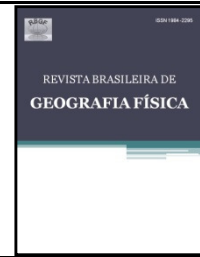




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## Hydraulic and Leaf Economics of Woody Plants of the Tropical Environment

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### ABSTRACT

Leaf photosynthesis and hydraulic traits are closely related to the maintenance of the plants, especially in tropical environments. There is scarce information about the xylem structure and hydraulic efficiency in tropical species, mainly considering the leaf. Environmental changes influence the species performance, conditioning differences of anatomical traits and functional efficiency of xylem cells related to the water flow inside the plant. The hydraulic conductivity and the theoretical leaf-specific conductivity allow estimating the xylem cells flow and inform about the efficiency of the water transport inside the plant. The relation among leaf biometry and anatomic/hydraulic characteristics of the xylem cells of leaves with different stages of growth, of five woody species from the tropical environment, was evaluated. Differences among leaves of different ages and species indicate to be responsible for the anatomical traits variations. The xylem hydraulic traits indicate a greater or smaller efficiency in leaves water transport and are related to the species. The hydraulic and structural differences indicate an adaptation to higher efficiency in water transport in leaves related to the prevailing environmental conditions during the leaf development.

Keywords: Hagen-Poiseuille Law, Huber value, Hydraulic diameter, Xylem characteristics, Leaf specific conductivity.

### Introduction

The crescent fragmentation of Atlantic Forest implies in a reducing of its biodiversity, and the knowledge about leaf traits, mainly those that are related to the photosynthesis and an efficient use of water, is crucial.

The tropical Atlantic Forest complex, the phytogeographic domain where wood plants are established, is among the 25 hotspots of world's biodiversity (Rôças et al., 2001), with high endemism index (Myers et al., 2000) and generalist plant species (Rôças et al., 1997). This forest complex shows an elevated level of environment fragmentation, only remaining 7.5% of its original area (Scarano, 2002), resulting in an urgency to achieve more profound knowledge concerning species acclimatization in these environments.

Plant species established at the woody tropical forests are under low resources available during its development, mainly by the presence of a sandy soil which has low water and nutrient retention capability (Rosado and Mattos, 2007).

Among the plant traits, the dependent relationships between morphoanatomical traits and hydraulic performance in leaves remain poorly studied (Yin et al., 2018) and the information about these traits and the leaf economics is scarce (Li et al., 2015).

The water transport efficiency is closely related to an appropriate plant development, mainly related to photosynthesis and transpiration that demand amounts of water (Baum et al., 2000).

The system of upward flow of water works in an integrated way, from the absorption of water by the roots, through the stem and its use in the leaves. In the leaf, the veins are a transport route of this water that will be used in the photosynthesis, resulting in the leaf blade growth.

Anatomical characteristics are associated with hydraulic characters to evaluate the vessels conduction functionality in some studies with species of temperate environments (Zwieniecki et al., 2002; Aasamaa et al., 2001; Lewis, 1992).

However, hydraulic system characteristics and functionality of xylem, considering the leaves, in species established in tropical environments are unknown. It is known that an efficient use of soil water available for plants is related to the anatomical and hydraulic characteristics of the water transport system, depending, mainly of the demanding from the leaves, dependent of the transversal area of the xylem and the hydraulic diameter of the vessels (Ewers, 1985; Sperry and Sullivan, 1992; Langan et al., 1997).

Xylem vessels into the petiole are water distribution networks that conduct water and minerals to the leaf blade that is related to its blade expansion (Karam, 2005; Murphy et al., 2012).

Xylem traits of the petiole, such as cross-sectional area, internal vessel area, and vessel density, affect the leaf physiological functions related to biomass production. Tyree and Zimmerman (2002), Yin et al. (2018), and Song et al. (2018) state that anatomical traits of xylem are closely linked to the hydraulic performance in plants.

