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WOOD HYDRAULIC CHARACTERISTICS IN TWO PROVENANCES OF *Myracrodruon urundeuva* Allemão (Anacardiaceae) TREES[1]

CARACTERÍSTICAS HIDRÁULICAS DA MADEIRA EM ÁRVORES DE DUAS PROCEDÊNCIAS DE *Myracrodruon urundeuva* Allemão (Anacardiaceae)

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ABSTRACT – We compared the hydraulic features in wood of *Myracrodruon urundeuva* trees planted in Experimental Forest Station of Luiz Antônio, the seeds were collected from two natural populations in Ilha Solteira – IS and Pederneiras – PE, three cities in the state of São Paulo, Brazil. In a previous study of the same plantation, we observed radial variation differences in vessel diameter and frequency in the main stem between two seed provenances, leading us to hypothesize that this variation could be traced back to the origin of seeds. To test this hypothesis in the present work, branches approximately 2 cm in diameter were collected from ten trees, five from each provenance. We used the standard techniques for wood anatomy. Experimental values of hydraulic conductivity were obtained with the Sperry apparatus. The higher hydraulic conductivity found in IS could be explained by the wider vessel diameter when compared with vessel diameter and higher percentage of embolized vessels in PE. Therefore, it is possible that the characteristics of vessel width and embolization could be related to genotype in that the mother trees in IS may be more adapted to high water deficit. Vessel length did not vary between provenaces, this feature could not be used to explain the variations found in hydraulic conductivity. Our results show that different provenances have different strategies for water use and that the lower density in IS could be related to wider vessel diameter and, hence, more efficient water distribution.

Keywords: hydraulic conductivity; aroeira; vessel diameter.

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RESUMO – Comparamos as características hidráulicas de árvores de *Myracrodruon urundeuva* provenientes de sementes de duas populações naturais de Ilha Solteira – IS e Pederneiras – PE, no Estado de São Paulo, Brasil, que cresceram no mesmo ambiente, a Estação Experimental de Luiz Antônio, São Paulo. Em um estudo anterior da mesma plantação, observamos variação radial no diâmetro e frequência dos vasos no tronco principal entre as duas procedências de sementes. Hipotetizamos que há variação na condutividade hidráulica entre as árvores de duas procedências e que esta variação deve estar relacionada com a origem das sementes. Estudamos galhos de aproximadamente 2 cm de diâmetro, retirados de dez árvores, cinco de cada procedência. Utilizamos técnicas padrão para a anatomia da madeira. Os valores experimentais de condutividade hidráulica foram obtidos com o aparato de Sperry. O comprimento dos vasos não variou entre as procedências, portanto, esta característica não explica as variações encontradas na condutividade hidráulica. A maior condutividade hidráulica encontrada em IS pode ser explicada pelo maior diâmetro dos vasos quando comparados com aqueles de PE, além da maior porcentagem de vasos embolizados em PE. Ambas as características podem estar relacionadas ao genótipo, uma vez que, as árvores-mãe em IS podem estar adaptadas ao maior déficit hídrico de IS quando comparado com PE. Portanto, a maior condutividade hidráulica em IS pode ser uma estratégia para permitir uma distribuição mais eficiente de água na planta em um ambiente com maior estresse hídrico. Nossos resultados sugerem que diferentes procedências têm diferentes estratégias de uso de água. A menor densidade aparente da madeira de IS pode estar relacionada ao maior diâmetro do vaso.

Palavras-chave: condutividade hidráulica; aroeira; diâmetro do vaso.

