

Variations in leaf characteristics of two species of *Miconia* in the Brazilian cerrado under different light intensities

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Abstract: The relationships between several leaf attributes (leaf area, mass, volume, density, thickness, organic matter content, anatomy and leaf specific mass) in two sympatric shrub species, *Miconia ibaguensis* and *M. stenostachya* (Melastomataceae), in Brazilian cerrado were explored. Leaf traits were assessed in two environments : a sun-exposed cerrado and in a shaded understory riparian forest. Area, mass, density and thickness of the leaves of both species varied significantly between the two habitats (t-tests, $p < 0.05$ all). Variations in leaf specific mass were correlated with leaf mass, density, and thickness in both species (Pearson correlation, $p < 0.001$). Fully sun-exposed leaves were denser and thicker due to an increase in the length of the palisade parenchyma cells (*M. ibaguensis*: sun = $93 \pm 3 \mu\text{m}$; shade = $61 \pm 2 \mu\text{m}$; *M. stenostachya*: sun = $150 \pm 5 \mu\text{m}$; shade = $92 \pm 4 \mu\text{m}$). *Miconia ibaguensis* and *M. stenostachya* presented an increase of 13% and 17% in stomatal density in the sunny habitat, respectively. *Miconia ibaguensis* also showed an increase of 57% in trichome density under high light conditions. These two species showed high leaf structure plasticity in relation to environmental conditions.

Resumen: Se estudiaron las relaciones de varios atributos de las hojas (área, peso, volumen, densidad, espesor, materia orgánica, anatomía y peso específico foliar) de dos especies arbustivas simpátricas, *Miconia ibaguensis* y *M. stenostachya* (Melastomataceae), expuestas al sol y en la sombra soto de en el bosque del cerrado brasileño. El área, peso, densidad y espesor de las hojas de ambas especies variaron significantivamente entre los dos habitats (best t, $p < 0.05$). Las variaciones en el peso específico foliar estuvieron correlacionadas con la masa, densidad y espesor de las hojas en ambas especies (Coeficiente de correlación de Pearson, $p < 0.001$). Las hojas expuestas completamente al sol fueron más densas y con mayor espesor debido al aumento de la extensión de las células del parénquima en empalizada (*M. ibaguensis*: sol = $93 \pm 3 \mu\text{m}$; sombra = $61 \pm 2 \mu\text{m}$; *M. stenostachya*: sol = $150 \pm 5 \mu\text{m}$; sombra = $92 \pm 4 \mu\text{m}$). *M. ibaguensis* y *M. stenostachya* presentaron un aumento en la densidad de estomas de 13% y 17%, respectivamente; en el habitat con sol, *M. ibaguensis* presentó un aumento de 57% en la densidad de tricomas. Estas dos especies mostraron una alta plasticidad foliar en relación a las condiciones ambientales.

Resumo: Foram estudadas as relações entre os vários atributos foliares (área, massa, volume, densidade, espessura, matéria orgânica, anatomia e massa foliar específica) de duas espécies arbustivas simpátricas, *Miconia ibaguensis* e *M. stenostachya* (Melastomataceae) no cerrado brasileiro. As características foliares foram avaliadas em dois ambientes: cerrado exposto ao sol e à sombra do subbosque da mata ripária. A área, massa, densidade e espessura foliares das duas espécies variaram significantivamente entre os dois habitats (teste t, $p < 0.05$). As variações na massa foliar (MFE) estavam correlacionadas com a massa, densidade e espes-

foliares em ambas as espécies (Correlação de Pearson, $p < 0.001$). As folhas completamente expostas ao sol apresentaram-se mais densas e espessas devido ao aumento do comprimento das células do parênquima paliçádico (*M. ibaguensis*: sol = 93 ± 3 mm; sombra = 61 ± 2 mm; *M. stenostachya* : sol = 150 ± 5 mm; sombra = 92 ± 4 mm). As folhas de *M. : ibaguensis* e *M. stenostachya* apresentaram um aumento na densidade estomática de 13% e 17%, respectivamente, no habitat ensolarado. A *M. ibaguensis* apresentou um aumento de 57% na densidade dos tricomas sob essas condições. Essas duas espécies mostraram uma alta plasticidade foliar em relação às condições ambientais.

Key words: Cerrado, leaf plasticity, light intensity, *Miconia ibaguensis*, *Miconia stenostachya*, morphological adaptations.

