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Differences in morphological and physiological leaf characteristics between *Tabebuia aurea* and *T. impetiginosa* is related to their typical habitats of occurrence

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RESUMO

(Diferenças em características morfológicas e fisiológicas foliares entre *Tabebuia aurea* e *T. impetiginosa* estão relacionadas aos seus ambientes típicos de ocorrência). *Tabebuia* é um gênero representativo do bioma Cerrado, ocorrendo em formações savânicas e florestais, que diferem em termos de microclima, disponibilidade hídrica e propriedades do solo. Neste trabalho foi realizado um estudo comparativo de parâmetros morfológicos e fisiológicos entre duas espécies, sendo *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore típica de ambientes savânicos, como o cerrado *sensu stricto*, enquanto *T. impetiginosa* (Mart. ex DC.) Standl é tipicamente encontrada nas matas de galeria, que margeiam os cursos de água. As duas espécies foram amostradas em ambientes savânicos, expostas a condições semelhantes de alta luminosidade. A espécie savânica apresentou maiores valores de espessura foliar, massa foliar específica, espessura do pecíolo, assimilação máxima de CO₂, condutância estomática, transpiração e concentração foliar de carotenóides. A espécie de mata destacou-se pelos maiores valores de área foliar específica, comprimento do pecíolo e de assimilação de CO₂ em base de massa, parâmetros que contribuem para maior taxa de crescimento e de tolerância ao sombreamento. Esta distinção funcional entre as duas espécies em vários atributos foliares, mesmo quando situadas num mesmo tipo de ambiente, pode ser o resultado da história evolutiva dessas espécies em resposta às diferentes pressões seletivas nos ambientes típicos de ocorrência.

Palavras-chave: assimilação de CO₂, área foliar; cerrado, pigmentos fotossintéticos, *Tabebuia*

ABSTRACT

(Differences in morphological and physiological leaf characteristics between *Tabebuia aurea* and *T. impetiginosa* is related to their typical habitats of occurrence). The genus *Tabebuia* is representative of the Cerrado biome, occurring in savanna and forest formations. These vegetation types are associated with distinct environmental conditions in terms of water availability, microclimate and soil properties. We compared morphological and physiological traits between *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore, which is typical of the savanna vegetation, and *T. impetiginosa* (Mart. ex DC.) Standl, which is commonly found in the gallery forests that occur along streams and rivers. Both were sampled in savanna conditions under full sun. The savanna species had higher values of leaf and petiole thickness, specific leaf mass, maximum CO₂ assimilation on a leaf area basis, stomatal conductance, transpiration and in leaf concentration of carotenoids. The forest species stood out by higher values of specific leaf area, petiole length and of CO₂ assimilation on a mass basis, parameters related to shade tolerance and higher growth rates. This functional distinction in a range of leaf traits that was maintained when both were naturally growing under similar environmental conditions, suggests that these are probably the result of differences in the evolutionary history of the two species in response to the contrasting environmental conditions in the typical habitats where they occur.

Key words: Cerrado, CO₂ assimilation, leaf area, photosynthetic pigments, *Tabebuia*

