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Morphoanatomical Leaf Plasticity Of Tree Species In Riparian Microenvironments

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ABSTRACT

BACKGROUND: Riparian areas show strong environmental heterogenity, which is the result of numerous cycles of flooding and drought. Tree species are able to modify morphoanatomical traits in according with the environmental conditions. **OBJECTIVE:** The present study characterized and evaluated anatomical traits of leaves of two plant species, *Byrsonima intermedia* A. Juss. and *Byrsonima verbascifolia* L. DC, in response to two differents luminosity and water regime.We compared morphoanatomical characteristics in populations of *Byrsonima* Rich. in order to understand about the coexistence of genus in distincts riparian microhabitats. **RESULTS:** According to the anatomical studies *B. intermedia* and *B. verbascifolia* exhibited morphoanatomical plasticity and for both species the greater thicknesses of palisade parenchyma were found in the population from dry microenvironment, not riparian. In relation to the spongy parenchyma, both studied species did not show significant differences of thickness among populations. The length and width of stomata were significantly different for *B. intermedia* and partly for *B. verbascifolia*. The number of stomata varied according to luminosity of microhabitats. In relation to the sclerophylly leaf, *B. intermedia* showed significant differences on leaf length while *B. verbascifolia* showed variation in leaf width. The cuticle varied according to riparian microhabitats. The leaves of *B. intermedia* and *B. verbascifolia* showed uniseriate epidermis, thicker on adaxial surface. The leaf thickness was significantly different for *B. intermedia* and not for *B. verbascifolia*. We found significatives differences in parenchyma and stomata. These anatomical structures are the most sensitive to environmental variations in both species. **CONCLUSION:** We found significatives differences in parenchyma and stomata. These anatomical structures are the most sensitive to environmental variations in both species

INTRODUCTION

The tropical forests comprise vegetal communities distributed accordingly to environmental heterogeneity (Naiman and Décamps, 2005). The establishment of plants in these places occurs by means of microevolutionary processes developed along time (Linhart and Grant, 1996). Depending on the species, individuals from the same population may develop distinct morpho-physiologic characteristics and capabilities to establish themselves in diversified environments, such as the margins of riparian areas (Naiman and Décamps, 1997). This capacity, named phenotypic plasticity, allows that changes in their reproductive and vegetative organs compensate the negative effects of the environment to which they are submitted (Gratani, 2014; Donohue, 2003).

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The riparian areas are composed of microclimatic zones, also named microenvironments or microhabitats (Naiman, 2005; Naiman and Décamps, 1997), which are effetively associated to luminosity (Nascimento *et al*., 2015), to the soil flooding and drying cycles (Mitton *et al*., 1998) and to the pedological alteration (Schilling and Lockaby, 2005; Naiman *et al*., 2005). Generally, the spatial scale of the microenvironments varies with the slope, and it can be within the range of few centímeters up to kilometers (Linhart and Grant, 1996; Savolainen *et al*., 2007). In a study with tree species populations established in different microenvironments, it was observed that there is a distinct morpho-physiological response compared to the adjacent population (Heathcote *et al*., 1987). This response may be attributed to the greater gene flow between individuals (Mitton *et al*., 1998; Rocha Filho and Lomônaco, 2006), in virtue of the presence of pollinators and diffusers adapted to the site (Alcantara and Rey, 2003; Edward, 2005).

Comparative studies of morpho-anatomical characters are important investigation tools for phenotypic plasticity present in several tree species. This plasticity refers to the final product of physiological regulation mechanisms and the leaves, besides being the main organs exposed to the environmental conditions, are more vulnerable to the changes in the environment. Changes in foliar structure in their structures have been the focus of interpretation to the adaptation to the specific microhabitats of riparian areas (Wang *et al*., 2014; Rossato and Kolb, 2010). Thus, the knowledge on the behavior of vegetal species sensitive to the microenvironmental gradients might aggregate information about mechanisms of dispersal and adaptation to these zones, or even verify relationships with the functional and/or ecological groups of such species.

