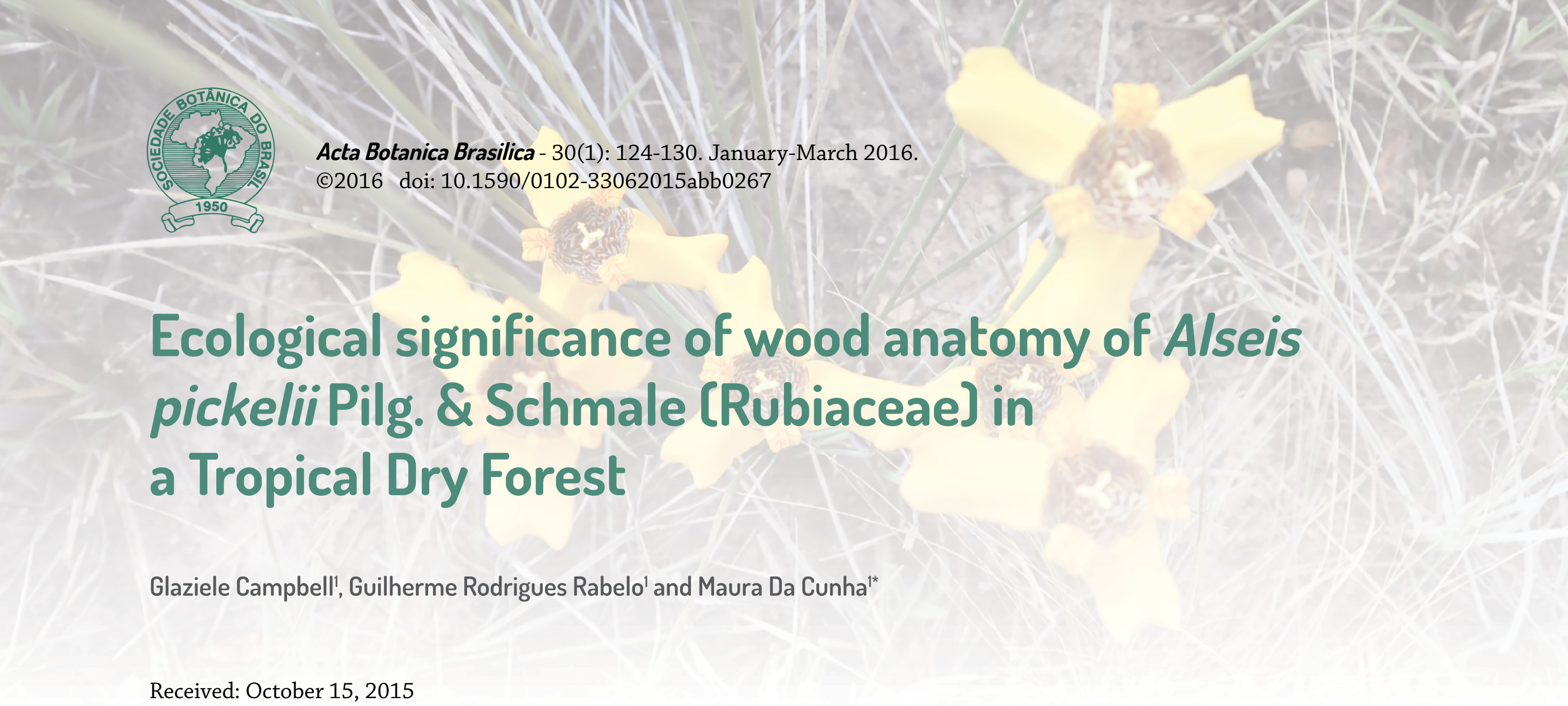

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Ecological significance of wood anatomy of *Alseis pickelii* Pilg. & Schmale (Rubiaceae) in a Tropical Dry Forest

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ABSTRACT

This work describes, analyzes and compares the wood anatomy of *Alseis pickelii* from two distinct sites in Tropical Dry Forest. One site is an exploited forest that was disturbed by deforestation whereas the other site is preserved and has not been logged since selective logging in the 1960's. For the evaluation of wood anatomy, plant material was processed following standard techniques for light microscopy and histochemical tests. The results indicated that *A. pickelii* did not vary qualitatively between the two sites. The histochemical tests indicated the presence of prismatic crystals and starch in radial parenchyma of samples from both sites. Some quantitative parameters differed significantly between the two sites including: vessel frequency; vessel length and lumina area; intervessel pits; diameter, lumina, length and wall thickness of fibres; and radial parenchyma width. In general, these quantitative parameters had higher values in the samples from the exploited site, suggesting an adjustment to the more severe drought conditions there. Quantitative anatomical differences in the samples from the two sites show the influence that environmental conditions can have on wood anatomy. The observed anatomical characteristics may also be useful for taxonomic and ecological studies of this species and genus.