Introduction

Cerrado is a type of vegetation which predominates on the Central Brazilian Plateau, similar to savanna in physiognomy. It ranges from pure grassland (campo limpo) to nearly closed canopy of medium height trees overlying grass (cerrado, campo cerrado and campo sujo) (Lopes & Cox 1977). There are physiognomic gradients based on the amount and size of woody plants. The woody components of the Brazilian cerrado are typically sclerophyllous, resistant to annual fires, and seem to have access to the water table, therefore, remaining photosynthetically active throughout the year (Medina & Silva 1990). The differences in physiognomic gradients of cerrado have been hypothesized as an evolutionary consequence of selection pressure imposed by the oligotrophic soils (Lopes & Cox 1977).

A common feature of the cerrado is the presence of narrow riparian forests along rivers, washes, and creeks (Meguro *et al.* 1996). In these riparian forests, light intensity is lower on shrub and herb strata, and water and nutrient availability are higher (Eiten 1990). Some species are found in cerrado and in riparian forest, but they show structural modifications. These features are the basis for the study of leaf plasticity under different environmental conditions in habitats separated only by a few meters.

Leaves of many plant species are known for their great growth plasticity varying in morphology and anatomy, as well as in physiology. For a particular plant species phenotype may change in response to nutrient and/or moisture availability (Jurik *et al.* 1982; Witkowski & Lamont 1991),

temperature (Ku & Hunt 1973), altitude (Korner 1989), and light intensity (Nobel *et al.* 1975; Sims & Pearcy 1992; Upadhyaya & Furness 1994). These variations may involve changes in life form (Garnier & Laurent 1994), leaf pubescence (Ehleringer & Mooney 1978), leaf area (Jurik *et al.* 1979), leaf thickening (Turner 1994), and photosynthetic rate (Holmes & Cowling 1993; Romero-Aranda *et al.* 1997).

This study concerns two common sympatric cerrado shrubs species, *Miconia ibaguensis* (Bonpl.) Triana and *Miconia stenostachya* Schrank & Mart. ex DC. (Melastomataceae), that have been found growing together in sunny and shady habitats. *Miconia ibaguensis* is primarily from riparian forest while *M. stenostachya* is from campo cerrado (Martins *et al.* 1996). These species vary in architecture, which suggests differences in leaf structure. Few studies have examined natural variation in leaf anatomy in relation to light acclimation. The aim of the present work was to determine the variations of leaf characteristics of these two shrubs in two different light intensity habitats. These studies may elucidate aspects of inter- and intra-specific adaptation to heterogeneous light environments in Brazilian cerrado.

Methods

Study site

The study was conducted in the Serra do Cipó National Park, Minas Gerais, southeastern Brazil at the southern end of the Espinhaço Mountains ($19^{\circ}20$ S, $43^{\circ}44$ W) at 800 m altitude above sea level (Fig. 1). The climate is tropical, with moist and warm summers, and with a de-

fined dry season (Fig. 2). The annual rainfall averages 1600 mm.

Site characteristics

Habitats studied were selected by their distinctiveness in light intensity. They were categorized by photosynthetic photon flux density (PPFD), measured with quantum sensors LI-189, as : (a) sunny habitat (integrated PPFD of $70 \text{ mol m}^{-2} \text{ day}^{-1}$) and (b) shady habitat (integrated PPFD of $6.8 \text{ mol m}^{-2} \text{ day}^{-1}$). The sunny habitat is located in "campo cerrado" that consists of a continuous grass cover with open or sparse shrubs or low trees, which cover less than a third of the surface. *Miconia ibaguensis* and *M. stenostachya* are approximately 1 m high in this habitat distributed in distinct groups. The shady habitat is located in a riparian forest, composed of medium tall (5 - 7 m) arboreal forms with either closed or semi-open tree canopy. In this habitat *M. ibaguensis* is nearly 2.5 m high, while *M. stenostachya* may have a procumbent stem; both are components of the riparian

forest understorey.

The habitats were also characterized in relation to the relative humidity (%), vapor pressure deficit (Kpa), and soil fertility (Table 1). All environmental data presented were obtained, in one single day, between 7:00 a.m. and 5:00 p.m. every 30-minute in the middle of spring (October 1996). Relative humidity (%) and vapor pressure deficit (Kpa) of the air were obtained with a psychrometer (ICOTERM). The amount of soil organic matter (SOM) was determined after the incineration of three soil samples at 500°C for two hours, the percentage of SOM being the difference between the weights. The pH was determined by the method of Raij & Quaggio (1983). We used the Student t-test to statistically compare all the leaf traits under the two distinct environments (Zar 1984).

