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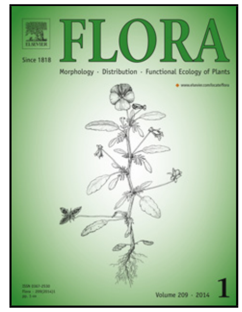

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Intraspecific variation of *Paubrasilia echinata* (Fabaceae) wood along a latitudinal gradient in Brazil

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Highlights

- *Paubrasilia echinata* morphotypes present variation in wood anatomy according to a latitudinal range.
- Specimens from higher latitudes show higher axial parenchyma percentage and larger vesses.
- Café and Laranja morphotypes share more wood anatomical traits.
- The wood anatomy do not corroborate previous molecular studies of *P. echinata*.
- The wood anatomy do not support the categorization into subspecies or variety.

Abstract

Molecular and taxonomy approach have been made to understand the differences among the three morphotypes of *Paubrasilia echinata*, termed laranja, café and arruda. However, there is no wood anatomic study considering these morphotypes and their probable anatomical similarity. Considering as an endangered species with historical relevancy, it is crucial to recognize its wood anatomy to its conservation. This study aims to investigate the wood anatomy of *P. echinata* collected along its occurrence area (between 5º53'S 34º04'W and 22º56'S 42º30'W) and to examine the anatomical relationship among arruda, laranja and café morphotypes that was previously reported by molecular studies. The results indicate that the wood anatomy varied along its range of distribution a gradient of axial parenchyma and vessel features between the lower and higher latitudes was observed. Since arruda occurs in the collection sites of all four states studied, while café and laranja only in Bahia, the three morphotypes can be identified into of two groups based on wood anatomy: one formed by arruda samples and another by café and laranja, which differs from the previous molecular analysis. Combinations between higher percentage of axial parenchyma and wider vessels were observed in samples from RJ guarantying conductance and safety, while samples from RN and PB have smaller solitary vessels and scanty axial parenchyma, which could prevent embolisms. The present results do not support the categorization into subspecies or varieties. The findings also suggest that café and laranja share similar features than with arruda morphotype.

Keywords*:* Atlantic Forest, axial parenchyma, comparative wood anatomy, vessels, xylem

Introduction

Paubrasilia L. was recently recognized as a phylogenetically isolated genus, constituting a new monospecific genus in Caesalpinioideae, Fabaceae (Gagnon et al., 2016). The genus has only one species, *Paubrasilia echinata* (Lam.) E. Gagnon, H.C. Lima & G. P. Lewis, a tree species popularly known as Brazilwood, with a very hard and dense wood, varying in colour from orange-chestnut to blackish red (Cunha and Lima, 1992; Lewis, 1998). *P. echinata* grows in semideciduous dry seasonal forest and in the sandy marine soil of Brazil's Atlantic coast (Cardoso et al., 1998; Bueno and Lima, 2002). It has an exceptionally large distribution between Rio Grande do Norte (5º S - 35ºW) and Rio de Janeiro (22ºS - 42ºW) (Fig. 1) (Cunha and Lima, 1992; Lewis, 1998; Bueno and Lima, 2002). Its pattern of distribution was originally fragmented because of cyclical climate changes during the Quaternary, expanding Brazilwood populations during dry and cold periods. With the prevailing hot and humid climate, the specimens were restricted to a few forests fragments with similar conditions to those of the expanding periods, which are near to densely populated urban areas of Brazil (Bigarella and Andrade-Lima, 1982; Lima et al., 2002).

Up to the 19th century, *P. echinata* wood was exploited to produce dyes and afterwards for the manufacture of high quality bows for stringed instruments (Bueno, 2002). An estimated 200 m^3 of Brazilwood is used annually for this purpose (CITES, 2007). Because its history of wood exploitation, the tree is included as an endangered species (CITES 2007, Varty, 1998, Martinelli and Moraes, 2013, MMA 2014). Its harvest from natural forests is prohibited, and its legal commercial use has been restricted since 2007 (CITES 2007).

Although only one species is recognized, Brazilwood populations along its general distribution present marked genetical (Cardoso et al. 1998; Lira et al. 2003) and morphological (Lewis 1998; Lima et al. 2002) differences, enabling the distinction of three morphotypes by the variants in leaflet size and shape and wood colour. The first morphotype, termed arruda, occupies the widest range between Rio Grande do Norte and Rio de Janeiro (between 5º S - 35ºW and 22ºS - 42ºW). It presents smaller, but numerous, pinnas and leaflets (5-10 pinnas and 12-21 leaflets, approximately 4 centimetrers), and the wood has an orange-chestnut colour. The second morphotype, termed café, occurs in Espírito Santo and Bahia (between 14ºS - 39ºW and 19ºS - 40ºW) and has larger, but less numerous, pinnas and leaflets (3-5 pinnas and 3-8 leaflets, approximately 7 cm), with reddish orange heartwood. The third variant, termed laranja, has large leaflets approximately 12 cm long and blackish red wood and is known from the south of Bahia (between 15ºS - 35ºW and 39ºS - 52ºW) (Cunha and Lima, 1992; Lewis, 1998; Lima et al., 2002). The three variants can occur in allopatric and sympatric populations, and they co-occur in natural populations in Bahia State (Juchum et al., 2008). The same authors also suggested that the morphotypes arruda and café are genetically similar, but laranja could be considered a distinct taxon (Juchum et al. 2008).Others studies observed that the variation resulting from geographical localization of *P. echinata* is greater than within-populations, reflecting a low gene flow among the regions (Cardoso et al., 1998; Lira et al., 2003). Gagnon et al. (2016) highlights that more efforts are needed to comprehend if these morphotypes worthy a taxonomic recognition.