Keywords: acclimation, Atlantic Forest, intraspecific variation, Rubiaceae, wood anatomy

Introduction

Throughout history, plants have developed anatomical strategies and adaptations for accomplishing certain functions in different environmental conditions. Thus, physiological processes can affect the structure of tissues and organs and so plant anatomy is essential to understand the processes of growth and water and nutrient transport in trees (Kramer & Kolowski 1960). Plant anatomy is also a valuable source of characters that distinguish species. Therefore, it is important to describe wood anatomy including its several constituent cells types and their function, organization and structural peculiarities. Moreover, comparative anatomy provides benefits to phylogenetic studies of ecological strategies, because it is possible to examine structural changes under different environmental pressures (Dickison 1975).

The Atlantic Forest is one of the most biodiverse biomes in the world. However, this biome has been fragmented and currently only 5% of its original area remains (Murray-Smith *et al*. 2009). As a result it has been classified among the top five biodiversity "hotspots" of the world in terms of conservation priority due to its high degree of plant species richness and endemism (Myers *et al*. 2000; Mittermeier *et al*. 2005; Eisenlohr *et al.* 2015).

Both legal and illegal logging of forests is a serious problem worldwide and one of main causes of tree fall gaps in Brazilian forests (Rondon Neto *et al*. 2000). Consequently these gaps induce the growth of secondary vegetation (Whitmore 1989) and promote qualitative changes

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in irradiance, humidity and temperature (Pinheiro *et al.* 2013). This forest fragmentation has been continuing over the years due to deforestation caused by the production of coal, farming and selective logging (Silva & Nascimento 2001; Villela *et al.* 2006).

Prior to being selectively cut, an Atlantic Forest canopy is comprised mostly of commercial valuable tree species (Silva & Nascimento 2001). As a consequence of one such disturbance at Guaxindiba Ecological Station (GES), Souza (2005) identified two distinct forest sites. The first, named the "unlogged stand" (US), has had no selective logging for the last 45 years and is without traces of selective logging or forest fires. The second, named the "logged stand" (LS), suffered selective logging and consequently the composition and structure of vegetation has been modified (Nascimento & Souza 2003; Souza 2005).

Among the trees naturally occurring in the Atlantic Forest many belong to the family Rubiaceae and one species in particular, *Alseis pickelii* is the subject of this study. Worldwide Rubiaceae contains about 13,673 species placed in 609 genera (The Plant List 2013), and 1,401 species in 125 genera in Brazil (Barbosa *et al.* 2013). The family contains plants of diverse habit and is particularly diverse in the Atlantic Forest (Bittencourt & Braz 2002; Struwe 2002). The genus *Alseis* belongs to the tribe Calycophylleae (Cinchonoideae), is distributed throughout the Neotropics, and contains 16 species of trees and shrubs, nine of which occur in Brazil (Bittencourt & Braz 2002; Mendonza *et al.* 2004).

Alseis pickelii is a late successional species and composes the understory (12 to 20 m) of the forest at the Guaxindiba Ecological Station (GES) (Silva & Nascimento 2001). A study of the effects of selective logging on the anatomical characteristics of sun and shade leaves of *A. pickelii* found that the "unlogged stand" produce trees with typical leaves of "sun" and "shade", but, in contrast, the "logged stand" produced trees with less variation among types of leaves (Rabelo *et al.* 2012).

Following this reasoning, one may expect that the anatomical characteristics of wood may be experiencing different modifications in function due to the different pressures exerted by the environment in these two sites at GES. Therefore, the present study aims to characterize the wood anatomy of *A. pickelii* in two these sites of forest at GES in order to determine the qualitative and quantitative characteristics of the constituent cells, and how they are related to strategies developed by this species in this ecosystem.

