

# Structural and functional leaf traits of two *Gochnatia* species from distinct growth forms in a sclerophyll forest site in Southeastern Brazil

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## RESUMO

(Atributos foliares estruturais e funcionais de duas espécies de *Gochnatia*, de formas distintas de crescimento, em uma floresta esclerófila do sudeste do Brasil). O gênero *Gochnatia* é comumente encontrado em diferentes fitofisionomias do Cerrado do Estado de São Paulo, crescendo desde ambientes mais abertos até áreas florestais mais fechadas. Aqui foram comparadas a anatomia foliar e alguns parâmetros ecofisiológicos de duas espécies do gênero *Gochnatia*, uma arbustiva (*Gochnatia barrosii* Cabrera) e a outra arbórea (*Gochnatia polymorpha* (Less.) Cabrera), ambas ocorrendo em área de cerradão na Estação Ecológica de Assis, SP. Encontraram-se diferenças estruturais qualitativas entre as espécies, com *G. barrosii* apresentando folhas anfiestomáticas, com epiderme unisseriada e *G. polymorpha* apresentando folhas hipoestomáticas, com epiderme múltipla ou hipoderme, na face adaxial. Além disso, as folhas de *G. barrosii* apresentaram menores valores para a espessura dos tecidos (com exceção da epiderme na face abaxial) e da folha em relação a *G. polymorpha*. Foram observadas diferenças na assimilação de CO<sub>2</sub> tanto em base de área quanto de massa seca foliar, além de diferenças na área foliar específica, sendo esta maior em *G. barrosii*. Apesar das folhas de *G. barrosii* possuírem estrutura bem menos escleromorfa do que as folhas de *G. polymorpha*, não foram encontradas diferenças na eficiência do uso de água. Os resultados sugerem que espécies de formas distintas de crescimento de um mesmo gênero possuem características foliares diferenciadas para lidar com as variações ambientais a que são submetidas.

**Palavras-chave:** anatomia foliar, Cerrado, estômatos, trocas gasosas

## ABSTRACT

(Structural and functional leaf traits of two *Gochnatia* species, with distinct growth forms, from a sclerophyll forest in Southeastern Brazil). *Gochnatia* is very common in different phytophysiognomies in the Cerrado of São Paulo State, occupying open and closed areas. In this study, we compared the leaf anatomy and some ecophysiological traits of two species of *Gochnatia*, one a shrub (*Gochnatia barrosii* Cabrera) and the other a tree (*Gochnatia polymorpha* (Less.) Cabrera), which both occur in an area of "cerradão" at the Estação Ecológica de Assis, SP. We found qualitative structural differences between the species, with *G. barrosii* presenting amphistomatic leaves with a uniseriate epidermis and *G. polymorpha* showing hypostomatic leaves and a multiple epidermis or hypodermis on the adaxial surface. Moreover, the *G. barrosii* leaves had lower values in tissue thickness (with the exception of the epidermis on the abaxial surface) and leaf thickness in relation to *G. polymorpha*. There were differences in CO<sub>2</sub> assimilation both in area and leaf dry mass basis, and differences in specific leaf area, which was higher in *G. barrosii*. Although the *G. barrosii* leaves were much less sclerophyllous than the *G. polymorpha* leaves, we found no differences in the efficiency of water use. The results suggest that plants from the same genus, but with distinct growth forms, differ in their leaf traits to deal with the environmental variations that they grow in.

**Key words:** Cerrado, gas exchange, leaf anatomy, stomata

## Introduction

The widespread distribution of areas of "Cerrados" in central Brazil (approximately from latitude 2° N to 42° S) is reflected in their high diversity of landscapes and types of

vegetation (Oliveira-Filho & Ratter 2002). The savanna-like vegetation, regionally called cerrado *sensu stricto*, dominates most of the "cerrados" landscape and can be found growing in a great diversity of climates and soils (Ribeiro & Walter 2008). Forest vegetation occurs within the savanna vegetation

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(Oliveira-Filho & Ratter 2002) and is represented by gallery forests that follow small rivers (Ribeiro & Walter 2001), seasonal deciduous forests on shallow soils and sclerophyllous forests on mesotrophic or dystrophic soils (Ribeiro & Walter 2008). The “cerradão”, a sclerophyllous forest or semi-closed woodland with about 60% tree cover, is the most dominant type of forest, especially in the southern regions of the Cerrado (Ribeiro & Walter 2008).

