Wood hydraulic characteristics of pioneers/early secondary and non-pioneer species

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Abstract We aimed to determine any differences in hydraulic conductivity between pioneer species/early secondary and non-pioneers. To make this determination, we measured maximum vessel length (Mvl), specific hydraulic conductivity (Ks), percentage of embolized vessels (Pev), leaf hydraulic conductivity (Kl) and wood density at equilibrium moisture content-12% (Wd_{12}). The pioneer/early secondary species we examined were *Guazuma ulmifolia*, *Inga marginata* and *Maclura tinctoria*. The non-pioneers we examined were *Paubrasilia echinata*, *Cariniana legalis* and *Myroxylon peruiferum*. The results were submitted to statistical analyses, including multiple comparison tests and *t* test, to verify differences between successional groups and regression analysis to verify the relationship between Ks and the other variables. Pioneer species had higher Ks than non-pioneers. Non-pioneers had a higher percentage of embolized vessels and wood density. Successional groups did not differ in Mvl, which is positively related to hydraulic conductivity in both successional groups since the percentage of embolized vessels was related negatively. Wood density is positively related to Ks in non-pioneer species, while a negative correlation was observed between Ks and Kl in the pioneer species.
Keywords: wood anatomy, physiology of trees, ecological groups and water transport

Introduction

Tree species are separated by ecological groups; this classification is based on successional dynamics, the process of opening and closing gaps and natural regeneration (Maciel et al., 2003). Over the years, different approaches have been employed to assess forest dynamics and the separation of species into ecological groups. We will use the proposal by Swaine and Whitmore (1988) who consider two ecological groups: pioneers and climaxes (not pioneers). Pioneers are those species capable of growing in a completely open environment, while non-pioneer species need to develop canopy.

Few studies have investigated the adaptive strategies of trees in these ecological groups when considering wood anatomy in relation to hydraulic efficiency (e.g., Wagner et al., 1998; Baas et al., 2004). Hydraulic efficiency can be determined and/or estimated from hydraulic conductivity tests and quantitative vessel analyses (Sperry et al., 2008; Fonti et al., 2010; McCulloh et al., 2012).

The analyses of wood structure, along with wood properties, allow us to establish the adaptive strategies of woody species. In this context, the comparative study of wood from different ecological groups makes it possible to understand these strategies, especially given the age of plants and the

climatic and soil characteristics of their habitat, all of which fit within the scope of the present study.

We hypothesize that early pioneer / secondary species have greater conductivity than non-pioneer species, suggesting the tendency of early pioneer/secondary species to have larger diameter vessels when compared to non-pioneer species. Thus, we aim to determine any statistical differences between the two groups in terms of hydraulic conductivity.

Methods
Sampling

Alberto Löfgren State Park - PEAL (Portuguese) is located in the northern area of São Paulo City, São Paulo State, Brazil (23°47′S, 46°38′W, elevation 814 m). Climate is Cwa in the Köppen classification, mesothermal and humid with rainy summers and dry winters (Rossi et al., 2009). Ombrophilous Dense Forest is the main vegetation

formation of PEAL; anthropic areas are also found with arborets of one or more species (Arzolla et al., 2009). The trees investigated in this study are located in one of these arborets, denominated "Commemorative Arboretum of 500 years of Brazil". In 2000, 24 native species were planted at the site, with 4 x 5 m spacing, occupying an area of one hectare (Bonucci et al. 2007). Three pioneer/early secondary species were selected (*Guazuma ulmifolia* Lam., *Inga marginata* Willd. and *Maclura tinctorial* (L.) D. Don ex Steud.), and three non-pioneer species were selected (*Paubrasilia echinata* Lam., *Cariniana legalis* (Mart.) Kuntze and *Myroxylon periuferum* L.f.). The height and DBH (diameter at breast height, 1.3 m from the ground) of trees were determined (Table 1). The study material (branches from 30 trees) was collected in 2013 when the trees were 13 years old.

Table 1. Dendrometric data of 13-year-old pioneer and non-pioneer species. Height (m) and DBH = diameter at breast height (cm).