Variability in secondary xylem structure in species of wide distribution is common among tree species (Liu and Noshiro, 2003), but the results are conflicting (Aguilar-Rodríguez et al., 2006). This variability could occur in response to different genetic and biochemical factors (Savidge, 1996; Ye, 2002), likewise to abiotic parameters (Mota et al. 2017; Begum et al., 2017; Nabais et al., 2018). Some studies evaluated the correlations between secondary xylem structure with climatic and abiotic parameters, such as altitude, latitude, temperature, rainfall and soil, showing that wood characters can be related to some of these parameters (e.g., van den Oever et al., 1981; Baas and Carlquist, 1985; Baas and Schweingruber, 1987; Noshiro et al., 1994; Noshiro and Suzuki, 1995; Alves and Angyalossy-Alfonso, 2000; Marcati et al., 2001; Alves and Angyalossy-Alfonso, 2002; Luchi 2004; Lens et al., 2004; Ribeiro and Barros, 2006; Aguilar-Rodrigues et al., 2006; Barros et al., 2006; Terrazas et al., 2008; Bosio et al., 2010; Heklau and von Wehrden, 2011; Zheng and Cabrera 2013). On the other hand, no significant ecological trends in wood structure at species level was reported(e.g., Sastrapradja and Lamoureux, 1969; van der Graaff and Baas, 1974; Noshiro and Baas, 2000; Liu and Noshiro, 2003).

Despite the wood anatomy of Brazilwood has been studied by several authors and differences in wood anatomy has been reported (e.g., Mainieri, 1960; Angyalossy et al., 2005; Amano, 2007; Alves et al., 2008; Gasson et al., 2009), no previous study comparing the three morphotypes based on samples collected throughout its geographic distribution was made. Therefore, the present paper compared the wood anatomy of the three morphotypes and investigated if it is possible distinguish them by wood anatomy and pointed out its importance for the taxonomic studies of this widely distributed Brazilian tree species.

Materials and methods

2.1. Sampling sites and sample preparation

An intensive survey was conducted throughout most of the study area (15 municipalities of four different states) to collect *P. echinata*. A total of 33 wood samples resulted from this fieldwork (Table 1) and are held at the Herbarium of Rio de Janeiro (RBw).The climate diagrams of the different sites were obtained using DIVA-GIS software (Fig. 1).

The height of the collected trees varied between 3 m to 15 m, with a mean of 9 m. A summary of the specimens and site collection is given in Table 1. As expected for a threatened tropical species, it was difficult to find samples in the field with the requirements for sampling, such as straight, unforked, and undamaged trunks with a diameter at breast height ≥ 10 cm.

The arruda samples from Rio Grande Norte (RN), Paraíba (PB) and Rio de Janeiro (RJ) were collected from semideciduous dry seasonal forest remnants, while those from Bahia (BA) were sampled in a range of successional stages: semideciduous dry forest, cabruca (a remnant forest used to plant cocoa), capoeira (disturbed remnant forest, in early successional stages) and pasture. In the Southern Bahia the cocoa (*Theobroma cacao* L.) plantations was established under the Atlantic Forest after thinning, in a system called cabruca.

After the collection, the wood sections were prepared in three planes (Transverse Section-TS, Radial Longitudinal Section-RLS and Tangential Longitudinal Section-TLS), and their thickness ranged from 15 to 20 µm. All samples were bleached, stained with safranin and astra blue (Bukatsch, 1972), dehydrated (Johansen, 1940; Sass, 1958) and mounted in synthetic resin. Macerations were prepared with Franklin's solution (Jane, 1956). The dissociated cell elements were stained with aqueous safranin 1% and mounted on semi-permanent slides with glycerine 50% (Strasburger, 1924). The descriptions, measurements and images were obtained with an Olympus BX50 light microscope with a digital image processing system (Image Pro Plus, version 3.0 for Windows) fitted with a video camera (Media Cybernetics CoolSNAP-Pro). The terminology followed the “IAWA List of Microscopic Features for Hardwood Identification” (IAWA Hardwood Committee 1989).

1.2.Data analysis

Thirty-four qualitative and quantitative anatomical features and climatic parameters were submitted to multivariate statistical analysis to determine the significant difference between morphotypes for each character measured. The site collection and the anatomical characters screened are summarized in Table 1. For normally distributed and homoscedastic variables, *t*-test (between two groups) or One-way ANOVA (between more than two groups) were performed. Principal component analysis (PCA) was used to establish the correlation between wood anatomical features and climatic parameters. All statistical analyses were performed using the STATISTICA 7 (StatSoft, Inc., USA).