The genus *Byrsonima* Rich. Ex. Kunth. (Malpighiaceae) has a wide distribution in tropical forest ecosystems, with several species occurring in Atlantic Forest and in distinct vegetations of Cerrado (Mamede, 2010). *B. intermedia* A. Juss. is a tree species often found in the Cerrado *sensu strictu,* (Rocha-Filho and Lomonaco, 2006) and rainforests of Brazil and its occurrence is restricted to wet and rocky fields areas (Durigan *et al*., 2011). *B. verbascifolia* (L.) DC., is restricted to the open areas (savannas) of South America from Colombia to southern Brazil (Mamede, 2010). Both species bloom from September to November, and each individual produces 100 to 500 fruit per year (Almeida *et al*., 1998). The density of occurrence varies according to the phytophysiognomy and region (Almeida *et al*., 1998). Its ecological traits are important for the restoration of riparian areas: their colorful flowers have oil glands at the base, attracting many pollinator insects (Sigrist and Sazima, 2004) in addition to the peculiar characteristics of ecophysiology (Durigan *et al*., 2011).

Studies with *Byrsonima* genus relate the association of morphological traits to abiotic stress conditions (fire) in savanna ecosystems (Higgins, 2007). The species present leaf morphology and anatomical structure (thick cuticles, thick parenchyma intercellular spaces) associated with regulation of water loss and energy balance (Higuchi 2007). Nevertheless, there are no published studies about morphoanatomical responses of plants distributed in microenvironments of riparian areas. At the local scale, extreme heterogenity conditions of soil, water and luminous regime might affect the behavior of individual trees of the same population exposed to such conditions. Thus, the success of individuals in establishing in heterogeneous microenvironments might be due to the plastic potencial of the species, acclimatizing morphological and anatomical traits to specific conditions (Alldredge and Moore, 2014; Magellan *et al*., 2013). In this context, this work aimed to test the hypothese that the coexistence of *B. verbascifolia* and *B. intermedia* in riparian microenvironments is due to differences in morphological and anatomical traits.

MATERIALS AND METHODS

Study site:

We conducted the study in riparian areas of Rio Doce river, Minas Gerais State, Brazil. This region have tropical humid climate, and the annual rainfall ranges between 900 and 1500 mm. The most pronounced dry period occurs from July to September (ANA, 2001). The annual average temperatures are high (28 - 30° C) for much of the year and even in the colder months, average temperatures are above 18 ° C. The humidity is high on average higher than 60%, and the daily temperature range is higher than the annual, ranging from 10 to 15 ° C.

Byrsonima species appear in riparian areas of two conservation units, the State Park of Rio Doce - PERD (*B. verbascifolia*, 19°47'05,0 S and 42°35'32,5 W) and the Environmental Station of Peti - PETI (*B. intermedia,* 19°53'34,1S "lat.-43°21'52,6"W.) (Figure 1). In each site, we defined two microenvironments according to the range where the light and the water level reach the vegetation (0-4m) (Mallik *et al*., 2001). Therefore, in the microenvironment of riparian vegetation edge (MMA) the tree population is exposed to flood cycles (dry and wet soil), and the alternating deposition of allochthonous sediments. In the dry microenvironment (MME) the tree population occurs where there is no soil exposure to flooding regime and their hearts are subject to indirect light the upper canopy.