Leaf attributes

In each site, five random mature leaf samples (5th node under shoot apex) of ten plants were taken per species. Leaves were oven dried at 70°C for a week to obtain leaf mass (mg) and leaf area

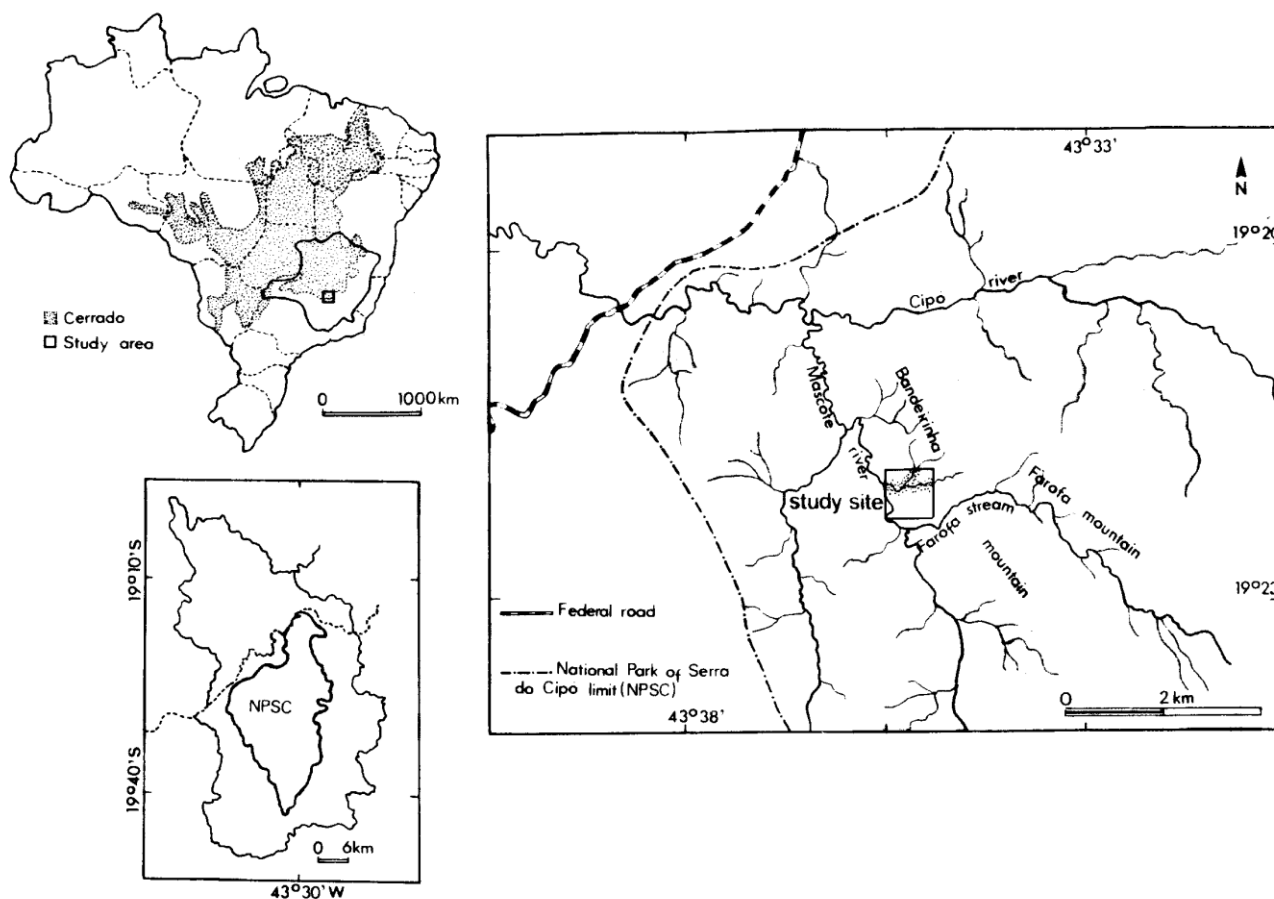


Fig. 1. National Park of Serra do Cipó, Minas Gerais, southeastern Brazil, where the study site was located.