Results

3.1. General description of wood anatomy of P. echinata

Growth ring boundaries are distinct, marked by marginal parenchyma, as well as thick-walled and flattened latewood fibres, but also with combinations of locally distended rays. Wood is diffuse-porous, vessels arranged solitary or in radial multiples of two to six vessels, some in tangential bands; circular to oval outline. Tangential diameter of vessels varied between 32 µm and 174 µm. Perforation plates are simple. Interverssel pits are minute or small (*ca*.4.2 µm), varying among the regions, alternate and rounded; vessel-ray pits and vessel-parenchyma pits are similar to the intervessel pits in shape and size. Ground tissue is composed of libriform fibres. Axial paratracheal parenchyma is mainly vasicentric, unilateral and lozange-aliform. The axial parenchyma is more abundant in samples from higher latitudes, with short confluences in BA, but tending to form bands in RJ and scanty in samples from lower latitudes (RN and PB) having a higher temperature and rainfall. Prismatic crystals in long chains are present in axial and radial parenchyma. Storied and irregularly storied rays are observed. Rays are homogeneous with 6-12/mm and 1-3 cells wide.

1.3.Comparisons among the morphotypes along their latitudinal range (Fig. 2 & 3)

In this analysis, both qualitative and quantitative differences were observed among samples, and both type/percentage of axial parenchyma and tangential vessel diameter were the main features influencing the characterization of morphotypes. ANOVA and PCA revealed that axial parenchyma percentage and tangential vessel diameter were the most varied among samples. Since arruda occurs in the collection sites of all four states, while café and laranja only in BA, analysis of wood anatomy of the three morphotypes resulted in the classification of two groups: one formed by arruda samples and another by café and laranja (Fig. 2). The formation of these two groups was based on PCA of 24 parameters that explain 48% of the total variation by two factors (Fig. 2A). Specifically, PC1 explained 29.37% of the variation, with scanty axial parenchyma and short confluences, axial parenchyma percentage, latitude, temperature and rainfall having loadings greater than 0.70. In PC2 (18.66 %), the highest loading was tangential vessel diameter (between 50 and 100 µm or greater than 100 µm). The ANOVA results for axial parenchyma percentage and tangential vessel diameter are presented in Fig. 2B and 2C, respectively. A summary of PCA and ANOVA results are given in Supplementary File I and II, respectively.

Arruda from RN (Fig. 3A) and PB (Fig. 3C) had axial parenchyma scanty and the lowest average percentage of axial parenchyma (11% and 12%, respectively), while arruda from BA (Fig.3E and F) had axial parenchyma with short confluences, and arruda samples from RJ (Fig. 3G) had confluences tending to form bands, constituting 23% of the tissue. Laranja (Fig. 3B) and café (Fig. 3D) had neither scanty parenchyma nor confluences tending to form bands. Nevertheless, the samples from BA (arruda, café and laranja) shared characteristics with arruda from RJ and with RN and PB, presenting axial parenchyma with short confluences (20% of the tissue).

As the percentage of axial parenchyma diminishes, fibre percentage increases. The highest mean percentage of fibre (53%) was found in arruda samples from RN, which also had the lowest mean percentage of radial parenchyma (15%). Table 1 summarizes the quantitative features of all sites.

Café and laranja morphotypes did have the lowest means of tangential vessel diameter. Two laranja samples from capoeira were segregated by presenting only small pits and having higher tangential vessel diameter than the café and the other two laranja samples. The arruda samples from RJ at the lower temperature and rainfall presented the highest mean of vessel diameter, 88 µm, and mean of estimated vessel area of 5.288 μm^2. In contrast, the arruda samples from RN and PB, with higher temperatures and rainfall, presented the lowest means of vessel diameter at 73 µm and vessel area at 4.222 µm, and 72 µm and 4.243 µm, respectively. The lowest average of vessel frequency was in RJ (26/mm^2), and the highest in RN (39/mm^2). The average vessel element length varied from 219 µm in RJ to 368 µm in BA. Most specimens presented small intervessel pits.

Discussion

P. echinata grows in environments characterized by dry climate and sandy soil of the Brazilian coastal zone. Wood features can be a sensitive variable for climate and for site conditions as observed by Heklau and von Wehrden (2011) studying *K. ceratoides*. They found widest vessels under a semi-humid climate (European provenances) and the narrowest ones in the arid-temperate climate of Central Asia towards to a safe strategy. It was reported that species with wider vessels are found in wet and warm sites (Baas, 1973; Carlquist, 2001). However, the different sites sampled here vary in relation to mean annual precipitation and temperature, and these differences can be related to anatomical features, such as tangential vessel diameter that was larger in RJ and smaller in RN, as well as vessel frequency that was lower in RJ and higher in RN. The southern sites, of the present study, are drier with lower temperature and rainfall. As a result, the specimens presented features more related to efficiency in conductance than to safety, such as larger vessels and low frequency, contrasting the literature cited above (Baas, 1973; Carlquist, 2001).