1 INTRODUCTION

Myracrodruon urundeuva is a Brazilian native species, but not endemic (Silva-Luz and Pirani, 2015). It presents geographic distribution in the North (Tocantins), Northeast (Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, and Sergipe), Midwest (Distrito Federal, Goiás, Mato Grosso do Sul, and Mato Grosso), Southeast (Minas Gerais and São Paulo) and South (Paraná, Rio Grande do Sul, and Santa Catarina), in the biomes of Caatinga, Cerrado and Mata Atlântica (Silva-Luz and Pirani, 2015). *M. urundeuva* heartwood is rot-proof. The high amount of phenolic extractives associated with lignin probably accounts for the high natural wood resistance (Queiroz et al., 2002). Combined with that, the wood's superior strength has, in the past, made it the wood of choice in the construction industry (Lorenzi, 1998). Unfortunately, natural populations have been devastated as a result of uncontrolled exploitation that has virtually extinguished large trees (Brandão, 2000). Consequently, *M. urundeuva* is currently considered endangered, and, as such, it is categorized as vulnerable in Brazil (Mendonça and Lins, 2000).

In the present study, we investigated the hydraulic conductivity in wood of *M. urundeuva*. Hydraulic architecture, a manifestion of efficiency and safety of water transport, is regulated, in part, by anatomical characteristics, such as arrangement, frequency, length, and diameter of vessels; vessel wall thickness and pit characteristics of conducting elements (Hacke et al., 2006, Sperry et al., 2006, Choat et al., 2008). Particularly, in woody angiosperms, long-distance water transport is carried on through vessel lumina, but it also occurs laterally, between adjacent vessels, through pit apertures. Vessel elements are interconnected longitudinally, forming vessels that, depending on the species, can reach several meters in length. Transpiration is the moving force that brings water all the way from roots upward through xylem to leaves. To accomplish the upward movement, transpiration utilizes the forces of cohesion and adhesion causing water molecules to form a column in the xylem through which water ultimately evaporates and leaves the plant via stomata (Fonti et al., 2010). Since vessel elements are the main water transporting cells in angiosperms, it is expected that any variaton in frequency and dimension of these cells, caused by the environment, will have a direct influence on hydraulic conductivity.

In a previous study in the same plantation (Longui et al. unpublished data)[5], we observed radial variation differences in vessel diameter and frequency in the main stem (DBH at breast height, 1.30 m) between two seed provenances, leading us to hypothesize that variation in hydraulic conductivity between the two provenances must exist. Therefore, in the present study, we aimed to determine whether seed origin affects hydraulic conductivity of *Myracrodruon urundeuva* wood and the resulting variation.

2 MATERIAL AND METHODS

2.1 Origin of Seeds and Area of Cultivation

Open-pollinated seeds were collected from *M. urundeuva* natural populations in two municipalities in the State of São Paulo, Brazil. In Ilha Solteira – IS (Cerrado), the seeds were collected in 1987, in the area has Red Latosols and Red Argisols (Empresa Brasileira de Pesquisa Agropecuária – EMBRAPA, 1999). In Pederneiras – PE (Seasonal Semideciduous Forest), the seeds collected in 1992, in the area has Latosols and Argisols (EMBRAPA, 1999). A study of silvicultural variation was then conducted between these two provenances during tree maturation (Gurgel-Garrido et al., 1997). Seedlings were produced and planted at the Luiz Antônio Experimental Station – LA (Cerrado), Luiz Antônio City, São Paulo, during 1988 in IS and 1993 in PE. In the LA area has Red Latosols (EMBRAPA, 1999). Climatic data of collection location of seeds and planting of trees are shown in Figure 1.