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Introduction

The central part of Brazil is covered by a complex mosaic of grasslands, savanna and forests, known locally as the Cerrado, which originally covered an area of over 2 million km². The position and large extent of this biome favored the occurrence of a wide range of soils and forms of relief, which are reflected in the variety of vegetation types in this biome (Ribeiro & Walter 1998; Oliveira-Filho & Ratter 2002). The most prominent vegetation types are the cerrado *sensu stricto*, a savanna physiognomy highly diverse in terms of herbaceous and woody species (Ribeiro & Walter 1998) and gallery forests, which form narrow strips of arboreal vegetation along river basins and contain approximately one third of the tree species that are found within the Cerrado biome (Felfili 1995, Ribeiro & Walter, 2001). Cerrado *sensu stricto* and gallery forests are subjected to drastically different environmental pressures that impose strong constraints on species distributions in these two types of physiognomies. In cerrado *sensu stricto*, plants are subjected to high irradiances (Franco & Lüttgugue 2002), low nutrient availability (Haridasan 2008), seasonal drought (Meinzer *et al.* 1999; Franco 2002) and the presence of fire (Hoffmann *et al.* 2003). Gallery forests are generally associated with soils that have greater water and nutrient content than the surrounding savanna (Oliveira-Filho & Ratter 2002; Silva *et al.* 2008). On the other hand gallery forests are characterized by a dense tree canopy layer that considerably reduces incoming solar irradiance and produces strong spatial and temporal heterogeneity in the light environment (Felfili *et al.* 2001). Thus, the species of savanna and forest should behave as distinct functional groups due to different selective pressures imposed by these environments (Hoffmann *et al.* 2005).

Studies using congeneric pairs, in which a species typical of savanna (cerrado *sensu stricto*), and another species that occurs preferentially in the gallery forest, indicate that these two functional types differ in patterns of early growth and biomass allocation with a greater investment by savanna species in underground structures (Hoffmann & Franco 2003) and fire resistance (Hoffmann *et al.* 2003). The two groups also differ in some leaf characteristics such as lower leaf nutrient concentrations and more leathery leaves in savanna trees (Hoffmann *et al.* 2005), when compared to forest trees. Forest species have a greater investment in aerial biomass, especially in leaf area and stem biomass (Hoffmann & Franco 2003; Hoffmann *et al.* 2005), which suggests that forest and savanna trees differ greatly in their responses to the contrasting light conditions they encounter in the two physiognomies (Barros *et al.* 2011). According to Hoffmann & Franco (2008), comparison of characteristics of species adapted to different environmental conditions can elucidate the selective pressures that led to morphological and functional plant diversity in these systems. In fact, to understand how plant communities would respond to

climatic and environmental changes, it is necessary to understand ecophysiological differences between populations of species that inhabit different vegetation types (Lemos Filho *et al.* 2008).

The aim of this study was to compare morphological and physiological leaf traits of two species of the genus *Tabebuia*, *T. aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore and *T. impetiginosa* (Mart. Ex DC.) Standl, which are typical of savanna and forest, respectively (Lorenzi 2002). It was postulated that the species typical of gallery forests would have leaves that show evidence of a preferential investment in traits that minimize the effects of competition for light, while leaves in the savanna species would more strongly express traits that were related to tolerance to high amounts of light, water shortage and low availability of nutrients. It is further postulated that these differences would continue to be expressed in spite of the fact that both species have been sampled in savanna environments, subjected to similar conditions of high irradiance.

Material and methods

Study site and plant material

This study was conducted at the Ecological Reserve of IBGE (Recor), located 35 km from the center of the city of Brasilia, DF, Brazil. The administrative headquarters of the Reserve are located in the following geographical coordinates: 15°56'S, 47 ° 52'W. The reserve is located at an average altitude of 1100 m. Mean annual rainfall is about 1453 mm, with a distinct dry season from May to September and a mean annual temperature of 22 °C (www.recor.org.br). The months of June, July and August are often devoid of precipitation. Several vegetation types typical of the Cerrado vegetation are found within the Reserve including: several types of grasslands, typical savanna vegetation (cerrado *sensu stricto*), woodlands (cerradão), and gallery forests (Oliveira-Filho & Ratter 2002).

The studied species were *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore and *T. impetiginosa* (Mart. Ex DC.) Standl. Ten individuals of each species were sampled in May 2011 (end of wet season). The morphological and physiological data were collected from three leaves of each individual. Trees of *T. aurea* were located in a transition between a *campo sujo* (an open savanna with scattered shrubs and few trees) and cerrado *sensu stricto*, while *T. impetiginosa* was measured in a cerrado *sensu stricto* site. Both species were exposed to similar light conditions during the period of measurements. Photon flux density averaged 1700 ± 456 μmolm⁻²s⁻¹ for sampled leaves of *T. impetiginosa* and 1719 ± 465 μmolm⁻²s⁻¹ for *T. aurea* (t-test= 0.54, P > 0.35).