The arruda morphotype occurring from Rio Grande do Norte to Rio de Janeiro can be identified by such morphological characters as small, but numerous, pinnae and leaflets (5-10 pinnae and 12-21 leaflets, approximately 4 cm) and orange-chestnut wood colour. Species of wide distribution usually present differences in the cell length, diameter, wall thickness and frequency of elements across their latitudinal distributions (Liu and Noshiro, 2003). Based on the qualitative and quantitative analyses of wood anatomy correlated with climatic factors, it was possible identify the specimens of arruda by geographical regions.

Specimens from the drier sites of RJ presented axial parenchyma confluent tending to form bands. Axial parenchyma percentage was higher in RJ and lower in Paraíba (PB) and RN. Samples from BA presented axial parenchyma with short confluences, showing some gradation between those from southern and northern regions, since samples from the northeast presented scanty parenchyma. Higher percentage of axial parenchyma associated with wider vessels (samples from RJ) could be related to the parenchyma function of long-distance water transport (Morris et al., 2018).

Carlquist (2018) pointed out that “the distribution of axial parenchyma in angiosperms supports the idea that conduction in vessels is supported or maintained by the action of adjacent axial parenchyma cells”. Both, axial parenchyma and the vessel, are not isolated but operate together. Parenchyma cells are important for exchange between apoplast and symplast in wood tissue, including carbohydrate storage, defense against pathogens and transport (Spicer and Holbrook, 2007), structural support of turgor, water storage, as auxiliary cells in latewood (Carlquist 2018). Morris et al. (2018) also showed the dependence on axial parenchyma for hydraulic maintenance in some tropical families, such as Fabaceae, and that water transport is controlled by living cells. Then, samples from RJ have wood features related to higher conductance (wider vessels) and to safety (vessels associated with paratracheal axial parenchyma).

Studying *Ilex*, Baas (1973) observed a tendency toward more abundant axial parenchyma at lower latitudes, but Aguilar-Rodríguez et al. (2006) did not observe such variation in *Buddleja cordata*. Alves and Angyalossy-Alfonso (2002) showed that the abundance of axial parenchyma in trees from Brazilian semideciduous forest tend to occur in warmer climates, this observation differs from those reported, since samples from the warmer regions exhibited scanty axial parenchyma.

Calrquist (2012) showed that shorter vessels are common in dry environments, representing a conductive compromise. Luchi (2004) also found a correlation between low vessel frequency and dry sites in *Croton urucurana*, such as that observed here. In higher latitudes, Chalk (1983) mentioned that the size of the cells decreases, while the wall thickness increases, improving xylem resistance. In *Buddleja cordata*, the vessel frequency increased with the increase of annual temperature range and the maximum temperature of the warmest period, and the decrease in rainfall (Aguilar-Rodríguez et al., 2006). In the present analysis, samples from Rio de Janeiro (RJ) (latitude 22º), which has the lowest mean precipitation, are similar to those observed in the *B. cordata* study, possess shorter vessels and the lowest mean of vessel frequency.

Barretta-Kuipers (1981) also described axial parenchyma as a relevant taxonomic feature for the genus "*Caesalpinia*" where it was shown that banded parenchyma occurs in many species. These axial parenchyma and tangential vessel diameter also had some taxonomic value in the tribe Sophoreae, albeit related to the habitat (Gasson, 1994). The axial parenchyma types were also an important feature to separate seven *Tachigali* (Caesalpinioideae) species into two groups occurring in Brazil (Macedo et al., 2014). Heklau and von Wehrden (2011) revealed that wood variables could be rather sensitive to climate and site conditions. The differences observed among arruda samples corroborate these and previously reported data from molecular analyses, which suggest that differences between regions were greater than within-populations (Cardoso et al., 1998; Lira et al., 2003), confirming the variety among populations from different states of Brazil. Cardoso et al. (1998) analyzed five arruda populations from RJ, Espírito Santo (ES) and BA and found that samples from RJ were distinct from the other two states. In addition, Lira et al. (2003) studied populations from RJ, ES, BA, PB and RN, and found relationships between populations of RN and PB similar to those observed here based on wood anatomy.

Café samples had the lowest mean of fibre percentage and only minute intervessel pits, which was the significant feature in the statistical analysis. In addition, laranja samples from semi-deciduous dry forest and capoeira differ by the tangential vessel diameter, vessel wall thickness and intervessel pit size. The quantitative features were important to characterized the three morphotype samples, but they do not allow us to clearly distinguish the morphotypes.

Our analysis indicates that café and laranja morphotypes share similar features than either alone shares with arruda. The present results did not corroborate the molecular analyses previously conducted for the arruda, café and laranja morphotypes from Bahia (Juchum et al. 2008). These authors investigated the relationships among the three morphotypes occurring in eight municipalities of southern BA, and some were from the same sites as our samples (Potiraguá and Porto Seguro). They found a clear molecular divergence between laranja and the café-arruda group, and such differentiation suggests an additional taxon. Café and arruda are more closely related to each other, and laranja should be recognized as a distinct taxon by genetics analysis (Juchum et al. 2008). However, in the present paper, we observe a closer relationship between café and laranja.