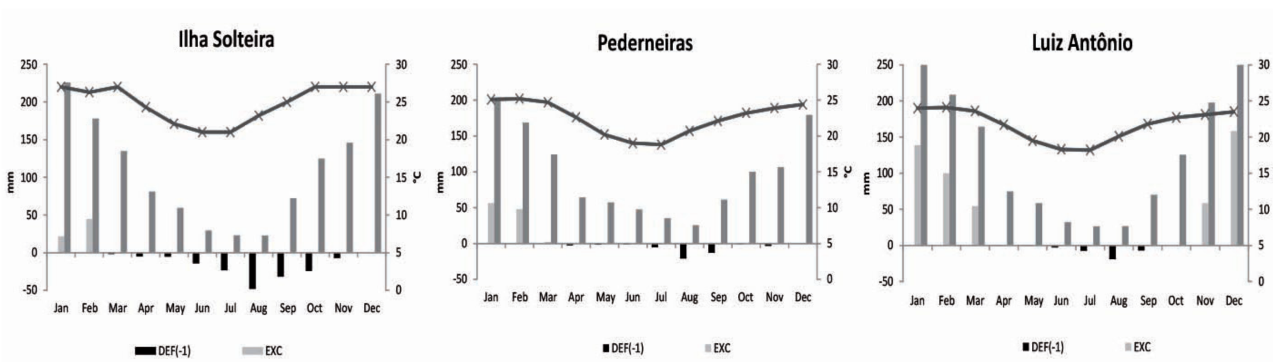

Figure 1. Average monthly precipitation, water deficit (DEF-1), water excedent (EXC) in bars, and mean temperature in lines of three areas – 1961-1990 (Centro de Pesquisas Meteorológicas e Climáticas Aplicadas à Agricultura – CEPAGRI, 2016).

Figura 1. Precipitação média mensal, déficit hídrico (DEF-1), excesso de água (EXC) em barras e temperatura média em linhas das três áreas – 1961-1990 (CEPAGRI, 2016).

2.2 Initial Procedure

Dendrometric data of trees are shown in Table 1. With the aid of a Jameson Big Mouth Pruner, two branches, at the bottom of the crown, approximately 2 cm in diameter and 1.5 cm in length, were collected from each plant. We emphasize that samples come from young branches, then there is no presence of heartwood, which in this species presents vessels obstructed by tyloses. Five specimens from each provenance were selected, totaling 10 trees and 20 branches. Immediately after cutting the first branch of each tree, it was immersed in a water container made with a PVC tube 15 cm wide and 100 cm long, sealed tightly at its bottom, and transported to the laboratory to determine hydraulic conductivity – Kh, percentage of embolized vessels – PLC and density – SG. The second branch from each tree was used to measure maximum vessel length – MVL) and was pruned and transported to the laboratory (Figure 2).

[5]LONGUI, E.L. et al. Genetic versus environmental influence on radial variation in *Myracrodruon urundeuva* wood. **FLORAM – Revista Floresta e Ambiente**, 2017. (no prelo).

Table 1. Dendrometric data of 23-year-old (Ilha Solteira) and 18-year-old (Pederneiras) *Myracrodruon urundeuva* trees. DBH = diameter at breast height.

Tabela 1. Dados dendrométricos das árvores de *Myracrodruon urundeuva* aos 23 anos (Ilha Solteira) e aos 18 anos (Pederneiras). DBH = diâmetro à altura do peito (DAP).

Ilha Solteira			Pederneiras		
Tree	Height (m)	DBH (cm)	Tree	Height (m)	DBH (cm)
IS 1	16	23	PE 1	20	19.5
IS 2	15	26	PE 2	17	14
IS 3	17	26	PE 3	16	17.5
IS 4	20	26	PE 4	16	14
IS 5	19	24	PE 5	15	15.5
Mean	17.4	25	Mean	16.8	16.1