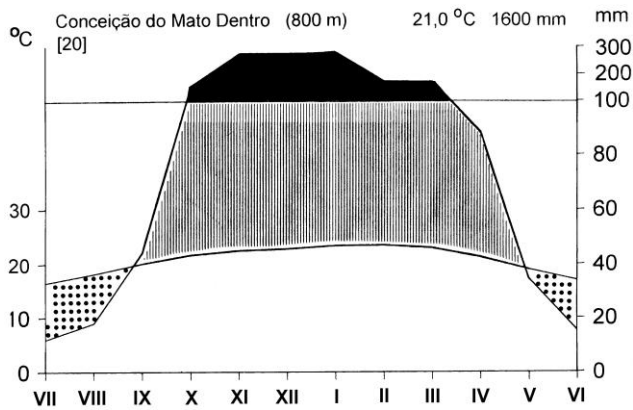


Fig. 2. Climate diagram for Conceição do Mato Dentro, at 800 m altitude, Serra do Cipó, southeastern Brazil. (black areas = perhumid season, vertical shading = relatively humid season, dotted = period of relative drought for climate region concerned).

(cm^2). Leaf area was obtained using an area meter (model MK2, Delta T Devices). Leaf specific mass (LSM), the most widely used index of sclerophylly, was calculated based on leaf mass and area (g mm^{-2}), while leaf density (g mm^{-3}) was calculated by dividing LSM by leaf thickness (Witkowski & Lamont 1991). Leaf thickness (m) was obtained from leaves fixed in alcohol 70% and measured midway between the margin and the midrib at the widest part of leaf. Major leaf veins were avoided. Leaf volume (mm^3) was calculated as the product of leaf area and mean leaf thickness (Garnier & Laurent 1994). The content of leaf organic matter (mg cm^{-2}) was determined by incineration of 0.2 g of tissue at 500°C for 2 h and the chlorophyll content (mg cm^{-2}) was obtained as Lichtenthaler & Wellburn (1983).

Five random mature leaf samples from each of the ten selected plants were fixed in alcohol 70%

and then transferred to Jeffrey Solution (Johansen 1940) for epidermis dissociation, stomata counting, and measurements of trichome density. Ten fields of view of known area (1 mm^2) were examined per leaf and the mean counts converted to stomata and trichome density. Mesophyll comparisons were made from leaf transverse sections in paraffin. Cross sections $10 \text{ }\mu\text{m}$ thick were cut with a microtome, and slides with mounted tissue were stained with Blue-Astra and Fuchsin (see Johansen 1940). Leaf anatomical features and thickness were then quantified under a microscope with a micrometer eyepiece. Cell counting was done using the number of cells over ten lines (1 mm) for palisade parenchyma and number of cells per mm^2 for spongy parenchyma on ten different sections from each species in both exposed and shaded sites. We used Pearson linear correlations to analyze the relationship between LSM and the various leaf attributes of the plant species (Zar 1984).

Results

In general, *M. ibaguensis* and *M. stenostachya* showed consistent differences in leaf area, volume, LSM, thickness, and organic matter content between sunny and shady habitats (Table 2). The area of leaves in the shady habitat of both species was 70% and 12% greater than leaves in sunny habitat, respectively. Leaves of *M. ibaguensis* in the shady habitat had 20% more volume than leaves of sunny habitat; in contrast, leaves of *M. stenostachya* from sunny habitat had 91% more volume than leaves of plants in the shady habitat. The dry mass of leaves of *M. stenostachya* in the sunny habitat was 92% greater than leaves in the shady habitat while *M. ibaguensis* showed no sta-

Table 1. Soil and environmental characteristics ($\bar{X} \pm \text{SE}$) of the habitats studied in the Serra do Cipó, Brazil. (Data were obtained in one single day, between 7:00 a.m. and 5:00 p.m. every 30-minute in the middle of spring (October 1996).

Traits	Cerrado	Riparian Forest
Soil (10-20 cm)		
Organic Matter (%)	$1.07 \pm 0.00 - 0.81 \pm 0.00$	$1.31 \pm 0.03 - 1.13 \pm 0.01$
pH	$4.99 \pm 0.01 - 4.95 \pm 0.04$	$4.81 \pm 0.01 - 5.03 \pm 0.03$
Environmental (min - max.)		
Air Relative Humidity (%)	37 - 65	43-73
Vapor Pressure Deficit (KPa)	2.06 - 4.25	1.94 - 2.99
Air Temperature ($^\circ\text{C}$)	18.0 - 31.5	17.0 - 24.0
Integrated 11-HR PPFD ($\text{mol.m}^{-2}.\text{day}^{-1}$)	70.0	6.8

tistical differences between the habitats. Plants in sunny habitat had leaves with higher LSM and density compared to leaves of shady habitat (Table 2). The same pattern was observed in organic matter content which was 77% greater in *M. ibaguensis* and 114% greater in *M. stenostachya* in the sunny habitat than in the shady habitat. Likewise, leaves of both species in the sunny habitat were thicker than those in the shady habitat (Table 2). The chlorophyll content for both species was higher in shady than in sunny habitat (Table 2).