The hydraulic diameter calculation ( $D_h$ ) and the theoretical specific conductivity ( $K_t$ ) is used since the 1990s to evaluate the water transport functionality of the xylem vessels (Tyree and Ewers, 1991). Despite more than twenty years of studies dedicated to xylem cells functionality, rare research has been undertaken in Brazilian tropical species. None of them considered the petiole, the part of the leaf that conduct the water to the blade, which has the tissues that use it to the photosynthesis. The hydraulic measurements in the petiole were measured, but no relationship with the blade and its economy was made (Song et al., 2018, Tombesi et al., 2014).

In this study, we investigate the xylem anatomical traits of the petiole related to water flow and leaf economics efficiency in tropical woody species under marine and fluviomarine influence. This study aims to improve the knowledge on water relations and contribute to elucidate species-specific differences in water use strategies

### Material and Methods

The five species, growing in a forest fragment under marine and fluviomarine influence, known as restinga vegetation, were selected based on a phytosociological study (Almeida Jr. et al., 2009), considering its higher Importance Value Index (IVI), growing in an area of 130 ha, 08°31'48''S and 35°01'05''W. The climate, according Köppen, is As' and the annual precipitation is of 2.533 mm, approximately (INMET, 2005).

From each species, five individuals were selected and, from each of them, three healthy, young and mature leaves were collected with the petiole included. The leaves were assembled in labeled plastic bags and taken to the laboratory where they were scanned and fixed in FAA 50 (Sass, 1958). Young leaves were collected in the 2<sup>nd</sup>. and third nodes from the branch extremity and the mature leaves were considered those with an entirely developed blade starting from the 8<sup>th</sup> node. For standardization purposes, all the collected leaves were exposed to the sun, collected in branches with similar diameter and in the medium portion of the crown.

The median portion of petioles was sampled from five species of woody plants (shrub and tree) to compare the morphological and anatomical traits, relating the hydraulic performance (Table 1)

Table 1. Woody species occurring in a forest fragment of a restinga vegetation and functional types.

Species	Family	Functional type
<i>Casearia javitensis</i>	Flacourtiaceae	shrub
<i>Guettarda platypoda</i>	Rubiaceae	shrub
<i>Hancornia speciosa</i>	Apocynaceae	tree
<i>Myrcia bergiana</i>	Myrtaceae	shrub
<i>Sacoglottis mattogrossensis</i>	Humiriaceae	tree

Scan images of the leaves were used for leaf area (cm<sup>2</sup>), leaf blade length (cm), maximum width and petiole length (cm) estimate. Also, specific leaf weight (SLW) of the leaf blade expressed as the ratio of leaf dry weight to leaf area determined after drying the leaf samples for up to 3 days.

All measurements were made in digital images using the software *ImageJ-Fiji* (Schindelin et al., 2012).

Leaf volume (cm<sup>3</sup>) was obtained as a product of leaf area and thickness values. Considering the leaf format characterization, the leaf index was used (IF = leaf length/leaf width), leaves with IF  $\cong$  1 (um) are round, in other words, isodiametric; IF < 1 is wider than long; IF > 1 are, proportionally, more prolonged (Reis, 2003).

Leaf structural traits such as leaf tissue thickness, thickness of the palisade parenchyma (PP), spongy parenchyma (SP), upper epidermis

cell (UEC), and lower epidermis cell (LEC) were compared between the five species.

Cross sections, handmade, were obtained from the petiole medium portion, stained with safranin and astra-blue, washed with distilled water and mounted in glycerin (Krauter, 1985). The best slides were examined with digital images obtained by optical microscope coupled with a digital camera with a 100x increase. Three images of the petiole cross sections were used to determine the transverse area occupied by the vascular bunch (ATX,  $\mu\text{m}^2$ ) and the xylem vessels density (DV,  $\text{n}^\circ.\mu\text{m}^{-2}$ ).