Materials and Methods

Study area

The GES is located in the São Francisco do Itabapoana district (21°24'S, 41°04'W) of northern Rio de Janeiro, Brazil. This area is the largest fragment of lowland forest on tertiary formations and encompasses 3260 hectares (Villela *et al.* 2006) with elevations ranging from 20 m to 200 m. Its low elevation distinguishes this forest as a lowland forest that differs from the Atlantic Forest in other regions along the Brazilian coast. The forest is classified as seasonal, semi-deciduous lowland forest, also known as *tabuleiro* forest because of its phytogeographic features (Rizzini 1979; RadamBrasil 1983; Veloso *et al.* 1991). Globally, however, it is known as Tropical Dry Forest (Quesada *et al.* 2009) with anthropic disturbance due to deforestation. The climate of the area is classified as Aw according to Alvares (2014) and is seasonal, being warm and moist during the rainy season in the summer, and with a dry season in the winter. The mean annual rainfall is ca. 1000 mm, and the mean temperature is 23°C (Villela *et al.* 2006).

The study took place in the same two sites studied by Rabelo *et al.* (2012) at GES, the "unlogged stand" (US) and "logged stand" (LS). These sites differ in irradiation, humidity and temperature, with LS having higher irradiation, and thus higher temperature and lower humidity than US.

Sampling, measurements and statistical analyses

For the present study, trees of *A. pickelii* Pilg. & Schmale were selected that were cylindrical, straight, without bifurcation or apparent defects, and with a DBH between 15 to 30 cm. Wood samples were collected from five individual trees of each site (US and LS) in a non-destructive manner using an increment borer at about 1.30 m above the soil. Wood samples were made and sectioned using a sliding microtome (SM2010 R, LEICA, Germany) in cross and longitudinal (radial and tangential) sections with an average thickness of 15 µm. The sectioned material was treated with sodium hypochlorite (50%), dehydrated in an ascending ethanol series and stained with Astra blue and hydro-alcoholic safranin (Johansen 1940). The sections were subsequently immersed in xylene and mounted on permanent slides with Entellan® (Burger & Richter 1991). For some measurements, like fibre and vessel length, fibre diameter, lumina and wall thickness, the sample body was macerated and dissociated by the Franklin method (Kraus & Arduin 1997), stained with safranin, and mounted on semi-permanent slides with an aqueous solution of glycerin. The descriptions, counts and cellular measurements follow the rules of the IAWA Committee (1989), and were made using the software Image-Pro Plus 4.0 for Windows after capturing images with a digital camera (PowerShot A640, CANON, USA) coupled to a light microscope (Axioplan, ZEISS, Germany). To test for the presence of starch, lignin, phenolics, lipids and crystals, microchemistry tests were performed on sections without previous treatment, and followed standard techniques of plant anatomy (Kraus & Arduin 1997). For study by scanning electron microscopy (SEM), samples were attached to aluminum stubs using double carbon sticky tape and sputtered with 20 nm gold (SCD 050, BAL-TEC, Germany) and observed using a ZEISS DSM 962 (Germany) scanning electron microscope. Sixteen quantitative parameters were used for the comparative analysis of individuals. The normality of the data was tested by the Shapiro-Wilk test (Shapiro & Wilk 1965) and descriptive statistics (averages and standard deviations) were calculated for each parameter for the two sites. Significant differences between averages of individuals in each of the two sites were determined using a T-test (Boneau 1960). All statistical tests were made with the software Statistica 7 (StatSoft 1993).

Results

The quantitative features of *A. pickelii* varied under the different microclimatic conditions between the forest sites at GES. Nine of the sixteen analyzed parameters differed significantly (T-test; Tab.1). *A. pickelii* in the LS site had higher values of frequency and length of vessel elements; intervessel pits; and diameter, lumina, length and wall thickness of fibre-tracheids. In contrast the vessel lumina area and ray width were higher in the US site. These results suggest that species change under the different environmental pressures, especially those related to the drought.

No differences in the qualitative characteristics were found between the two forest sites. The species is characterized bellow following the terminology of the IAWA Committee (1989). Figure 1 shows transversal (Fig. 1A), tangential (Fig. 1B) and radial sections (Fig. 1C) respectively, and representative examples of the characteristics of cellular elements (Fig. 1D-F).

Growth rings: boundaries distinct, including thick-walled and radially flattened latewood versus thin-walled early wood fibres (Fig. 1A).