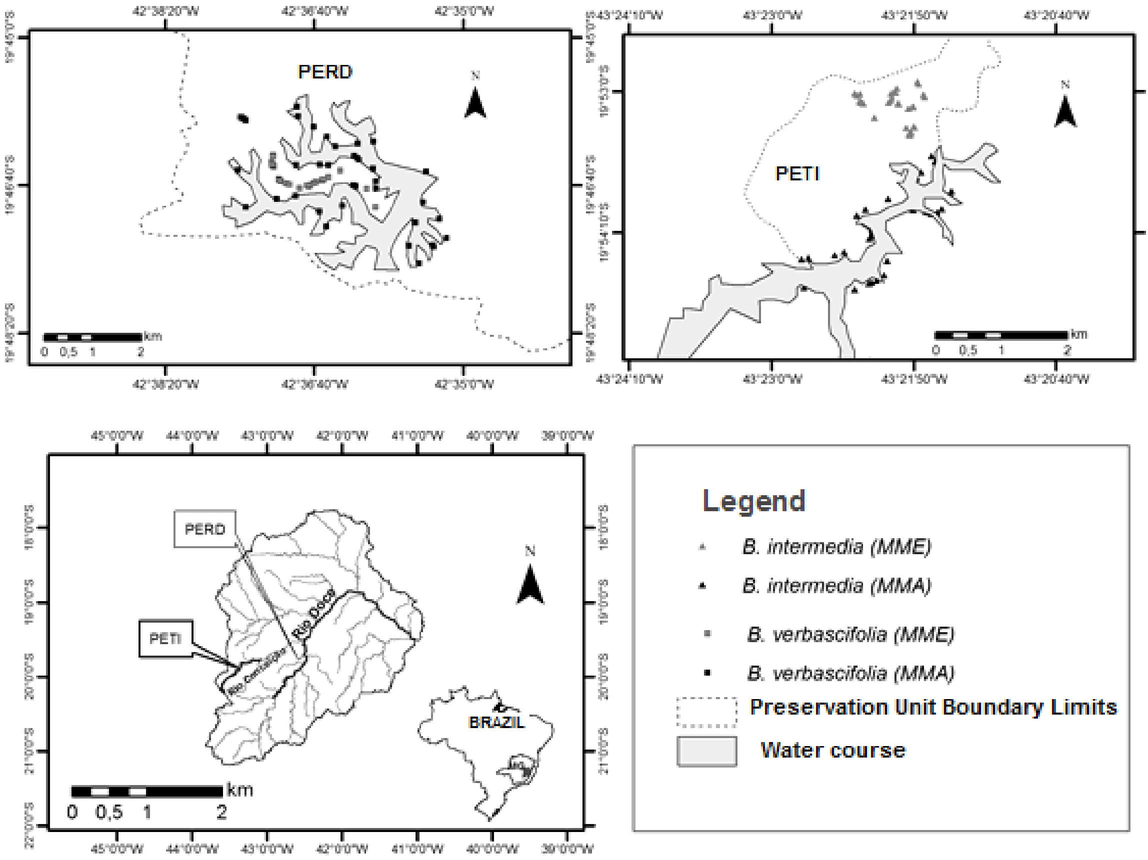

Fig. 1: Location of Protected Areas (PERD and PETI) with the distribution of individuals of Byrsonima Rich. Ex. Kunth. in microenvironments close (MMA) and away from the river (MME) in the Doce River, Brazil.

In the PETI site, the flood period occurs from March to August. In this area the microenvironment MMA have averaged higher incidence of photosynthetically active radiation about 113.86 µmol.m^{-2}.s^{-1}, while the microambeiente MME presented radiation near 43.11µmol.m^{-2}.s^{-1}. In PERD, flooding occurs for four months (October to March). The microenvironments do not have wide differences in the incidence of light luz (MMA = 225,31 µmol.m^{-2}.s^{-1}; MME = 234,10 µmol.m^{-2}.s^{-1}). The incidence of solar radiation was evaluated with Datalogger LI1400 coupled to a light sensor LI190SB model.

Sampling and anatomy:

In each microenvironment, were selected 25-42 individual trees, with a minimum distance of 100 m, to avoid sampled individuals from common parents (Brune, 1981). In each individual tree, four branches were removed in the lower and upper crown.

The sampled leaf material were fixed in fomaldeído solution of acetic acid and 70% ethanol (70 FAA) for 48 hours and then preserved in 70% ethanol (Johansen, 1940).

The anatomical analysis of leaves consisted in conducting cross and paradermic sections with manual microtome aid. Sections were cleared in 50% sodium hypochlorite for 20 minutes subjected to safranin staining in (paradermic sections) and safrablau (safranin solution astra blue and 7.5: 2.5) to obtain cross sections and mounted on slides with 50% glycerol (Kraus and Arduin 1997).

An Olympus U-TVOSXC-3 optic microscope was used, coupled to a PL-A662 digital camera, for recording the sections pictures. These were utilized for measuring the anatomic parameters, utilizing an image analysis program (Imagetool®).

The measured anatomic parameters in the cross sections were a) in the limb - cuticle of adaxial (Cad) and abaxial (Cab) surfaces; epidermis thickness of the adaxial (Ead) and abaxial (Eab) surfaces; cell layer thickness of the palisade (P) and spongy (L) parenchymae and limb thickness (M); b) in the mid rib region - cell diameter of metaxylem (DMX) and protoxylem (DPX); cell layer thickness of the phloem (F).

The calculated the follow anatomic parameters: stomata index, according with Cutter (1986), and stomata density and functionability, according (Castro, 2009).