Morphological parameters

Leaf area was measured with a leaf area meter (CL-202, CID). Leaf thickness and petiole length and thickness were measured with a caliper (Mitutoyo, resolution of 0.001 mm). Leaves were collected and dried at 60 °C for 120 hours, and then weighed on a precision balance (± 0.0001 g). Specific leaf area (SLA, $\text{g}^{-1} \text{cm}^2$) was calculated as the ratio of leaf area to leaf dry mass. Leaf density (g cm^{-3}), was calculated by dividing the specific leaf mass (the ratio of leaf dry mass to leaf area) by the thickness of the leaf blade according to Wright & Westoby (2002).

Physiological parameters

Maximum CO_2 assimilation (A_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) with simultaneous measurements of transpiration (E ; $\text{mmol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_s ; $\text{mol m}^{-2} \text{s}^{-1}$) were taken between 08:00 and 11:00 h with a portable system for measuring photosynthesis and transpiration (LCi, ADC BioScientific Ltd.). The system was connected to an external halogen lamp which delivered a photon flux density (DFF) of $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the leaf surface. Measurements were taken every 30 seconds for 2 minutes. Maximum CO_2 assimilation on a mass basis (A_{mass} ; $\mu\text{mol kg}^{-1} \text{s}^{-1}$) was calculated by multiplying the specific leaf area by A_{max} and 0.1 to account for differences in units. Measurements of dark respiration (Resp ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) were obtained by covering the chamber of the IRGA with aluminum foil and waiting for the stabilization of the CO_2 exchange rates. Intrinsic water use efficiency (IWUE) was calculated as the ratio of A_{max} and g_s (Larcher 2000).

Photosynthetic pigment concentration was determined by using leaf discs of 0.5 cm in diameter placed in Eppendorf microcentrifuge tubes of amber color which contained 2 ml of DMF (N, N – dimethylformamide, Vetec). Two leaf discs were taken from each sampled leaf. The tubes were kept in the dark at 4 °C for a period of 48 hours. The samples were analyzed in a spectrophotometer Genesys 2 (Thermo Spectronic) to determine the absorbance at wavelengths of 480, 645 and 663 nm. The absorbance values were then used to calculate the concentrations of chlorophyll *a*, chlorophyll *b*, total chlorophyll (*a* + *b*) and carotenoids according to Wellburn (1994).

Statistical analyses

In the analysis of morphological and physiological parameters, we used an ANOVA followed by Tukey's test when the F test was significant. The significance level was set as 0.05. All data presented normality according to the Kolmogorov-Smirnov test ($P > 0.50$). We also tested whether the linear relationships between the different parameters differed in their slope and intercept between the two species. Differences in the regression lines between the two species were tested with the SMATR software (Warton et al. 2006).

Results

Morphological parameters

The savanna species had thicker leaves with higher specific leaf mass, while leaf density and specific leaf area were higher for the species typical of the forest environment (Tab. 1). The two species showed no statistical differences in relation to leaf area (Tab. 1).

Tabebuia aurea had thicker and shorter petioles in relation to the forest species. Only the thickness of the petiole showed a significant linear relationship with leaf area (Fig. 1) for both *T. aurea* ($r^2 = 0.741$, $P < 0.001$) and *T. impetiginosa* ($r^2 = 0.602$, $P = 0.008$). These relationships did not differ in slope (Wald statistic = 0.456, $P = 0.512$), but differed in their intercept (Wald statistic = 24.552, $P < 0.001$), so that to support the same leaf area, the species typical of savanna environments had thicker petioles. There was no significant relationship between SLA and petiole thickness and SLA and petiole length ($r^2 < 0.01$, $P > 0.50$).