Plants living in “cerradão” forest may deal with water seasonality (Franco 2002), frequent fires (Coutinho 1978) and well-weathered soils with low nutrient availability (Haridasan 1992). Forest formations, however, have an additional constraint that species should be able to deal with: the great variation in light availability along the vertical continuum through the canopy (Felfili *et al.* 2001). The differences in light conditions may impose adaptation or acclimation of leaves according to the level of light availability: leaves of emergent or canopy trees are exposed to high light intensities and normally are small and thick (Valladares & Niinemets 2008), whereas large and thin leaves of understory species may be a response to limited light conditions (Evans & Poorter 2001; Santiago & Wright 2007). Understanding responses to the local availability of light is fundamental to understanding the adaptation of such species to the forest environment (Hoffmann & Franco 2008).

The “cerradão” flora is dominated by trees (Ribeiro & Walter 2008), but shrubs and herbs also occur in its understory (Christianini & Cavassan 1998). In the State of São Paulo two sympatric species of *Gochmatia* are particularly common and dominant in border areas of the “cerradão”. *Gochmatia barrosii* Cabrera is a shrub that can reach 1-1.5 meters in height, and produces yellow- to white-haired branches and leaves, whereas *Gochmatia polymorpha* (Less.) Cabrera is a tree that can reach 5-6 meters in height, with a well-suberised and tortuous trunk (Durigan *et al.* 1999; Rossatto *et al.* 2008). Both species are woody and evergreen. These sympatric species may differ in their leaf functional aspects in relation to light availability and growth form (Santiago & Wright 2007). Leaves are the most important organs that influence the growth of plant species (Niklas *et al.* 2007) and learning about their functional traits may contribute important information to understanding the process of adaptation of distinct growth forms in their natural environments (Santiago & Wright 2007).

The goal of this study was to compare the leaf structural and functional traits of two *Gochmatia* species that have different growth forms. Despite the fact that both species share similar ecologies, we expected structural and functional divergences in leaf traits due to their different growth forms (Santiago & Wright 2007) and the differences in light intensity and quality that a tree (*G. polymorpha*) and a shrub (*G. barrosii*) experience along the borders of a forest (Habermann *et al.* 2011). We expected that the shrub species would present mesomorphic leaves with low investment in tissues thickness, thinner and bigger leaves, with higher values of specific leaf area and mass basis carbon assimilation, a set

of traits that would allow the shrub to deal with the lower light availability, and a common condition experienced in the forest understory. The tree species, in contrast, would present sclerophyllous leaves, with high investment in tissue thickness, thicker and smaller leaves, lower values of specific leaf area and higher area basis carbon assimilation, which are characters that deal with higher light intensities found in the canopy of emergent trees.

## Material and methods

### Study site

This study was carried out at Estação Ecológica de Assis (EEA), near the city of Assis, São Paulo State, Brazil, which is located at 22°33'20"S and 50°21'27"W, at an elevation of approximately 600 m above sea level. The climate at the EEA is Cwa and Cfa according to the Köppen classification. The average annual rainfall recorded at the study site is around 1400 mm, with a markedly dry season from June to September and a mean annual temperature of 22.0°C. The soils are predominantly well-weathered dystrophic oxisols (Juhász *et al.* 2006). The EEA's vegetation comprises the more closed and denser physiognomies of cerrado *sensu lato*, where the “cerradão” physiognomy predominates (Durigan *et al.* 1999).

### Species and sampling

We selected two evergreen and sympatric species from *Gochmatia* Kunth (Asteraceae), which are abundant in the “cerradão” of EEA and show contrasting growth forms: *Gochmatia barrosii* Cabrera is a shrub and *Gochmatia polymorpha* (Less) Cabrera is a tree. The voucher of *G. polymorpha* was deposited in Herbário Irina Felanova Gemtchjnicov of UNESP Botucatu, under the number BOTU-23842, whereas the *G. barrosii* voucher was deposited in the SPSF herbarium under the number SPSF-37024. Both species were sampled at the edge of the “cerradão” (i.e., the interface between the forested and a non-forested area existing inside the EEA). For each species, we selected 12 sun-exposed individuals along the edge; these individuals were at least 5 meters apart from each other and possessed the maximum height that each species commonly attains in the field. For both species, light intensity was measured at the leaf level with a spherical sensor coupled to a Li-cor photometer (Li-250A, Biosciences, Lincoln, USA). The measurements were taken in February 2009, and were carried out in three sunlit leaves per plant (n=6 individuals, per species) between 11:00 a.m. and 12:00 p.m. Leaves of *G. polymorpha* were exposed to higher values (t-test = 11.74  $P < 0.05$ ) of light intensity ( $1928.33 \pm 209.88 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ ) than leaves of *G. barrosii* ( $735.01 \pm 133.93 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ ).