Data analyses:

Statistical analyzes were performed according to the need of interaction of information obtained on the microenvironments and morphoanatomical characters. The anatomical structures of the populations were compared by paired analysis (t test). Correlation curves were plotted in order to compare the behavior of the anatomical structures between species in their respective riparian microenvironments.

Results:

B. intermedia and *B.verbascifolia* leaves presented a very similar anatomic structure (Figura 2a e 2b). The cuticle is thick in both foliar surfaces. The biggest thickness was achieved in the MMA subpopulation, with 0.38 µm for *B. intermedia* and 0.33 µm for *B. verbascifolia*. A significant difference between the microenvironments was found for cuticle only for *B. verbascifolia*.

In both species, the abaxial surface is thicker than the adaxial surface and both presented regular shape and distinct responses in function of the microenvironments (Table 1). The greatest thickness was found in *B. intermedia*, in both foliar faces, in the MME subpopulation. On the adaxial surface, the average was 9.90 □m and 3.10 µm for the abaxial one. *B. verbascifolia* presented greater epidermis thickness in the MMA subpopulations (subp.), with superior average of 4.70 µm in the adaxial surface, and 2.70 µm in the abaxial surface (Table 1).

The species have uniseriate palisade parenchyma and well developed. The palisade parenchyma presented dimensional variation compared to spongy parenchyma, and in B. intermedia the difference between the microenvironments was significant ($p < 0.01$). Larger values ranged on average 19.20 uM in MMA and lower values were 17.20 µm in the MME. For B. verbascifolia, higher values were also found in MMA population with 14.40 µm. The spongy parenchyma is formed by cells in loose arrangement and irregular distribution, with intercellular spaces (Figure 2b).

Simple multiple-cell not glandular trichomes are present only on the abaxial surface of the leaves of *B. intermedia* (Fig. 2). This characteristic is also present in the abaxial surface of *B. verbascifolia*, although with smaller expression (Fig. 3 and 4).

