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Water deficit affects wood vessels of *Croton floribundus* Spreng. in different vegetation types, São Paulo State, Brazil

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ABSTRACT - (Water deficit affects wood vessels of *Croton floribundus* Spreng. in different vegetation types, São Paulo State, Brazil). In this paper we showed that water deficit affects the wood vessels of *Croton floribundus* in five areas with different vegetation types: Rain Forest, Semi-deciduous Forest and Woody Savanna. We concluded that variations in the vessels are due especially to water deficit and the number of months with water deficit. Larger diameter vessels occurred in areas with higher water deficit, which may represent a strategy to optimize the water transport in favorable periods. Vessels with smaller diameters occur in areas with lower deficit, which may be related to lower minimum temperatures and frost occurrence, which like drought can cause vessel embolism. In Caetetus Ecological Station, a Semi-deciduous Forest (area of highest water deficit), we observed investments in efficiency and safety, with the occurrence of larger diameter vessels associated with one of the lowest vulnerability indexes and highest proportions of multiple vessels of four or more elements.
Key words: Ecological anatomy, mesomorphy, vulnerability, water availability

RESUMO - (Déficit hídrico interfere nos vasos do lenho de *Croton floribundus* Spreng. em diferentes tipos de vegetação, SP, Brasil). O déficit hídrico influenciou na formação dos vasos da madeira de *Croton floribundus* ocorrentes em cinco áreas com as seguintes vegetações: Floresta Ombrófila, Floresta Estacional Semidecidual e Cerradão. As variações dos vasos devem-se especialmente ao déficit hídrico e número de meses com déficit hídrico. Vasos de maior diâmetro ocorreram em áreas com maior déficit hídrico, o que pode indicar uma estratégia para otimizar o transporte de água em épocas favoráveis. Vasos com menores diâmetros ocorreram em áreas com menor déficit hídrico, possivelmente influenciados pelas menores temperaturas mínimas e a ocorrência de geadas, que semelhante a seca, causa a embolia dos vasos. Na Estação Ecológica de Caetetus, Floresta Estacional Semidecidual (área com maior déficit de água) observaram-se investimentos em eficiência e segurança, com a ocorrência de vasos de maior diâmetro associados a um dos menores índices de vulnerabilidade e maior proporção de vasos múltiplos de quatro ou mais elementos.
Palavras-chave: Anatomia ecológica, disponibilidade hídrica, mesomorfia, vulnerabilidade

Introduction

In this study we aimed to identify variations in the vessel features of *Croton floribundus* Spreng. wood with respect to variations in climatic data, especially the water deficit. We hypothesized that vessels show features related to greater safety in water transport in dry environments and are related to water deficit.

Expanding knowledge about the influence of water deficit in Brazilian native trees is important, because the water deficiency is one of the main factors that limit plant growth due to its influence on photosynthesis, production of sugars employed in produce energy and the construction of cell walls. Thus, the efficient water transport in plants allows for increased photosynthetic uptake of CO_2 for a given vascular investment and should improve fitness through enhanced growth and reproduction (Pittermann *et al*. 2005). The availability of water interferes in the formation of wood cells, especially vessel elements, the responsible cells for the water transport in angiosperms. In this context, trees have

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variations in size, frequency and vessel elements grouping as an adaptive response to the environment, tending to a greater efficiency or safety depending on water availability (Carlquist 2001).

Vessels with a smaller diameter are safer in water transport, while larger vessels are more efficient, which can increase the capacity of photosynthesis (Hacke *et al*. 2005, Carlquist 2001). According to Tyree *et al*. (1994), the law of Hagen-Poiseuille, which assesses the dynamics of fluids through cylindrical tubes, also serves to explain the water flow through the wood vessels, which can also be compared to pipes. According to the authors, one vessel with 40 µm diameter is as conductive as 16 vessels with 20 µm diameter each or as 256 vessels with 10 µm diameter each. Moreover, historically vessels with smaller diameters are associated with drier or colder environments (Baas 1982, Carlquist 2001). There is also a trend towards an increase in vessel grouping in areas of high water deficit (Carlquist & Hoekman 1985, Fahn *et al*. 1986).

Aiming to evaluate ecological trends and the susceptibility of wood vessels to develop embolism, Carlquist (2001) introduced some indexes as ecological indicators: vulnerability index (VI); mesomorphy index (MI) and vessel grouping index (VGI). Based on these indicators, it is determined that vulnerability index lower than one (< 1) reflect adaption to drier areas, while values greater than three (> 3) are found in plants living in areas with high water availability (Carlquist 2001). For mesomorphy index, values less than 100 indicate plants that grow in dry environments (xeric) or in regions with a dry period for several months in the year, while higher mesomorphy index values are found in species that grow in mesic environments (Carlquist 2001, Lens *et al*. 2003). For vessel grouping index, the value of one (> 1) indicates exclusively solitary vessels; beyond that, as higher the value, greater is the vessel grouping index. Therefore plants adapted to water stress environments have higher vessel grouping index (Carlquist 2001).

Due to the wide distribution and occurrence in different vegetation types, *Croton floribundus* Spreng. (Euphorbiaceae) becomes an interesting species for studies of ecological wood anatomy and evaluation of the ecological indexes mentioned. The species is pioneer, heliophyte, deciduous or semi-deciduous; has very fast growth and short life cycle, and does not tolerate low temperatures. *C. floribundus* naturally occurs in different vegetations in São Paulo State, as rain forest, semi-deciduous forest and woody savanna (Durigan *et al*. 1997, Lorenzi 2002, Carvalho 2003). These vegetations have distinct characteristics of precipitation, temperature and water deficit, enabling assessment of anatomical aspects under different environmental conditions, which in turn contributes to increase the ecological knowledge of this species.