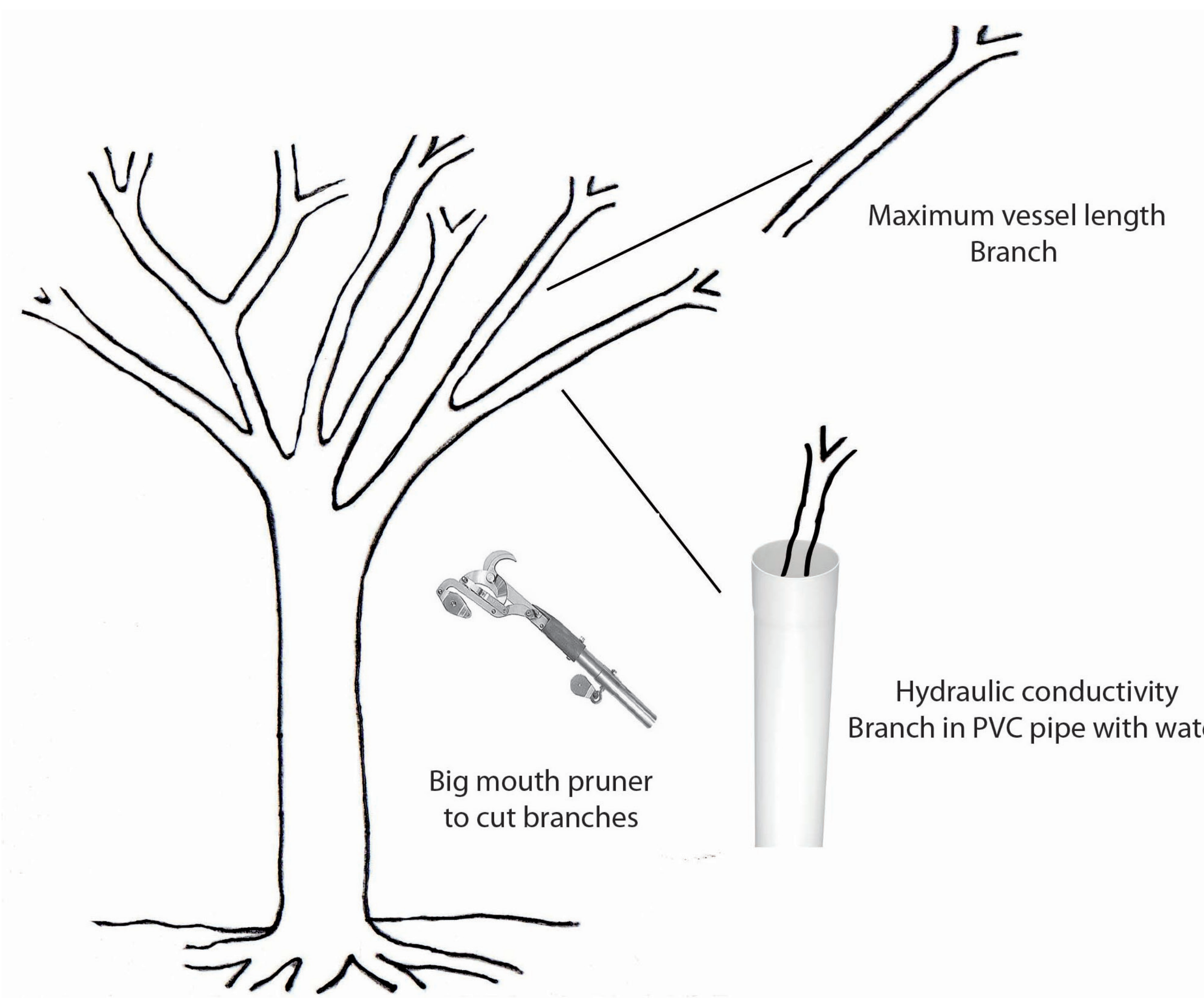

Figure 2. Illustration of sampling design for hydraulic conductivity analysis.

Figura 2. Ilustração da amostragem para as análises de condutividade hidráulica.

2.3 Maximum Vessel Length (MVL)

The technique described by Ewers and Fisher (1989) was used to measure MVL. It is important to determine MVL in order to make certain that the segments used to measure hydraulic conductivity have, at least, one vessel end. This, assuming that vessel end distribution is hazardly distributed inside the branches (Tyree and Zimmermann, 2013). Once leaves were removed, both ends of each branch were cut with the aid of prunning scissors. A final shaving was made using new razor blades to remove debris. One branch end was debarked for a length of 2 cm to allow connection to an air compressor using high pressure-resistant (up to 50 KPa) plastic tubing, aided with connectors and fasteners. The opposite branch end was kept immersed in water. Once the system was perfectly mounted with no air leaks, air was blown into the branch, carefully checking for the presence of bubbles coming out of the branch end immersed in water. If no bubbles were present, a segment 2 cm long was removed from the distal end and reimmersed in water. The procedure was repeated as many times as needed, until the first bubble was observed coming from the open vessels (Figure 3a-c). After this procedure, the branch segment remaining was measured with a measuring tape, adding 1 cm to compensate for the uncertainty of the last cut (length of segment removed each time, divided by two). This measurement provides a good approximaton of MVL.