Conclusions

The anatomical features indicate a similarity between café and laranja morphotypes in contrast to the leaf morphology and the molecular data. The arruda morphotype presents phenotypic variation along its range of distribution, such as type of axial parenchyma, tangential vessel diameter and percentage of axial parenchyma. Higher percentage of axial parenchyma associated with wider vessels in samples from RJ can guarantee higher conductance and safety, while the populations from RN and PB could prevent embolism having smaller solitary vessels and scanty axial parenchyma. The arruda wood anatomy variation is related to the variation of temperature and rainfall along the latitudinal gradient.

Declarations of interest

None.

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Figure 1. Distribution range of *Paubrasilia echinata* on the Atlantic Forest between Rio Grande do Norte (RN) (5º S - 35ºW) and Rio de Janeiro (RJ) (22ºS - 42ºW), the dots and numbers indicate the sites collections. Map and climates diagrams were compiled by DIVA-GIS software. Climatic diagrams for sites collection in the Atlantic Rain Forest, grey-square: temperature monthly maximum, black-square: temperature monthly minimum, white-rectangle: rainfall.

Figure 2. Statistical analysis of morphotypes. (A) Principal Components Analysis. Dark square: arruda from Rio Grande do Norte, black circle: arruda from Paraíba, asterisk: arruda from Bahia, dark grey circle: arruda from Rio de Janeiro, light grey circle: laranja, white circle: café. AP: axial parenchyma. AP: axial parenchyma, big circle: includes laranja and café samples. (B) General tendencies in the axial parenchyma percentage. (C) General tendencies in the tangential vessel diameter. The degrees of freedom and F and p values are provided for each graph.

Figure 3. Transverse sections (TS) of morphotypes. (A) Arruda from Rio Grande do Norte, (B) Laranja from Bahia, (C) Arruda from Paraíba, (D) Café from Bahia, (E) Arruda from Bahia, (F) Arruda from Bahia, (G) Arruda from Rio de Janeiro. Bars=100 µm. *arrow*: growth ring boundary, *asterisk*: axial parenchyma unilateral, *circle*: axial parenchyma vasicentric, *square*: axial parenchyma with short confluences, *triangle:* axial parenchyma lozenge-aliform, *stars*: axial parenchyma forming bands, *arrowhead*: vessels with higher diameter.

