughout the ray cell; deposits in some vessel lumina. Tracheids: vascular tracheids present (Fig. 2 G). Fibers: with distinctly bordered pits in both tangential (Fig. 2 H) and radial (Fig. 2 I) walls. Axial parenchyma: apotracheal diffuse to diffuse-in-aggregates (Fig. 2 C, D); 3–4 cells per parenchyma strand; amount of 5% of axial parenchyma in individuals from the cerrado and 6% of axial parenchyma in individuals from the caatinga; storage starch in axial parenchyma. Rays: 1 to 3 cells wide, with multiseriate portion as wide as uniseriate portion (Fig. 2 H); fused rays (Fig. 2 H); body ray cells procumbent with over 4 rows of upright and/or square marginal cells (Fig. 2 I); perforated ray cells present (Fig. 2 J); storage starch in rays. Chrome Azurol-S test: positive, more pronounced in individuals from the cerrado.

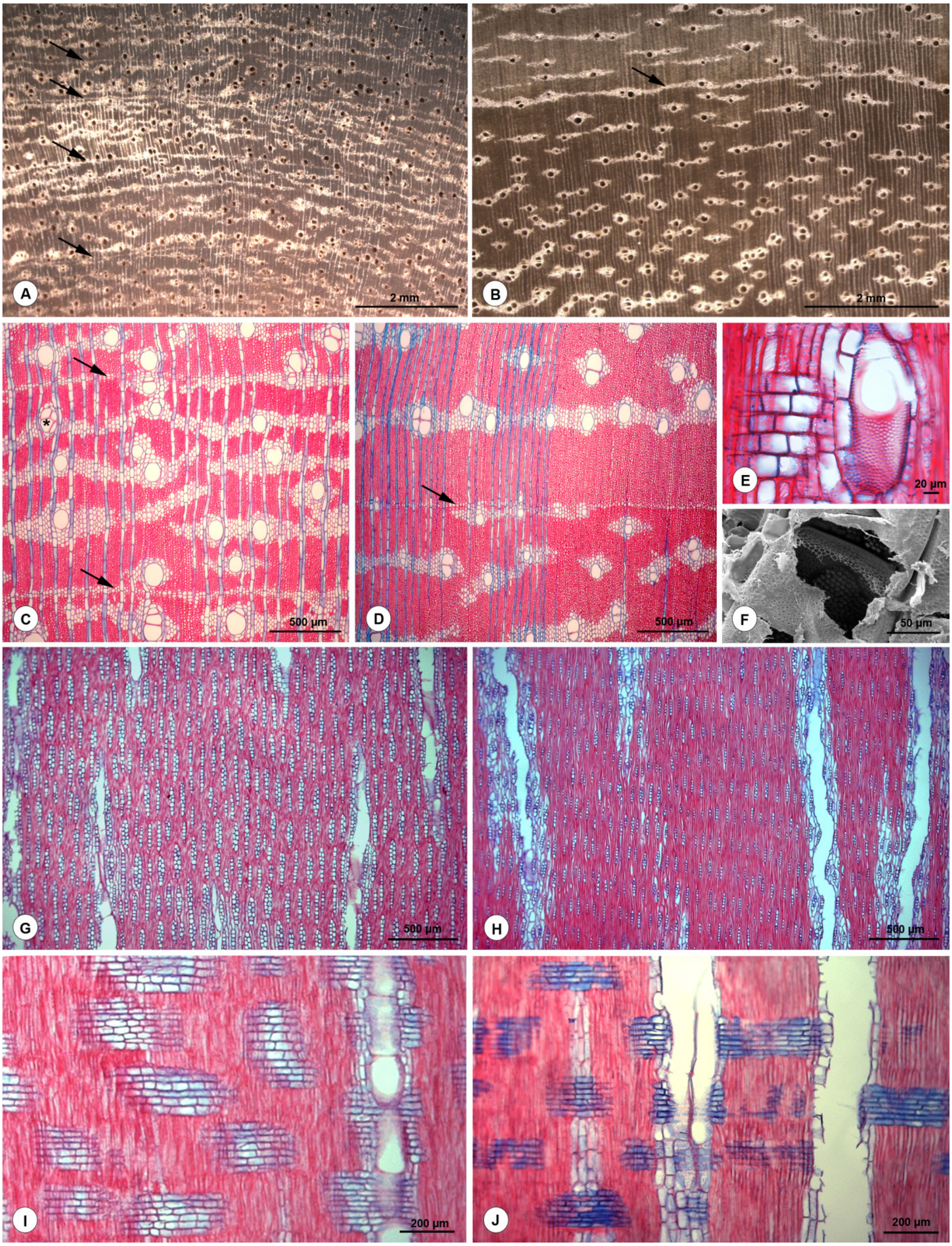

Figure S1 • Macroscopic and microscopic images of *Tabebuia aurea* secondary xylem. A–D. Cross sections. Growth rings delimited by marginal lines/bands of axial parenchyma (arrows), wood diffuse-porous, and paratracheal axial parenchyma in individuals from the cerrado (A, C) and from the caatinga (B, D). Note narrower growth rings and vessel cluster (*) in individuals from the cerrado (A, C). E. Simple perforation plate in radial longitudinal section. F. Foraminate perforation plate broken by technical artifact in scanning electron microscopic. G–H. Tangential longitudinal sections. G. Two-seriate and irregularly storied rays in individuals from the cerrado. H. Uniseriate regularly storied rays in individuals from the caatinga. I–J. Radial longitudinal section. Ray cells procumbent in individuals from the cerrado (I) and in individuals from the caatinga (J).