Pioneer						Non-pioneer					
Guazuma ulmifolia		*Inga marginata*		*Maclura tinctoria*		*Paubrasilia echinata*		*Cariniana legalis*		*Myroxylon peruiferum*	
Height	DBH	Height	DBH	Height	DBH	Height	DBH	Height	DBH	Height	DBH
12	38.2	15	25.3	13.5	24.5	11.5	15.5	8.7	12	13	15
14	29.6	15	27.7	15	20.6	7.5	8	13	20	13	11.6
15	36.9	15	26.5	11	14.5	7.2	7	10.2	14	13	14.3
15	24.8	13	19	13.5	23	9.3	6	7.3	9	13	11.2
15	26.7	14	22	135	22.5	8	7.5	14	22	13	14.5

Initial procedure

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. Since samples came from young branches, no heartwood had developed, which, in this species, would present 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 measure maximum vessel length (Mvl), specific hydraulic conductivity (Ks), percentage of embolized vessels (Pev), leaf hydraulic conductivity (Kl) and wood density at equilibrium moisture content-12% (Wd$_{12}$). The second branch from each tree was used to measure Mvl. For all hydraulic determination procedures, we consider Scholz et al. (2013).

Maximum vessel length

We measured Mvl according Ewers and Fisher (1989). It is important to determine Mvl to make certain that the segments used to measure hydraulic conductivity have, at least, one vessel end. We assumed that vessel ends would be distributed

in a haphazard manner inside the branches (Tyree and Zimmermann 2013). Once leaves were removed, both ends of each branch were cut with the aid of pruning scissors. Finally, shaving was performed by using new razor blades to remove debris from the cut surface.

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 re-immersed in water. The procedure was repeated as many times as needed, until the first bubble was observed coming from the open vessels. 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 approximation of Mvl.

Specific hydraulic conductivity (Ks)

After determining Mvl, it was possible to obtain shorter segments (15 cm). 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.

To measure hydraulic conductance, a solution of 1% acetic acid in distilled water was prepared to avoid fungal and bacterial growth during measurements. To measure the flux of solution through each branch segment in the manifold, a container, i.e., 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. 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., 60×10^{-3} MPa. After this, the valve leading to that branch segment was closed, and the next one was opened to repeat the procedure.

Hydraulic conductance for each segment was calculated by multiplying the water flux times the quotient of pressure gradient ($dp = 0.006$ MPa), divided by the branch segment (dl), as

$$K_h = Flux \ \frac{d_p}{d_l} \qquad \left[\frac{kg \ . \ MPa}{sec \ . \ m}\right] \qquad \text{Eqn. 1}$$

This represents hydraulic conductance before removing embolisms. To remove embolisms from the system, the solution container was elevated to 7 m, using a support with a pulley placed outside of the laboratory building to connect to the manifold. At this step, passage of this solution was forced through all the segments at the same time for 20 minutes in order to remove embolisms. Following 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 Khi. To ensure that all embolisms had been removed, the system was subjected again to high pressure for 20 minutes, and Khf was calculated, as described. In all cases, no significant differences were observed between Khf and Khi. Therefore, it was assumed that one round of removing embolisms was enough to allow for accurate calculation of the maximum Kh.

Then, the initial (without embolism removal) and final or maximum (after embolism removal) specific hydraulic conductivities (Ks) were calculated by multiplying the conductance by sample length and dividing by the xylem cross-sectional area of samples, as

$$K_{si} = khi \ x \ \frac{L}{CSA} \qquad \text{Eqn. 2}$$

$$K_{sf} = khf \ x \ \frac{L}{CSA} \qquad \text{Eqn. 3}$$

where Ks = specific hydraulic conductivity (in kg m*MPa^{-1}*s^{-1}), Khi = initial hydraulic conductance, Khf = final hydraulic conductance, L= sample length (m), and CSA = cross-sectional area of sample (m^2). Ksi = initial specific hydraulic conductivity, and Ksf = final specific hydraulic conductivity.