Material and methods

Experimental areas - The samples was collected in five areas of the São Paulo State: 1. Cantareira State Park (CSP), 2. Carlos Botelho State Park (CBSP), 3. Itapeva Experimental Station (IES), 4. Assis Ecological Station (AES) and 5. Caetetus Ecological Station (CES) (figure 1, table 1).

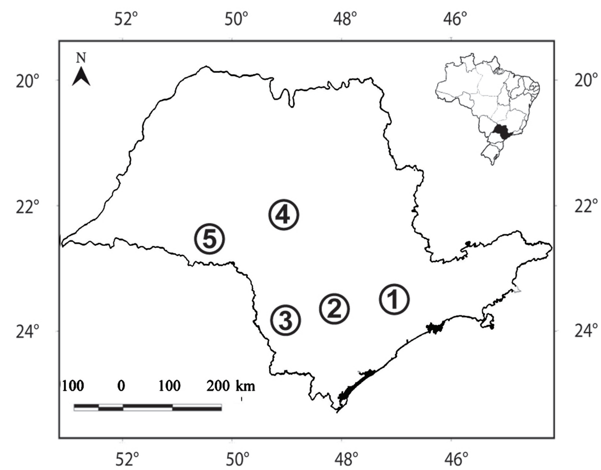

Figure 1. Map with location of the sampling areas for *Croton floribundus* wood, São Paulo State, Brazil. 1. Cantareira State Park (CSP), 2. Carlos Botelho State Park (CBSP), 3. Itapeva Experimental Station (IES), 4. Assis Ecological Station (AES) and 5. Caetetus Ecological Station (CES).

Tree sampling - Wood samples were collected at breast height (DBH - 1.30 m) of three trees from each area with estimated heights between 5-8 m, totaling 15 trees. Samples were collected between April and July, the beginning of the drier season in all areas (figure 2). BBH, means of DBH and xylarium number of *Croton floribundus* trees are described on table 2.

Anatomical analysis - Blocks of 1.5 cm^3 were cut from each sample. The blocks were softened in boiling water and glycerin (4:1), and 15-20 µm thick sections were prepared on a sliding microtome. The transverse and longitudinal sections (A) were bleached with sodium hypochlorite (60%), washed in water, and stained with safranin (1%) (Johansen 1940). Macerations (B) were prepared according to the modified Franklin method (Berlyn & Miksche 1976). A and B were stained with

Table 1. Vegetation types, geographical coordinates and climatic data of the sampling areas, São Paulo State, Brazil.

	Areas				
	CSP[1]	CBSP[2]	IES[2]	AES[2]	CES[2]
Vegetation type	RF	RF	Transition between SF and WS	WS	SF
Altitude (m)	1150	740	660	480	660
Latitude (S)	23°25”	24°00”	24°16”	22°33”	22°23”
Longitude (W)	46°40”	47°58”	49°03”	50°27”	49°41”
Mean precipitation (mm)	1345	1395	1278	1441	1385
Mean temperature (ºC)	19.9	20.4	20.1	22.1	22.1
Mean minimum temperature (ºC)	11.4	9.7	9.4	11	11.1
Sum of Water deficit (mm)	-2.7	-0.1	-0.1	-2.8	-13.5
Months with water deficit and no water surplus in the soil	6	2	2	4	6

Data: 1. Rossi *et al*. (2009). 2. Centro de Pesquisas Meteorológicas e Climáticas Aplicadas a Agricultura – CEPAGRI (2010). RF: Rain Forest, SF: Semi-deciduous Forest. WS: Woody Savanna. Cantareira State Park (CSP). Carlos Botelho State Park (CBSP). Itapeva Experimental Station (IES). Assis Ecological Station (AES). Caetetus Ecological Station (CES).

aqueous safranin and mounted in a solution of water and glycerin (1:1). The terminology followed the IAWA list (IAWA Committee 1989).

Slides were prepared for the analysis and measurement of the following anatomical features: diameter, frequency and vessel element length, diameter of intervessel pits and vessel-ray pits. For each feature n = 25 was used initially, except for the pits, where n = 10 was adopted.

We investigated the vulnerability (VI), mesomorphy (MI) and vessel grouping index (VGI) (Carquist 2001). According to the formulas:

$$VI = \frac{\overline{X}\,VD}{\overline{X}\ VF} \qquad MI = \frac{VI}{\overline{X}\,VEL} \qquad VGI = \frac{\Sigma VF}{VG}$$

Where: VD: vessel diameter. VF: vessel frequency, VEL: Vessel element length. VG: Vessel grouping (solitary, multiples of 2, 3 and multiples of 4 or more vessels).

The percentage of vessel area was determined on transverse sections in 25 squares of 1 mm^2 each, distributed among the sections of each sample.

All anatomical measures were performed on a microscope (Olympus CX 31) equipped with a camera (Olympus Evolt E330) and a computer with image analyzer software (Image-Pro 6.3).

Statistical analysis - We initially performed descriptive statistical analysis and comparison between means and standard deviations to test the differences between the groups. With the results, "t-test sample size" were used to determine the number of measurements to the power 0.8. For comparison of each anatomical feature, based on the normal distribution of data, a parametric analysis of variance (One Way Analysis of Variance) was performed. When a significant difference was observed, Tukey test to identify pairs of significantly different means were used. Relation among vessel features, indexes and the climatic data were perfomed by linear regression.