### Leaf anatomy

Leaf samples from the two species were collected at EEA in October-2008 (during the wet season). We

selected leaves from the most peripheral branches of the canopy of each individual, sampling non-damaged leaves from the third node from the apex in both species. One leaf from each of the 12 individuals of each species was sampled. Each sample consisted of a 1-cm<sup>2</sup> middle section between the main vein and the leaf margin of fully expanded leaf. Samples were fixed in 70% formalin-acetic acid- alcohol (FAA 70), dehydrated in a graded ethanol series, infiltrated and embedded in paraffin and cut into 8- $\mu$ m sections. The cross-sections obtained were stained with astra blue-basic fucine and permanently mounted in entellan. Fifty measurements were taken for each sample, from different regions of the transversal cuts, for leaf traits (thickness of cuticle, abaxial and adaxial epidermis, palisade and spongy parenchyma). The stomata density and guard cells length were obtained by using epidermal prints of dissociated material in 1% sodium hypochlorite solution stained with safranin. Stomatal counts were made from the abaxial and adaxial leaf surfaces in three fields per sample. The stomata size was measured for 60 stomata per sample.

#### Leaf gas exchange and specific leaf area

In February 2009 (peak of the wet season), six sun-exposed individuals were selected. We randomly selected 6 individuals from the 12 previously chosen in the anatomical study for each species. The gas exchange parameters were measured using an open and portable photosynthesis system (LcPRO, ADC, Hoddesdon, UK). Maximum CO<sub>2</sub> assimilation in area basis ( $A_{\text{area}}$ ) and stomatal conductance (gs) were determined under ambient conditions with a led light source providing a light intensity between 1200-1300  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The chamber temperature was maintained at  $24\pm 2$  °C. The measurements were carried out with three sunlit leaves per plant between the hours of 09:00 and 11:00 a.m. The assimilation values in area basis were used to calculate assimilation in mass basis ( $A_{\text{mass}}$ ) (the product of specific leaf area ( $\text{cm}^2\cdot\text{g}^{-1}$ ) and assimilation in area basis ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )). We also calculated the IWUE (intrinsic water use efficiency) dividing  $A_{\text{area}}$  by gs. The leaves used for the gas exchange measurements were collected for determination of specific leaf area (SLA). Each leaf was scanned on a flatbed scanner and its area determined using the free software Area (Caldas *et al.* 1992), then they were dried at 70°C for 3 days and weighed to determine the specific leaf area ( $\text{cm}^2\cdot\text{g}^{-1}$ ).

#### Statistical analyses

The leaf histometric data were analyzed using a MANOVA analysis followed by ANOVAs to verify differences between species. The ecophysiological data were analyzed through an ANOVA followed by Tukey's test. All anatomical and ecophysiological data were normally distributed according to Kolmogorov-Smirnov test ( $P > 0.25$ ) and homogeneity of variances according to Levene's test ( $F < 1.20$ ,  $P > 0.06$ ). In all cases we adopted an  $\alpha = 0.05$ .

## Results

### Leaf anatomy

*Gochnatia barrosii* leaves are dorsiventral (Fig. 1) with few scleromorphic aspects, such as cells with lignified walls in the vascular bundle sheath, with extensions towards the epidermis (Fig. 1), and the presence of tector trichomes on both surfaces. In this species, the abaxial and adaxial leaf epidermis surfaces are uniseriate (Fig. 1). The mesophyll is composed of a single palisade parenchyma layer and three spongy parenchyma layers (Fig. 1), which are compactly arranged. The leaves are amphihypostomatic, with anomocytic stomata (Fig. 2-3) elevated in relation to the leaf epidermal cells (Fig. 1). The stomata are of similar size on both faces (Tab. 1). The leaves have glandular (Fig. 4) and stellate, thick-walled, tector trichomes (Fig. 5). The glandular trichomes occur only on the abaxial leaf surface.