In 10 cells at each vascular bunch, the largest and the smallest perpendicular length of the xylem cells lumen were measured (Sellin et al., 2008), as well as the wall thickness of these vessels ( $\mu\text{m}$ ). The mean xylem vessel diameter (D) was calculated following Eq. 1.

$$D = \frac{\sum_{i=1}^n \sqrt{a_i b_i}}{n} \quad \text{Eq. (1)}$$

where  $a_i$  is the smallest and  $b_i$  is the largest perpendicular diameter of the xylem vessel (Sellin et al. 2008). The hydraulic diameter ( $D_h$ ) was calculated using Eq. 2 (Sperry et al., 1994; Kolb and Sperry, 1999; Sellin et al., 2008).

$$D_h = \frac{\sum_{i=1}^n (\sqrt{a_i b_i})^5}{\sum_{i=1}^n (\sqrt{a_i b_i})^4} \quad \text{Eq. (2)}$$

The theoretical xylem-specific conductivity (Kt), relating the xylem anatomy with the ideal water flux efficiency by the Hagen-Poiseuille equation, modified to the elliptic transverse area (Calkin et al., 1986), adding the

water density parameters and transverse area occupied by the xylem (Sellin et al., 2008), was obtained by Eq. 3.

$$K_t = \frac{\pi \rho}{64 \eta A_x} \sum_{i=1}^n \frac{a_i^3 b_i^3}{a_i^2 + b_i^2} \quad \text{Eq. (3)}$$

where  $\rho$  is the water density ( $\text{kg.m}^{-3}$ ),  $\eta$  is the dynamic water viscosity (both for  $35^\circ\text{C}$  water) and  $A_x$  are the transverse areas occupied by the xylem ( $\mu\text{m}^2$ ). The Theoretical Leaf-specific Conductivity (LSC) ( $\text{LSC}_i; \text{kg.m}^{-1}.\text{s}^{-1}.\text{MPa}^{-1}$ ), was calculated as a product between  $K_t$  and the Huber value ( $\text{HV} = \text{xylem area/leaf area}$ ) (Sellin et al., 2008).

To identify interspecific variations between young and mature leaves the mean comparison test (ANOVA) was used for whole the tested variables. Linear correlations were accomplished to evaluate the relationships among the analyzed parameters.

## Results

### Intraspecific Variations

The young and mature leaves presented differences in the maximum width and length of the leaf blade (cm), leaf area ( $\text{cm}^2$ ), petiole length (cm), and leaf volume ( $\text{cm}^3$ ) in all the studied species, and  $\text{IF} > 1$ , characterizing an elongated blade for all plants (Table 2).

Considering the five woody species dominant in the restinga forest, only *C. javitensis*, and *S. mattogrossensis* did not present significant differences in the blade length and area between young and mature leaves (Table 2). Among the five species, the leaf blade maximum width varied significantly between young and mature leaves of *H. speciosa* (Table 2).

Table 2. Differences in seven petiole traits of five wood species of restinga vegetation. Young (Y) and mature (M) leaves.

Traits	Leaf age	Species				
		<i>Casearia javitensis</i>	<i>Guettarda platypoda</i>	<i>Hancornia speciosa</i>	<i>Myrcia bergiana</i>	<i>Sacoglottis mattogrossensis</i>
Leaf lamina						
Area ( $\text{cm}^2$ )	Y	317.67 ± 78.77 a	193.52 ± 76.27 b	34.49 ± 7.14 b	166.25 ± 44.87 b	273.08 ± 69.01 a
	M	325.35 ± 104.01 a	299.06 ± 129.94 a	50.01 ± 6.33 a	196.00 ± 30.21 a	303.59 ± 57.92 a
Length (cm)	Y	34.29 ± 4.56 a	21.30 ± 4.02 b	10.27 ± 1.56 b	23.80 ± 3.20 b	29.04 ± 3.42 a
	M	32.82 ± 5.62 a	25.82 ± 5.69 a	11.96 ± 0.97 a	26.78 ± 2.67 a	30.34 ± 3.54 a
Width (cm)	Y	12.27 ± 1.92 a	12.28 ± 2.76 a	4.42 ± 0.43 b	10.16 ± 2.17 a	13.28 ± 1.90 a
	M	12.87 ± 2.34 a	14.47 ± 4.19 a	5.55 ± 0.43 a	11.20 ± 1.48 a	14.01 ± 1.98 a
LAI	Y	2.82 ± 0.31 a	1.76 ± 0.27 a	2.32 ± 0.33 a	2.41 ± 0.48 a	2.20 ± 0.26 a
	M	2.56 ± 0.27 b	1.85 ± 0.39 a	2.16 ± 0.22 a	2.43 ± 0.40 a	2.19 ± 0.34 a

