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Original Article

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Caatinga Tree Wood Anatomy: Perspectives on Use and Conservation

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ABSTRACT

This work describes the anatomical analysis of the wood of four Caatinga tree species in order to determine the anatomical characteristics necessary for species segregation in functional groups, to relate them to the regional environmental conditions, as well as to infer about their management and conservation. Qualitatively, the species showed peculiar adaptations to xeric environments such as high frequency of low caliber vessels or parenchyma cells. Quantitatively, the four taxa were divided into three functional groups related to the precipitation and temperature of the Caatinga. The relationships between anatomy and the environment have shown their vulnerability to climatic variations, and have warned of the damage that can be generated by anthropogenic action. It is advisable to use the energy of the species or for use in civil construction, with the exception of *Tabebuia aurea*, which is appropriate for carpentry. It was verified that the anatomy of the wood has potential as a subsidy for the use, management and conservation of the studied species.

Keywords: wood anatomy, xeric environments, functional groups.

1. INTRODUCTION

Even though tropical forests cover less than 7 percent of the land surface, they play a key role in maintaining the balance of biogeochemical and hydrological cycles (Wright, 2010), as well as providing clean water, fuel and food for millions of people around the world (Schmidt & Ticktin, 2012). These regions have high levels of biodiversity, contribute to one-third of primary terrestrial productivity (Bonan, 2008), and account for about 30% of global carbon (Pan et al., 2011).

Tropical dry forests such as the Brazilian Northeast Caatinga are crucial to these ecosystem services and are vulnerable to changes in climate, as they occur in areas considered prone to change and with high concentrations of people (Pan et al., 2011). The population in these regions has a direct economic dependence on the forest products from the wood, which increases the pressure on the arboreal remnants and potentiates the effect of the climate on the vegetation (Araújo et al., 2007; Araujo et al., 2010; Albuquerque et al., 2012). Most of the demand generated by the population is concentrated on timber resources used for various purposes, from construction to energy use (Araújo et al., 2007; Albuquerque et al., 2012).

Wood is exploited throughout the year in the Brazilian Caatinga; however, its extraction increases significantly in the months that make up the dry period (Figueirôa et al., 2006; Albuquerque et al., 2012). Among other factors, water scarcity restricts agriculture and livestock activities during this period, thus evidencing the resources (wood) in the Caatinga landscape, making them a source of subsistence for communities until the rainy season (Araújo et al., 2007; Albuquerque et al., 2012). This impacts on the structure of tree communities (Araújo et al., 2007), as well as gradually decreases the wealth of the region's wood and carbon stocks (Pan et al., 2011; Albuquerque et al., 2012).

These types of pressure generate changes at the ecosystem level, but also at a specific level in the functional traits of tree species, such as in the anatomical structure of the wood (Carlquist, 2010; Baas & Wheeler, 2011; Reich, 2014). These changes present latitudinal and pluviometric patterns, and are used as a support to define the main climatic regions of the globe (Zuidema et al., 2013). Extreme anatomical variations are evidence of *trade-offs* between the mechanical stress of the wood and the hydraulic architecture (Pineda-García et al., 2015; Gleason et al., 2016), and in some cases are explained in up to 92% by the changes in the climate (Roque et al., 2007). Conduction and storage structures are the main functional characters of wood, responsible for maintaining the physiology of trees under water stress (Pineda-García et al., 2015), and make up the functional models of these taxa (Zanne et al., 2010).

In this sense, understanding the anatomical arrangement of the wood assists in determining the possible causes of stress, whether they are environmental or anthropic (Figueirôa et al., 2006; Albuquerque et al., 2012; Anderegg & Meinzer, 2015), as well as in the framework of their potential use (Benites et al., 2015; Brand et al., 2016) and proper management and conservation (Albuquerque et al., 2012; Santos et al., 2014).

In this way, the present work aimed to describe and quantify the wood anatomy of four common tree species in Caatinga regions of the state of Sergipe, Brazil, in order to verify the influence of environmental conditions on the anatomical characters of these species, to describe their organization in functional groups, and to determine its proper use, handling and conservation.

2. MATERIAL AND METHODS

2.1. Study area

This study was carried out in two sites: (Site 1) the conservation unit Grota do Angico Natural Monument, located in the northwest of Sergipe state on the São Francisco River (9°41' S 38°31' W), in an area of 2,183 hectares of dry forest (Ferraz et al., 2013; Silva et al., 2013; SEMARH, 2016) (Figure 1); (Site 2) a remnant of Caatinga with preserved shrub-tree vegetation located to the north at São Pedro Farm (10°02.266' S 37°24.965' W), with 50 hectares and an average altitude of 168 m (Oliveira et al., 2013) (Figure 1).

The climate of the region is semi-arid, dry and hot, marked by a rainy season between April and July, and a dry season between August and December (Köppen, 1948). The total annual precipitation varies from 380 to 760 mm for Site 1 (Figure 2a), and between 300 and 700 mm for Site 2 (Figure 2b), as well as annual mean air temperature between 18 and 25 °C, and annual potential evapotranspiration greater than the annual precipitation in the two areas. The municipalities where the two study sites are located have a high degree of deforestation, and they have the highest number of drought events among the counties of Sergipe (Bomfim et al., 2002; Jungles et al., 2011).

2.2. Selected species

Considering floristic surveys (Ferraz et al., 2013; Silva et al., 2013) in Poço Redondo (Oliveira et al., 2013) and in Porto da Folha, four species of heliophyte habit were selected: *Aspidosperma pyrifolium* Mart.

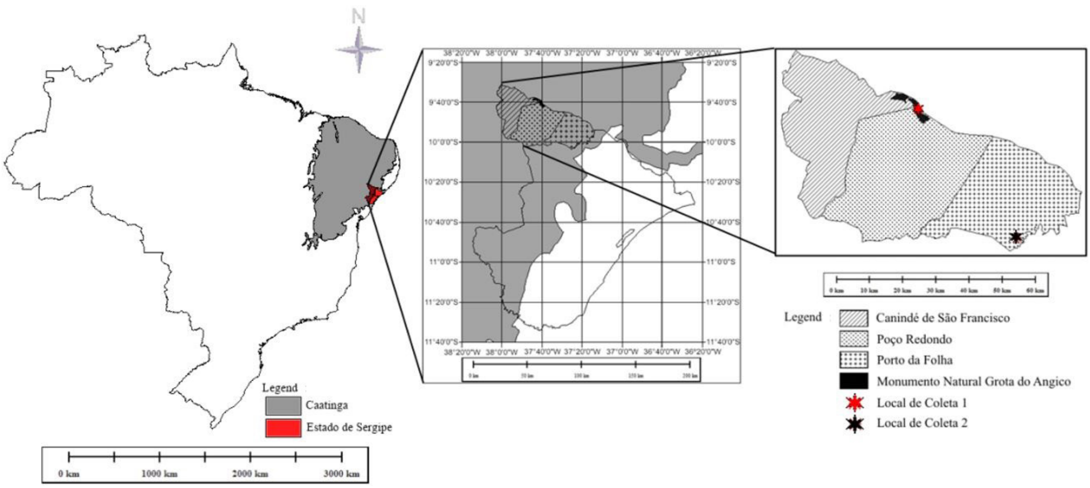

Figure 1. Study sites: Natural Monument Conservation Unit of Angico Grota (light star), municipalities of Canindé do São Francisco and Poço Redondo (S1); Fragment of Caatinga (dark star), municipality of Porto da Folha (S2), Sergipe state, Brazil.