LSM did not correlate with leaf area, but correlated significantly with volume in leaves in the shady habitat of both species (Table 3). Likewise LSM correlated significantly with leaf thickness only in the shady habitat for both species (*M. ibaguensis* $r = 0.66$; *M. stenostachya* $r = 0.54$).

The differences in LSM were influenced by changes in the thickness of cuticle, epidermis, pa-

lisade, and spongy parenchyma. All anatomical parameters measured differed between sunny and shady habitats in both species. Structural development of leaf mesophyll in the sunny habitat was greater compared to shady habitat. The differences in the development of the mesophyll were probably caused by an increase in the tissue thickness, in the number of cells per area, and in the cell size (Table 4).

Leaves of *M. ibaguensis* in the sun were 20% thicker than leaves of plants in the shady habitat, while leaves of *M. stenostachya* in the sunny habitat were 100% thicker than those in the shady habitat (Table 4). Although the epidermis did not differ in thickness for *M. ibaguensis*, the thickness of leaf cuticle in the sunny habitat contributed to an increase in the leaf thickness in this species, and for *M. stenostachya* cuticle and epidermis were thicker in sunny habitat (Figs. 3 and 4 and Table 4). The thickness of mesophyll of both species in

Table 2. Leaf traits ($X \pm SE$) of *Miconia ibaguensis* and *M. stenostachya* (Melastomataceae) in sunny and shady habitats. (Test t, * = $P < 0.05$ and NS = not statistically significant, LSM denotes leaf specific mass).

Leaf Traits	<i>Miconia ibaguensis</i>		<i>Miconia stenostachya</i>	
	Sun	Shade	Sun	Shade
Structural traits				
Area (cm ²)	20.6 ± 0.76	34.9 ± 1.33*	34.1 ± 1.35	38.3 ± 1.65*
Volume (mm ³)	404 ± 17	484 ± 21*	940 ± 42	491 ± 24*
Dry mass (mg)	307 ± 12	299 ± 14 ^{ns}	735 ± 32	383 ± 20*
L.S.M. (g mm ⁻²)	151 ± 5	85 ± 2*	214 ± 3	99 ± 3*
Density (g mm ⁻³)	786 ± 26	616 ± 11*	792 ± 19	780 ± 18 ^{ns}
Thickness (m)	173 ± 3	142 ± 3*	273 ± 17	132 ± 3*
Chemical traits				
Chlorophyll content (mg cm ⁻²)	10.2 ± 0.9	14.8 ± 1.9*	12.8 ± 1.2	15.6 ± 0.8*
Organic matter content (mg cm ⁻²)	14.5 ± 0.22	7.7 ± 0.05*	20.0 ± 0.01	9.3 ± 0.03*

Table 3. Linear (Pearson product moment) correlations between leaf specific mass (LSM) and various leaf traits of *Miconia ibaguensis* and *M. stenostachya* (Melastomataceae) in sunny and shady habitats. (* = $P < 0.05$ and ns = not statistically significant), different letters indicate significant differences between habitats (Test t, $P < 0.001$).

Leaf Traits	<i>Miconia ibaguensis</i>		<i>Miconia stenostachya</i>	
	Sun	Shade	Sun	Shade
Area	-0.255 ^{ns a}	0.194 ^{ns b}	0.187 ^{ns a}	0.150 ^{ns ak}
Volume	-0.136 ^{ns a}	0.401 ^{* a}	0.148 ^{ns a}	0.350 ^{* a}
Dry mass	0.526 ^{*a}	0.632 ^{*a}	0.483 ^{*a}	0.559 ^{*a}
Density	0.833 ^{*a}	0.750 ^{* b}	0.606 ^{*a}	0.572 ^{* b}
Thickness	0.273 ^{ns a}	0.658 ^{* b}	-0.016 ^{ns a}	0.538 ^{* b}

the sunny habitat was greater than in shady habitat. This was caused by an increase either in the palisade parenchyma and/or in the spongy parenchyma. The leaf mesophyll of *M. ibaguensis* was thicker in the sunny habitat mainly because of the increased thickness of the palisade parenchyma, which reflects increased cell number and length while the spongy parenchyma did not differ between plants in the habitats (Fig. 3 and Table 4). In *M. stenostachya* the increase in thickness of the mesophyll was influenced by both parenchyma. The palisade parenchyma increased two more cell layers and the spongy parenchyma was significantly thicker because of the increased number of cells, as well as the increased cell width and length (Fig. 4 and Table 4). Cells of the spongy parenchyma of this species were larger and of irregular shape (due to branching). In addition, the distance between veins was reduced forming cavities where the stomata were protected by trichomes (Fig. 4).