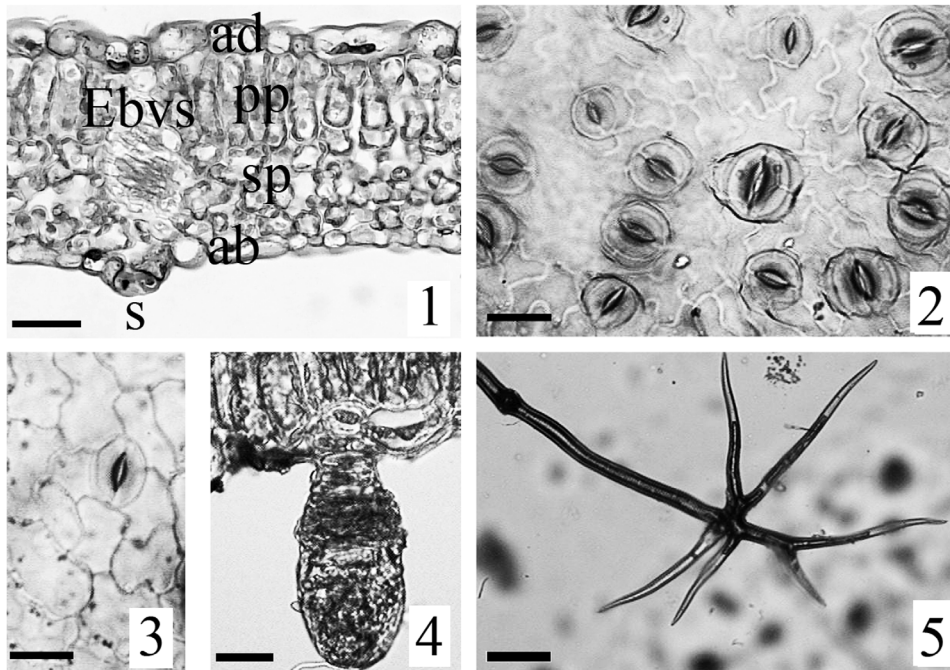
*Gochnatia polymorpha* leaves are dorsiventral (Fig. 6) with 2-3 layers of palisade parenchyma and 5-6 layers of well-developed spongy parenchyma (Fig. 7). The epidermis on the adaxial surface is 2-cell layers (Fig. 7) or, more rarely, 3-cell layers. The second and third cell layers can also represent a hypodermis; however, this was not investigated by an ontogenetic study. In contrast, the epidermis on the abaxial surface is uniseriate (Fig. 7). The lateral veins have bundle sheaths that extend towards the epidermis, presenting thick-walled cells (Fig. 6-7). Leaves from this species are hypostomatic, with anomocytic stomata (Fig. 8) that are elevated in relation to the epidermal cells (Fig. 6). Tector (Fig. 8) and glandular (Fig. 9) trichomes are present only on the abaxial leaf surface.

*Gochnatia barrosii* presented larger ( $F_{1,10} = 10.14$ ,  $P = 0.009$ ) and thinner ( $F_{1,10} = 16.04$ ,  $P = 0.002$ ) leaves than *G. polymorpha* (Tab. 1). In general terms, leaf tissues of *G. barrosii* were thinner (Tab. 1) (MANOVA Wilk's = 0.01,  $F_{4,19} = 298.65$ ,  $P = 0.000$ ). The only exception was the epidermis from abaxial leaf surface ( $F_{1,22} = 137.66$ ,  $P < 0.001$ ), which was thicker in relation to that found for the leaf of *G. polymorpha* (Tab. 1). *Gochnatia barrosii* had smaller stomata ( $F_{1,22} = 766.51$ ,  $P < 0.001$ ) and higher values of stomatal density ( $F_{1,2} = 145.65$ ,  $P < 0.001$ ) when compared to *G. polymorpha* (Tab. 1).