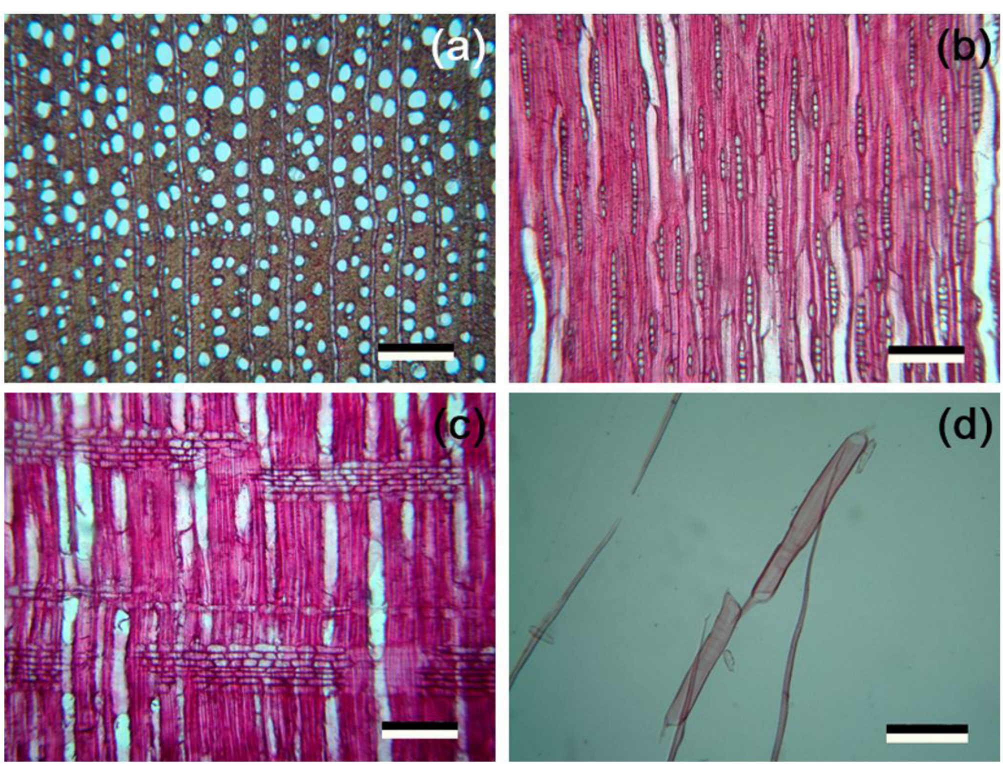

Figure 2. Histological sections of the *A. pyrifolum* wood collected in site 1 (S1) and site 2 (S2), Sergipe state, Brazil: (a) transversal plane, bar; (b) tangential longitudinal plane; (c) radial longitudinal; (d) macerated; Bar = 200 μm.

(Apocynaceae), pioneering and deciduous; *Libidibia ferrea* (Mart. Ex Tul.) L. P. Queiroz (Fabaceae), secondary and semi-deciduous; *Tabebuia aurea* (Silva Manso) Benth. & Hook. F. S. ex. Moore (Bignoniaceae), early secondary and semi-deciduous; and *Ziziphus joazeiro* Mart. (Rhamnaceae), pioneering and evergreen. These occur in both locations having high ecological and economic relevance for the region (Gandolfi et al., 1995; Carvalho et al., 2012; Andrade et al., 2015), and represent the growth dynamics of the Caatinga in Sergipe.

2.3. Wood anatomical data collection

Six subjects were randomly set for each species at each study site during the rainy season with wood samples being removed using a motorized core (Sthil BT45) (in trees with a diameter at breast height - DBH greater than 130 cm). Three samples of each specimen were collected for anatomical analyzes for a total of six individuals per species at each study site, with all samples containing heartwood, sapwood and bark. These were packed in paper bags and then dried in a refrigerator at –6 °C at the Laboratory of Vegetable Anatomy and Dendroecology of the Federal University of Sergipe. Circumference at breast height (C.B.H.) of the trees was measured with tape, then diameter at breast height (D.B.H.) was calculated and the geographical coordinates were recorded for each individual.

2.4. Environmental data collection

The regional climatic data used in the analyzes were collected from the data platform of the National Institute of Meteorology (INMET), the Agrometeorological Monitoring System of Embrapa (AGRITEMPO), and the state platforms of each study Site. The values obtained for the environmental variables were adequate according to calculations of the platform WorldClim 2017 (WorldClim, 2017), where the regional values were standardized according to the 19 environmental layers (Bio's) of this platform. The most important environmental layers were submitted to statistical analyses with the anatomical data of the wood in order to observe the species' responses to the climate.

2.5. Biological analyses

For the anatomical analyses, the sapwood samples of each species were collected close to the shell in cubes of 2 cm^3, and softened in water/glycerin solution (3:1). They were then sectioned in the three anatomical planes (transversal, tangential and radial), and 30 sections of each plane of each specimen were removed. Samples were clarified with sodium hypochlorite (20%), dehydrated in an alcoholic series (30-50%) and stained with alcoholic Safranin (1%) (Johansen, 1940). The chemical maceration of each sample stained (Brown, 1919) with aqueous Safranin (1%) was also obtained, and the anatomical elements were visualized separately. The tissues were visualized using a Bioval microscope under transmitted light at 40×, 100× and 400× magnification and photographed with a digital camera attached to the microscope. Characterization of the anatomical elements was performed according to the rules of the International Association of Wood Anatomists (IAWA) (Wheeler et al., 1989), and its measurement was carried out using the ImagePro-plus program (version 4.5.0.29 for Windows) (with an accuracy of 0.01 mm).