Figure 3. Methods for measuring maximum vessel length (a-c), hydraulic conductivity (d-g) and percentage of embolized vessels (h-i).

Figura 3. Métodos para medir o comprimento máximo do vaso (a-c), condutividade hidráulica (d-g) e porcentagem de vasos embolizados (h-i).

2.4 Hydraulic Conductivity

Once the MVL was known, segments shorter than MVL were obtained from a different branch, keeping the branch under water to avoid introducing air into the exposed vessels. Both ends of these new segments were trimmed with a cutter and retrimmed with new razor blades (Sperry et al.; 1988, Tyree and Ewers, 1991; Davis et al., 2009) to keep vessels open.

One end of each segment was connected to a set of multiple connectors (a manifold), using plastic fasteners to seal the connection. If the branch was too thick for the hose, a band of bark 2 cm wide was removed, as necessary. If, on the contrary, the branch was thinner than the hose, a band 2 cm wide of a thinner hose was inserted in one branch end and then the branch and hose were inserted into the manifold (Figure 3d-g).

To measure water conductivity, a solution of 1% acetic acid in distilled water was prepared, to avoid fungal and bacterial growth during measurements. This solution was kept under refrigeration until use. Just before use, this solution was subjected to vacuum for 24 hours to eliminate air dissolved in the solution, to avoid introducing air into the vessels. To measure the flux of solution through each branch segment in the manifold, a container (a bag originally used for intravenous infiltration) filled with the degassed acetic acid solution, as described above, was kept at a height of 60 cm from the working surface. The valve connecting the container to the manifold was opened, while the valves connecting each branch segment were kept closed. After confirming that the system was air-free, the valve connected to the first branch segment was opened, allowing the solution to flow through that branch segment. At the other end of the branch, the solution coming out the branch segment was collected in a glass vial that was previously weighed. The vial was tagged to identify it as belonging to that particular branch segment. Then, the vial with the collected solution was weighed using an electronic balance with a precision of 0.001 mg (Figure 3d-g). The amount of water collected in 1 minute was calculated by subtracting the weight of the vial from the weight of the vial with the collected solution. The same procedure was repeated 10 times to obtain the amount of water flowing through each branch segment during one minute in response to the pressure differential created by the water head at 0.6 m, *i.e.*, 60 X 10^{-3} MPa. After this, the valve leading to that branch segment was closed, and the next one was opened to repeat the procedure.

Hydraulic conductivity for each segment was calculated by multiplying the water flux times the quotient of pressure gradient (dp), divided by the branch segment (dl):

$$k_h = \text{Flux}\,\frac{d_p}{d_l} \quad \left[\frac{\text{Kg . MPa}}{\text{seg . m}}\right]$$

This represents hydraulic conductivity before removing embolisms. To remove embolisms from the system, the solution container was elevated to 7 m, using a support with a pulley placed on the outside of the laboratory building to connect to the manifold (Figure 3d-g). At this step, passage of this solution was forced through all the segments at the same time, during 20 minutes, to remove embolisms. After this, the system was again brought up to the original height of 0.6 m, and the *Kh* was calculated again for each branch segment to obtain maximum *Kh1*. To make sure that all embolisms had been removed, the system was subjected again to high pressure during 20 minutes, and *Kh2* was calculated, as described. In all cases, no significant differences were observed between *Kh2* and *Kh1*. Therefore, it was assumed that one removal of embolisms was enough to allow for accurate calculation of the maximum *Kh*. The difference between maximum and mimimum *Kh* gives the percentage of embolisms in the branch at the time of its collection:

$$\%\ \text{embolism} = \left(\frac{\text{maximum } K_h - \text{minimum } K_h}{\text{maximum } K_h}\right) \text{x } 100$$

2.5 Percentage of Embolized Vessels

Other segments of the same branches used to measure *Kh* were used to obtain the percentage of embolized vessels. A 0.01% aqueous safranin solution was added into a 1% acetic acid solution and passed twice through a Whatman filter No. 1 to eliminate any particles that could clog the vessels (Ewers and Fisher, 1989).