Physiological parameters

Values of A_{max} differed significantly between the two species. A_{max} averaged $16.10 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *T. aurea* compared to $14.01 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *T. impetiginosa* (Fig. 2A). There was a statistically significant difference for the two species in relation to g_s (Fig. 2B) and E (Fig. 2C), with higher values for the species typical of savanna, *T. aurea*. Differences in the degree of stomatal opening between the two species were associated with differences in A_{max} , as A_{max} was lin-

Table 1. Leaf morphological parameters of *Tabebuia aurea* and *T. impetiginosa*. Different lowercase letters indicate differences between the two species according to Tukey's test ($P < 0.05$). Data expressed as mean (\pm SE).

Morphological parameters	<i>Tabebuia aurea</i>	<i>Tabebuia impetiginosa</i>
Leaf area (cm^2)	403.54 \pm 32.93 a	318.44 \pm 29.27 a
Specific leaf area (cm^2/g)	48.92 \pm 2.00 a	78.58 \pm 5.44 b
Specific leaf mass (g/cm^2)	0.0208 \pm 0.0007 a	0.0132 \pm 0.0007 b
Leaf blade thickness (mm)	0.538 \pm 0.0092 a	0.244 \pm 0.0072 b
Leaf density (g/cm^3)	0.3863 \pm 0.0099 a	0.5413 \pm 0.0265 b
Petiole thickness (mm)	3.84 \pm 0.15 a	2.23 \pm 0.10 b
Petiole length (mm)	88.185 \pm 6.272 a	115.122 \pm 6.309 b

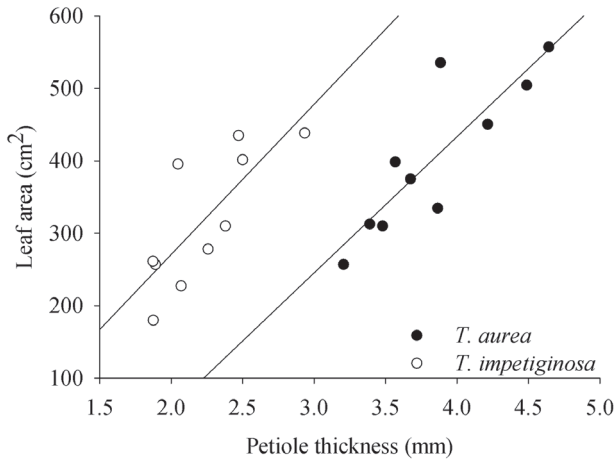


Figure 1. Relationship between petiole thickness and the area of the leaf blade for the two studied species. The lines represent linear regressions fit to the data for *T. aurea* ($r^2 = 0.741$, $P < 0.001$) and *T. impetiginosa* ($r^2 = 0.602$, $P = 0.008$).

early related to g_s (Fig. 3) in both *T. aurea* ($r^2 = 0.688$, $P = 0.003$) and *T. impetiginosa* ($r^2 = 0.469$, $P = 0.029$). These relationships shared the same slope (Wald statistic = 0.21, $P = 0.632$), but with a displacement of *T. aurea* in relation to *T. impetiginosa* along the same axis of inclination (Wald statistic = 23.55, $P < 0.01$).

The forest species showed lower investment in non-photosynthetic leaf tissue producing leaves with higher SLA (Tab. 1). These differences in SLA were reflected in higher A_{mass} for *T. impetiginosa* in comparison to *T. aurea* (Fig. 2D). Both species showed a significant positive linear relationship between SLA and A_{mass} ($r^2 = 0.401$, $P = 0.049$ for *T. aurea* and $r^2 = 0.782$, $P = 0.001$ for *T. impetiginosa*; Fig. 4), whose slopes (Wald-statistic = 1.57, $P = 0.21$) and intercepts (Wald-statistic = 2.73, $P = 0.11$) did not differ between the two species, but with a displacement of *T. impetiginosa* in relation to *T. aurea* along the same axis of inclination (Wald-Statistics = 12.40, $P = 0.00001$).