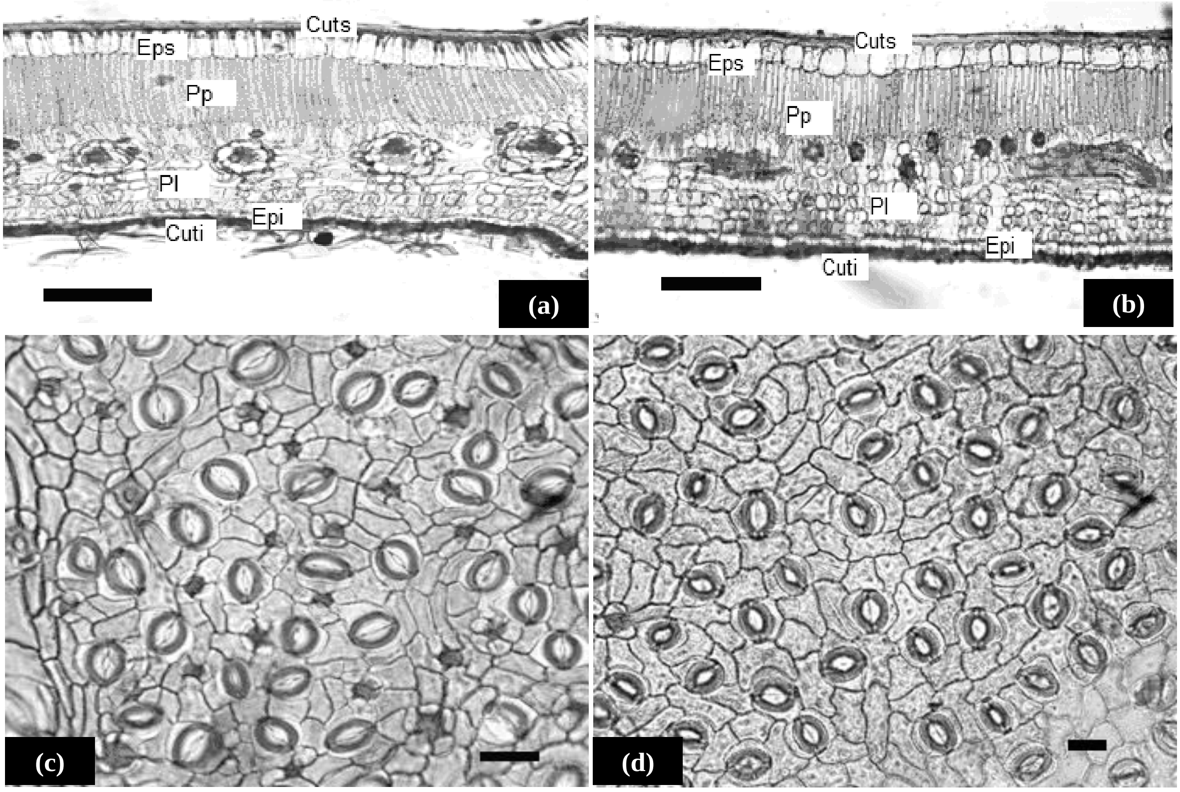

Fig. 2: Morphological and anatomical characters in leaves: Cross section in leaves of B. intermedia (a) and B. verbascicolia (b) Cuts = upper cuticle;. Eps. = Upper epidermis; Pp = palisade parenchyma.; Pl = spongy parenchyma.; Epi. = Lower epidermis; Cuti. = Lo

The leaves of the studied species are hypostomatic with anomocytic stomata (Figura 2c e 2d). The stomata are at the same level as the other epidermal cells; While the subsidiary cells are much smaller than the other cells. Stomatal measurements, such as polar diameter, show that the B. intermedia species presented significant differences, being the highest values found without MMA (12.20 µm). Both tree species showed significant variation in stomatal equatorial diameter (Table 1) between populations. For *B. intermedia* the highest value was found in the population MME (9.10 µm; p =0,01), and for *B. verbascifolia*, the highest value was found in the MMA population (8.60 µm; p = 0.05). In relation to stomatal density, the mean values for *B. intermedia* were 432.4 – 440.1 mm^{-2} and for *B. verbascifolia*, 397.0 – 415.9 mm^{-2} stomate. Regarding the number of cells, there were significant differences for the two species, and the highest values found in the MME (*B. intermedia*, 3907.6 células.mm^{-2}, *B. verbascifolia*, 3331.9 células.mm^{-2}).

Measurements performed in the central axis of the limb showed significant differences between the subpopulations for cell diameter of the protoxylem in *B. intermedia* (p < 0.01) and phloem cell diameter in *B. verbascifolia* (p < 0.01). The biggest values were observed in MME with average diameter of 1.70 µm in the protoxylem and 7.80 µm in the phloem cells. For metaxylem cell diameter, no significant differences were found between the microenvironments for both species (*B. intermedia*, p = 0.83; *B. verbascifolia*, p = 0.637) (Table 1).

Table 1: Variability of foliar anatomic structures of *Byrsonima* Rich. Ex. Kunth. in the respective riparian microenvironments: Cut. – Upper cuticle; Eps. – Superior epidermis; Epi. – Inferior epidermis; Pp. – Palisade parenchyma; Pl. – Spongy parenchyma; Dpe. – Stomata polar diameter; Dee. Stomata equatorial diameter; Dcel. – Cell density; Dest. Stomata density; Dmet. – Metaxylem cell diameter; Dprt. – Protoxylem cell diameter; Efl.- Phloem cell diameter; Efol. – Foliar thickness; Cfol. – Foliar length; Dfol. - Foliar diameter.