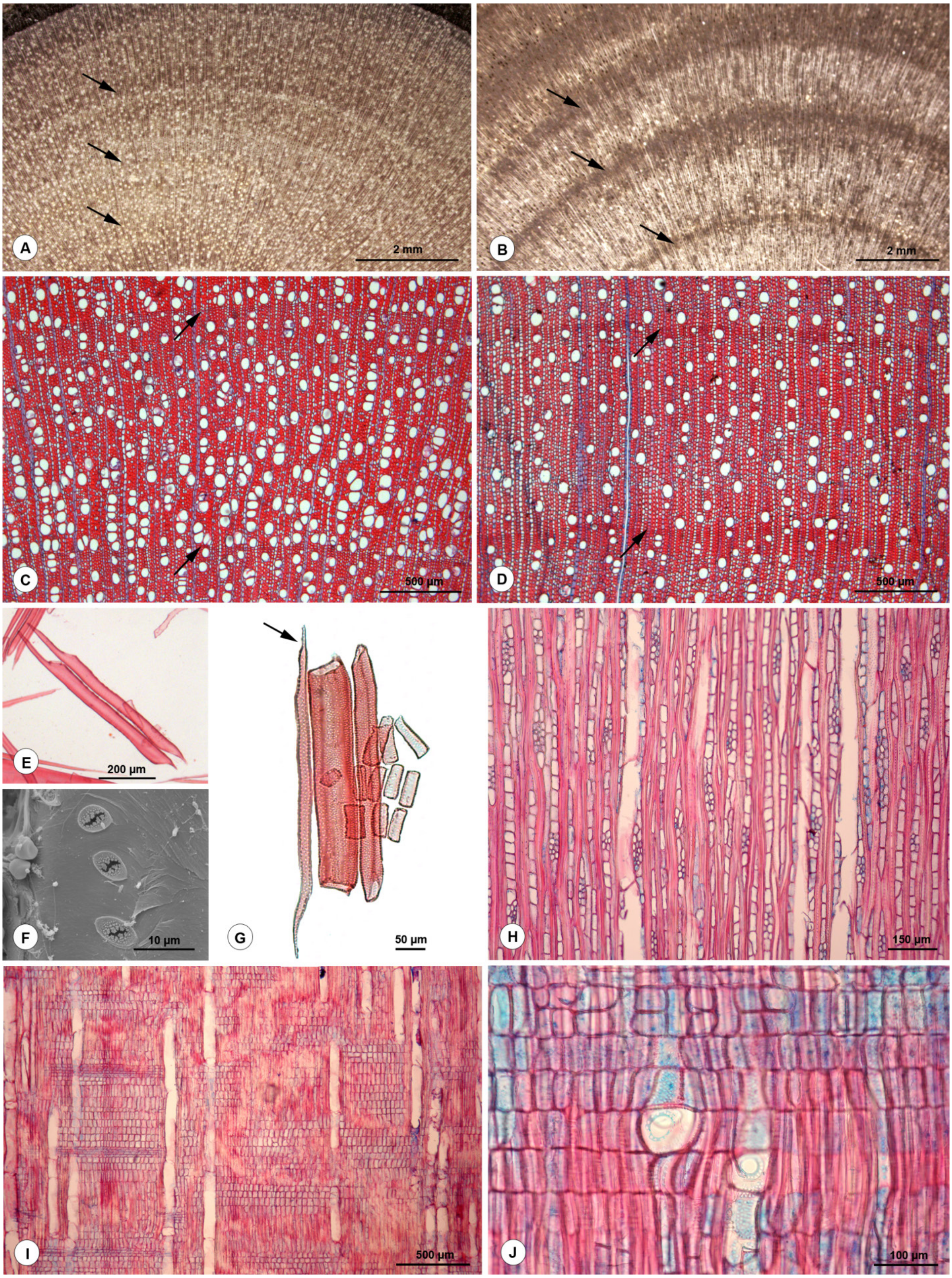

Figure S2 • Macroscopic and microscopic images of *Tocoyena formosa* secondary xylem. A–D. Cross sections. Growth rings delimited by thick-walled and radially flattened latewood fibers, wood diffuse-porous, and diffuse to diffuse-in-aggregates in individuals from the cerrado (A,C) and from the caatinga (B, D). Note growth markers more pronounced in individuals from the caatinga (B, D). E. Conspicuous tails of vessel elements in macerate. F. Intervessel vestured pits in scanning electron microscopic. G. Vascular tracheid (arrow) and simple perforation plate in macerate. H. Rays 1–3 cells wide with multiseriate portion as wide as uniseriate portion, fused rays in tangencial longitudinal section. I–J. Radial longitudinal sections. I. Heterogeneous rays. J. Perforated ray cells.