There were no statistical differences between the two species in the values of dark respiration (Fig. 2E) and of intrinsic water use efficiency (Fig. 2F). The analysis of the leaf concentration of photosynthetic pigments also revealed no differences between the two species in chlorophyll *a*, chlorophyll *b*, total chlorophyll, chlorophyll *a:b* and chlorophyll:carotenoid ratios (Figs. 5A,B). However, leaf concentration of carotenoids was significantly higher for the savanna species (Fig. 5A). The relationship between A_{max} and total chlorophyll and between A_{max} and carotenoid concentrations were not significant.

Discussion

In relation to the savanna species, the forest species had higher SLA, corroborating the studies of Hoffmann *et al.* (2005) and Rossatto *et al.* (2009a), and thinner leaves. Higher values of SLA can be the product of a proportionally lower investment in

biosynthesis of tissue for support and protection, which would result in a thinner leaf (Grime 1979, Franco *et al.* 2005). Leaf thickness is higher in species that grow in environments with high incidence of light (Grime 1979, Reich *et al.* 1999, Dahlgren *et al.* 2006), and is usually an effect caused by increased investment in structures and protective tissues, such as the cuticle and thickened cell walls (Fahn Cutler 1992). This strategy of high investment in these non-photosynthetic structures may serve to reduce the penetration of ultraviolet radiation (Turner 1994). The light environment can also influence other leaf structures, resulting in adjustments in leaf area and in the thickness of photosynthetic tissues (Goulet & Bellefleur 1986). Indeed, higher light intensities induce a thicker palisade parenchyma, and differences in the total number of cells within this tissue (Gratani *et al.* 2006).

Differences in thickness and size of the petiole between the two species and its correlation with functional variables such as leaf area, suggest that the two species have different strategies with regard to the capture of ambient light (Poorter & Bongers 2006). So to improve the capture of light, the forest species have invested in thinner leaves with longer and thinner petioles (Poorter 2008), which would provide greater capacity to capture light, when it is subjected to shaded conditions. Longer petioles would reduce aggregation of leaf area around the stem (Tanekaka 1994) and also provide a more optimal placement of the leaves in relation to neighboring leaves of other trees in forest environments (Poorter 2008). The fact that the forest species maintained higher values for these characteristics in the high light conditions where both species were measured, suggests that these traits were selected and remained conserved in the species typical of the forest environment (Ackerly 2009).

The savanna species had higher A_{max} in relation to the forest species, a pattern also found for two congeneric species of the genus *Styrax*, one of them of typical forest and the other of savanna (Habermann & Bressan 2011). The values of A_{max} are within the range reported by Prado *et al.* (2004) and Franco *et al.* (2005) for savanna species, and by Nogueira *et al.* (2004) for forest species (between 7-23 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Although the concentration of chlorophyll often explains differences in photosynthetic capacity among species (Lichtenthaler *et al.* 2007), this is apparently not the case for the species studied here, since there was no difference in the concentration of these pigments (Fig. 5A), which also showed no significant correlation with A_{max} . The higher concentrations of carotenoids of the savanna species could contribute to a more efficient regulation of electron transport by the photosystems, as these pigments would act in protective mechanisms against high irradiances (Sims & Gamon 2002). However, this has to be considered with caution because other biochemical and physiological mechanisms of photoprotection are commonly found in plants of environments with high irradiance and carotenoid composition has to be taken into consideration (Gonçalves *et al.* 2001, Franco *et al.* 2007, Lichtenthaler *et al.* 2007).