The vessels' frequency per mm^2 (VF), ray frequency (RF) (mm), vessel diameter (VD) (10 per cut) (μm), vessel area (VA) (10 per cut) (μm^3), ray height (RH) (10 per cut) (μm), ray width (RW) (10 per cut) (μm), fiber length (FL) (30 measures) (mm), fiber wall thickness (FWT) (30 measures) (μm), and fiber lumen thickness (FLT) (30 measures) (μm) were measured for each section. The following were also calculated: vulnerability index (VI), wood mesomorphism index (MI) (Carlquist, 1977), wall thickness (WT), wall fraction (WF), flexibility coefficient (FC), and Runkel index (RI) (30 measures for all) (Runkel, 1952). In total, 2,340 measurements were made per sample and 28,080 per species.

2.6. Statistical analyses

The results of the four species in both study sites were submitted to the Shapiro-Wilk normality test followed by the t-test for comparison of the means and evaluation of possible differences in the responses between the studied sites. The anatomical data of the taxa along with the environmental data were staggered (by deviations from the means in units of standard deviation) and submitted to principal component analysis (PCA) (under correlation matrix between groups) in order to consider the influence on the functional anatomical features of the trees. A Cluster analysis (in paired groups under the distance of Manhattan) and clustering by

K-means were performed in order to determine the relationship of the species' biological responses. Next, the values of the three more explanatory environmental variables were compared to the anatomical data from generalized linear model (GLM) tests in order to elucidate the possible environmental influence of each variable on the samples. The anatomical values significantly influenced by environmental variables were subsequently submitted to the Pearson correlation (r) in order to observe the type of relationship between the data and the climate (direct or antagonistic). All analyses were performed using R 3.2.1. and Past 2.17c software programs.

3. RESULTS

3.1. Anatomical description of wood

3.1.1. Aspidosperma pyrifolium

3.1.1.1. Macroscopic analysis

Heartwood is distinct from sapwood by its coloration, as heartwood is dark brown and sapwood is beige; it exhibits moderate brightness, bitter taste and imperceptible scent, and is a hard wood to cut with direct grains, a fine texture and growth layers that are distinct to the naked eye. Its axial parenchyma is only visible under lens; its rays are invisible to the naked eye, very thin to thin, and numerous; its vessels are only visible under lens, very small to small, very numerous to numerous, of diffuse porosity and in radial arrangement without obstruction; it has low rays, only visible in the tangential plane under a lens, not stratified, and little contrasted in the radial plane.

3.1.1.2. Microscopic analysis

Vessels: diffuse porosity, predominantly solitary, radially grouped, rarely twinned or multiple, very small, very frequent, circular in shape, appendices at one or both ends, or completely absent (Figure 2a and 2d). They have a simple oblique perforation plate, which is small with alternating and bordered intervessel pits (Figure 2d).

Growth ring: distinct, with occurrence of fiber flattening and presence of uniseriate marginal parenchyma line; the growth layer is also characterized by vessel size and clustering, where vessels are more clustered and larger at the beginning of the growth layer, and less clustered and smaller at their end (Figure 2a).

Axial parenchyma: scarce paratracheal (Figure 2a).

Radial parenchyma: non-stratified, predominantly unisseriate with the occurrence of multiseriate of up to three cells, very fine, extremely low, very numerous, with the presence of substances in its interior; heterogeneous, poorly contrasted, with procumbent cells and presence of substances (Figure 2b and 2c).

Fibers: medium-length, narrow, septa-free, thick-walled libriformes with reduced lumen, numerous simple points evident throughout the fibers (Figure 2d).

3.1.2. Ziziphus joazeiro

3.1.2.1. Macroscopic analysis

Heartwood is distinct from the sapwood by coloration, as the heartwood is black and the sapwood is yellow; it exhibits moderate brightness and imperceptible scent, is an intermediate-soft wood to the cut with direct grain, a fine texture, with the axial parenchyma and the growth layers being indistinct to the naked eye; its rays are invisible to the naked eye, very thin to thin, numerous; its pores are visible to the naked eye, small to medium, very infrequent and of diffuse porosity in radial arrangement with possible obstruction; it has low rays which are only visible in the tangential plane under a lens, not stratified, and little contrasted in the radial plane.

3.1.2.2. Microscopic analysis

*Vessels: a*re not uniform, diffuse array grouped tangentially, are mostly solitary in multiples of 2-6 and in clusters (up to 3), rarely solitary, and eventually blocked by tyloses. They have medium length, are very numerous, very short and circular in shape with no appendages, or rarely short and may have appendages on one end (Figure 3a and 3d). They have simple oblique or straight perforation plates and the intervessel points are small, alternate and bordered (Figure 3d).

Growth ring: distinct, semi-porous ring with occurrence of fiber flattening and presence of a narrow line of unisseriate marginal parenchyma (Figure 3a).

Axial parenchyma: scarce paratracheal and apotracheal in lines. It has a marginal formation parallel to fiber flattening next to the growth layer (Figure 4a).

Radial parenchyma: non-stratified, predominantly multiseriate, occurring from 2 to 4 cells, fine, extremely low, very numerous and with the presence of crystals in its interior; heterogenous, poorly contrasted and with procumbent cells (Figure 3b and 3c).