Thickness ( $\mu\text{m}$ )	Y	201.83 $\pm$ 34.15 a	162.96 $\pm$ 17.16 a	316.74 $\pm$ 38.11 b	334.61 $\pm$ 46.99 a	308.71 $\pm$ 44.49 a
	M	220.35 $\pm$ 29.45 a	144.54 $\pm$ 16.71 b	356.00 $\pm$ 45.97 a	332.56 $\pm$ 45.56 a	287.15 $\pm$ 44.89 a
Volume ( $\text{cm}^3$ )	Y	8.52 $\pm$ 2.42 a	4.39 $\pm$ 1.73 a	1.46 $\pm$ 0.41 b	8.35 $\pm$ 2.98 a	11.84 $\pm$ 2.53 a
	M	9.66 $\pm$ 3.48 a	5.42 $\pm$ 2.06 a	2.38 $\pm$ 0.57 a	10.01 $\pm$ 2.21 a	12.25 $\pm$ 3.16 a
----- Petiole -----						
Length (cm)	Y	1.88 $\pm$ 0.23 b	3.30 $\pm$ 1.59 a	2.02 $\pm$ 0.52 a	2.42 $\pm$ 0.33 a	2.34 $\pm$ 0.41 b
	M	2.68 $\pm$ 0.51 a	4.09 $\pm$ 1.99 a	2.32 $\pm$ 0.43 a	2.59 $\pm$ 0.47 a	2.64 $\pm$ 0.37 a

Equal letters between young and mature leaves, by species, did not statistically differ, based on Tukey test at  $P < 0.05$ .

The leaf blade thickness varied in opposite sides between young and mature leaves of *G. platypoda*, *M. bergiana*, *S. mattogrossensis* presenting thicker young leaves in the first one and thicker mature leaves in the second (Table 2).

The leaf blade volume varied between young and mature leaves only in *H. speciosa* (Table 2). The petiole length presented higher values only in mature leaves of *C. javitensis* and *S. mattogrossensis* (Table 2).

The xylem hydraulic structure in the petiole of the five-species studied was diverse for all the appraised characters (Table 3). The

transverse area occupied by the xylem vessels and its number were higher values to the mature leaves in all analyzed species (Table 3). The vessels wall thickness was larger in mature leaves of *C. javitensis*, and the other species remained without significant variations (Table 3). The vessels internal diameter (hydraulic diameter,  $D_h$ ) in petiole did not change variance significantly between the leaves age in *G. platypoda*, *M. bergiana*, and *S. mattogrossensis*, however, it was larger in young leaves of *C. javitensis* and smaller in young leaves of *H. speciosa* (Table 3).

Table 3. Hydraulic related traits of petiole of the five-woody species of restinga vegetation. Vessel area (VA); vessel density per transverse xylem area (VD); vessel wall thickness (EPV); Huber value (HV); mean hydraulic diameter ( $D_h$ ); specific conductivity ( $K_t$ ) and theoretical leaf-specific conductivity ( $LSC_t$ ). Different letters in the same line indicate significant differences between species ( $P < 0.05$ ).