Differences in morphological and physiological leaf characteristics between *Tabebuia aurea* and *T. impetiginosa* is related to their typical habitats of occurrence

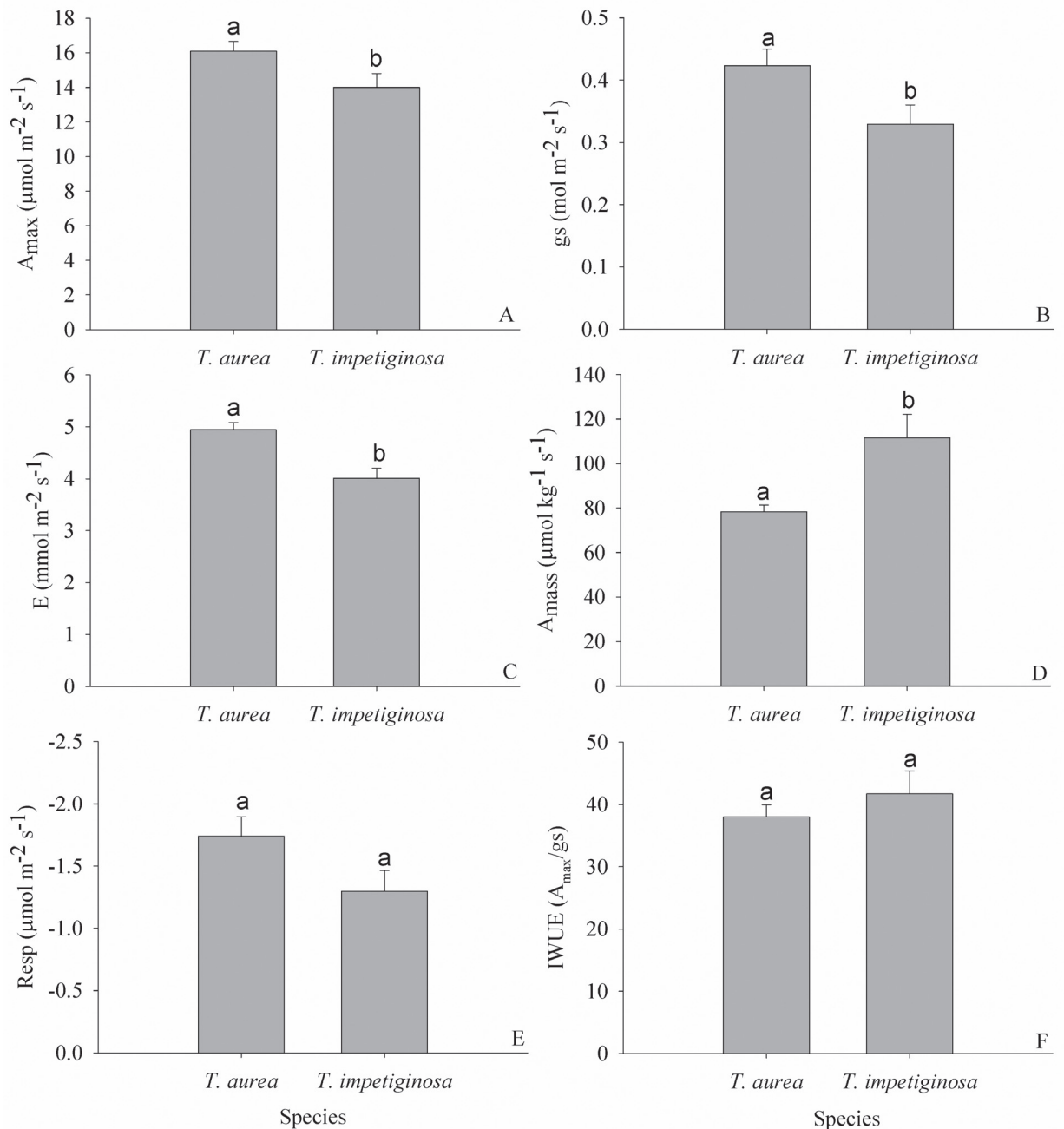


Figure 2. Leaf characteristics related to gas exchange for *T. aurea* and *T. impetiginosa*. A- Maximum CO₂ assimilation (A_{max}); B- Stomatal conductance (g_s); C- Transpiration (E); D- Maximum CO₂ assimilation on a mass basis (A_{max}); E- Dark respiration (Resp) and F – Intrinsic water use efficiency (IWUE). Error bars are the standard errors of the means. Different lowercase letters indicate differences between the two species according to Tukey's test (P < 0.05).