Both species were hypostomatous in both habitats. The number of stomata per leaf area in plants in shady habitat was significantly lower than those in sunny habitat (Table 4). *Miconia*

ibaguensis and *M. stenostachya* had trichomes only on abaxial leaf surface, and their number varied significantly between the species, being more in *M. stenostachya*. Leaves of *M. ibaguensis* had more trichomes in sunny habitat than in shade, however, for *M. stenostachya* no statistically significant differences in trichome density between the habitats were observed (Table 4). The ratio trichome/stomata for *M. ibaguensis* was higher in sunny habitat (0.021) than in shady habitat (0.008). In spite of this, *M. stenostachya* showed a slightly greater trichome/stomata ratio in shade (0.677) than in sun (0.551).

Discussion

Light acclimation may be mediated by distinct mechanisms that involve structural, physiological and biochemical changes (Chazdon & Kaufmann 1993). Plants of both species studied had larger leaf thickness, higher density, and higher LSM in sunny habitat, in which moisture and nutrient availability were lower, in agreement with several experimental studies (e.g., Boardman 1977; Sims

Table 4. Some anatomical parameters leaf stomatal density (stomata. mm⁻², X ± SE, n = 10 plants), and leaf trichome density (trichomes. mm⁻²; X ± SE, n = 10 plants) in *Miconia ibaguensis* and *M. stenostachya* (Melastomataceae) in sunny and shady habitats) (significance level of student t-test for comparison of means of each species; * = P < 0.05 and ns = not statistically significant).

Leaf Traits	<i>Miconia ibaguensis</i>		<i>Miconia stenostachya</i>	
	Sun	Shade	Sun	Shade
Total leaf thickness (m)	173 ± 3	142 ± 3 *	273 ± 7	132 ± 3 *
Cuticle thickness (m)	4	2 *	6	4 *
Upper epidermis thickness (m)	8	8	18	16 *
Lower epidermis thickness (m)	7	7	7	8 *
Mesophyll thickness (m)	154 ± 3	122 ± 3 *	242 ± 7	104 ± 3 *
Palisade Parenchyma				
Thickness (m)	93 ± 3	57 ± 1 *	150 ± 5	46 ± 2 *
First layer cell				
Cell number (mm ⁻¹)	71 ± 2	60 ± 1 *	55 ± 1	51 ± 1 *
Cell width (m)	16 ± 1	17 ± 1 ns	20 ± 1	19.0 ± 0.1 ns
Cell length (m)	62 ± 2	41 ± 2 *	88 ± 1	30 ± 2 *
Spongy Parenchyma				
Thickness (m)	61 ± 2	65 ± 3 ns	92 ± 4	58 ± 4 *
Cell number (mm ⁻²)	2170 ± 67	1960 ± 64 *	1770 ± 98	1360 ± 78 *
Cell width (m)	26 ± 1	26 ± 1	25 ± 1	32 ± 2 *
Cell length (m)	18 ± 1	16 ± 1 ns	23 ± 1	17 ± 1 *
Stomatal density (stomata mm ⁻²)	289 ± 10	251 ± 7 *	316 ± 1	263 ± 5 *
Lower surface trichome density (trichomes mm ⁻²)	6 ± 1	2 ± 1 *	174 ± 7	178 ± 3 ns