Traits	Leaf age	Species				
		<i>Casearia javitensis</i>	<i>Guettarda platypoda</i>	<i>Hancornia speciosa</i>	<i>Myrcia bergiana</i>	<i>Sacoglottis mattogrossensis</i>
VA ( $\times 10^{-3} \mu\text{m}^2$ )	Y	160.68 $\pm$ 43.77 b	275.46 $\pm$ 124.22 b	47.45 $\pm$ 24.10 b	136.72 $\pm$ 42.09 b	259.04 $\pm$ 40.71 b
	M	359.36 $\pm$ 114.77 a	410.16 $\pm$ 174.62 a	90.77 $\pm$ 26.85 a	178.38 $\pm$ 31.14 a	319.90 $\pm$ 67.82 a
VD ( $\text{n}^\circ \cdot \mu\text{m}^{-2}$ )	Y	207.24 $\pm$ 53.76 b	412.81 $\pm$ 235.83 b	81.82 $\pm$ 28.54 b	200.58 $\pm$ 56.82 b	222.98 $\pm$ 54.47 b
	M	308.48 $\pm$ 71.11 a	794.11 $\pm$ 345.81 a	130.46 $\pm$ 33.61 a	256.78 $\pm$ 58.85 a	279.76 $\pm$ 76.28 a
EPV ( $\mu\text{m}$ )	Y	3.50 $\pm$ 0.45 b	3.60 $\pm$ 0.64 a	3.34 $\pm$ 0.62 a	3.43 $\pm$ 0.63 a	2.25 $\pm$ 0.47 a
	M	4.19 $\pm$ 0.67 a	3.89 $\pm$ 0.41 a	3.54 $\pm$ 0.57 a	3.78 $\pm$ 0.31 a	2.13 $\pm$ 0.28 a
$D_h$ ( $\mu\text{m}$ )	Y	20.19 $\pm$ 2.63 a	17.68 $\pm$ 2.72 a	18.17 $\pm$ 1.49 b	15.33 $\pm$ 2.91 a	25.63 $\pm$ 2.23 a
	M	17.82 $\pm$ 2.34 b	17.31 $\pm$ 1.65 a	20.56 $\pm$ 1.70 a	15.47 $\pm$ 2.43 a	25.58 $\pm$ 2.20 a
HV	Y	0.53 $\pm$ 0.20 b	1.44 $\pm$ 0.42 a	1.35 $\pm$ 0.55 b	0.91 $\pm$ 0.60 a	1.02 $\pm$ 0.37 a
	M	1.11 $\pm$ 0.17 a	1.43 $\pm$ 0.46 a	1.82 $\pm$ 0.51 a	0.92 $\pm$ 0.15 a	1.05 $\pm$ 0.14 a
$K_t$ ( $\times 10^{-3} \text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ )	Y	310.35 $\pm$ 163.86 a	124.03 $\pm$ 70.05 a	777.39 $\pm$ 365.91 a	122.37 $\pm$ 83.94 a	452.46 $\pm$ 158.07 a
	M	84.45 $\pm$ 40.53 b	71.83 $\pm$ 31.28 b	582.45 $\pm$ 170.03 a	96.26 $\pm$ 54.36 a	345.91 $\pm$ 95.44 b
$LSC_t$ ( $\times 10^{-3} \text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ )	Y	152.27 $\pm$ 71.99 a	165.00 $\pm$ 74.34 a	900.07 $\pm$ 251.16 a	104.43 $\pm$ 81.10 a	467.02 $\pm$ 224.00 a
	M	92.53 $\pm$ 43.92 b	102.70 $\pm$ 50.83 b	1026.11 $\pm$ 308.65 a	86.77 $\pm$ 44.22 a	362.86 $\pm$ 108.44 a

Sap flow efficiency inside xylem that supplies the leaf blade with water in mature leaves was significantly more prominent in *C. javitensis*

and *H. speciosa*. No significant variations were found in the other species (Table 2).

The theoretical specific conductivity did not vary between young and mature leaves of *H.*

*speciosa* and *M. bergiana*; in the other species, young leaves always showed the most significant values (Table 2).

The theoretical leaf-specific conductivity varied in *C. javitensis* and *G. platypoda*, which showed larger values in young leaves (Table 2).

The theoretical leaf-specific conductivity was larger in young and mature leaves of *H. speciosa*, followed by *S. mattogrossensis*; the other species showed identical values (Table 3).

#### Interspecific Variations

The largest area medium values of the leaf area in young leaves were significantly equal for *C. javitensis* and *S. mattogrossensis* (317.67 and 273.08 cm<sup>2</sup>, respectively), followed by *G. platypoda* and *M. bergiana* (193.52 and 166.25 cm<sup>2</sup>, respectively); *H. speciosa* (34.49 cm<sup>2</sup>) stood out with the smallest significant value for this parameter (Table 2). The leaf area of mature leaves was significantly equal in *C. javitensis*, *G. platypoda* and *S. mattogrossensis*, proceeded with smaller values by *M. bergiana* and *H. speciosa*, (196 and 50.01 cm<sup>2</sup>, respectively) (Table 2).