Results

Regardless of experimental area, the vessel elements have simple perforation plate; there are elements without and with tails at one or both ends (figure 3a). Intervessel pits with medium size, alternate (figure 3b); vessel-ray pits similar to intervessel pits (figure 3c). The specimens have diffuse pores (figures 5a-e).

There are quantitative differences among the sampling areas in all the anatomical features studied. Vessel diameter was wider in CES (figure 4a); shorter vessel element length and less frequent vessels in CSP (figure 4b-c), see transverse sections in figure 5.

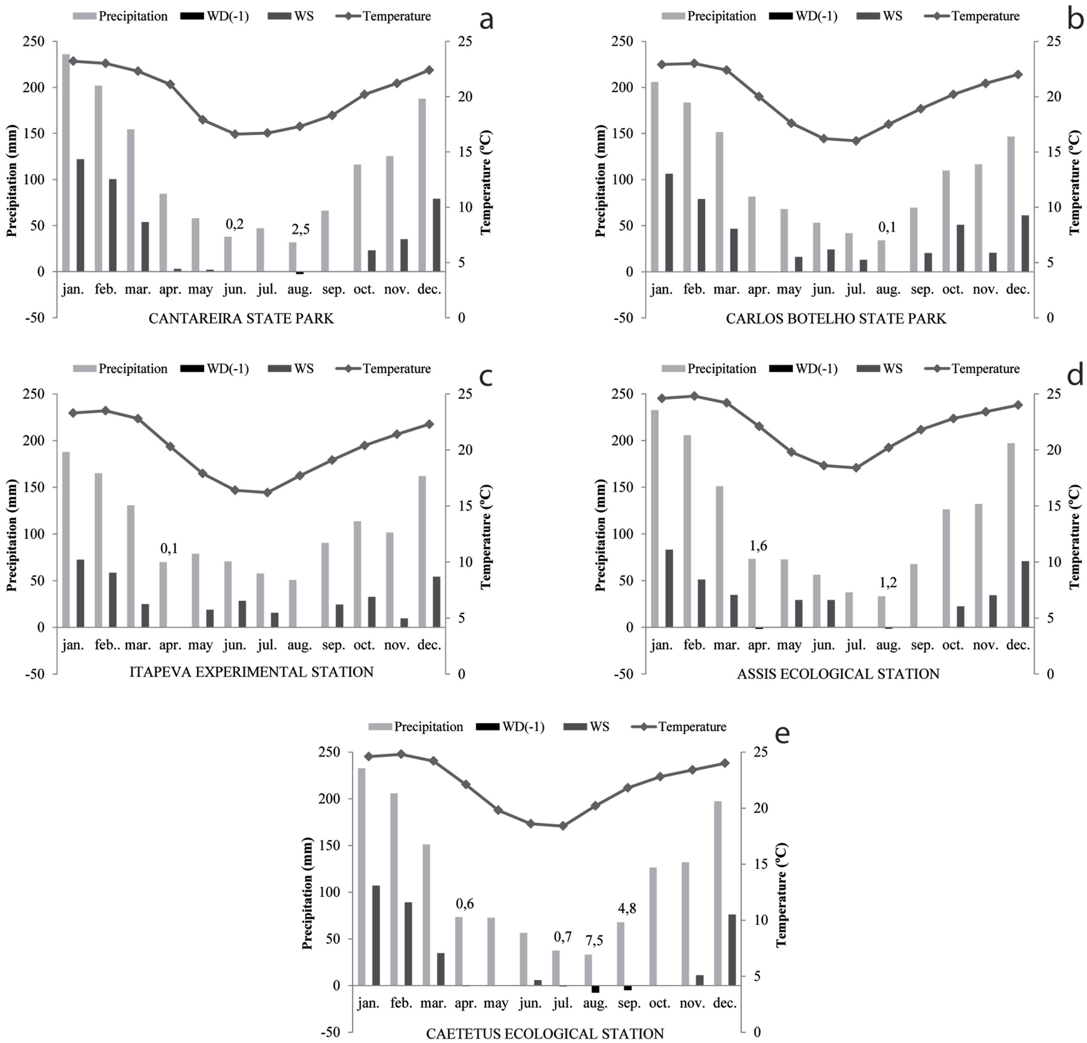

Figure 2. Average monthly sum of precipitation, water deficit (WD) and water surplus (WS) in bars and average mean temperature in lines at the sampling areas of *Croton floribundus* wood, São Paulo State, Brazil. Measurement period: CSP 1992-2008, other areas 1961-1990. Data: CSP Rossi *et al*. (2009), others areas CEPAGRI (2010).

The vessel area was greater in IES, AES and CES (figure 6a). The pit diameters revealed no trend among the five areas (figure 6b-c).

All ecological indexes showed variation among the areas (figure 7a-c). The vessel grouping (figure 8) differed among study areas, mostly solitary vessels were observed only in IES samples. The lowest percentage of solitary vessels was noted in the samples of CBSP. The percentage of vessels multiples of two and three did not vary among the samples of different areas, whereas the highest percentage of vessels multiples of four or more occurred in the samples of CBSP, AES and CES (figure 8).

All significant relations were positive (table 3). The Vessel diameter was related with the mean temperature (MT), mean minimum temperature (MMT), water deficit (WD) and months with water deficit (MWD). The vulnerability index was related with MMT and MWD while the mesomorphy index was correlated with the MMT, WD and MWD.