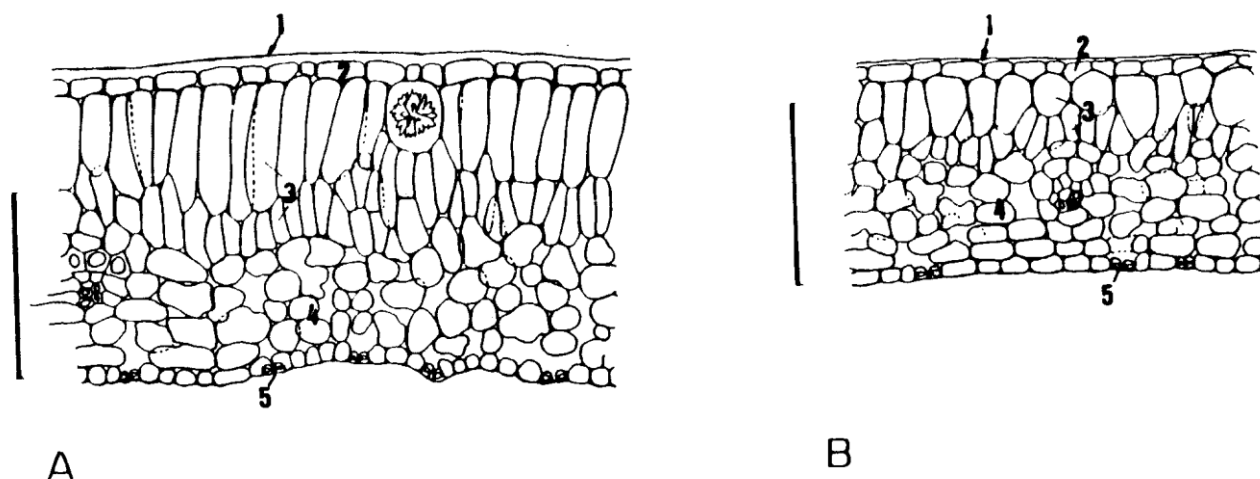


Fig. 3. A cross section of *Miconia ibaguensis* leaf in the sunny habitat (A) and in the shady habitat (B). 1, cuticle; 2, epidermis; 3, palisade parenchyma; 4, spongy parenchyma; 5, stomata. Bar = 100 μ m. (x 250).

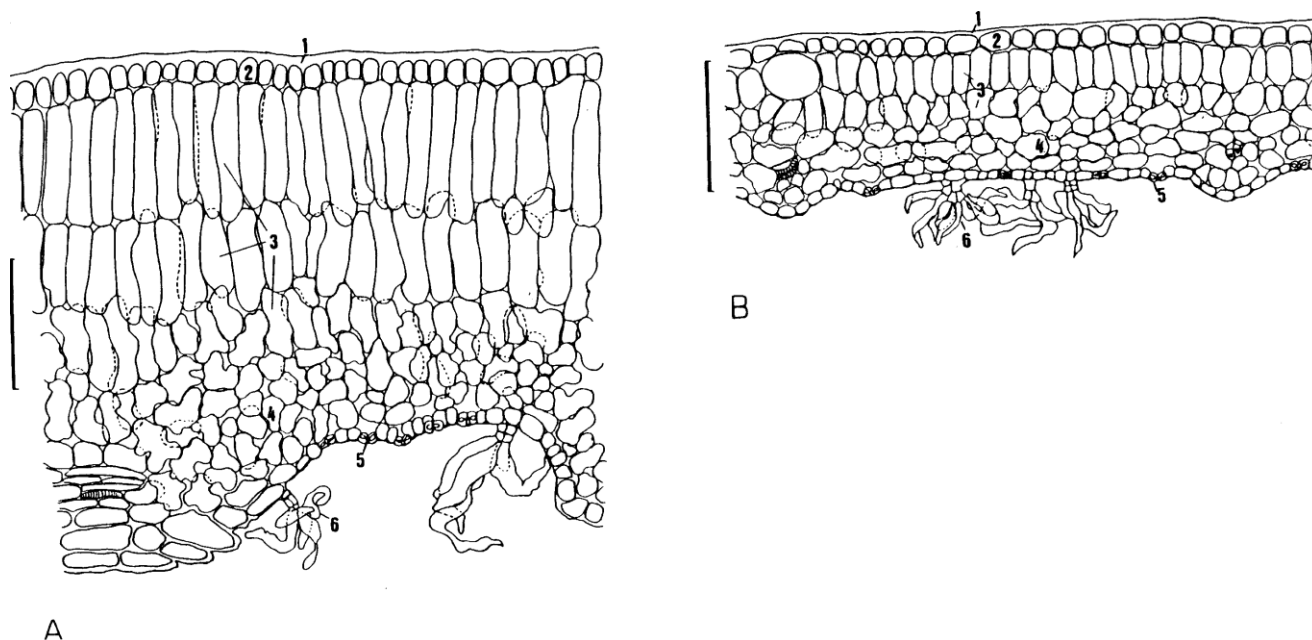


Fig. 4. A cross section of *Miconia stenostachya* leaf in the sunny habitat (A) and in the shady habitat (B). 1, cuticle; 2, epidermis; 3, palisade parenchyma; 4, spongy parenchyma; 5, stomata; 6, trichomes. Bar = 100 μ m. (x 250).

& Pearcy 1992; Witkowski & Lamont 1991). Plants in the understory of the riparian forest had thinner leaves resulting in greater area but lower density and LSM as reported by Corré (1983).