Percentage of embolized vessels (Pev)

Other segments of the same branches used to measure Ks 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 et al. 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 vertically, attached to a support, with a vial under the branch. The water in the tube was replaced with the 0.01% aqueous safranin solution described 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.

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. Here, % of embolized vessels = [(# conductive vessels – # nonconductive vessels)/ Total vessel number] x100).

Leaf hydraulic conductivity (branch conductance per unit leaf area, Kl)

The procedure for measuring leaf area was performed based on Leigh et al. (2017). For this analysis, we considered all leaves from branches that we had previously measured for hydraulic conductivity. We carefully removed the leaves from the petioles and stored them in paper envelopes, after which we separated out 20 leaves per crown position (base, middle and top, 60 leaves per tree). The leaves were pressed to prevent shrinkage and

contortion, followed by drying in a laboratory kiln for three days. Subsequently, we weighed all leaves individually to determine their masses (g), and their individual areas were measured using an LI-3100C Area Meter.

The leaves left in the paper envelopes were placed in the laboratory oven at 60-70°C and left to dry for three days. After this period, we obtained the total weight of leaves. For calculation of total area, a regression was elaborated with values of area and mass from each of 60 leaves.

Leaf conductivity (Kl) was calculated by dividing the maximum hydraulic conductance (Kh) of branch segment by the corresponding leaf area.

Wood density (□12)

Density was determined at equilibrium moisture content (EMC-12%) condition and calculated by the relationship 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).

Statistical analysis

We initially undertook descriptive statistical analysis and used Box Plot graphics to detect outliers. Thus, values 1.5 times higher than the 3rd quartile and values 1.5 times lower than the 1st quartile were excluded from the analysis. Normality tests were performed to check the distribution of data, and when a normal distribution was not observed, data were square root-transformed. Then, we performed a parametric analysis of variance (one-way analysis of variance-ANOVA). When a significant difference was observed, Tukey's test was used to identify pairs of significantly different means between species in successional groups. We used a *t* test to verify differences between successional groups. We also used regression analyses to verify the relationship between Ks and the other variables.

Results and discussion

Maximum vessel length did not differ between ecological groups. The pioneer species *I. marginata* and *G. ulmifolia* presented the highest values, differing from *M. tinctoria*. In the non-pioneer species, *M. peruiferum* presented the highest averages, followed by *P. echinata*, and the lowest averages were those of *C. legalis* (Figure 1a).

Specific hydraulic conductivity was higher in pioneer species when compared to non-pioneer species. Among the pioneers, *I. marginata* presented the highest average, differing from *M. tinctoria*, while *G. ulmifolia* did not differ from the other two species. In the non-pioneer species, *M. peruiferum* showed the highest average, differing significantly from *C. legalis* (Figure 1b).

The non-pioneer species had the highest percentage of non-conducting vessels. In the pioneers, *M. tinctoria* had the highest average, differing from *G. ulmifolia*. *I. marginata* did not differ