Discussion

The samples of this study were collected at the beginning of the dry season between April and June, so all samples examined were from between growth layers, *i.e.*, formed before the cambium cessation when the plants had water available.

The qualitative vessels features corroborate Pollito (2004) for the presence of simple perforation

Table 2. Wood samples collected at breast height (DBH), means of DBH and xylarium number of *Croton floribundus* trees, São Paulo State, Brazil.

Area	Tree number	DBH (cm)	Mean DBH (cm)	Xylarium number (SPSFw)
CSP	1	36.4		3451
	2	38	34.46	3452
	3	29		3453
CBSP	4	24		3454
	5	20.5	23.66	3455
	6	26.5		3456
IES	7	33		3458
	8	22	30.66	3459
	9	37		3460
AES	10	21		3530
	11	22	22.66	3531
	12	25		3532
CES	13	31		3533
	14	27	26.66	3534
	15	22		3535

Cantareira State Park (CSP), Carlos Botelho State Park (CBSP), Itapeva Experimental Station (IES), Assis Ecological Station (AES) and Caetetus Ecological Station (CES).

Table 3. Regression equations showing the relation among the anatomical features (dependent variables) of *Croton floribundus* and environmental data (independent variables) in the five areas, São Paulo State, Brazil. *F*: statistical significance test, *P*: significance levels and R^2: coefficient of determination.

Equation	*F*	*P*	R^2
VD = -95.075 + (11.000 * MT)	7.130	0.019	0.35
VD = -36.170 + (16.275 * MMT)	14.745	0.002	0.53
VD = 123.017 + (3.117 * WD)	38.798	0.001	0.74
VD = 105.188 + (14.929 * MWD)	59.638	0.001	0.82
VI = -24.494 + (3.577 * MMT)	21.173	0.001	0.62
VI = 9.522 + (1.808 * MWD)	5.326	0.038	0.29
MI = -12937.722 + (2025.729 * MMT)	9.807	0.008	0.43
MI = 7364.713 + (261.202 * WD)	4.926	0.045	0.27
MI = 5677.648 + (1347.653 * MWD)	6.982	0.020	0.34

VD: vessel diameter, VI: Vulnerability index, MI: Mesomorphy index, MT: Mean temperature, MMT: Mean minimum temperature, WD: Water deficit and MWD: Months with water deficit.

plates and for the type of pits. The vessel diameter was related positively with temperature (table 3), indicating that higher temperatures, such as occur at CES, are associated with larger vessel sizes. Moreover, the positive relation between vessel diameters with water deficit (WD) and the number of months with water deficit (MWD) indicates that plants from areas with higher values of water deficit and number of months with water deficit develop vessels with a larger diameter (efficiency), a contrary result of many studies in ecological wood anatomy.

We suggest that our results may represent a strategy of these plants to optimize the water transport in months with adequate rainfall to grow. Plants of the CES, *e.g.*, have four months with water deficit, in seven months of dry period in which there is no

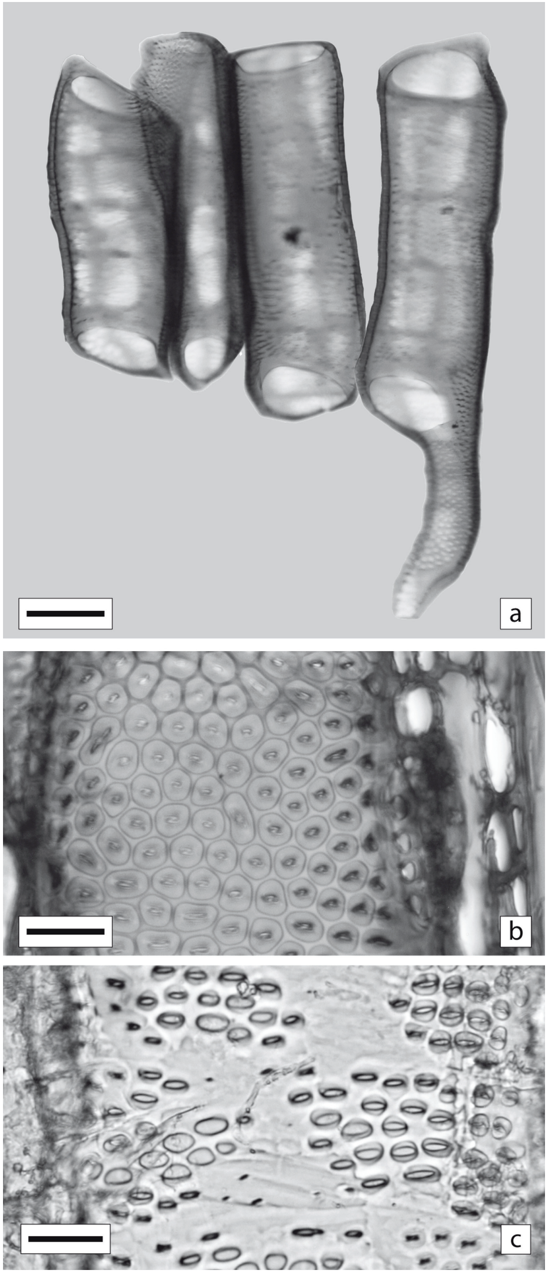

Figure 3. a. Variation in vessel elements, simple perforation plates and the presence or absence of tails, b. Intervessel pits, c. Vessel-ray pits. Scale bars: a = 100 μm; b,c = 25 μm