Vessels: vessel frequency numerous, 102 vessels mm-2; diffuse vessels with long appendices in both extremities (Fig. 1D); solitary, in radial pattern with multiples of two to five elements or in clusters of four elements, outline rounded; simple perforation plates and lateral plates; intervessel pits alternate, minute and vestured (Fig. 1E); vessel-ray pits similar to intervessel pits; mean tangential diameter of 37 µm; mean length of 731 µm.

Fibres: fibre-tracheids with simple pits with chambers of over 3 µm; septate fibers present (Fig. 1B), with thin to thick walls; starch present (Fig. 1F); mean length of 1,415 µm.

Axial Parenchyma: absent or extremely rare.

Rays: mean 7 mm-1; multiseriate, width one to three cells or mean 38 µm; composed of body ray cells procumbent with mostly 2-4 rows of upright and/or square marginal cells; mean height 428 µm; presence of perforated ray cells and fusion rays (Fig. 1C). Prismatic crystals and starch are present in procumbent and square cells.

Table 1. Quantitative anatomical parameters of the wood of *Alseis pickelii* (Mean and Standard Deviation –SD) in both sites (US and LS) at Guaxindiba Ecological Station, city of São Francisco do Itabapoana, state Rio de Janeiro, Brazil.

Parameters	Stands	Mean ± SD
Vessels		
Frequency (vessels.mm^{-2})	US	93.92 ± 17.22
	LS	111.15 ± 18.44 *
Length (µm)	US	664.79 ± 137.75
	LS	753.97 ± 184.51 *
Diameter tangential (µm)	US	36.94 ± 5.65
	LS	36.6 ± 4.67
Vessel lumina area (µm^2)	US	1339.18 ± 394.56 *
	LS	1223.15 ± 353.64
Wall thickness (µm)	US	4.28 ± 1.12
	LS	4.02 ± 1.02
Intervessel pits (µm)	US	4.54 ± 0.58
	LS	5.22 ± 0.72 *
Vessel-ray pits (µm)	US	3.71 ± 0.53
	LS	3.87 ± 0.58
Fibres		
Diameter (µm)	US	22.59 ± 4.5
	LS	25.25 ± 4.24 *
Lumina (µm)	US	11.49 ± 3.28
	LS	13.4 ± 3.52 *
Length (µm)	US	1368.03 ± 313
	LS	1514.07 ± 253 *
Wall thickness (µm)	US	5.54 ± 1.26
	LS	5.93 ± 1.28 *
Pits (µm)	US	5.78 ± 1.62
	LS	5.71 ± 1.5
Radial parenchyma		
Frequency (rays.mm^{-1})	US	6.47 ± 1.7
	LS	6.9 ± 1.37
Length (µm)	US	433.05 ± 117.28
	LS	408.43 ± 116.57
Width (µm)	US	34.58 ± 7.4 *
	LS	32.41 ± 5.63

Notes: * Statistically different parameters (T-test $p < 0.05$).