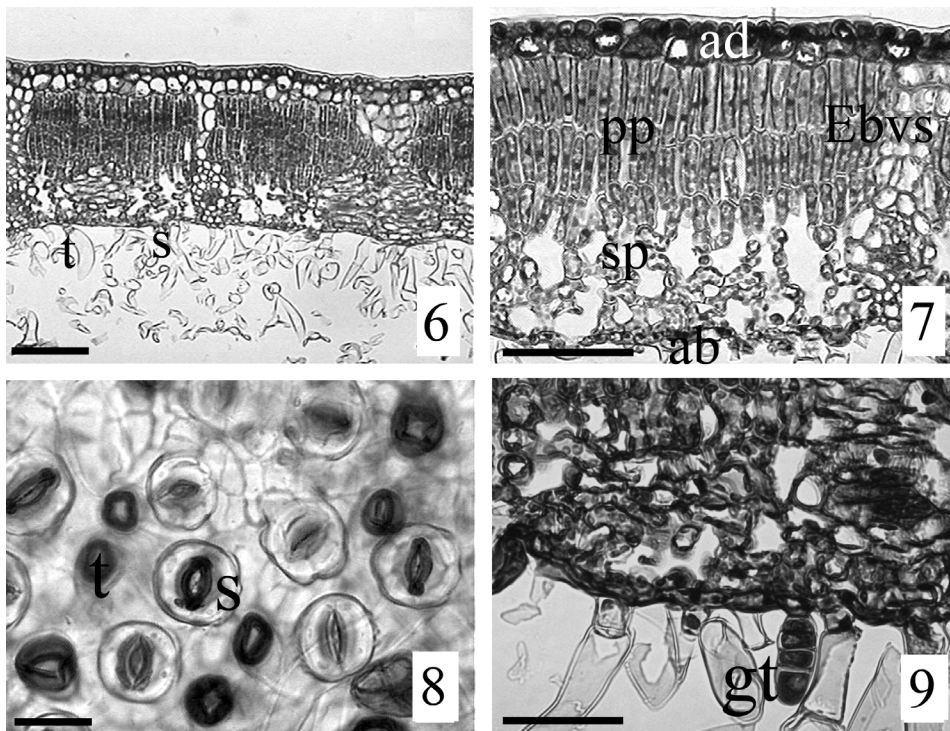
### Functional traits

We found differences in the specific leaf area of the species ( $F_{1,10} = 86.69$ ,  $P < 0.001$ ), in *G. polymorpha* showing lower values (Tab. 1). In terms of gas exchange, the sclerophyllous leaves of *G. polymorpha* showed higher values (around 15  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) of carbon assimilation in area basis than leaves of *G. barrosii* ( $F_{1,10} = 13.04$ ,  $P = 0.004$ ) (Fig. 10A). The carbon assimilation in leaf mass basis also differed between species ( $F_{1,10} = 32.15$ ,  $P < 0.001$ ), with *G. barrosii* showing a average rate of 225  $\mu\text{mol}\cdot\text{kg}^{-1}\cdot\text{s}^{-1}$ , in comparison with 116  $\mu\text{mol}\cdot\text{kg}^{-1}\cdot\text{s}^{-1}$  for *G. polymorpha* (Fig. 10B).





**Figures 1-5.** Leaf anatomy of *Gochnatia barrosii* Cabrera. 1. Transversal cut showing the epidermis from adaxial surface (ad), palisade parenchyma (pp), spongy parenchyma (sp), vascular bundle sheath with extension towards the epidermis (Ebvs) and epidermis of the abaxial surface (ab). Scale bar = 100  $\mu$ m. 2. View of the abaxial leaf surface. Scale bar = 20  $\mu$ m. 3. View of the adaxial leaf surface. Scale bar = 20  $\mu$ m. 4. Glandular trichome on the abaxial leaf surface. Scale bar = 20  $\mu$ m. 5. Stellate trichome in detail. Scale bar = 20  $\mu$ m.



**Figures 6-9.** Leaf anatomy of *Gochnatia polymorpha* (Less.) Cabrera. 6. Transversal cut showing a general view of leaf structure, tector trichomes (t) and stoma (s) on the abaxial leaf surface. Scale bar = 100  $\mu$ m. 7. Transversal cut showing the epidermis from adaxial surface (ad), palisade parenchyma (pp), spongy parenchyma (sp), vascular bundle sheath with extension towards the epidermis (Ebvs) and epidermis of the abaxial surface (ab). Scale bar = 100  $\mu$ m. 8. View of the abaxial leaf surface showing the stomata (s) and the tector trichome base (t). Scale bar = 30  $\mu$ m. 9. Glandular trichome on the abaxial leaf surface (gt). Scale bar = 50  $\mu$ m.

**Table 1.** Measurements of leaf traits (mean  $\pm$  s.d.,  $n = 12$ ) for two *Gochnatia* species in a “cerradão” forest at the Estação Ecológica de Assis, southeastern Brazil. Different letters represent statistical differences according to the Tukey’s test ( $P < 0.05$ ). \* For this study we considered the 2-3 cell layers above the palisade parenchyma as the adaxial surface epidermis. \*\*na – not applicable.