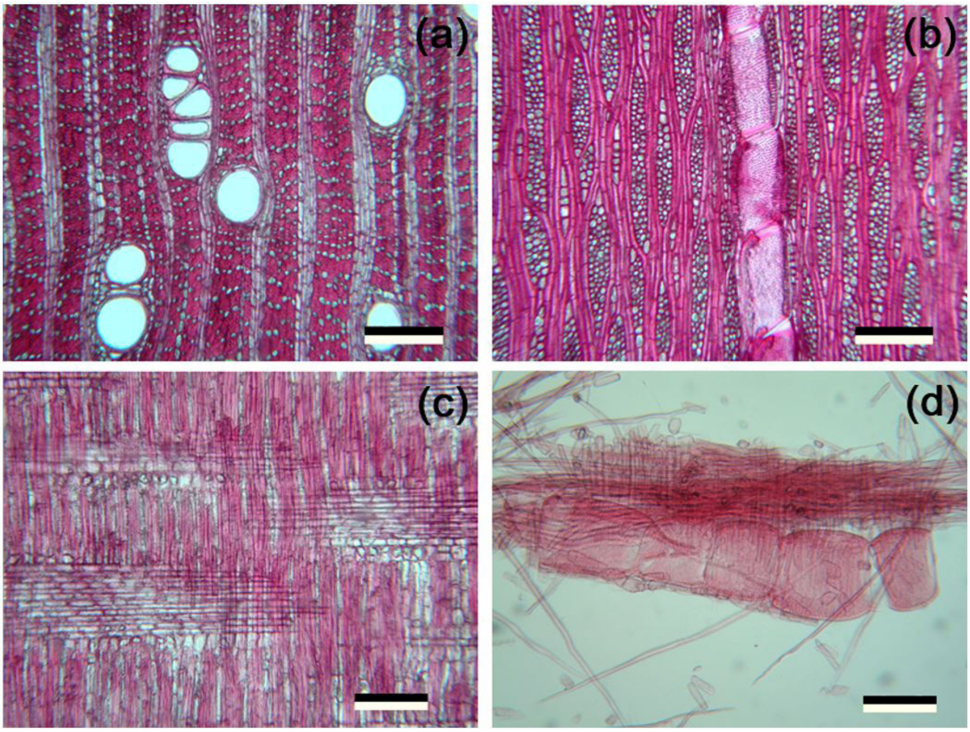

Figure 3. Histological sections of the *Z. joazeiro* wood collected in site 1 (S1) and site 2 (S2), Sergipe state, Brazil: (a) transversal plane, bar; (b) tangential longitudinal plane; (c) radial longitudinal; (d) macerated; Bar = 200 μm.

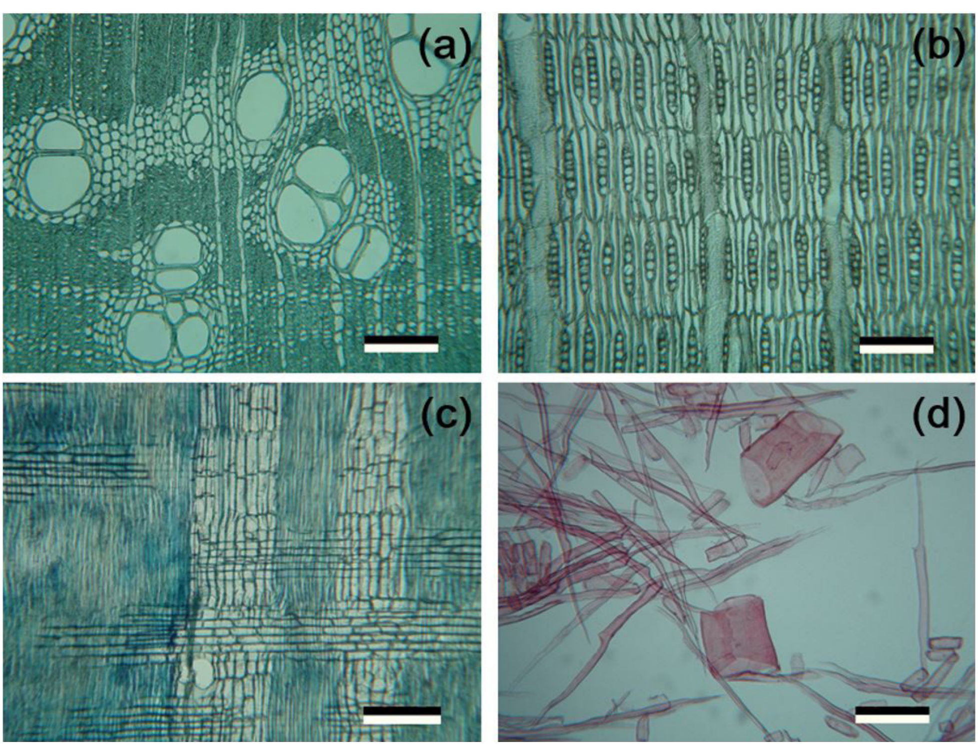

Figure 4. Histological sections of the *T. aurea* wood collected in site 1 (S1) and site 2 (S2), Sergipe state, Brazil: (a) transversal plane, bar; (b) tangential longitudinal plane; (c) radial longitudinal; (d) macerated; Bar = 200 μm.

Fibers: Libriform, moderately short in length, narrow, with very thick walls and reduced lumen (Figure 3d).

3.1.3. Tabebuia aurea

3.1.3.1. Macroscopic analysis

Heartwood is distinct from sapwood by coloration, as the heartwood is dark brown and sapwood is light brown; it has a moderate brightness and imperceptible odor, soft cutting wood, irregular grain, fine texture, axial parenchyma and growth layers are distinguished by the naked eye; its rays are invisible to the naked eye, very fine, very numerous; its pores are visible to the naked eye, medium, few, diffuse porosity and in radial arrangement with possible obstruction; it has low rays which are only visible in the tangential plane under a lens, moderately stratified, and little contrasted in the radial plane.

3.1.3.2. Microscopic analysis

Vessels: arranged in semiporous rings, grouped tangentially or radially, are mostly multiples of 2-8 and in bunches (up to 6), are rarely solitary and eventually obstructed by tyloses. They are large in diameter, few in number, very short and circular in shape, absent in appendages, or they may rarely have short appendages at one end (Figure 4a and 4d). They have simple oblique or straight perforation plates, and the intervessel points are small, alternating and bordered (Figure 4d).

Growth ring: distinct with occurrence of fiber flattening and presence of unisseriate marginal parenchyma line (Figure 4a).

Axial parenchyma: paratracheal, vasicentric aliform of angular extension, confluent. It has marginal formation parallel to the growth layer, and may or may not occur in ring formation (Figure 4a).

Radial parenchyma: partially laminated with a predominantly multiseriate wavy stratification, occurring from 2 to 5 cells, very thin, extremely low, and very numerous; heterogeneous, poorly contrasted and with procumbent cells (Figure 4b and 4c).

Fibers: Libriform, moderately short in length, narrow and thick-walled (Figure 4d).

3.1.4. Libidibia ferrea

3.1.4.1. Macroscopic analysis

Heartwood is distinct from sapwood by coloration, as the heartwood is black and the sapwood is yellow; presents moderate brightness and imperceptible scent, it is a hard wood to cut with direct grain and a fine texture, with axial parenchyma and growth layers being distinct to the naked eye; its rays are invisible to the naked eye, very thin to thin, numerous; its pores are only visible under a lens, small, numerous, and of diffuse porosity in radial arrangement with possible obstruction; it has low rays, only visible in the tangential plane under a lens, moderately stratified, and little contrasted in the radial plane.

Vessels: their arrangement is in semiporous rings, tangentially grouped, are mostly multiples of 2-4 and in bunches (up to 6), rarely solitary, and eventually obstructed by tiloses. They are medium, not very numerous, very short and circular in shape with absent appendages, or they may rarely present short appendages at one end (Figure 5a and 5d). They have simple (foraminated) oblique or straight perforation plates, and the intervessel points are small, alternate and bordered (Figure 5d).

Growth ring: distinct, with marginal parenchyma line uniseriate together with thickening in the fiber walls in the latewood; the growth layer is also characterized by vessel size and clustering, where vessels are less clustered and larger at the beginning of the growth layer, and less clustered and smaller at their end (Figure 5a).