from the other two species. In the non-pioneer species, *C. legalis* and *M. peruiferum* presented higher averages (Figure 1c).
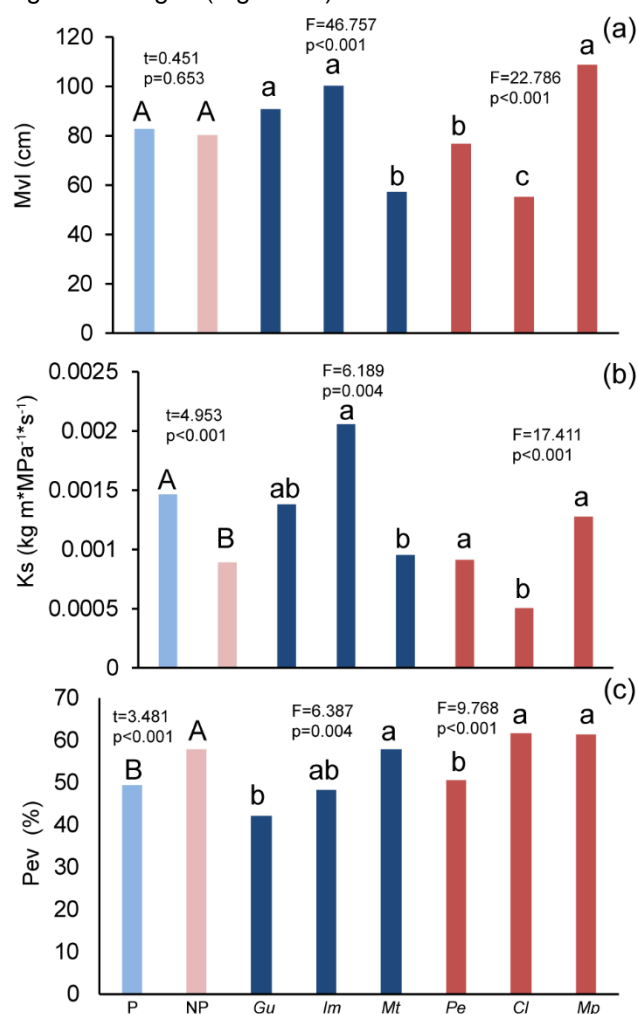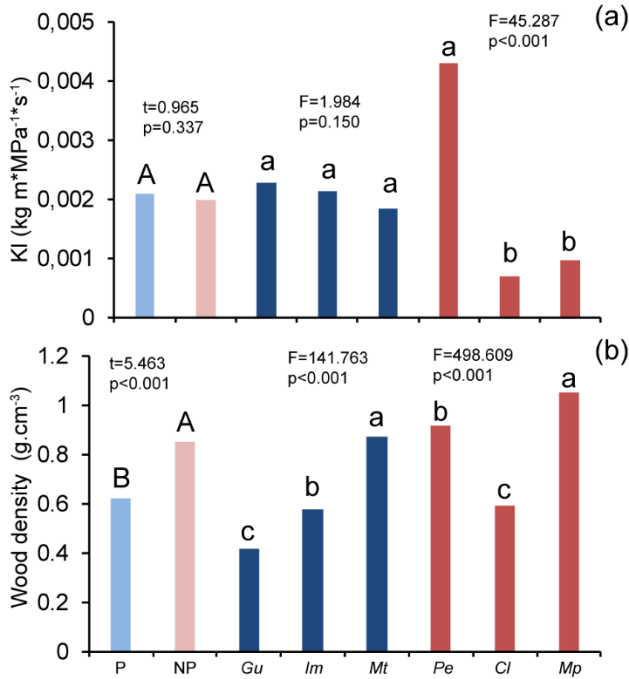

Figure 1. (a) Maximum vessel length (Mvl). (b) Specific hydraulic conductivity (Ks). P=pioneer, NP=non-pioneer species, *Gu= Guazuma ulmifolia*, *Im=Inga marginata*, *Mt=Maclura tinctorial*, *Pe=Paubrasilia echinata*, *Cl=Cariniana legalis*, *Mp=Myroxylon peruiferum*. The difference between ecological groups is represented by uppercase letters (*t* test), and in each group is represented by lowercase letters (Tukey's test).

Leaf hydraulic conductivity did not differ between pioneer and non-pioneer species. Among the pioneers no variation was noted, but among the non-pioneers, *P. echinata* showed the highest values (Figure 2a).

The non-pioneer species showed higher wood densities when compared to non-pioneer species. Among pioneer species, *M. tinctoria* had the highest values, followed by *I. marginata*, and the lowest values were found in *G. ulmifolia*. In the non-pioneer species, *M. peruiferum* had the highest density, followed by *P. echinata*, while *C. legalis* had the lowest values (Figure 2b).

In the regression analyses, specific hydraulic conductivity was positively related to maximum vessel length in both ecological groups (Figure 3a-b). The pioneer and non-pioneer species did not differ in terms of maximum vessel length

(Figure 1a), but this characteristic showed a significant relationship with conductivity for the two ecological groups (Figure 3a-b), showing that the greater the maximum vessel length, the greater the specific hydraulic conductivity will be for these species.