Despite the higher A_{max} of the savanna species, the species of the forest had higher A_{max}mass, suggesting a greater capacity and better competition for light in light-limiting conditions (Valladares & Niinemets 2008), even though both species were studied in high irradiance environments. A_{max}mass was positively correlated to SLA (Fig. 4). This type of relation has been previously reported for a number of species and environments (Prior *et al.* 2004, Franco *et al.* 2005).

The two species had similar dark respiration rates; although the respiration rates of the forest species were

marginally lower (Fig. 2E). This marginal difference would suggest that the leaves of savanna species have a higher metabolic cost, probably linked to a higher thickness of the photosynthetic parenchyma tissue (Dahlgren *et al.* 2006). Studies of the leaf anatomy of both species coupled with detailed gas exchange measurements are necessary to better evaluate any differences in leaf carbon costs.

Relative to the forest species, *Tabebuia aurea* showed higher E due to a greater degree of stomatal opening, which suggests greater water transport capacity on a leaf area basis

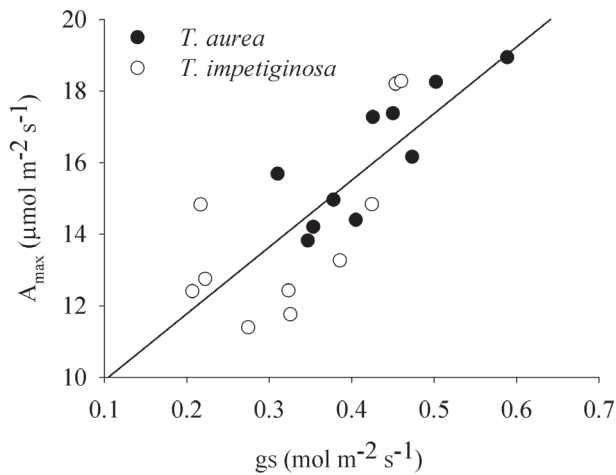


Figure 3. Relationship between stomatal conductance (g_s) and maximum CO_2 assimilation (A_{max}). Individual linear regressions were significant for *T. aurea* ($r^2 = 0.688$; $P = 0.003$) and *T. impetiginosa* ($r^2 = 0.469$; $P = 0.029$).