Axial parenchyma: paratracheal, vasocentric aliform of angular extent, confluent, and with the presence of amyloplasts. It has a marginal formation parallel to the growth layer, and may or may not occur in the formation of the rings (Figure 5a).

Radial parenchyma: partially laminated with predominantly multiseriate undulating stratification, occurring from 2 to 4 cells, thin, extremely low, numerous, and with the presence of substances (starch) and crystals in its interior; heterogeneous, poorly contrasted and with procumbent cells (Figure 5b and 5c).

Fibers: Libriform, medium length, narrow, with very thick walls and reduced lumen (Figure 5a).

3.2. Anatomical variation of wood

The anatomical elements evaluated among the four species had significant variations with emphasis on frequency, diameter, length and area of vessels, fiber length, vulnerability index, mesomorphism and Runkel (Table 1). The mean anatomical values of the individuals of each species in the two study sites also varied, suggesting different responses among the sites, with significant values (Table 1).

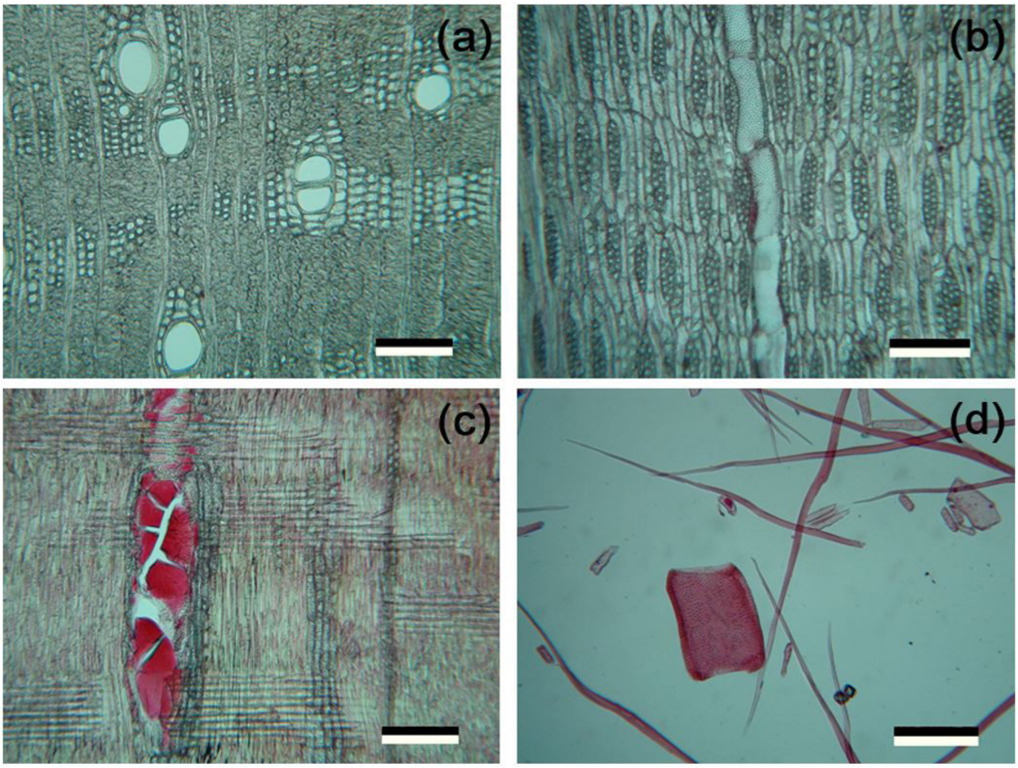

Figure 5. Histological sections of the *L. ferrea* wood collected in site 1 (S1) and site 2 (S2), Sergipe state, Brazil: (a) transversal plane, bar; (b) tangential longitudinal plane; (c) radial longitudinal; (d) macerated; Bar = 200 μm.

Table 1. Mean values of the anatomical elements of *A. pyrifolium, Z. joazeiro, T. aurea*, and *L. ferrea*, collected in site 1**(S1)** and site 2 **(S2)**, Sergipe state, Brazil. ± = standard deviation; **Bold values** = significant at $p < 0.05$ From the comparison between sites by the T-test.

	A. pyrifolium_SI	*A. pyrifolium_S2*	*Z. joazeiro_S1*	*Z. joazeiro_S2*	*T. aurea_S1*	*T. aurea_S2*	*L. ferrea_S1*	*L. ferrea_S2*
VF	**243.04 ±16.78**	**211.34 ±12.78**	7.81 ± 1.25	8.38 ± 1.49	**9.36 ± 1.45**	**7.44 ± 0.31**	**8.72 ± 2.12**	**6.33 ± 1.21**
RF	11.19 ± 0.73	11.05 ± 0.20	**13.47 ± 0.36**	**11.48 ± 0.80**	12.59 ± 0.83	12.58 ± 1.26	10.38 ± 1.82	9.86 ± 0.90
VD	**36.38 ± 2.15**	**46.07 ± 0.57**	111.53 ± 9.96	109.41 ±11.03	**121.41 ±13.28**	**140.99 ±11.17**	115.05 ±13.50	130.86 ±18.46
VL	602.36 ±97.89	600.55 ±53.80	298.07 ±18.55	274.73 ±24.25	259.96 ±19.33	264.50 ±18.49	**291.73 ±30.55**	**254.60 ±16.10**
VA	**1.50 ± 0.13**	**2.61 ± 0.17**	14.29 ± 2.56	13.42 ± 2.99	**16.67 ± 2.81**	**20.97 ± 3.63**	14.54 ± 2.81	17.61 ± 4.28
RH	162.95 ±15.42	163.19 ±12.91	395.53 ±27.50	354.84 ±46.41	150.76 ±14.32	151.08 ±12.19	175.86 ±19.03	185.66 ± 5.30
RW	16.08 ± 0.55	16.24 ± 0.73	49.78 ± 3.68	48.53 ± 5.03	27.85 ± 2.41	30.45 ± 4.89	37.55 ± 6.21	40.62 ± 5.31
FL	1.06 ± 0.11	1.17 ± 0.18	0.80 ± 0.06	0.88 ± 0.07	**0.68 ± 0.05**	**0.80 ± 0.06**	1.05± 0.07	1.06 ± 0.06
FWT	1.54 ± 0.03	1.50 ± 0.14	1.01 ± 0.09	1.01 ± 0.08	1.07 ± 0.12	1.01 ± 0.07	1.59 ± 0.09	1.51 ± 0.06
FLT	0.64 ± 0.03	0.63 ± 0.09	0.41 ± 0.04	0.43 ± 0.02	0.75 ± 0.04	0.67 ± 0.06	0.48 ± 0.03	0.44 ± 0.05
VI	**0.15 ± 0.02**	**0.22 ± 0.02**	14.59 ± 2.75	13.40 ± 2.70	**13.33 ± 3.02**	**18.98 ± 1.83**	**14.04 ± 4.46**	**21.06 ± 3.86**
MI	**0.09 ± 0.02**	**0.13 ± 0.07**	4.35 ± 0.88	3.68 ± 0.84	**3.44 ± 0.67**	**5.04 ± 0.78**	4.18 ± 1.67	5.38 ± 1.19
WT	0.77 ± 0.02	0.75 ± 0.07	0.51 ± 0.04	0.50 ± 0.04	0.53 ± 0.06	0.50 ± 0.03	0.79 ± 0.04	0.76 ± 0.03
WF	70.52 ± 1.38	70.34 ± 3.12	70.98 ± 0.66	69.93 ± 1.27	58.62 ± 2.20	60.02 ± 2.29	76.73 ± 4.41	77.42 ± 2.14
CF	29.48 ± 1.38	29.66 ± 3.12	29.02 ± 0.66	30.07 ± 1.27	41.38 ± 2.20	39.98 ± 2.29	23.27 ± 4.41	22.58 ± 2.14
RI	2.40 ± 0.16	2.40 ± 0.37	2.45 ± 0.08	2.33 ± 0.14	1.42 ± 0.14	1.51 ± 0.14	3.31 ± 0.25	3.46 ± 0.38
EI	48.39 ± 5.21	54.63 ± 5.87	57.16 ± 7.83	61.51 ± 7.35	**37.72 ± 4.41**	**48.15 ± 6.25**	51.11 ± 5.62	54.61 ± 3.68