The transverse area occupied by xylem vessels in the petiole medium portion of young leaves was significantly more prominent in *G. platypoda* and *S. mattogrossensis*, followed by *C. javitensis* and *M. bergiana*; the smallest values were observed in *H. speciosa* (Table 2). In mature leaves, this parameter was significantly equal to *C. javitensis*, *G. platypoda*, and *S. mattogrossensis*; and more prominent to *H. speciosa* and *M. bergiana* who presented similar areas (Table 2).

In the transverse area of young leaves, the xylem vessels density was significantly higher in *G. platypoda*, followed by *C. javitensis*, *M. bergiana*, and *S. mattogrossensis*; *H. speciosa* showed the smallest vessel density (Table 3). The vessels density in mature leaves was significantly higher in *G. platypoda*; *C. javitensis*, *M. bergiana* and *S. mattogrossensis* showed similar density, standing out *H. speciosa*, which presented similar values to the last two mentioned species (Figure 1C).

The xylem vessels  $D_h$  in the vascular bunch of the petiole medium portion in young leaves was significantly higher in *S. mattogrossensis*, proceeded by *C. javitensis* which was equal to *H. speciosa*; this one was equal to *G. platypoda*, which was equal to *M. bergiana* (Figure 1D). In mature leaves,  $D_h$  was significantly higher in *S. mattogrossensis*, followed by *H. speciosa*; in *C. javitensis* and *G. platypoda*,  $D_h$  was the same, and this last species showed a similar value to *M. bergiana* (Figure 1D).

The hydraulic conductivity in the xylem vessels of young leaves was larger in *H. speciosa*, followed by *S. mattogrossensis* and *C. javitensis*; *C. javitensis* showed equal values to *G. platypoda* and *M. bergiana* (Figure 2A). In mature leaves, *H. speciosa* showed the higher value, proceeded by *S. mattogrossensis*, while the other species showed identical values (Table 3).

#### Discussion

Differences among the leaves age (young and mature) and the species regarding the studied morphological characters were found. Variability, considering the analyzed characters, was due to the species diversity, which belongs to different families, and respond through differences in morpho-anatomical traits, based on the environmental stimuli. Leaves diverge in agreement with space and temporal distribution of the species, individuals' height, light availability, leaf age, genetic influences and biotic or abiotic stresses (Bongers and Popma, 1990; Tsukaya, 2017). According to Larcher (2004), when leaf development is slow, mature leaves tend to show significant differences in leaf length and area, as verified in *G. platypoda*, *M. bergiana*, and *H. speciosa*.

The theoretical leaf-specific conductivity could define the xylem hydraulic system efficiency in young and mature leaves between five woody species dominant in the tropical environment. Studies about the hydraulic behavior of Brazilian species are rare. Machado et al. (2006) studied the sap flux in orange tree individuals (*Citrus sinensis*), Naves-Barbiero et al. (2000) evaluated the sap flux in two woody species of Cerrado, and Oliveira (2018) studied effects of water stress in hydraulic stem system of young *jatropha curcas* plants. Studies with vegetation from regions with Temperate and Mediterranean climate are abundant, especially in vegetative organs as stems and roots (Tyree, 1997; Chiu and Ewers, 1992; Schultz and Matthews, 1993; Aou-ouad et al., 2018, Battipaglia et al. 2016), and some studies with leaves (Salleo et al., 2000; Nardini et al., 2001; Xiong et al., 2016).

Chiu and Ewers (1992) affirm that differences in the xylem characteristics and structures have an adaptative value in plants, suggesting that the intraspecific variations of the hydraulic structure have a relationship with the species phenotype plasticity. Is known that the amplitude of each's phenotypic plasticity enables many variations in the leaf anatomical characters (DeWitt et al., 1998; Tsukaya, 2017). According to the environmental conditions, the phenotype plasticity and the diverse plant organs adaptations

are observed during the several phases of the vegetative development and are not reversible during maturity (Larcher, 2004; Bjorkman, 1981).

During the leaf expansion, the xylem vessels show a growing lignification of its walls promoting their enlargement during the cells maturation (Cutter, 1986). Mature leaves have a higher amount of wholly formed xylem vessels observed in the five studied species (Cutter, 1986; Fahn, 1990). In *C. javitensis*, the wall medium thickness value was considerably larger in mature leaves.