Anatomic parameter		*B. intermedia*		*B. verbascifolia*		P-value (Test t)	
		Population					
		MMA	MME	MMA	MME	B.int.	B.verb.
Cut.	µm	3.80 ± 1.60	3.60 ± 1.20	3.30 ± 0.90	2.80 ± 0.60	0.213	<0.01
Eps.	µm	8.70 ± 2.70	9.90 ± 2.00	4.80 ± 1.50	4.70 ± 1.20	<0.01	0.634
Epi.	µm	3.00 ± 0.90	3.10 ± 0.80	2.70 ± 0.70	2.40 ± 0.50	0.326	<0.05
Pp.	µm	17.20 ± 4.30	19.20 ± 3.60	13.80 ± 2.50	14.40 ± 2.60	<0.01	0.081
Pl.	µm	23.40 ± 4.20	24.00 ± 5.10	23.50 ± 6.30	23.20 ± 6.40	0.456	0.752
Dpe.	µm	12.20 ± 1.30	11.90 ± 1.00	11.80 ± 0.80	11.80 ± 1.00	<0.05	0.932
Dee.	µm	8.70 ± 1.00	9.10 ± 0.80	8.60 ± 0.80	8.40 ± 0.80	<0.01	<0.05
Dcel.	n.cel. mm^{-2}	3554.1 ± 558.0	3907.6 ± 559.9	3084.7 ± 380.4	3331.9 ± 370.1	<0.01	<0.01
Dest.	n.estom. mm^{-}	440.1 ± 120.5	432.4 ± 107.7	397.0 ± 101.2	415.9 ± 103.3	0.478	0.155
Dmet.	µm	3.00 ± 0.25	2.90 ± 0.19	2.90 ± 0.25	3.00 ± 0.19	0.83	0.637
Dprt	µm	1.4º ± 0.31	1.70 ± 0.25	1.70 ± 0.19	1.50 ± 0.25	<0.01	0.527
Efl.	µm	9.60 ± 2.70	9.80 ± 2.50	4.60 ± 1.20	7.80 ± 0.49	0.691	<0.01
Efol.	µm	56.10 ± 7.40	59.8 ± 7.10	48.00 ± 8.10	47.50 ± 8.10	<0.01	0.687
Cfol.	Cm	9.23 ± 1.88	8.38 ± 1.28	15.76 ± 2.29	16.32 ± 3.19	<0.05	0.393
Dfol.	Cm	3.37 ± 0.47	3.24 ± 0.53	5.73 ± 0.87	6.26 ± 1.13	0.285	<0.05

The foliar limb thickness of *B. intermedia* is greater than *B. verbascifolia* (Table 1). Significant differences were found only between the subpopulations of *B. intermedia* (subp. MMA = 56.10 µm; subp. MME = 59.80 µm; p < 0.01). *B. verbascifolia* did not present significant differences between the subpopulations (pvalue = 0.687). The foliar limb length in *B. intermedia* was significantly different between the subpopulations (Tab. 1). The biggest values were obtained in the subp. MMA (9.23 cm) compared to the subp. MME (8.38 cm). *B. verbascifolia* presented significant differences in foliar diameter values (Subp. MMA = 5.73 cm; Subp. MME = 6.26; p = 0.05).

When assessing the stomatal index, a significant difference was observed between the subpopulations only for *B. intermedia* (p = 0.04) (Fig. 3 and 4). For the two species, lower stomatal index values were found for the individuals in the MME microenvironment (*B. intermedia* = 10.18%; *B. verbascifolia* = 11.10%). Regarding stomata functionality, the values found for studied species did not present the same response . For *B. intermedia*, the biggest values were found in MMA with 1.41 while for *B. verbascifolia* 1.42 was found in MME.

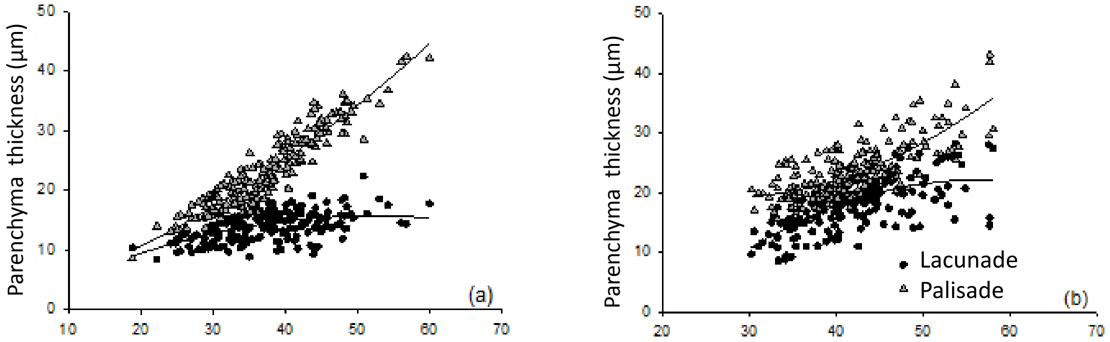

Fig. 3: Correlation between leaf thickness and thickness of the parenchyma: (a) palisade (Y=32.790+0.0309x+0.0247x2; R2 = 0.40; p < 0.001) and spongy (Y=30.963-0.897x+0.0169x2; R2 = 0.57; p<0.001) em B. intermedia; (b) palisade (Y=-0.918+0.638x-0.00612)