Figure 1

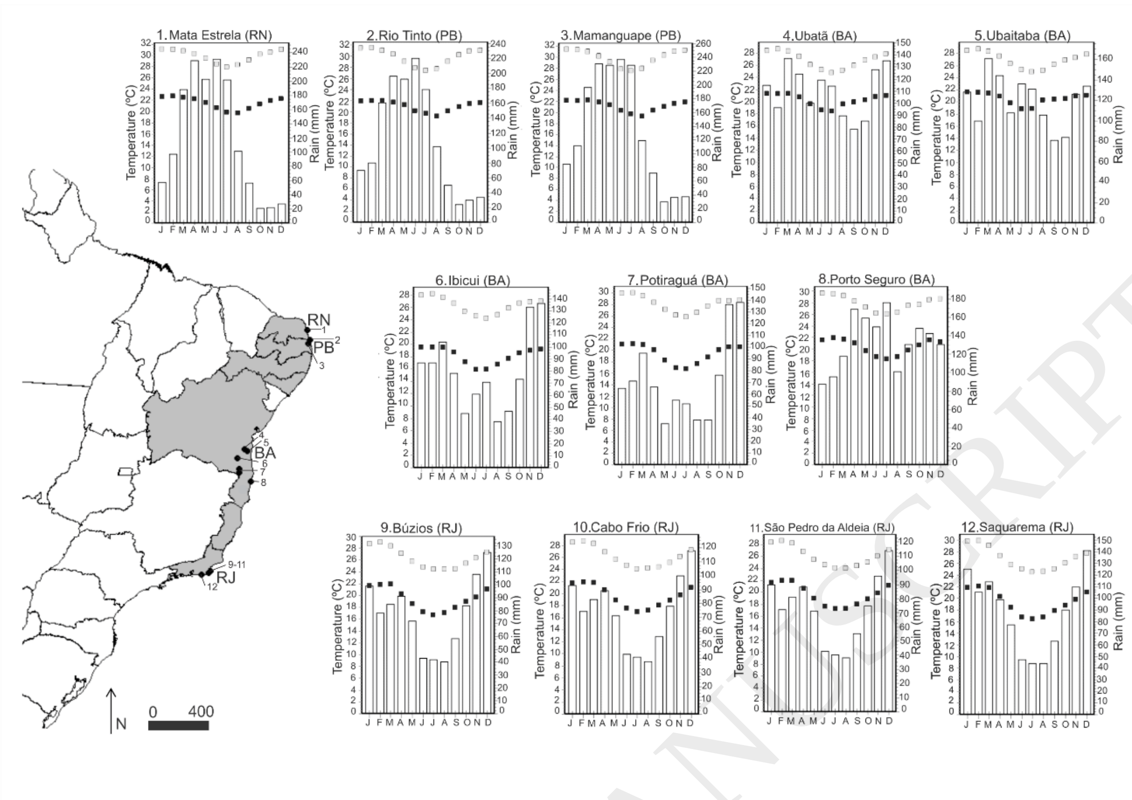

Figure 2

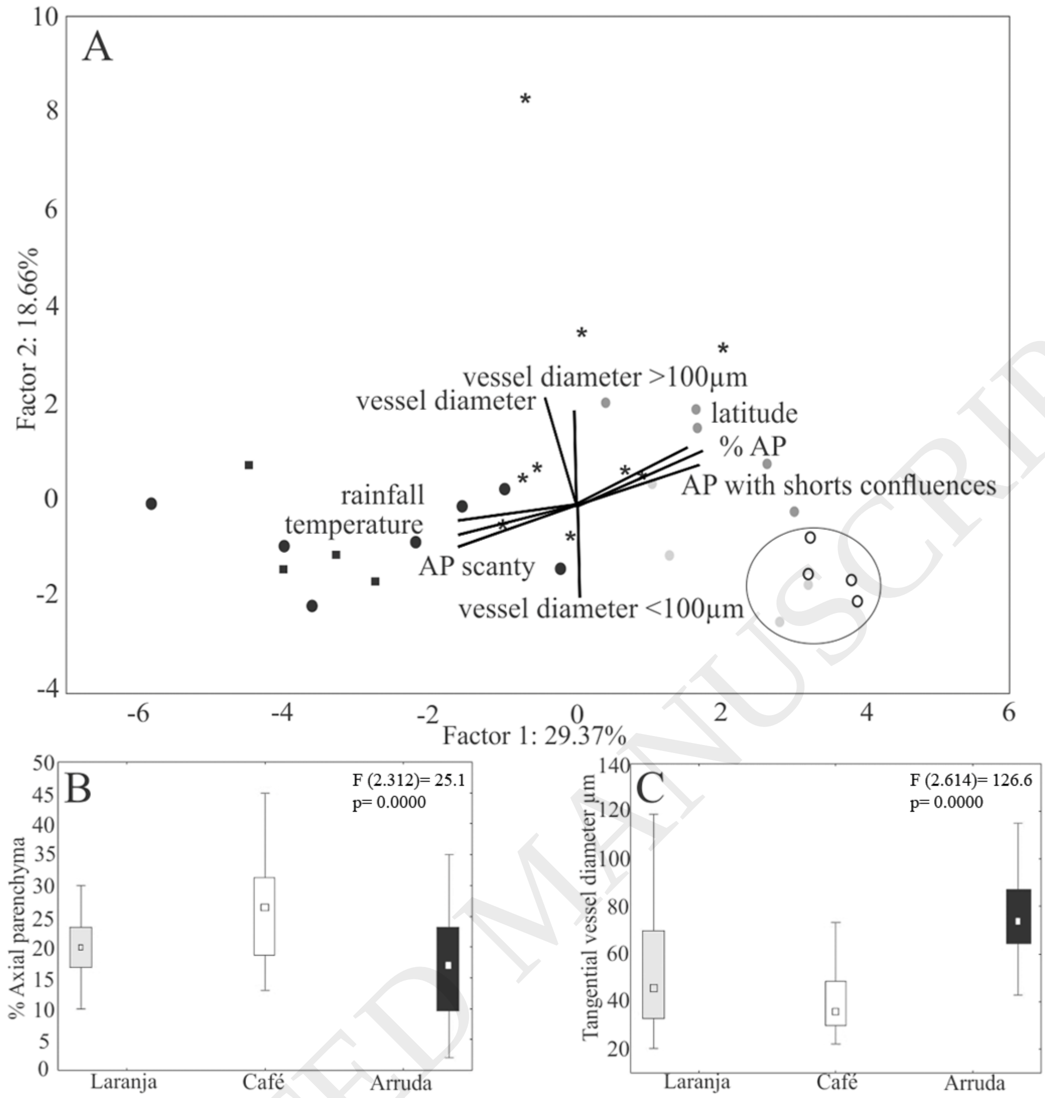
A
Factor 2: 18.66%
Factor 1: 29.37%
vessel diameter >100µm
vessel diameter
latitude
% AP
AP with shorts confluences
rainfall
temperature
AP scanty
vessel diameter <100µm
B
F (2.312)= 25.1
p= 0.0000
% Axial parenchyma
Laranja
Café
Arruda
C
F (2.614)= 126.6
p= 0.0000
Tangential vessel diameter µm
Laranja
Café
Arruda