Traits	<i>Gochnatia barrosii</i>	<i>Gochnatia polymorpha</i>
Cuticle from adaxial surface ( $\mu\text{m}$ )	2.89 $\pm$ 0.10 a	5.23 $\pm$ 0.53 b
Epidermis from adaxial surface ( $\mu\text{m}$ )*	14.28 $\pm$ 2.48 a	35.02 $\pm$ 5.59 b
Palisade parenchyma ( $\mu\text{m}$ )	38.28 $\pm$ 5.56 a	103.36 $\pm$ 5.94 b
Spongy parenchyma ( $\mu\text{m}$ )	44.49 $\pm$ 1.97 a	53.93 $\pm$ 5.44 b
Epidermis from abaxial surface ( $\mu\text{m}$ )	9.52 $\pm$ 1.56 a	6.00 $\pm$ 0.56 b
Leaf thickness ( $\mu\text{m}$ )	107.91 $\pm$ 11.46 a	215.33 $\pm$ 9.74 b
Total leaf area ( $\text{cm}^2$ )	143.42 $\pm$ 36.94 a	25.92 $\pm$ 4.49 b
Specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ )	189.8 $\pm$ 30.42 a	73.23 $\pm$ 4.32 b
Guard cell length (abaxial) ( $\mu\text{m}$ )	21.48 $\pm$ 1.21 a	26.07 $\pm$ 1.36 b
Guard cell length (adaxial) ( $\mu\text{m}$ )	19.50 $\pm$ 1.01	na**
Stomatal frequency (abaxial) ( $\text{n}^\circ \text{mm}^{-2}$ )	675.11 $\pm$ 78.44 a	442.27 $\pm$ 32.43 b
Stomatal frequency (adaxial) ( $\text{n}^\circ \text{mm}^{-2}$ )	122.57 $\pm$ 44.50	na**

Differences in carbon assimilation occurred despite similar values ( $F_{1,10} = 5.32$ ,  $P = 0.08$ ) for stomatal conductance ( $0.15$ – $0.20 \text{ mol m}^{-2} \text{ s}^{-1}$ ) (Figure 10C). The water use efficiency was similar ( $F_{1,10} = 1.32$ ,  $P = 0.21$ ) between species (Fig. 10D).

## Discussion

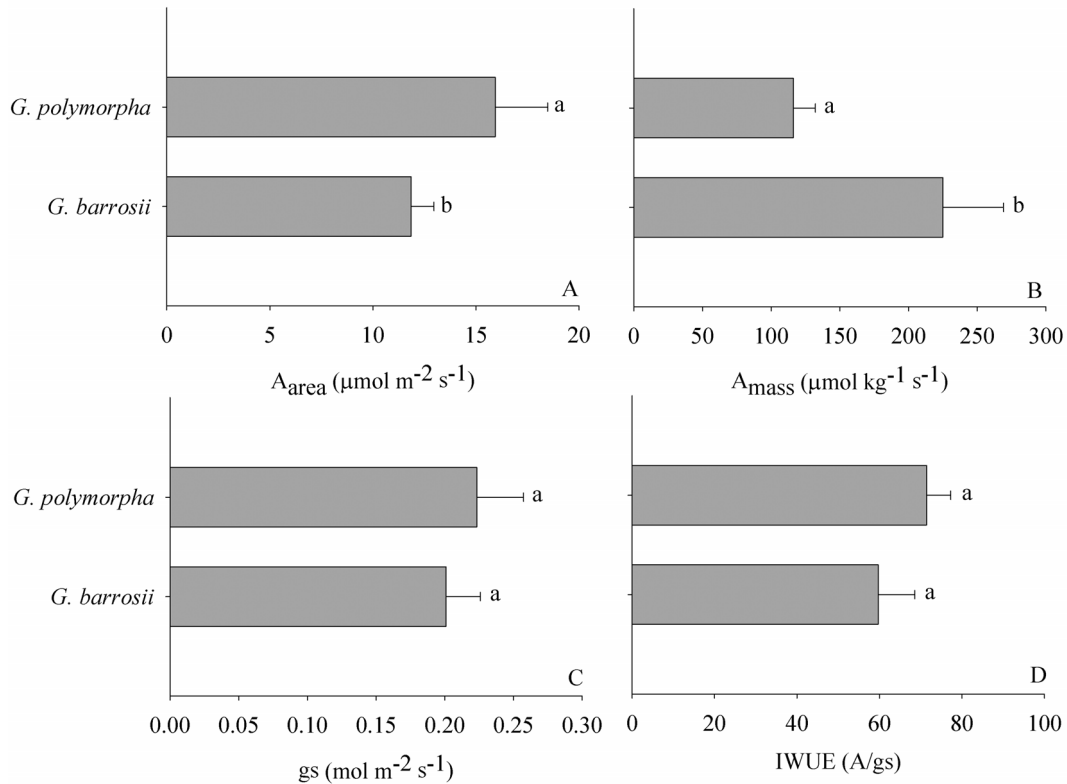
The congeneric species studied here showed some contrasting morphological and physiological leaf traits, even though they grow in a same site. These differences were markedly different for the quantitative aspects of the leaf anatomy and physiological traits. We observed that the tree (*G. polymorpha*) had a greater number of sclerophyllous leaf traits, which are normally reported for woody, “Cerrado” species. These traits include smaller and thicker leaves, well developed parenchyma (Bieras & Sajo 2009), high stomatal density (Rossatto *et al.* 2009a), higher photosynthetic rates ( $A_{\text{area}}$ ) and lower values of specific leaf area (Rossatto *et al.* 2009b). On the other hand, the shrub (*G. barrosii*) presented more mesophytic leaf traits, bigger and thinner leaves, higher values of specific leaf area and lower photosynthetic rates ( $A_{\text{area}}$ ), which are reported for woody species that grow in lower light environments (Sefton *et al.* 2002; Dahlgren *et al.* 2006).