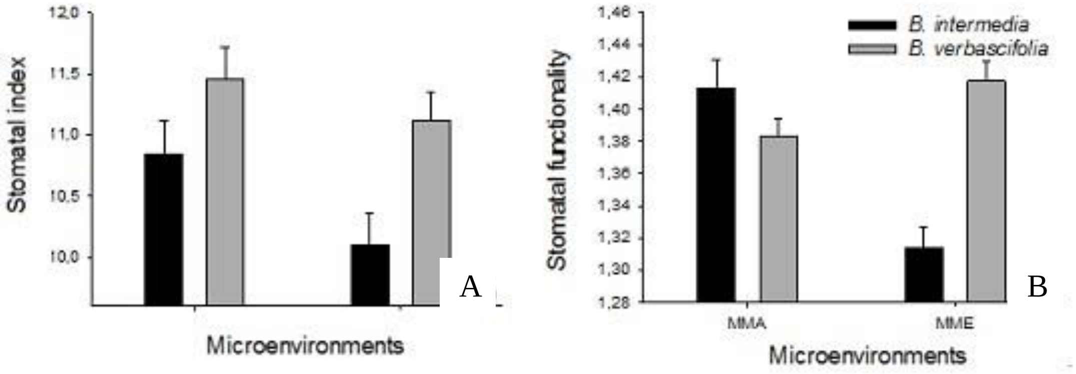

Fig. 4: Stomatal characteristics of tree species. Stomatal index B. intermedia, p = 0.04 e B. verbascifolia, p = 0.33 (a); Stomatal functionality B. intermedia, p < 0.05 e B. verbascifolia, p < 0.05 (b)

Discussion:

According to the anatomical studies performed in leaves of *B. intermedia* and *B. verbascifolia,* their subpopulations present morpho-anatomic plasticity in response to the distinct riparian microenvironments, and this may significantly reflect in the metabolic activity of the plant (Boardman 1977). These anatomic differences found may be caused by the soil properties, like nutrients and moisture (Rossato and Kolb, 2006). This may possibly yield physiologic adaptations in different levels (Dias *et al*. 2007).

In the far microenvironment of the river, the nutrients are more available in the soil solution and hence to the roots (Casanova, 2015). Fair *et al*. (2005) evaluated the anatomical plasticity *Xilopia brasiliensis* Mart. observed that the palisade parenchyma tissue was greater plasticity in response to climate station, the size of the tree and the type of environment. They also observed that the leaves with thicker palisade parenchyma showed high coefficient of light extinction, so it is expected that such sheets have higher photosynthetic rate (Bolhar-Nordenkampf and Draxler, 1993).

About spongy parenchyma, studies with the species showed that its thickness did not present significant differences between the subpopulations. In a study with *Erythroxylum* populations in different types of sandbanks, Mantuano *et al*. (2006) also did not observe significant differences between microhabitats. In general, environments of greater water availability of *B. verbascifolia* presented thicker y parenchyma, which suggests a plant mechanism to increase gas concentration in the mesophile and consequently promote the increase on its photosynthetic rate (Pearce *et al*. 2006).

Length and stoma diameter indicates greater plasticity of the species *B. intermedia* compared to *B. verbascifolia*. The polar diameter may be associated with water saving that individual trees present as the environment in which they occur (Nolf *et al*., 2014; Justo *et al*., 2005). Leaves with smaller stomata have higher water use efficiency and the difference in the diameter of the stomata opening is greater control over the distribution of water than on the diffusion of CO_2 (Abrams *et al*. 1994). The change in the equatorial diameter of the stoma found in *B. intermedia* indicates that this structure is more flexible than the polar diameter due to the variation of cellular turgor, which is decisive for the opening movement and stomatal closure (Taiz and Zeiger, 1998). The stomatal frequency varied according to photosynthetic photon flux density (PPFD) in the microenvironments, in the areas with higher luminosity stomatal frequency was higher (Rossato and Kolb, 2010). This feature promotes efficiency in gas exchange because it is associated with stomatal conductance and consequently with photosynthetic rates (Galmes *et al*. 2007).

The characteristic of cuticle varied according to the submitted environmental conditions, and found the greatest thickness of the structure in higher light environments. This probably show the sensitivity of the cuticle brightness in natural environments. This feature assists the species to colonize and become established in different environments (Fahn and Cutler, 1992). The temperature must also be a stimulus responsible in changing the thickness (Rossato and Kolb, 2010). At higher intensity light environments cuticle as a protection that prevents the temperature rise in the mesophyll and prevents impairment of the organs of metabolism (Fahn and Cutler, 1992).