Figure 3

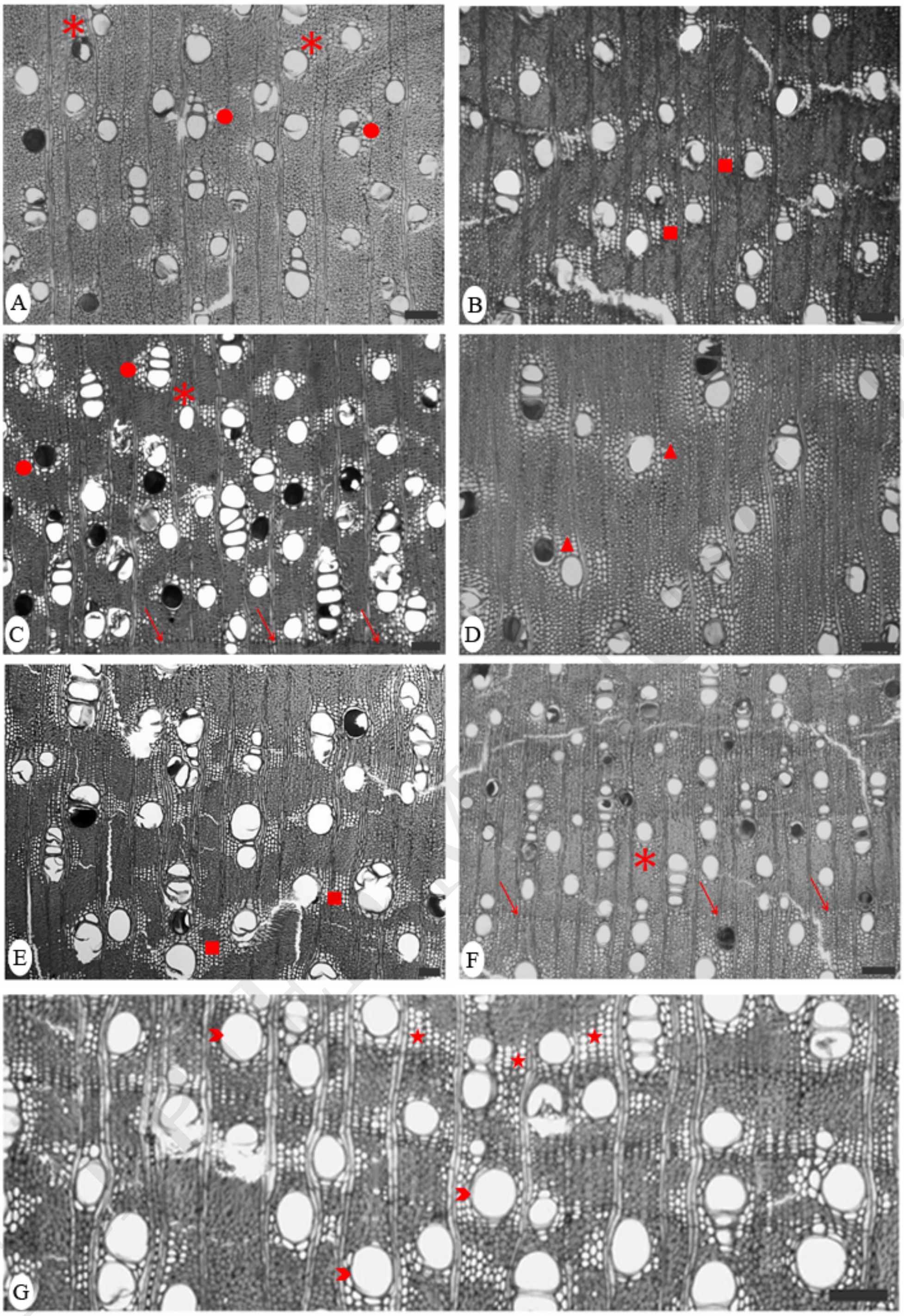
A
B
C
D
E
F
G

Table 1. Specimens, site collection and means of the wood characters analyzed. Brazilian regions: NE=Northeastern, SE=Southeastern. States: RN=Rio Grande do Norte, PB=Paraíba, BA=Bahia, RJ=Rio de Janeiro. Veg.= vegetation. Wood characters: VF= vessel frequency; VL=vessel length; VD=tangential vessel diameter; VW=vessel wall thickness; VA= vessel area; IP= mean intervessel pits; FL=fibre length; FW=fibre wall thickness; AP= axial parenchyma distribution: 1= scanty, 2= unilateral, 3= vasicentric, 4=lozange-aliform, 5= shorts confluences, 6= confluent tending to form bands, 7= marginal; RF= ray frequency; % V= percentage of vessels; % AP= percentage of axial parenchyma; % F= percentage of fibres; % R= percentage of rays.