With regards to stomata anatomy, both species had stomata above the level of the epidermal cells, a rarely reported pattern in the literature for Asteraceae species (Sajo & Menezes 1994; Luque 1995). Leaves of *G. polymorpha* presented stomata only on the abaxial leaf surface, while *G. barrosii* possessed stomata on both surfaces. The presence of stomata on both leaf surfaces can be variable in Asteraceae (Breitwieser 1993; Milan *et al.* 2006). The presence of amphistomatic leaves is variable also among “Cerrado” species (Morretes 1969; Elias *et al.* 2003; Rossatto *et al.* 2009a), despite that the general pattern reported for plants from this vegetation

is hypostomatic leaves (Bieras & Sajo 2009). Stomata size was variable and the guard cell length of *G. barrosii* stomata was shorter. Guard cell length is important because it can influence the pattern of stomatal frequency and stomatal conductance (Hetherington & Woodward 2003; Rossatto *et al.* 2009a) because smaller stomata are more responsive to environmental changes (Hetherington & Woodward 2003; Galmes *et al.* 2007).

The values of stomatal frequency were high for both species and within the range reported for other “Cerrado” species (Rossatto *et al.* 2009a). Studies about the patterns of stomatal density suggest high stomata densities in leaves subjected to high light intensities and/or low water availability (Pearce *et al.* 2006) are factors associated with “Cerrado” vegetation and also the forest canopy. However, stomatal frequency differed between the studied species, with *G. barrosii* showing the highest values of stomatal density on the abaxial leaf surface. The smaller stomata and the higher stomatal frequency in *G. barrosii* can be related to better and faster responses to environmental variations (better use of sunflecks), conferring an improved carbon uptake under forest understory conditions. It is assumed that stomatal density can affect carbon uptake and water use efficiency (Galmes *et al.* 2007); however, despite that we found differences in stomatal density between the species, we did not find significant differences in stomatal conductance or even in water use efficiency. This may indicate that stomatal density cannot account alone for photosynthetic differences between the species.

For both species, we described the occurrence of glandular and tector trichomes, however the presence of the latter structure on leaf surfaces was variable depending on the species. In terms of glandular trichomes it is possible that it is a shared trait in the genus *Gochnatia* that may allow an adaptive defense against herbivores, a common



**Figure 10.** Physiological leaf traits of *Gochmatia polymorpha* (Less.) Cabrera and *Gochmatia barrosii* Cabrera. A – Carbon assimilation rates on an area basis ( $A_{area}$ ) and B – mass basis ( $A_{mass}$ ); C – stomatal conductance (gs); D – Intrinsic water use efficiency (IWUE). Horizontal bars show standard deviation ( $n = 6$ ). Different letters represent statistical differences according to Tukey's test ( $P < 0.05$ ).

aspect in the savanna vegetation (Marquis *et al.* 2001). The presence of tector trichomes on both surfaces of *G. barrosii* and on the abaxial leaf surface of *G. polymorpha* are also probably more related to phylogenetic proximity than to an adaptive mechanism to avoid the overheating of leaves (Gianoli & Gonzalez-Teuber 2005). However, because a high number of trichomes occurred on the abaxial surface of *G. polymorpha* leaves, it is possible that the trichomes play a role in water balance in the plant (Fahn 1986; Fahn & Cutler 1992; Larcher 2000).