The leaves of *B. intermedia* and *B. verbascifolia* presented epidermis thicker on the adaxial surface. This feature has been marked in the species *B. intermedia*, possibly guarantee their coexistence in higher ambient light compared to the occurrence of *B. verbascifolia* environments. Rossato and Kolb (2010) observed in *Gochnatia polymorpha* (Less.) the third layer of epidermis in leaf adaxial surface with a significant association to light. Other authors found an association thickness of epidermis with soil fertility (Feller, 1996). The occurrence of different thicker leaf types in species of these of population can reflect their adaptations to different environmental conditions, and present results indicate that the species growing in different environments indeed significant differences in the composition intrapopulation (Garssen *et al*., 2015).

The low stomatal index for the studied populations can be attributed to evaporative demand of difference between the two microenvironments because the MME showed no edge effect characterized by high density of plants, possibly resulting in a drier microclimate, as confirmed by Justo *et al*., (2005). According Cutter (1986), the stomatal index is usually constant for a given species, and is mainly affected by moisture.

The blade thickness was significantly different for *B. intermedia* ($p < 0.001$) and indifferent to *B. verbascifolia* ($p = 0.687$). According to Yamashita *et al* (2002), small variations in the thickness of the sheet result in significant changes in photosynthesis in some species, while others show great plasticity in leaf thickness with little variation in photosynthetic capacity. In a study of *Xylopia brasiliensis* Mart. a positive correlation was observed between the assimilation of CO_2 and the blade thickness (Justo *et al*., 2005). Palva *et al*. (2003) observed that some plants have different leaf morphology in response to light in these environments.

About the contribution of the parenchyma in the sheet thickness, the palisade and spongy parenchyma were important structures that differentiate tree species (Figure 3a and 3b). Similar behaviors have been found in plant species of the Mediterranean (Gratani *et al*. 2006). The results also show that both tree species had the thickest parenchyma in populations of MME, which may be associated with bright light and soil properties. On the other hand, individual trees of MMA had the highest coefficient of variation in the thickness of the parenchyma, which is possibly associated with greater environmental heterogeneity of this microenvironment, such as brightness (Klich, 2000) and water availability in the soil system (Larcher, 2003). This can promote a new discussion about the capacity that the new individuals acquire for establishing in these environments, especially to the degree of exposure to the system of flooding and luminosity, since they are subject to an important to improve the source of morphogenetic variation capable of obeying different degrees of tolerance physiological (Kissmann, 2014). In order to infer about the characteristics of the parenchyma there is some relation that these populations converged to different paths of the functional adaptation (Kawecki & Ebert, 2004), future investigations are necessary.

Therefore, tree species from differents riparian microenvironments have morphoanatomical traits which allow various phenotypic changes and to transfer to their progenies (Magalhães *et al*., 2013). And through management reforestation of ripariass areas programs, these progeny can be inserted in these areas according to their source environment and time necessary at the stabilishment (Zou *et al*., 2009), which might contribute to the increased success of individuals for the recovey of degraded area an for economical purposes (Costa *et al*., 2015; Nolf *et al*., 2014). In this sense, studies on the heritability of morphological and anatomical features in tree species should be carried out with the aim of supporting information on the relevance of tree species in riparian microhabitats, especially representation in the collection of propagules at the population level and at the microscale (Sterk *et al*., 2016).

Conclusion:

The species B. intermedia and B. verbascifolia shownd similar foliar anatomical traits but B. intermedia shown higher morpho-anatomic plasticity for the upper epidermis and palisade parenchyma, stomatal diameter, diameter of protoxilema, cell density and leaf length and leaf thickness.On the other hand, B. verbascifolia shown significant variation in cuticle thickness, stomatal and cellular diameter, phloem thickness and leaf diameter. Considering the thickness of the parenchyma, it was observed that B. intermedia and B. verbascifolia presented a pattern as a function of the heterogeneity of the microenvironments, which represents an important characteristic for ecology studies of arboreal species in riparian areas.

After successive generations, local adaptations in plant anatomy and physiology may arise in response to the specific natural selection of different habitats, leading to ecotypes. The implementation of criteria for the management of seedlings as a function of these microenvironments seems to be an important variable in programs for the recovery of degraded areas.

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