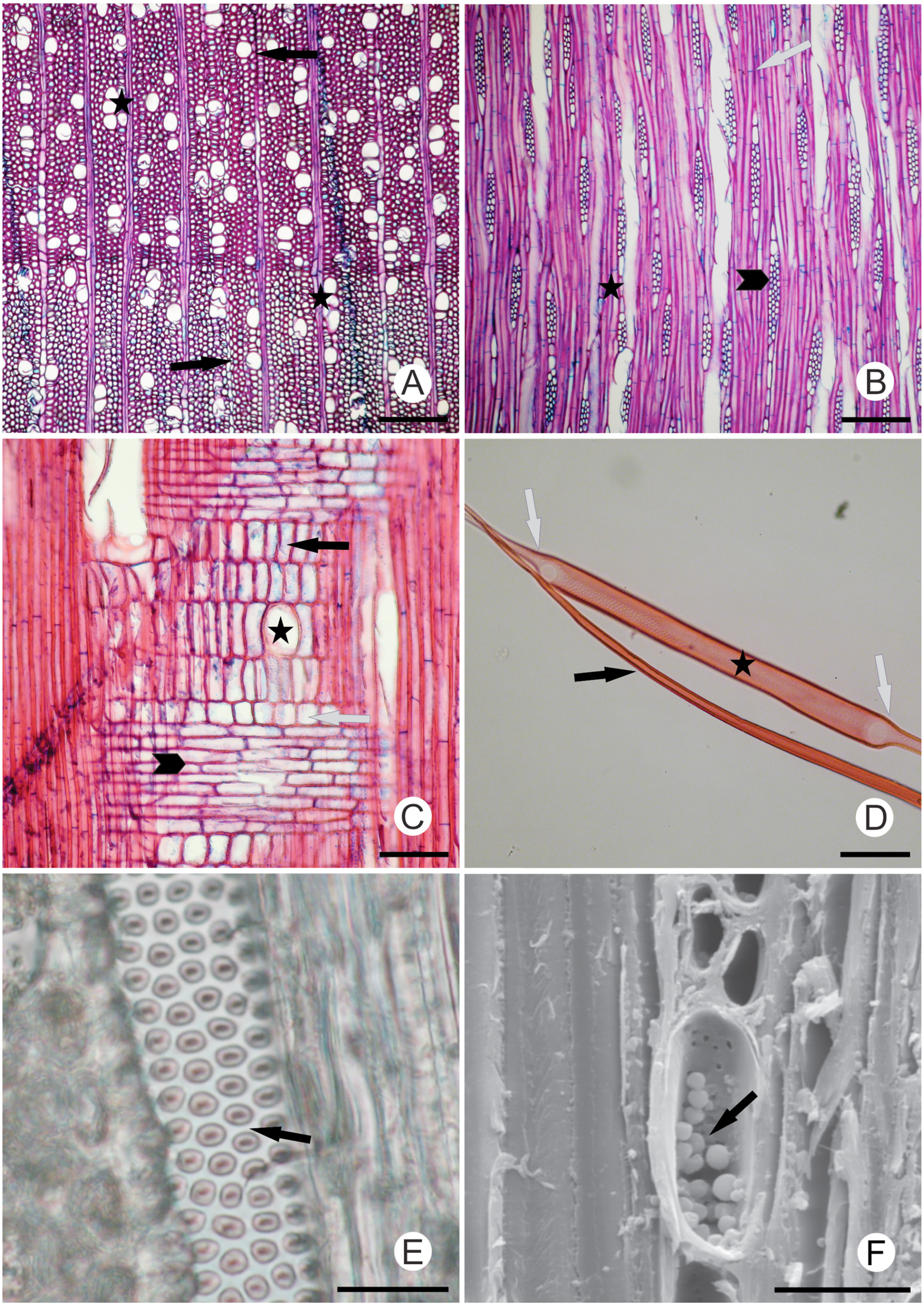

Figure 1. Wood anatomy of *Alseis pickelii* at Guaxindiba Ecological Station, city of São Francisco do Itabapoana, state Rio de Janeiro, Brazil. **A-E.** Light microscopy. **A.** Cross section, growth rings distinct, vessels with solitary (black arrow) and clustered (star) diffuse pores. **B.** tangential longitudinal section, radial parenchyma multiseriate (arrow head), and septate fibre-tracheids (gray arrow) and fusion rays (star). **C.** radial longitudinal section, rays composed of procumbent cells (arrowhead), square cells (gray arrow), upright cells (black arrow), and perforated ray cells (star). **D.** Macerated sample showing fiber-tracheids (black arrow) and a vessel (star) with simple perforation and appendices (gray arrow). **E.** Intervessel pits alternate, minute and vestured (black arrow). **F.** Scanning electron microscopy. The presence of starch in ray cells (black arrow). Scale bars: A and B: 200 µm, C and D: 100 µm; E and F: 20 µm.

Discussion

Wood growth is associated with seasonal variation, which results in the formation of growth rings that are visible due to specific anatomical features (Dickison 2000). Other anatomical features that result from seasonal variation are vessel diameter, length, and frequency (Carlquist 1977), all of which are features that help plants deal with excessive water stress in dry environments (Markesteijn *et al*. 2011; Scholz *et al*. 2014). In the tropics, periods of the drought and rain may produce differential growth, particularly in regions of marked seasonality (Costa *et al*. 2006). This annual dry season, with lower monthly rainfall, may lead to the formation of annual rings in tropical trees (Worbes 1995). The marked seasonality at GES (Silva & Nascimento 2001; Villela *et al*. 2006), likely explains the presence of distinct growth rings in *A. pickelii* growing there.

The simple perforation plates on the side walls of the vessel elements and perforated ray cells found in the wood of *A. Pickelii* have been described for the families Combretaceae, Euphorbiaceae, Monimiaceae and Rubiaceae (Costa *et al*. 2006). The presence of these features in *A. pickelii* suggests that they assist in long and short transport, respectively. The vestured pits serve an important role in the prevention of cavitation and in improving vessel performance by helping to repair embolisms (Dickison 2000; Jansen *et al*. 2003; Sperry 2003; Costa *et al*. 2006); they are also a useful taxonomic character for many botanical groups (Wheeler *et al*. 1989; Carlquist 2001).