VF = vessel frequency (mm^2); **RF** = ray frequency (mm); **VD** = Vessel diameter (μm); **VL** = vessel length (μm); **VA** = vessel area (μm^3); **RH** = ray height (μm); **RW** = ray width (μm); **FL** = fiber length (μm); **FWT** = fiber wall thickness (μm); **FLT** = fiber lumen thickness (μm); **VI** = vulnerability index; **MI** = mesomorphism index; **WT** = wall thickness; **WF** = wall fraction; **CF** = coefficient of flexibility; **RI** = Runkel index; **EI** = enfeltrament index.

When weighted on the environmental variables by PCA, the anatomical data of the wood explained 93% of the values in the first two axes (axis 1 – 73%, axis 2 – 20%), which shows its strong relation with the climate and the different strategies used by the taxa for water use in the wood (Figure 6). The cluster analysis (Cluster and K-means) similarly revealed significant levels of organization between the groups for the anatomical values of the wood (0.968) (Figure 6). There was then a complete distinction between the

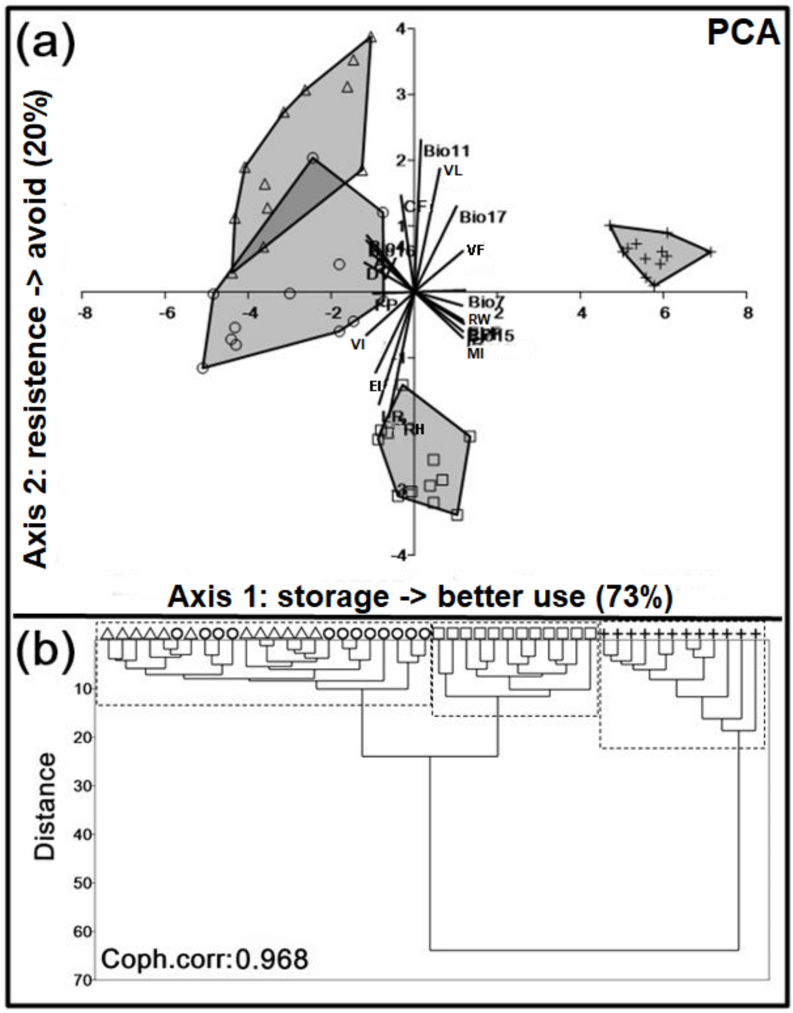

Figure 6. Principal components analysis (PCA) (a) and clustering (b) for the anatomical characters of the wood of four tree species of Caatinga in relation to six environmental variables of temperature and precipitation in (S1) and (S2); + = *A. pyrifolium*; □ = *Z. joazeiro*; Δ = *T. aurea*; ○ = *L. ferrea;* Coph.corr = coefficient of cophonetic correlation. **VF** = vessel frequency (mm^2); **RF** = ray frequency (mm); **VD** = Vessel diameter (µm); **VL** = vessel length (µm); **VA** = vessel area ($µm^3$); **RH** = ray height (µm); **RW** = ray width (µm); **FL** = fiber length (µm); **FWT** = fiber wall thickness (µm); **FLT** = fiber lumen thickness (µm); **VI** = vulnerability index; **MI** = mesomorphism index; **WT** = wall thickness; **WF** = wall fraction; **CF** = coefficient of flexibility; **RI** = Runkel index; **EI** = enfeltrament index; **Bio1** = Annual Mean Temperature; **Bio2** = Mean Diurnal Range (Mean of monthly (max temp - min temp)); **Bio3** = Isothermality (Bio2/Bio7) (*100); **Bio4** = Temperature Seasonality (standard deviation *100); **Bio5** = Max Temperature of Warmest Month; **Bio6** = Min Temperature of Coldest Month; **Bio7** = Temperature Annual Range (Bio5-Bio6); **Bio8** = Mean Temperature of Wettest Quarter; **Bio9** = Mean Temperature of Driest Quarter; **Bio10** = Mean Temperature of Warmest Quarter; **Bio11** = Mean Temperature of Coldest Quarter; **Bio12** = Annual Precipitation; **Bio13** = Precipitation of Wettest Month; **Bio14** = Precipitation of Driest Month; **Bio15** = Precipitation Seasonality (Coefficient of Variation); **Bio16** = Precipitation of Wettest Quarter; **Bio17** = Precipitation of Driest Quarter; **Bio18** = Precipitation of Warmest Quarter; **Bio19** = Precipitation of Coldest Quarter.