Figure 2. (a) Leaf hydraulic conductivity (Kl). (b) Wood density (ρ12). P=pioneer, NP=non-pioneer species, *Gu= Guazuma ulmifolia*, *Im=Inga marginata*, *Mt=Maclura tinctorial*, *Pe=Paubrasilia echinata*, *Cl=Cariniana legalis*, *Mp=Myroxylon peruiferum.* The difference between ecological groups is represented by uppercase letters (*t* test), and in each group is represented by lowercase letters (Tukey's test).

Specific hydraulic conductivity was negatively related to the percentage of non-conducting vessels for both ecological groups (Figure 4a-b).

Specific hydraulic conductivity was positively related to wood density in the non-pioneer species and negatively related to leaf hydraulic conductivity in the pioneer species (Figure 5a-b, respectively).

According to Tyree (1993), as cited by Evert (2006), vessel length was defined as the maximum distance that water can travel without crossing a vessel to the adjacent vessel through the pit membrane. The vessel elements, in addition to having pits on their walls, also have perforations which are areas where primary and secondary walls are absent and through which the elements intersect. Perforations generally occur in the terminal walls where the connection between the vessel elements occurs, forming long continuous columns called vessels. Perforations may also be present in the side walls, as each vessel element that makes up a vessel has a perforation plate on each end portion of the wall, except vessels that occupy the upper and lower terminal positions. The vessel element in the upper terminal position of the vessel does not have a perforation plate at its upper end, and the element that occupies the lower terminal position of that same vessel does not have a perforation plate at its upper end. Therefore, the movement of water and solutes from one vessel to another vessel occurs through the pairs of pits on its adjacent walls (Evert, 2006).
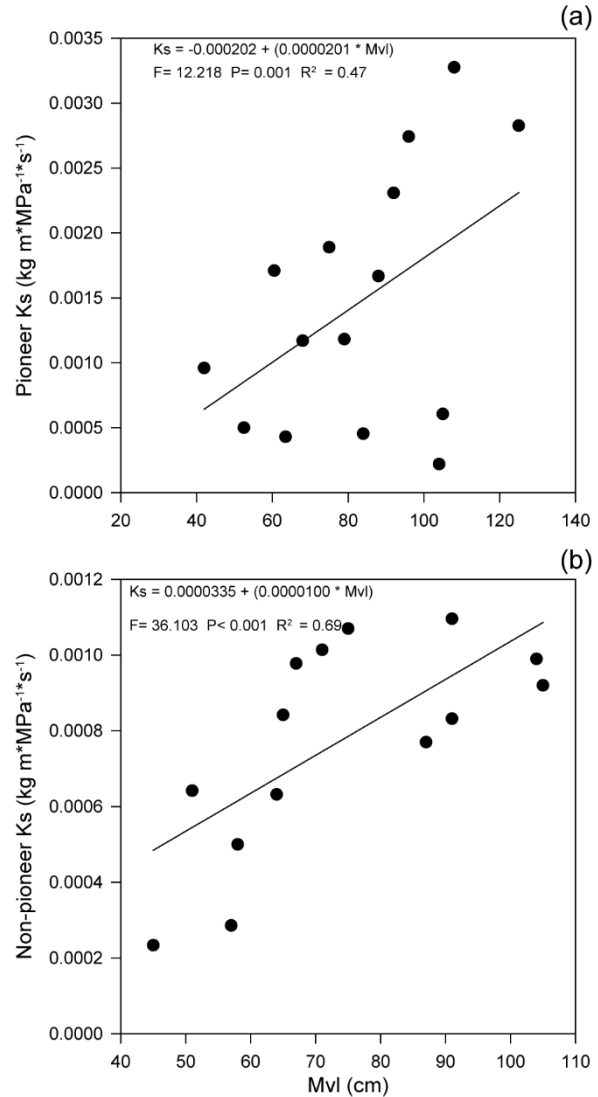
Figure 3. Relationships between specific hydraulic conductivity and maximum vessel length. (a) Pioneer species. (b) Non-pioneer species.
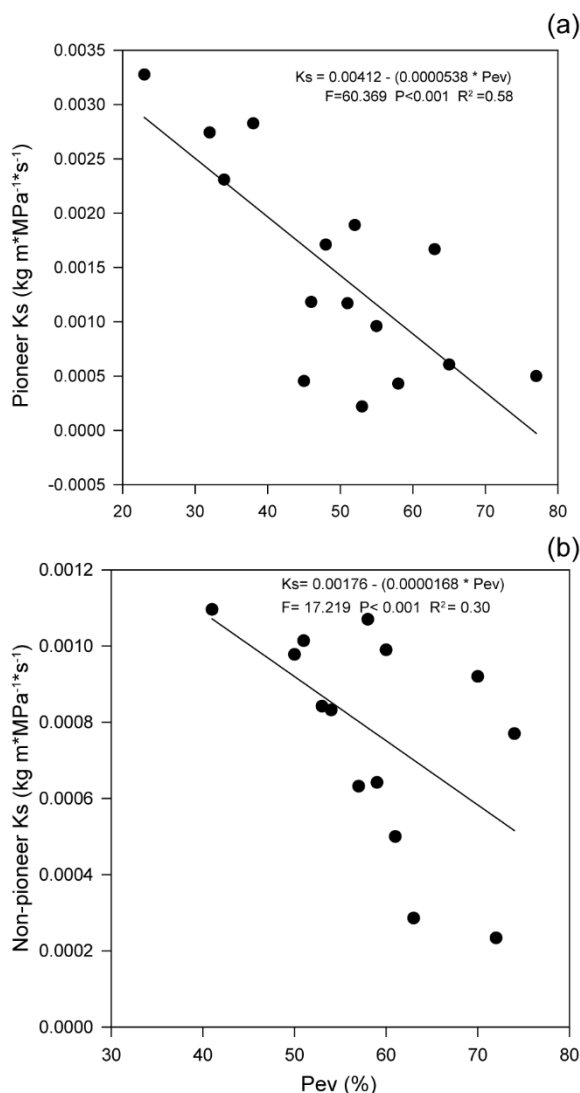
The higher values of specific hydraulic conductivity in the pioneer species must result from the larger vessel diameters presented in these species, thus confirming our hypothesis that the larger vessel diameter may interfere with hydraulic conductivity. Larger diameter vessels imply a greater flow of water through the plant, essentially because doubling vessel diameter causes its hydraulic conductivity potential to increase by 16 times (Tyree and Zimmermann, 2002).