Our data showed that there was no significant relationship between LSM and leaf thickness in either species studied in sun-exposed cerrado. However, for plants from understory LSM was positively correlated with leaf thickness. Con-

trasts between the correlations of LSM and thickness have been reported in several studies (e.g., Dijkstra & Lambers 1989; Garnier & Laurent 1994; Kebede *et al.* 1994; van Arendonk & Poorter 1994). On the other hand, LSM was positively correlated with leaf mass and leaf density in both species and habitats. Our data corroborate the findings of Pammenter *et al.* (1986), Kebede *et al.* (1994) and Garnier & Laurent (1994) in which leaf density played a major role in the determination of

LSM in the sunny habitat. The effects of thickness and/or leaf density on LSM have also been shown in the study of Witkowski & Lamont (1991), with shrub species growing in different environments.

Variation in leaf density can be brought about by several factors which pertain to chemical composition and anatomy (Lambers & Poorter 1992). Anatomical characters leading to a high leaf density are essentially those that result in a high amount of cell wall per unit volume. This occurs when the proportion of tissues with thick walled cells is high relative to tissues with thin walled cells and/or the cells of one or several tissues are small (Garnier & Laurent 1994). The species studied here showed increased mesophyll cell size and number which was reflected in mesophyll thickness and density, therefore, contributing to either an increase in the amount of the cellular walls or in the percentage of organic matter (see also Turner *et al.* 1993).

Leaf thickness is influenced by variations in the palisade tissue (number of layers and cell length), number of layers and length of mesophyll, epidermis, hypodermis, and indumentum, as well as by increased cell size (Esau 1977; Fahn & Cuttler 1992; Garnier & Laurent 1994; Sims & Pearcy 1992; Thompson *et al.* 1992; Witkowski & Lamont 1991). Our results showed an increase in thickness of cuticle and epidermis of leaves in the sun-exposed cerrado in *M. stenostachya* whereas, *M. ibaguensis* increased only in cuticle thickness. Chazdon & Kaufmann (1993) suggest that the increase in thickness of the upper epidermis may increase leaf reflectance. A thicker epidermal layer alters light-scattering processes within mesophyll tissue or protect photosynthetic tissues from excessive irradiance (Roth 1934). Thus, our data indicate that *M. stenostachya* may be more protected against light irradiation than *M. ibaguensis*.

The palisade parenchyma cells of *M. ibaguensis* and *M. stenostachya* were deeper in sun-exposed plants and the latter also showed more layers. Thompson *et al.* (1992) stated that high light irradiance induces the development of the mesophyll in the palisade and spongy parenchyma producing thicker leaves which have thinner aerial spaces. Conversely, leaves of shade plants have thinner blades and smaller and more densely packed leaf cells (Nobel *et al.* 1975).

Trichome and stomata density can also be influenced by light. For *M. ibaguensis*, the ratio tri-

chome/stomata was highest in the sunny habitat. This suggests that the increase in trichome density found in sunny habitat plays an important role in water regulation through an increase in the boundary layer and reduces the vapor pressure difference between leaf surface and the microclimate just above the leaf lamina, minimizing water losses (*e.g.*, Ehleringer & Mooney 1978; Gay & Hurd 1975; Johnson 1975). Although the number of trichomes of *M. stenostachya* was not statistically different between the habitats, the stomata of this species in sunny habitat are in deep cavities, feature that may reduce water loss (Fahn & Cuttler 1992). The greater number of stomata of *M. stenostachya* in sunny habitat could be related to the CO₂ diffusion rate because this species also has thicker leaves. Romero-Aranda *et al.* (1997) showed that the increase in leaf thickness and large mesophyll cell volume increase the biophysical resistance to CO₂ diffusion. Besides this, thicker leaves that increase the number of stomata per unit area may favor leaf CO₂ diffusion under high irradiance conditions (*e.g.*, Mott *et al.* 1982; Mott & Michaelson 1991).

For *M. ibaguensis*, leaf anatomical variations were less evident between habitats. Probably, *M. ibaguensis* invests in biochemical and physiological mechanisms that allow its survival in sunny habitat because the species primarily occurs in shady habitat (Martins *et al.* 1996). *Miconia stenostachya*, which is primarily a sun plant (Martins *et al.* 1996), seems to invest more in leaf anatomical structures in order to gain more protection against high irradiations. When it grows in a shady habitat it exhibits more conspicuous morphological changes in the leaves.

We can conclude that sympatric species may show variations in leaf anatomy, density, thickness and LSM that may be important ecological adaptations relative to light conditions, and that these features are very plastic structurally.

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