individuals of *A. pyrifolium* and *Z. joazeiro* in relation to *T. aurea* and *L. ferrea* (Figure 6) which, although appearing separated, presented some individuals merged in the grouping between the two taxa given their structural similarities (elements and vessel and axial parenchyma) (Figure 4 and 5).

In this sense, six environmental variables showed influence on the wood anatomy of the four species, namely: the seasonal variation of temperature (SVT), the mean annual temperature (MAT), mean temperature in the coldest period (MTC), seasonal variation of precipitation (SVP), wet (WP) and dry precipitation (DP) (Table 2).

3.3. Environmental influences on wood structure

Overall GLM's showed a greater influence of mean annual temperature on the anatomical structures of *A. pyrifolium* and *Z. joazeiro* (Table 2). *T. aurea* showed a strong relation of its anatomy with the precipitation that occurs in the dry period (Table 2), while *L. ferrea* revealed a proportional relation between the three environmental variables to which it was compared (seasonality of temperature, seasonal precipitation and wet period) (Table 2), all with high numbers of anatomical characters related to variations in the environment.

Pearson (r) correlations corroborated the influences shown by GLM (Table 2). In this sense, it is possible to highlight the relation between annual mean temperature and fiber length of *A. pyrifolium* (+95%) (Table 2) and rainfall in the wet period on its vessel diameter (+91%) (Table 2). Similarly, rainfall in the wet period had an influence on the frequency of *Z. joazeiro* rays (–93%) (Table 2), as well as on their wall thickness (–87%) (Table 2). Both taxa also showed strong relationships between the Runkel index and the annual average temperature (+93% in *A. pyrifolium* and –91% in *Z. joazeiro*), which points to the high influence of this variable on structure and quality wood of these species.

Among the correlations which occurred between precipitation in *T. aurea* during the dry period, the frequency of vessels (+86%) (Table 2), the fiber wall thickness (+76%), and the flexibility coefficient (+77%)

Table 2. Generalized linear models (GLM) and Pearson (r) correlations between the anatomical data of the four Caatinga tree species and environmental variables of the Brazilian Northeast.

	Aspidosperma pyrifolium			*Ziziphus joazeiro*			*Tabebuia aurea*			*Libidibia ferrea*		
	SVT	MAT	WP	SVT	MAT	WP	SVT	MTC	DP	MAT	SVP	WP
VF	**0.86***	-0.47_	-0.24_	0.16	0.52_	-0.47_	**0.68***	**0.69***	**0.84***	**0.85***	**0.70***	**-0.80***
RF	-0.41_	**0.95***	**-0.63***	0.18	**0.89***	**-0.95***	0.57_	**0.62***	**0.72***	**0.91***	**0.62***	-0.57_
VD	-0.46_	-0.41_	**0.91***	-0.29	**-0.59***	0.27_	-0.49_	**-0.67***	**-0.61***	**-0.86***	**-0.69***	0.52_
VL	**-0.82***	**0.68***	-0.02_	0.52	-0.13_	0.19_	0.44_	**0.50***	**0.64***	**0.87***	**0.89***	**-0.92***
VA	**-0.74**	**0.86***	-0.34_	-0.46	0.25_	-0.54_	-0.58_	**-0.78***	-0.51_	-0.46_	0.01_	-0.15_
RH	0.50_	**-0.90***	0.46_	-0.46	0.33_	-0.40_	-0.37_	-0.38_	-0.50_	**-0.59***	-0.53_	**0.75***
RW	-0.50_	**0.91***	-0.56_	0.21	0.14_	0.10_	0.22_	0.31_	0.17_	-0.50_	-0.26_	0.13_
FL	**-0.62***	**0.93***	-0.50_	-0.19	**0.87***	**-0.88***	0.40_	0.36_	**0.62***	**0.79***	**0.99***	**-0.91***
FWT	**-0.60***	**0.94***	-0.53_	-0.18	**0.88***	**-0.89***	0.49_	0.45_	**0.70***	**0.81***	**0.99***	**-0.92***
FLT	**-0.60***	**0.94***	-0.52_	-0.18	**0.88***	**-0.89***	0.48_	0.44_	**0.69***	**0.79***	**0.99***	**-0.92***
VI	**-0.62***	**0.93***	-0.51_	-0.43	0.42_	-0.58_	**-0.64***	**-0.76***	**-0.73***	-0.57_	-0.20_	0.36_
MI	**-0.61***	**0.93***	-0.51_	-0.25	**0.77***	**-0.85***	-0.25_	-0.36_	-0.03_	0.33_	**0.79***	**-0.63***
WT	**-0.60***	**0.93***	-0.52_	-0.18	**0.88***	**-0.89***	0.45_	0.41_	**0.67***	**0.79***	**0.99***	**-0.92***
WF	**0.74***	**-0.69***	0.19_	0.55	**-0.60***	**0.65***	**0.74***	**0.77***	**0.65***	0.02_	-0.58_	0.44_
CF	0.32_	-0.03_	0.18_	0.24	-0.12_	0.49_	**0.82***	**0.78***	**0.77***	**0.64***	0.36_	-0.35_
RI	**-0.60***	**0.93***	-0.54_	-0.15	**0.88***	**-0.91***	0.44_	0.42_	**0.66***	**0.81***	**0.98***	**-0.91***
EI	**-0.69***	0.02_	0.44_	-0.01	-0.43_	0.47_	**-0.68***	**-0.63***	**-0.65***	-0.05_	-0.27_	0.46_

VF = vessel frequency (mm^2); **RF** = ray frequency (mm); **VD** = Vessel diameter (µm); **VL** = vessel length (µm); **VA** = vessel area ($µm^3$); **RH** = ray height (µm); **RW** = ray width (µm); **FL** = fiber length (µm); **FWT** = fiber wall thickness (µm); **FLT** = fiber lumen thickness (µm); **VI** = vulnerability index; **MI** = mesomorphism index; **WT** = wall thickness; **WF** = wall fraction; **CF** = coefficient of flexibility; **RI** = Runkel index; **EI** = enfeltrament index; **SVT** = seasonal variation of temperature; **MAT** = mean annual temperature; **MTC** = mean temperature in the coldest period; **SVP** = seasonal variation of precipitation; **WP** = wet precipitation; **DP** = dry precipitation; * = GLM's significant at $p < 0.05$; Values in bold = *r* significant at $p < 0.05$.

may be highlighted (Table 2). The most significant correlations in *L. ferrea* were the average annual temperature with the lightning frequency (+94%) (Table 2), and the seasonal precipitation variation with fiber length (+99%) and Runkel (–91%) (Table 2). However, the environmental influences of annual mean temperature and precipitation events in different periods of the year were relevant in the wood structure of the evaluated species.