Wood collection (RBw)	State/ Brazilian Region	Veg.	Morphotype	VF	VL (µm)	VD (µm)	VW (µm)	EA (µm)	IP (µm)	FL (µm)	FW (µm)	AP (µm)	RF	% V	% AP	% F	% R
7726	RN/NE	Forest	Arruda	36	293	67	4	4280	5	1003	5	1,2,3,7	12	20	10	55	15
7729	RN/NE	Forest	Arruda	24	318	81	6	3933	5	1137	6	1,2,3,4,7	9	14	11	58	17
7730	RN/NE	Forest	Arruda	40	304	72	3	3980	4	1009	4	1,2,3,4,7	9	21	12	54	14
7731	RN/NE	Forest	Arruda	55	338	72	3	4694	6	1040	5	1,2,3,4,7	9	29	13	46	12
7732	PB/NE	Forest	Arruda	29	285	69	5	4643	5	930	6	2,3,4,5,7	10	23	21	40	16
7733	PB/NE	Forest	Arruda	26	246	77	5	4281	4	901	6	2,3,4,5,7	11	20	13	47	19
7734	PB/NE	Forest	Arruda	32	255	77	5	4554	4	772	5	1,2,3,7	10	22	7	53	18

Table 1. Continued

Wood collection (RBw)	State/ Brazilian Region	Veg.	Morphotype	VF	VL (µm)	VD (µm)	VW (µm)	EA (µm)	IP (µm)	FL (µm)	FW (µm)	AP (µm)	RF	% V	% AP	% F	% R
7735	PB/NE	Forest	Arruda	56	355	69	5	4736	5	1215	6	1,2,3,7	7	34	6	47	13
7738	PB/NE	Forest	Arruda	36	253	68	5	4341	4	1049	5	2,3,4,5,7	7	22	14	49	15
7739	PB/NE	Forest	Arruda	31	269	67	5	3490	5	1123	5	2,3,4,7	10	19	13	54	15
7740	PB/NE	Forest	Arruda	35	302	77	6	3657	4	1050	6	1,2,3,7	9	26	7	53	15
8515	BA/NE	Cabruca	Arruda	28	234	98	4	4823	5	934	6	2,3,4,5,7	11	17	17	49	17
8522	BA/NE	Pasture	Arruda	63	253	52	4	2440	4	762	5	2,3,4,5,7	12	20	16	49	15
8524	BA/NE	Cabruca	Arruda	34	294	74	3	5579	4	1040	7	2,3,4,7	10	18	19	50	14
8546	BA/NE	Forest	Arruda	27	362	69	4	4857	6	1292	6	3,4,7	10	12	15	65	8
8548	BA/NE	Forest	Arruda	32	326	74	4	4526	5	689	5	2,3,4,5,7	11	15	20	48	16
8550	BA/NE	Cabruca	Arruda	31	304	90	4	8810	5	1077	5	2,3,4,5,7	8	24	29	25	23
8553	BA/NE	Forest	Arruda	19	300	67	4	5640	6	1147	3	2,3,4,5,7	9	11	22	48	17
8555	BA/NE	Cabruca	Arruda	47	306	174	4	6293	5	971	3	2,3,4,5,7	9	26	24	29	21

Table 1. Continued

Wood collection (RBw)	State/ Brazilian Region	Veg.	Morphotype	VF	VL (µm)	VD (µm)	VW (µm)	EA (µm)	IP (µm)	FL (µm)	FW (µm)	AP (µm)	RF	% V	% AP	% F	% R
8556	BA/NE	Cabruca	Arruda	45	368	96	4	7905	5	1119	5	2,3,4,5,7	12	32	22	27	19
8501	RJ/SE	Forest	Arruda	17	255	91	5	5766	4	929	5	3,4,5,6,7	6	15	23	46	16
8502	RJ/SE	Forest	Arruda	19	237	83	5	5403	4	845	6	3,4,5,6,7	7	14	21	47	19
8503	RJ/SE	Forest	Arruda	28	219	65	5	3587	3	860	5	2,3,4,5,6,7	6	18	25	41	16
8504	RJ/SE	Forest	Arruda	26	235	82	6	5978	4	922	6	3,4,5,6,7	9	22	19	41	18
8505	RJ/SE	Forest	Arruda	40	271	78	5	5704	4	1132	7	2,3,4,67	8	27	26	33	14
8538	BA/NE	Capoeira	Laranja	17	289	73	4	6072	4	1302	6	2,3,4,5,7	12	14	22	48	19
8539	BA/NE	Capoeira	Laranja	20	322	64	4	2261	4	744	5	2,3,4,5,7	7	9	20	55	16
8541	BA/NE	Forest	Laranja	18	319	35	3	4588	2	1007	5	2,3,4,5,7	8	16	25	43	17
8542	BA/NE	Forest	Laranja	29	328	33	2	2929	2	1083	5	2,3,4,5,7	10	14	16	50	20
8532	BA/NE	Capoeira	Café	19	304	38	2	3348	2	1043	4	2,3,4,5,7	8	14	34	36	16
8533	BA/NE	Capoeira	Café	17	275	44	2	4373	3	951	4	2,3,4,5,7	10	14	22	42	22
8534	BA/NE	Capoeira	Café	10	305	32	2	4224	2.5	937	5	2,3,4,5,7	9	9	23	43	25
8544	BA/NE	Capoeira	Café	15	248	67	3	4716	4	776	5	2,3,4,5,7	8	12	25	41	22