A portion of stem about 15 cm long was cut under water to avoid entrance of air. Then, both ends of this segment were cut clean with safety razor blades to open closed vessels.

In one of the branch ends, a plastic tube 15 cm long was connected, using metal clamps to avoid solution leakage. The tube and branch were placed verticaly, attached to a support, with a vial under the branch. The water in the tube was replaced with the 0.01% aqueous safranin solution decribed above, filling it completely. When the solution passed through the branch, the tube was filled with a 1% solution of acetic acid in distilled water to remove excess of safranin from the branch (Figure 3h-i).

The branch was cut at the middle and sectioned with a safety razor blade. Images from these sections were obtained, followed by counting stained and unstained vessels (Figure 3h-i). Here, % of embolized vessels = [(# conductive vessels – # nonconductive vessels)/Total vessel number] x100).

2.6 Wood Anatomy

After determining hydraulic conductivity of a branch, we obtained samples (one from each branch) from the central portion of the same branch to determine vessel diameter and frequency. The samples were the branches themselves, however, in measurement of anatomical features only portions near to the bark were measured. Samples were softened in boiling water and glycerin (4:1) for approximately 1 h. Transverse sections 20-25 µm thick were cut using a sliding microtome. Sections were bleached with sodium hypochlorite (60%), washed thoroughly in water, and stained with 1% safranin (Johansen, 1940). Measurements followed the recommendations of the IAWA Committee (1989). Quantitative data are based on at least 25 measurements for each feature, and the statistical requirements for minimum numbers of measurements were fulfilled.

2.7 Density

Density ($\rho 12$) was determined at equilibrium moisture content (EMC-12%) condition and calculated by the relation between mass and volume at the same moisture content. Volume was evaluated by the volume of water displaced during immersion of the specimens (Glass and Zelinka, 2010), as $\rho 12 = M/V$,

where $\rho 12$ = density (kg.m^{-3}); M = wood mass at 12% moisture content (kg); and V = wood volume at 12% moisture content (m^3).

2.8 Statistical Analysis

Descriptive statistical analysis and comparison between means were performed to test diferences between groups. With these results, a “t-test sample size” was made to determine the number of measurements needed to reach a power of 0.9. A normality test was used to observe data distribution. According to data distribution, when a normal distribution was observed, a parametric t-test was applied, and the results were expressed as a mean and standard deviation. When a normal distribution of data was not observed, data were square root-transformed.

3 RESULTS AND DISCUSSION

Maximum vessel lengths did not differ between provenances. Hydraulic conductivity and vessel diameter were higher in IS. On the other hand, vessel frequency, percentage of embolized vessels and density were higher in PE (Table 2).

Table 2. Hydraulic features and wood density of 23-year-old (Ilha Solteira) and 18-year-old (Pederneiras) *Myracrodruon urundeuva* trees.

Tabela 2. Características hidráulicas e densidade da madeira de árvores de *Myracrodruon urundeuva* aos 23 anos (Ilha Solteira) e aos 18 anos (Pederneiras).

Hydraulic features and density	Ilha Solteira	Pederneiras
Maximum length of vessels (cm)	72a	66a
Hydraulic conductivity (kg.MPa.s^{-1}.m^{-1})	0.155a	0.124b
Percentage of embolized vessels (%)	33b	57a
Vessel diameter (µm)	65a	62b
Vessel frequency (n°mm^{-2})	28b	34a
Density (kg.m^{-3})	915b	1074a

Vessel diameter and frequency alone do not determine hydraulic conductivity in woody plants; however, maximum vessel length must be considered because the end-wall effect (connection between vessels) appears to reduce conductivity at a given diameter by a relatively constant 56% in angiosperms with simple perforation plates (Sperry et al., 2006). *M. urundeuva* has simple perforation plates, but since vessel length did not vary between provenances, this feature did not explain the variations found in conductivity, showing that, even at different ages, vessel length had reached its maximum value for the species. We did not find any other study on *Myracrodruon urundeuva* with which to compare maximum vessel length, since this parameter is not taken into account in anatomical studies where individual vessel element length is reported.