The hydraulic conductivity is, commonly, closely related to  $D_h$  and xylem vessels density, as found by Salleo et al. (1985) and Schultz and Matthews (1993), in leaves from Mediterranean species and *Vitis vinifera*, respectively. The results found in *C. javitensis*, *G. platypoda* and *S. mottogrossensis* corroborate these authors, allowing to affirm that  $D_h$  is a good indicator of the  $K_t$  and  $LSC_t$ , according to Tyree and Zimmermann (2002).

The larger volume of water is transported inside the xylem vessels with larger diameters, according to its hydraulic pressure and directly related to the soil water availability and the atmospheric water content (Choat et al., 2005). *C. javitensis* demonstrated to be more efficient in water transport in young leaves because of its larger  $D_h$  values, indicating a better condition to produce biomass as a result of the photosynthesis stimuli. Following this reasoning, mature leaves of *H. speciosa* showed similar behavior to the *C. javitensis* young leaves. Smaller values of  $D_h$ , responding to the larger pressure inside the xylem vessels, are considered by some authors (Carlquist, 1988; Yang and Tyree, 1992; Nardini et al., 2001; Mauseth and Plemons-Rodriguez, 1998), as an adaptable advantage of plants in dry environments due to its smaller vulnerability to embolism and cavitation.

*Sacoglottis mottogrossensis* individuals, less exposed to radiation and under higher relative air humidity, surrounded by higher plants, and *H. speciosa* individuals, more exposed to radiation because of the absence of other plants in its surroundings, resulting in a more prominent incentive to water loss by evapotranspiration, showed mature leaves with  $D_h$  values significantly equivalent. The other species, distributed in edge regions with higher light availability, and sandy soil with lower water retention capability, presented the smallest  $D_h$  values and, therefore, are less vulnerable to cavitation. Sellin (2008) observed that  $LSC_t$  is directly linked by the HV and found a high relationship ( $r$  Pearson = 0,829/ $P=0.001$ ) among these characters in *Betula*

*pendula* from Estonia forests. However, tropical environment species showed larger values of  $LSC_t$  in young leaves, and larger HV in mature leaves indicating that  $LSC_t$  is more strongly related to the  $K_t$  characters than the HV. The small diameter conduits also contribute to water transport. When the cross-sectional area is small, the pressure inside the conduit will be more significant resulting in a higher speed of movement of the fluid within the same (Martre et al., 2000).

Studies suggest that the most significant restriction to water flow in plants occurs in leaves, varying between 40 and 80% (Becker et al., 1999; Nardini and Tyree, 2000; Brodribb et al., 2002). That would explain the leaves need to invest in characters capable of improving the water transport and, consequently, to maintain the ascending axial flow in the stem. Mechanics and hydraulics demands concerning the plant water transport and distribution compromise the density of the xylem elements of conductivity and its  $D_h$  (Sellin et al., 2008). The smallest values of xylem vessels density and transverse area occupied by them found in *H. speciosa*, are balanced by the  $D_h$ ,  $K_h$  and  $LSC_t$  high values, which, according to Sellin et al. (2008), implies an integration of xylem hydraulic and mechanic stability, observed in other studies relating the xylem hydraulic structure and its efficiency (Mokany et al., 2003; Preston et al., 2006).

The hydraulic and structural differences observed in the xylem of the tropical environment species indicate a better efficiency in water transport and use in leaves based on its needs, promoting anatomic and hydraulic adaptations in its water transport system. Those needs can be stimulated by the microenvironment where the leaves are developed, by the species, by their place of establishment and by the individual crown structure.

To better understand those variations, additional studies are required to evaluate the variations between species in the same environment and between individuals of the same species in distinct environments with distinct characteristics closely related with water availability, temperature, and humidity.

## Conclusion

Tropical environment plant species develop specific anatomical structural features regarding xylem, aiming at maintaining the structure for water flow, ensuring the physiological functions related to respiration and photosynthesis and consequently the establishment of the species to those climatic conditions.

In the studied species, the leaf area is not directly related to  $D_h$  and HV, and  $K_t$  and  $LSC_t$  are more related to  $D_h$  than to HV.

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