4. DISCUSSION

The qualitative characteristics of the wood generally did not change due to the environmental conditions; however, the quantitative characteristics showed strong relations with the variations in the environment and revealed the existence of three different functional groups between the species. Thus, these characteristics showed potential use for evaluating functional groups in a similar way to the results corroborated by other researches developed in dry forests of Mexico and rainy forests in Australia (Pineda-García et al., 2015; Apgaua et al., 2017). The variations observed herein between species in the two study sites also corroborate the heterogeneity of the Caatingas (Costa et al., 2015), as well as alert us to environmental influences on this plant formation, thereby reiterating the need for its management and conservation as highlighted by other authors (Albuquerque et al., 2012).

The anatomical structural organization of the secondary xylem of the four species showed at least three distinct functional groups (Figure 6). *T. aurea* and *L. ferrea* differed from their storage structures (group 1), while *A. pyrifolium* had higher hydraulic safety, mainly in the water conduction structures of the wood (vessel elements) (group 2), and *Z. joazeiro* for presenting intermediate characteristics between these two groups (group 3), which corroborates other studies of the genus (Anderegg & Meinzer, 2015; Pineda-García et al., 2015; Gleason et al., 2016; Apgaua et al., 2017). The high proportion of parenchyma observed in the wood of *T. aurea* and *L. ferrea*, as well as of potting elements in *A. pyrifolium*, are characteristics which, according to Carlquist (2010) and Baas & Wheeler (2011), refer to the specializations that followed different evolutionary paths and allowed the occurrence of angiosperms in many environments. The high frequency of vessel elements and their reduced caliber are also framed as characteristics common to pioneer species that survive in xeric environments (Baas & Wheeler, 2011; Anderegg & Meinzer, 2015). Regardless of the type of adaptation, it is possible to highlight that the anatomical structures of all evaluated species presented common specializations for survival in extreme environments (Carlquist, 2010; Baas & Wheeler, 2011), as well as trade-offs between the best use of water or its storage, similar to that observed in other studies (Pineda-García et al., 2015; Gleason et al., 2016; Apgaua et al., 2017).

The observed relationships between the anatomical functional characters of the four species and the climatic conditions (Figure 6, Table 2) corroborate the hypothesis that different functional groups respond in a significant way to environmental variations, either under water conduction efficiency (axial and radial parenchyma) or wood support (fibers), as observed by Anderegg & Meinzer (2015) Gleason et al. (2016) and Apgaua et al. (2017).

Among the functional groups formed by the four species, it was possible to observe that the anatomy of the wood was influenced by temperature and precipitation (*A. pyrifolium*), precipitation in the dry period (*T. aurea*), or by seasonal variations of precipitation (*L. ferrea*); factors that act on the hydraulic conductivity (Anderegg & Meinzer, 2015) and generate damage that can make these species vulnerable in the near future (Santos et al., 2014). According to Baas & Wheeler (2011), the velocity of the effects generated by the changes in the climate inhibits the hydraulic and mechanical adaptive potential of the secondary xylem of the trees, which restricts their area of occurrence and consequently promotes impacts on the biodiversity of vascular plants. These effects are also capable of reducing the caliber of the potting elements, increasing the fibers density and disorganizing the parenchyma structures, which compromises the water balance as well as the whole photosynthetic process, and generates damage to the species' development (Baas & Wheeler, 2011; Anderegg & Meinzer, 2015). However, in an antagonistic way, *Z. joazeiro* did not show direct dependence of rainfall events, which suggests the existence of other types of adaptations, whether they be metabolic or root (Brunner et al., 2015), and allows the survival of this species in xeric environments.

The environmental influences highlighted for the anatomical characters were also observed in the wood quality indexes, mainly on the Runkel index (RI) (in *A. pyrifolium*, *Z. joazeiro* and *L. ferrea*) and the infiltration index (II) (in *T. aurea*), which warn of the impact of climate on wood quality (Carlquist, 2010; Baas & Wheeler, 2011; Anderegg & Meinzer, 2015; Gleason et al., 2016). In addition to environmental pressures, anthropic action may interfere with these relationships and aggravate their effect, since poor management of the timber waste/residue interferes with their quality and the survival of tree species (Figueirôa et al., 2006).

From the perspective wood use determined herein by the anatomical characters, it was possible to observe that the four species have mainly civil construction and energy use purposes, except for *T. aurea*, which presented quantitative characteristics (such as RI) in carpentry and paper production, but qualitatively had this last purpose discarded given the high presence of parenchyma structures (Runkel, 1952; Foelkel & Barrichelo, 1975; Longui et al., 2009). The use of these species by human communities established in Caatinga areas has extrapolated the limits of their purposes (Silva et al., 2014), contributed to the reduction of vegetated areas (Araújo et al., 2007; Albuquerque et al., 2012) or stagnation in intermediate succession stages of the forests, as observed in Site 1 (Ferraz et al., 2013).

However, there is a need for actions focused on detailed research in Caatinga areas (Albuquerque et al., 2012), mainly in relation to the use of the resources coming from this vegetation (Araújo et al., 2007; Araújo, 2011), as well as the adequate management of timber resources, which may have its quality compromised by the climatic conditions, in addition to anthropic action (cutting regime) (Figueirôa et al., 2006; Brand et al., 2016).

5. CONCLUSIONS

The four species had their anatomical characteristics influenced by the Caatinga environmental conditions, mainly by the precipitation and temperature of the region.

There was the distinction of three functional groups in the wood anatomy of the four species, responding to different environmental variables.

From the observed anatomical characters, it is recommended that *A. pyrifolium*, *Z. joazeiro* and *L. ferrea* have their wood destined to civil construction or to energy use, and *T. aurea* to carpentry or in studies directed at wood technology.

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