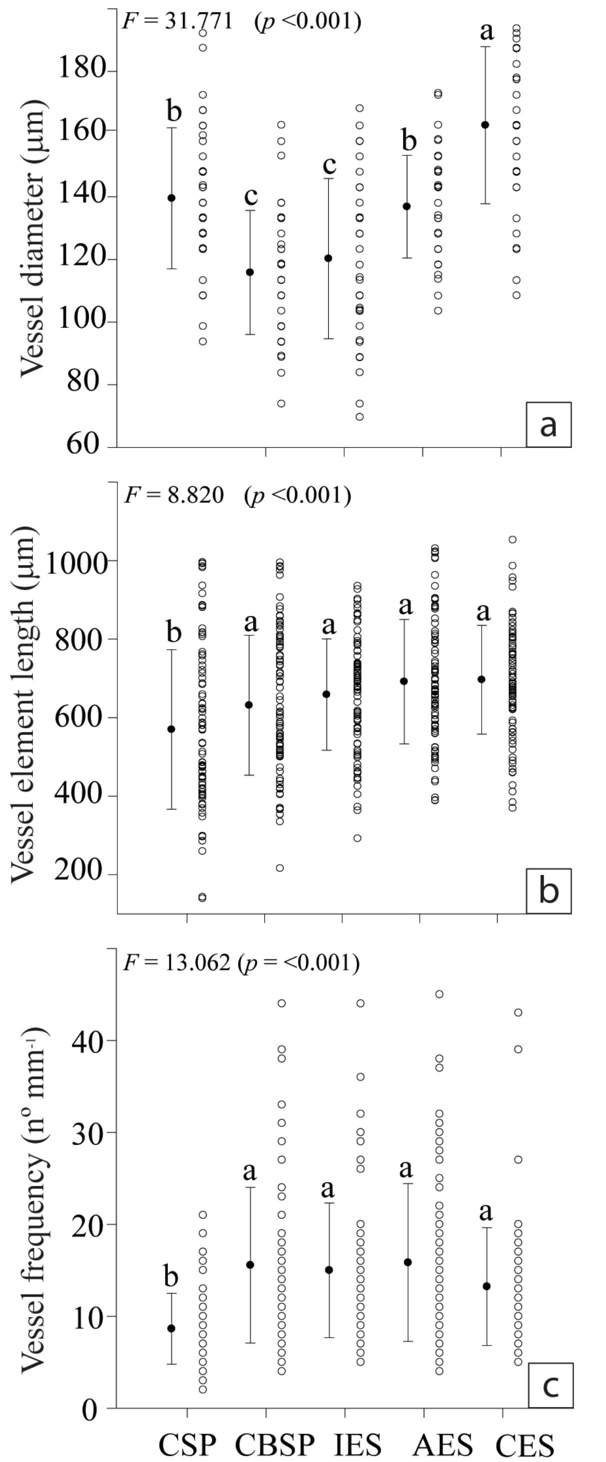

Figure 4. Variation in the vessel features among the experimental areas São Paulo State, Brazil. a. Vessel diameter, b. Vessel element length, c. Vessel frequency, 1. Cantareira State Park (CSP), 2. Carlos Botelho State Park (CBSP), 3. Itapeva Experimental Station (IES), 4. Assis Ecological Station (AES) and 5 Caetetus Ecological Station (CES). Distinct letters differ statistically by Tukey test, the *F* and *p* values are presented in each graph.

surplus water. Thus, these plants have only five months during the year to grow in appropriate water conditions (figure 2e).

Vessels with smaller diameters, safer and less efficient in water conduction, occurred in CBSP and IES. However, these two areas have the lowest values of water deficit and number of months with water deficit per year, with water available almost all year-round. Under these conditions we expected find vessels of larger diameter (more efficient); a possible explanation for the smaller vessel diameter in CBSP and IES are the lowest minimum temperatures and frost occurrence, which similar to an event such as drought, can cause vessel embolism (Carlquist 2001).

This result was reinforced by the positive relation between vessel diameter and minimum temperatures (table 3) indicating the largest diameter of the vessels in areas with higher MMT. Vessels with smaller diameters (safer) could represent a strategy to avoid xylem cavitation (Hacke *et al*. 2005), even without apparent risk of water deficits in the CBSP and IES. Martinez-Vilalta & Pockman (2002) observed that the cavitation induced by freezing is a limiting factor for the distribution of populations of *Larrea tridentata* (Sessé & Moc. *ex* DC.) Coville, which shows the potential importance of frost in the xylem anatomy.

To estimate the potential area of water transport, we measured the vessel area percentage in 1 mm^2. The highest values occurred in the IES, AES and CES. According to the climatic data, apparently, we did not observe any obvious feature shared by these three areas (table 1) because they are distinct in water deficit, precipitation and temperature.

These three areas have lower altitudes, but we do not believe that this feature should significantly influence the formation of wood in the direction of greater potential area of water transport. Additionally, CSP presents climatic characteristics related to water availability consistent with a greater area of vessels, despite showing the lowest value for this variable among study areas. One possible explanation for these results could be found from the analysis of soils, particularly water availability (Oliveira & Peichl 1986). Soils with low water availability, due to low water holding capacity or a higher position on the local topography, could counterbalance the small water deficit in the IES, inducing greater water transport than what would be expected based on the climatic characteristics of the study area. The mechanism of action could account for less potential of water transport observed in the CSP.