According to Carlquist (2001), the most common significance of the absence or sparseness of axial parenchyma is the presence of septate fibres, which thereby functionally substitute for the axial parenchyma, i.e. as a storage system. Starch deposits, such as those observed in radial parenchyma and in the fiber-tracheids of *A. pickelii,* serve as a survival strategy for plants that inhabit environments with defined seasonality and species that undergo periods of stress, especially at the end of the growing season (Scatena & Scremin-Dias 2006). The presence of crystals is an important taxonomic character in Rubiaceae (Jansen *et al*. 2001; 2002; Costa *et al*. 2006), and are found in the genera *Simira* (Callado & Silva Neto 2003), *Bathysa* (Barros *et al*. 2008) and *Psychotria* (Barros & Callado 1997; Marques *et al*. 2015). Prismatic and sand crystals were present in the wood of *A. pickelli*, as well as in the colleters (Tullii *et al*. 2013).

Quantitative changes in the anatomical structure of the wood of *A. pickelii* were due to variation in environmental conditions in both sites. According to Baas (1973), environmental factors influence the structure of secondary xylem. Thus, anatomical characteristics can influence the functional performance of xylem in various environmental conditions and under different ecological trends (Carlquist 2001). The variation found in the wood of *A. pickelii* may explain the fitness of this species to its environment, where wood plasticity counterbalances the lower leaf plasticity found for this late successional tree in this area (Rabelo *et al*. 2012). Other examples of fitness counterbalance by wood/leaf plasticity were the vessel lumina area and frequency that were higher in US, possibly allowing greater hydraulic conductance and, consequently, promoting a better water supply to the leaves, confirming that the leaf and wood plasticity can be related (e.g. Santiago *et al*. 2004; Jennifer *et al*. 2009, Markesteijn *et al*. 2011, Fu *et al*. 2012; Scholz *et al*. 2014).

Studies of intraspecific variation show that quantitative changes of fiber and vessel elements are related to environmental conditions, because they provide security and efficiency in the transport of water and solutes (Dickison 2000; Carlquist 2001; Ribeiro & Barros 2006). Individuals of *A. pickelii* of LS had narrower and more common vessel elements, and fibre-tracheids with thicker walls, greater diameters and larger lumina. Narrow, but numerous, vessel elements with a simple perforation plate evolved in dry conditions with low humidity in the atmosphere and soil (Dickison 2000), such as the conditions observed for *A. pickelii* at GES. However, larger vessel elements are more efficient in conducting water, although they provide less hydraulic safety (Bosio *et al*. 2010). This fact was noted for individuals of *A. pickelii* that were exposed to less radiation and more humidity, as were the conditions of US (i.e. where individuals had larger, but less frequent, vessel elements). The relationship between the frequency of vessel elements and their size, and the size of lumina of fibres is a structural adjustment related to the requirements for water by plants (Novaes *et al*. 2010). Thus, wide vessel elements can carry a greater volume of water, but are more prone to embolism (Sperry *et al*. 1994).

However, vessel frequency may balance water transport efficiency (Baas *et al*. 1983; Metcalfe 1983; Carlquist 2001). Thus, the density of vessels also affects hydraulic conductivity and vulnerability to embolism (Martinez *et al*. 2012). Individuals of *A. pickelii* in LS had more frequent, and narrower, vessel elements, which may be from the greater radiation, the higher temperatures and the lower humidity there.

The qualitative characteristics of wood usually do not vary among individuals in different environmental conditions (Noshiro & Suzuki 1995; Ribeiro & Barros 2006). Therefore, the findings of the present study are in agreement with those found in the literature for various species of Rubiaceae and of the genus *Alseis*. The quantitative results, on the other hand, demonstrated that the anatomical structure of the wood of *A. pickelii* is indeed influenced by environmental conditions, suggesting a better fit of individuals to conditions of high radiation and low humidity. For this reason, *A. pickelii* is well adapted to the semi-deciduous environment and exhibited differences between individuals from the two different sites. These results provide a basis for other studies on interspecific and intraspecific variation of woody species, acclimation mechanisms, and survival in the Atlantic Forest.

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