Pioneer species showed lower percentages of non-conducting vessels. This influences their greater conductivity when compared to non-pioneer

species. Such phenomenon can be explained by the negative relationship between hydraulic conductivity and percentage of non-conducting vessels. This means that species having a greater number of non-conductive vessels (e.g., filled with air) will conduct less water. According to Sperry (1988), embolism is the presence of air in the tracheids and vessels, causing, in turn, damage to xylem water transport, as this vessel, which is filled with air, no longer plays a role in conduction.
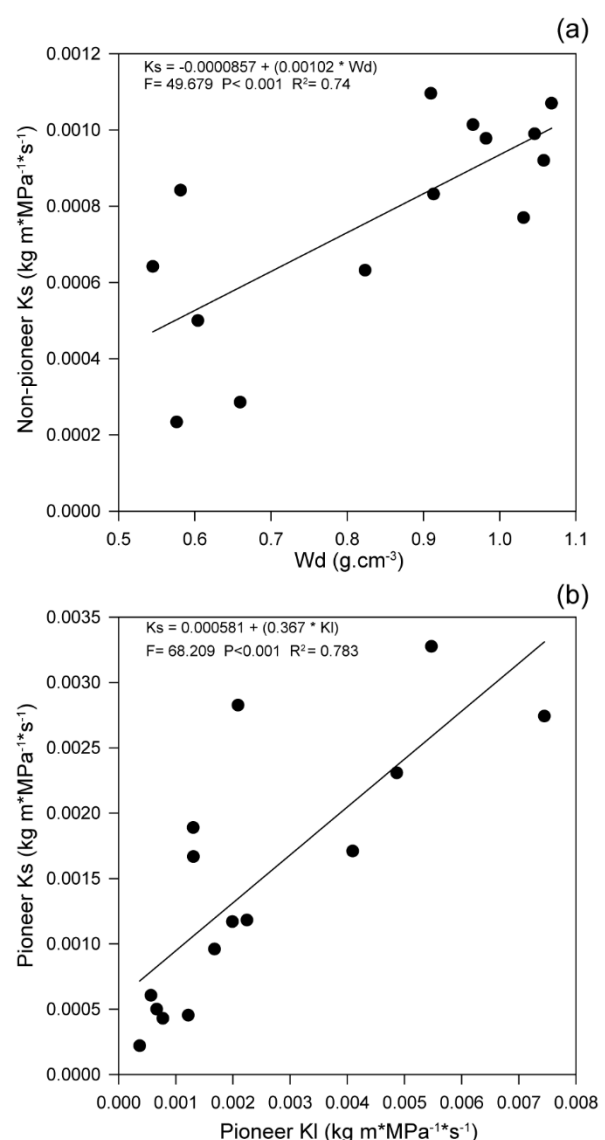
Leaf hydraulic conductivity did not differ between pioneer and non-pioneer; however, *P. echinata* did present high values when compared to other species. It is suggested that this may be related to the formation of its leaves composed of individually measured leaflets. Thus, if the area of all leaflets were added, it may turn out that *P. echinata* presents Kl values close to those of other species.

2000). Non-pioneer species showed greater density because they have vessels with smaller diameters (lesser proportion of empty spaces) and, consequently, greater proportion of tissue. According to Hacke et al. (2001), a good relationship exists between high wood density and low hydraulic conductivity based on the decreased water conduction in the lumen of vessels. Additionally, species with high wood density have a high cost in their construction and, thus, low growth rate (Larjavaara and Muller-Landau, 2010). Both hydraulic conductivity and wood density influence plant strategies to acquire resources. Thus, it is easy to understand the distribution of tree species during forest succession since these characteristics determine the allometric growth patterns that determine forest dynamics (Rüger et al., 2012).

(a)

$Ks = 0.00412 - (0.0000538 * Pev)$
$F=60.369 \quad P<0.001 \quad R^2 =0.58$

(b)

$Ks= 0.00176 - (0.0000168 * Pev)$
$F= 17.219 \quad P< 0.001 \quad R^2= 0.30$

Figure 4. Relationships between specific hydraulic conductivity and percentage of embolized vessels. (a) Pioneer species. (b) Non-pioneer species.

Wood density of pioneer species was lower, which can also be explained, in part, by vessel diameter. Since pioneer species have vessels with larger diameters, a greater proportion of empty spaces can be related to lower density (Hoadley

(a)

$Ks = -0.0000857 + (0.00102 * Wd)$
$F= 49.679 \quad P< 0.001 \quad R^2= 0.74$

(b)

$Ks = 0.000581 + (0.367 * Kl)$
$F= 68.209 \quad P<0.001 \quad R^2= 0.783$

Figure 5. (a) Relationships between specific hydraulic conductivity and wood density in non-pioneer species. (b) Relationships between specific hydraulic conductivity and leaf hydraulic conductivity in pioneer species.

Conclusion

The results demonstrated a difference between early and non-early pioneer/secondary

50

species in terms of hydraulic conductivity. Pioneer species show a higher hydraulic conductivity than non-pioneer species for the individuals studied.

The initial pioneer/secondary species, in addition to having the highest hydraulic conductivity, showed low densities and a smaller number of non-conducting vessels, indicating that these anatomical features influenced the result. Non-pioneer species, on the other hand, show lower hydraulic conductivity and higher values of wood density and percentage of non-conducting vessels. Thus, by investing in some features, such as higher vessel densities, they end up losing others, such as hydraulic conductivity.

Acknowledgment

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