Measured hydraulic conductivity presented statistical differences between provenances. IS showed higher values (Table 2), indicating that wood from both provenances differed in architecture and hydraulic transport efficiency, in spite of having different genotypes. We observed vessels with larger diameters in IS, compared with the PE, which indicates a potentially greater hydraulic efficiency in IS, essentially because wider vessels are more conductive than narrower ones (McElrone et al., 2004; Fan et al., 2012), a fact already well documented among wood anatomists. According to Carlquist (2001), larger diameter of conductive elements correlates with larger hydraulic conductivity, resulting in an increased rate of photosynthesis.

These variations can be explained in two ways:

1) first, seeds receive genetic information from the mother trees; therefore, differences in xylem traits could occur as a result of seed provenance. Since we did not perform heritability studies of this material, we cannot say whether this genetic information is maintained throughout the lifetime of the studied trees. However, since wood anatomists have agreed that anatomy is quite conservative compared to the more ephemeral parts of plants, such as the leaves, it is possible that trees express phenotypical variations influenced by their original environment, *e.g.*, climate and soil;

2) second, it is possible that these variations arise as a result of age. More specifically, at the time of collection, IS trees were 23 years old, while those of PE were 18 years old. This difference is mainly based on tree diameter measured as DBH (25 cm in IS and 16.1 cm in PE), not height, which exhibited, on average, less than one meter of difference between provenances.

It was noted above that changes in tree height between the two provenances were slight, making it impossible to establish a relationship between tree height and our results. Currently, studies, such as those of Anfodillo et al. (2006, 2013) and Olson and Rosell (2013), have shown that tree height influences vessel diameter. Olson and Rossel (2013), for example, claim that plant size is related to climate, leading indirectly to a vessel-climate relationship in which vessels are likely narrower in drier communities because dryland plants are, on average, smaller, not because they have narrow vessels for their stem sizes. It is a fact that wider vessels occurred in branches collected from IS, a place which undergoes more restrictive water stress than PE.

The higher presence ocurrence of embolisms in PE, associated with smaller vessel diameter, contributed to lower hydraulic conductivity compared to IS. According to Carlquist (2001), larger vessels are more susceptible to the development of embolisms, especially embolisms of larger size; therefore, it becomes correspondingly harder to revert it, impeding the refilling of the embolized vessel. In finer capillaries, embolisms are smaller and easier to dissolve. However, in the present study, just the opposite was observed.

IS trees, with wider vessels, presented a lower percentage of embolized vessels (Table 2). This contradiction could be explained by the environmental influence of mother tree origin. That is, IS presents more limited water availability (Figure 1); therefore, IS trees could be more adapted to water stress and could recover more quickly from embolisms than PE trees.

Xylem tensions causing cavitation vary with species. The ability to recover from embolisms may be associated with the presence of living cells adjacent to the vessels. According to Brodersen et al. (2010), parenchyma cells secrete solutes into the vessel, establishing an osmotic gradient, and water will gradually refill the air-filled vessels, either dissolving air micro-bubles in the solution or forcing them into the surrounding hydrophobic microchannels in the vessel wall.

Wood density is often negatively correlated with hydraulic conductivity (Bucci et al., 2004). In this study, we did not see this relationship; however, lowest densities are associated with wider vessel diameter (Hoadley, 2000). In this study, lower density in IS could be related to wider vessel diameter.

4 CONCLUSION

Vessel length did not vary between provenances; therefore, this feature does not explain the variations found in hydraulic conductivity. The higher hydraulic conductivity measured in IS can be explained by wider vessel diameter, when compared with smaller vessel diameter and higher percentage of embolized vessels in PE. Both characteristics could be related to the genotype since it is likely that the IS mother tree would have been more adapted to the higher water deficit in IS, as compared to PE. Therefore, given the water-deficient environment, a higher hydraulic conductivity in IS could be a strategy to allow a more efficient water distribution in the plant. Our results suggest that different provenances have different strategies for water use. Lower density in IS could be related to wider vessel diameter.

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