Despite the similar distribution of the parenchyma in both species, there was a variation in mesophyll thickness; *G. polymorpha* showed the highest thickness for these tissues, with well-developed palisade and spongy parenchyma. This strategy is commonly found in species subjected to high light intensities (Sefton *et al.* 2002; Boeger *et al.* 2006; Rossatto & Kolb 2010) and should promote good performance (carbon uptake and water economy) in such environments (Gratani *et al.* 2006). Besides the value of the thickness of the mesophyll, the ratio between thickness of spongy parenchyma and palisade parenchyma can reflect a mechanism for optimizing light capture. In an environment with higher luminous intensity a ratio greater than one is advantageous (Vogelmann *et al.* 1996); this relation was observed for the tree *G. polymorpha* (0.52), in contrast to that of the shrub *G. barrosii* (1.16). The thicker palisade parenchyma opti-

mizes the capture of direct light incident on the leaves of the canopy, while a thicker spongy parenchyma optimizes the capture of diffuse light, which predominates in the understory (Vogelmann *et al.* 1996). In terms of the leaf vascular system, the studied species showed some similar aspects, such as the occurrence of cells with lignified walls in the bundle sheath, with extensions towards the epidermis. The presence of such extensions has been reported for Asteraceae species (Breitwieser 1993; Melo-de-Pina 2004), and it has been suggested that these structures can transport and store water, which could be an adaptation in seasonal dry systems (Fahn & Cutler 1992).

One of the most important physiological traits that confer adaptation is the maximum photosynthetic rate in area basis (Franco *et al.* 2005). The values measured here for both species are within the typical values found in “Cerrado” species (between 6–20  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) (Franco *et al.* 2005). However, we were able to find differences in the carbon assimilation rates of the species; *G. polymorpha* showed the highest values in comparison to *G. barrosii*. The same trend was found in congeneric *Styrax* species growing on the edge and in the understory of a “cerradão” forest (Habermann *et al.* 2011). Differences in the amount of mesophyll tissues may partially explain these photosynthetic differences, as *G. polymorpha* heavily invested in mesophyll thickness in comparison to *G. barrosii*. *G.*



*polymorpha*, as a tree exposed to high light intensities may also possess efficient biochemical mechanisms to make a better use of this high light availability, such as a high efficiency electron transport mechanism (Lichtenthaler *et al.* 2007) due to high contents of chlorophyll in the palisade parenchyma (James *et al.* 1999) or higher concentration of carotenoids, which are important to avoid the damage of photosystems (Sarijeva *et al.* 2007).

In contrast to  $A_{\text{area}}$ , the carbon assimilation in mass basis was higher in *G. barrosii*. Higher values of  $A_{\text{mass}}$  are commonly reported for species growing in lower light environments (Prior *et al.* 2004, Rossatto *et al.* 2009b, Rossatto *et al.* 2010), which are indicative that understory species are better competitors for light (Valladares & Niinemets 2008). The differences in  $A_{\text{mass}}$  were likely to be influenced by the differences in SLA. Specific leaf area for both species showed values normally reported for “Cerrado” species (75–200 cm<sup>2</sup> g<sup>-1</sup>) (Hoffmann & Franco 2008), however, when comparing the values of SLA of the species we found lower values for *G. polymorpha* than for *G. barrosii*. Lower values of SLA are linked to a high investment in leaf thickness (Sefton *et al.* 2002; Dahlgren *et al.* 2006), which is a common aspect in leaves experiencing high light intensities or low nutrient availability (Turner 1994). Normally, leaves with a lower SLA invest a lot in non-photosynthetic tissues, such as the cuticle and leaf epidermis (Dijkstra 1990; Fahn & Cutler 1992), and have leaves with a lower leaf area. These aspects may be important in high-light environments where conservation of water resources leads to ecological success (Schulze *et al.* 1998), but also to a lower  $A_{\text{mass}}$ . In contrast, the higher values of SLA for *G. barrosii* may suggest a mesophytic aspect of its leaves, which also has lower leaf thickness and higher leaf area as a strategy to increase the capture of the diffuse light that penetrates the border of the canopy (Grime & Hunt 1975).

The small differences related to the qualitative aspects of leaf structure may suggest trait conservatism (Ackerly 2009) of leaf anatomical aspects of these species, despite their distinct growth forms. On the other hand, the quantitative anatomical data may suggest that the investment in the tissues may differ between the species according to the variation in light availability and that these differences may explain, at least in part, the physiological differences found between these two growth forms (Sefton *et al.* 2002). *Gochmatia polymorpha* is a very plastic species in relation to leaf anatomy (Rossatto & Kolb 2010), so this plasticity may help to explain its distribution in several physiognomies of the Cerrado that differ in light availability (Durigan *et al.* 1999). *Gochmatia barrosii* in turn can probably present plasticity, once it is able to grow not only in forest physiognomies but also in open Cerrado areas (Rossatto *et al.* 2008). Our results suggest that the evolutionary history and ecological adaptation to differences in light regimes should affect the leaf traits in these distinct growth form plants as a specialized response to deal with differences in resource availability in the habitats where they grow.

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