We did not observe any relation between the length and frequency of vessel elements of *C. floribundus* with the environmental variables. The lower frequency occurred in the CSP. In contrast, Longui *et al*. (2009a) found a higher vessel frequency in the CSP in *Piptadenia gonoacantha* (Mart.) J.F. Macbr. collected in CSP at CES. Studies show that vessel frequency is inversely proportional to vessel diameter (Baas *et al*. 2004). In the present study this relationship was not observed, because the vessel

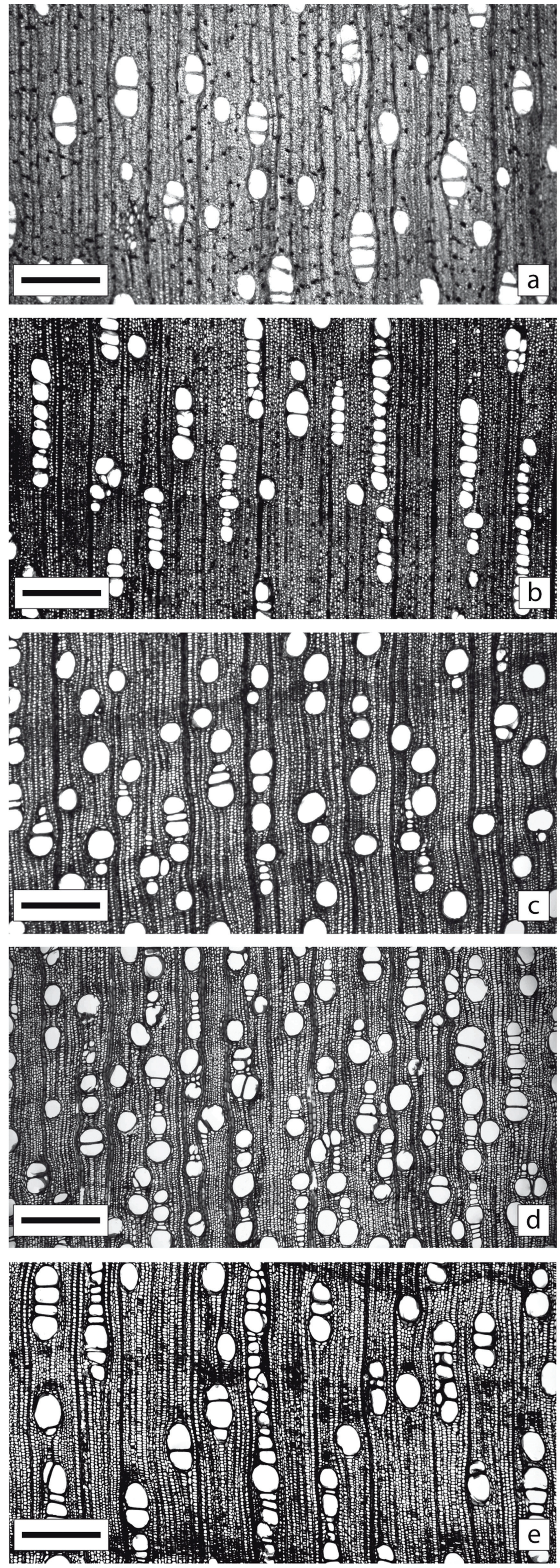

Figure 5. Transverse sections showing the variation in diameter, frequency and vessel grouping among the five areas. a. Area CSP (less frequency), b. Area CBSP (lower proportion of solitary vessels), c. Area IES (higher proportion of solitary vessels), d. Area AES, e. Area CES. (highest proportion of vessel multiples of four or more, also present in CBSP). Scale bar = 500 μm.