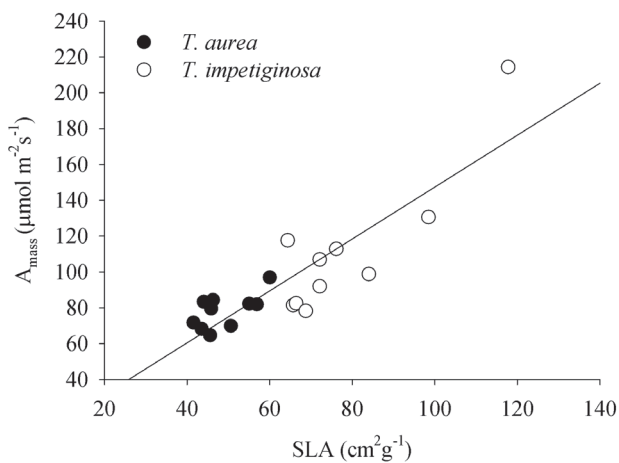
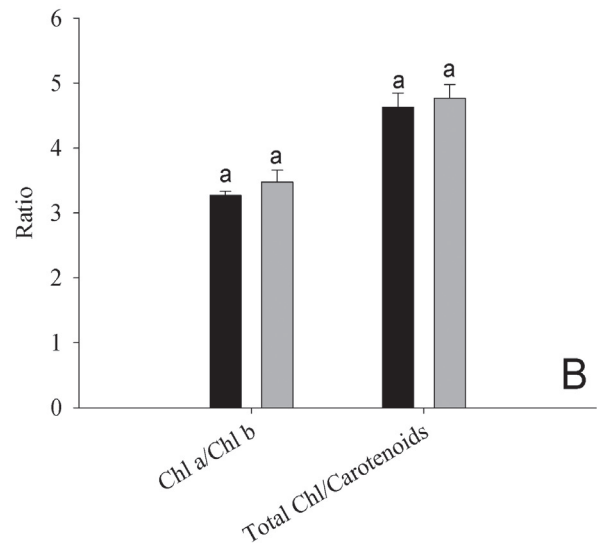
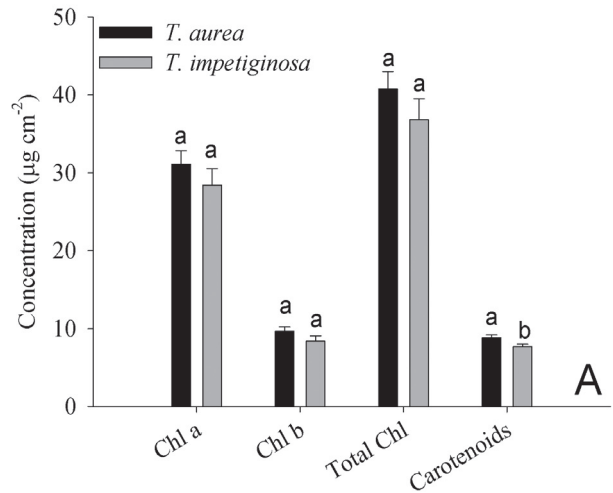


Figure 4. Relationship between specific leaf area (SLA) and maximum CO_2 assimilation on a mass basis (A_{mass}). Individual linear regressions were significant for *T. aurea* ($r^2 = 0.401$; $P = 0.049$) and *T. impetiginosa* ($r^2 = 0.782$; $P = 0.001$).

(Gotsch *et al.* 2010). However, as the savanna species also had higher values of A_{max} , intrinsic water use efficiency was similar between the two species. Differences in g_s and E are not always found between congeneric pairs of savanna and forest species. In fact, Rossatto *et al.* (2009b) measured g_s and E in 10 congeneric pairs and found significant differences in only three of these pairs; the savanna species showed higher transpiration in two of them.

The observed differences in the morphological and physiological parameters described here revealed a functional distinction between *T. aurea* and *T. impetiginosa*, even when exposed to the same environmental determinants. We suggest that such differences could be the result of the evolutionary history of these species, which were exposed to different selective pressures in the environments of origin. Thus, higher values of SLA, petiole length and A_{mass} of the forest species are indicative of functional variables evolutionarily shaped to increase the ability to capture light in shaded environments



Leaf pigments

Figure 5. A- Leaf concentrations of photosynthetic pigments for *T. aurea* e *T. impetiginosa*. A- Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Total Chl), and carotenoids. B- Chlorophyll *a:b* and total chlorophyll:carotenoid ratios. Error bars are the standard errors of the means. Different lowercase letters indicate differences between the two species according to Tukey's test ($P < 0.05$).

(Valladares & Niinemets 2008, Rossatto *et al.* 2010, Barros *et al.* 2011) and to achieve higher growth rates (Poorter & Bongers 2006). On the other hand, the higher values of A_{max} , leaf thickness and carotenoids and lower SLA in the savanna species would be adaptations to nutrient-poor soils (Haridasan 1992), high irradiance and dry environments (Turner 1994), which are typical conditions of savannas.

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