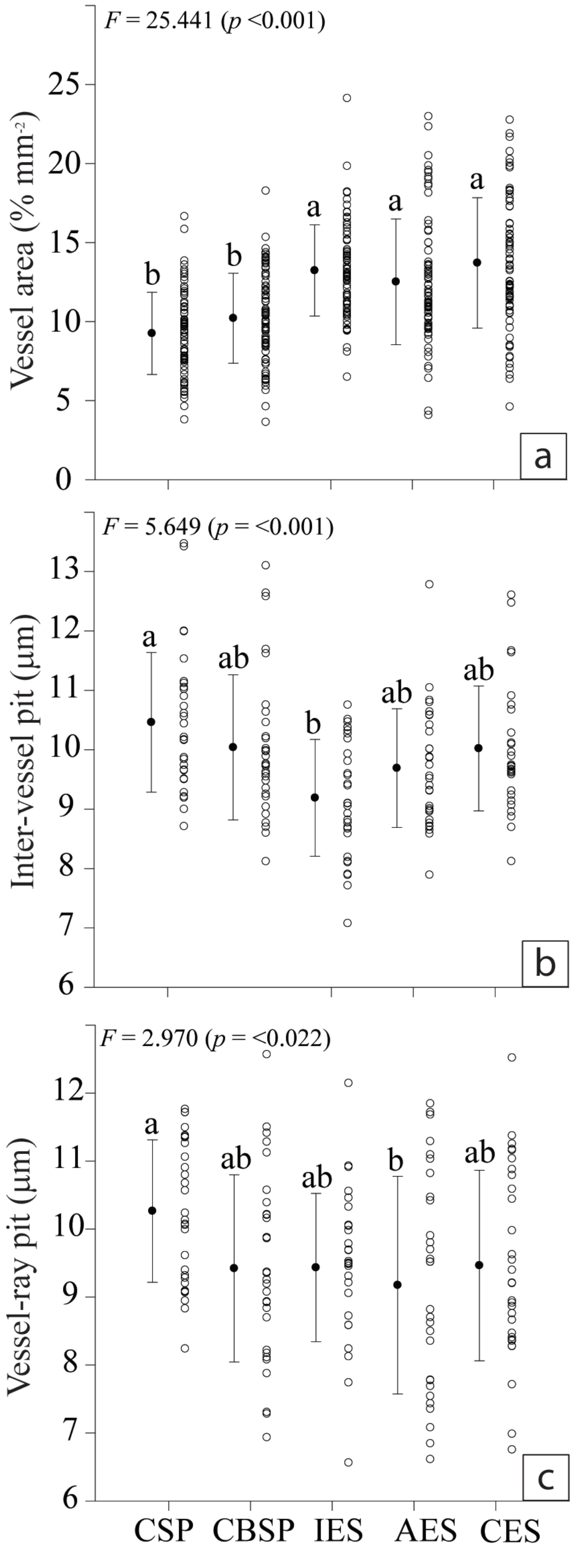

Figure 6. Variation in the vessel features. a. Vessel area %. b. Intervessel pits, c. Vessel-ray pits. Cantareira State Park (CSP), Carlos Botelho State Park (CBSP), Itapeva Experimental Station (IES), Assis Ecological Station (AES) and Caetetus Ecological Station (CES). Distinct letters differ statistically by Tukey test, the *F* and *p* values are presented in each graph.

frequency did not change in four areas (except in CSP), but the diameter varied. These results show that the relation frequency / diameter differs between species and that only with regards the frequency is difficult to establish a generalized trend in the adaptation of vessels to the environment.

Apparently the pit diameter in *C. floribundus* does not show an eco-anatomical response related to environmental variables because the values revealed no trends among the five areas. According IAWA Committee (1989), *C. floribundus* pits have medium (7-10 µm) to large (≥ 10 µm) diameter. Dickison (2000) mentions that in addition to vessel diameter, the danger of embolism is mainly related to the pit features. Thus, small pits (Baas *et al*. 1982), with small size apertures (Tyree *et al*. 1994; Sperry & Hacke 2004) offer a strategy to reduce the occurrence of cavitation, regardless of vessel size. Luchi (2004), studying *Croton urucurana* Baill. in soils with different moisture levels, found larger pits in specimens of wetland.

The positive relations between the vulnerability index with months with water deficit and mean minimum temperature and between mesomorphy index with water deficit, months with water deficit and mean minimum temperature (table 3) indicate a greater efficiency in more restrictive areas to the availability of water.

As mentioned in the introduction, vulnerability index values < 1 reflect high safe, while values > 3 are found in plants with highly efficient water transport (Carlquist 2001). We interpret that lower vulnerability index, the greater xylem safety. The CES and CSP are the two areas with the highest months with water deficit and without water surplus. In both areas there were the two higher vulnerability index (figure 7a). This index reflects that wood of CES and CSP is more efficient in transport to water, but more vulnerable to embolism in relation to the other three areas. Longui *et al*. (2009a), in *Piptadenia gonoacantha* (Mart.) J.F.Macbr., noted higher vulnerability index at CES with respect to the CSP.

We emphasize that the plants of CBSP, IES and AES showed lower values of vessel grouping index, and CBSP the lowest percentage of solitary vessels although Carlquist & Hoekman (1985) and Fahn *et al*. (1986) report that there is a tendency for greater vessel grouping in environments with higher water deficit. This conflict between the largest vessels grouping in an environment without water deficit, such as CBSP,

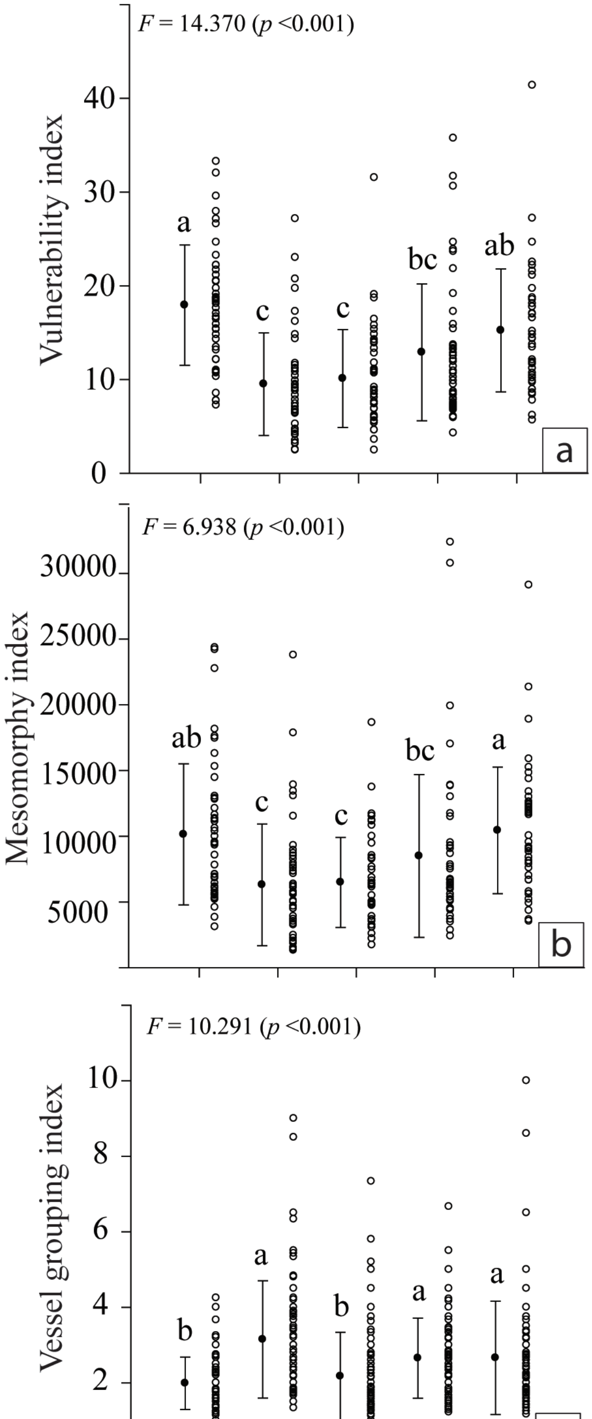

Figure 7. Variation in ecological indexes. a. Vulnerability index, c. Mesomorphy index, c. Vessel grouping index. Cantareira State Park (CSP), Carlos Botelho State Park (CBSP), Itapeva Experimental Station (IES), Assis Ecological Station (AES) and Caetetus Ecological Station (CES). Distinct letters differ statistically by Tukey test, the *F* and *p* values are presented in each graph.

might be explained, as previously mentioned, by low temperatures and frost, contributing in part to the results found for the grouping.

With respect to mesomorphy index, which relates mesic and xeric conditions, in Brazilian forests are moisture gradients with different climatic conditions. Thus we consider that plants adapted to mesic conditions present higher mesomorphy index in areas with a more humid climate. However, in the present study, the largest mesomorphy index occurred at CES and the CSP, both areas with high water deficit; according to the above we expected lower mesomorphy index in these areas.

According to Carlquist (2001), the higher value of vessel grouping index, up to 1, is the better adaptation to water stress. We did not observe a clear trend for the vessel grouping index, because the two areas with high water deficit have significantly different vessel grouping index: CSP showed lower vessel grouping index compared to CES. However, CSP did not differ from IES and CES did not differ from CBSP, the other two areas did not present apparent water restriction (figure 2). Noshiro & Baas (2000) also found no relations between vessel grouping index and the average temperature and precipitation in species of the genus Cornus. In this study, vessel grouping index was not a good indicator of eco-anatomical responses.

Regarding the vessels grouping, considering only CSP and CES, the latter seems to have an advantage in wood safety with a higher percentage of vessel multiples of 4 or more than the former (figure 8), a feature that can compensate for the larger vessel diameter. Marcati *et al*. (2001), in a study of *Copaifera langsdorffii* Desf. in forest and savanna, mentioned that specimens from savanna showed greater vessel diameter than the specimens from the forest, but trees in the savanna were also found a higher vessel frequency.

In the present study, there was no relation between precipitation and vessel features. On the other hand, the water deficit and number of months with deficit shows five significant relations, suggesting greater attention to these environmental data in the interpretation of changes in the wood vessels.

Besides the influence of the environment, changes in vessel diameter can also be caused by the radial position and reflect the changes between juvenile and mature wood, being influenced by the maturity of the vascular cambium (Tsoumis 1968). In many species of Brazilian tree an increase in vessel diameter in the

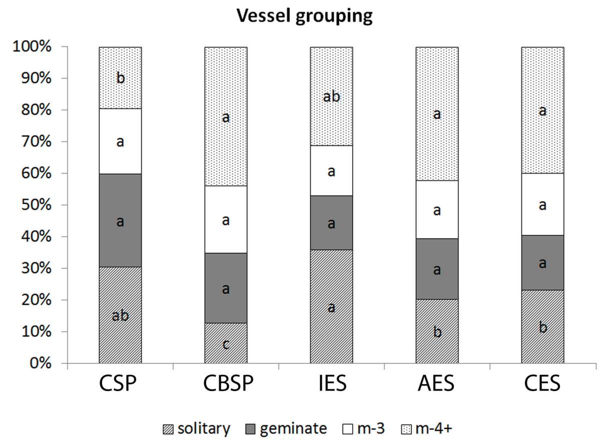

Figure 8. Variation in the vessel grouping among the five areas São Paulo State, Brazil. Different letters differ statistically by Tukey test. Cantareira State Park (CSP), Carlos Botelho State Park (CBSP), Itapeva Experimental Station (IES), Assis Ecological Station (AES) and Caetetus Ecological Station (CES). Distinct letters differ statistically by Tukey test, the F and *p* values are presented in each graph.

direction of bark is reported, *e.g.*, Longui *et al*. (2009b) in *Luehea divaricata* Mart. and Lima *et al*. (2010) also in *Croton floribundus* with different samples from CSP.

Conclusions

Our hypothesis was partially confirmed, because were observed larger diameter vessels in areas with higher water deficit, this results is not common in literature. We suggested a strategy to optimize the use of water in favorable periods. Vessels with smaller diameters occurred in areas with lower water deficit, we infer a relationship with lower minimum temperatures and frost occurrence, which similar to drought event may cause vessel embolism. In Caetetus Ecological Station semi-deciduous forest (area of highest water deficit) we observed investments in efficiency (a) and safety (b): a) larger diameter vessels associated with b) one of the lowest vulnerability index and highest proportions of vessel multiples of four or more elements. These conclusions emphasize the importance of variations in diameter and frequency of vessel and vessel grouping to adjust the water transport under diverse environmental conditions.

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