

## Leaf habit does not predict leaf functional traits in cerrado woody species

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### Abstract

Plant species with a high leaf life span (LLS) commonly have a low specific leaf area (SLA), leaf nitrogen per unit mass (N), and phosphorous concentration (P), whereas species with low LLS have a high SLA, N and P. However, LLS tends to be longer in species growing in low-nutrient soils and, therefore, differences in LLS and other leaf traits may not be consistent with a plant classification according to leaf habit. Here we investigated whether leaf habit is consistent with leaf economic spectrum trade-offs in cerrado (a Neotropical savanna) woody species. We analyzed the SLA, N and P of 125 woody species with a distinct leaf habit (deciduous, semideciduous, brevideciduous or evergreen). We also gathered data on the LLS (33 species), maximum net photosynthesis per leaf area ( $A_{area}$ , 56 species) and per leaf mass ( $A_{mass}$ , 31 species), comprising the most extensive database analyzed so far for the cerrado. Differences among leaf habit groups were tested using generalized linear mixed models and ANOVA. We did not find differences in SLA and N among species with a distinct leaf habit, but deciduous species had a higher leaf P concentration than evergreens. Species did not differ in LLS and  $A_{mass}$ , but  $A_{area}$  varied among groups. Semideciduous species had higher  $A_{area}$  values than deciduous and brevideciduous species, but all other groups had similar  $A_{area}$  values. Because of the small difference in the LLS, SLA, leaf N, leaf P and maximum net photosynthesis, we argue that deciduous, brevideciduous, semideciduous and evergreen species may not constitute different functional groups in cerrado woody species.

### Zusammenfassung

Pflanzenarten mit einer hohen Blattlebensdauer (LLS) haben gemeinhin eine geringe spezifische Blattfläche (SLA), sowie geringe Stickstoff- (N) und Phosphorkonzentrationen (P), während Arten mit geringer LLS hohe SLA-, N- und P-Werte aufweisen. Indessen tendiert die LLS dahin, bei Arten, die in nährstoffarmen Böden wachsen, länger zu sein, und deshalb könnten Unterschiede hinsichtlich der LLS und anderer Blatteigenschaften nicht mit einer Einteilung der Pflanzen nach Blattwurftypen übereinstimmen. Wir untersuchten an den Gehölzarten neotropischer Savannen (cerrado), ob der Blattwurfotyp mit den Zielkonflikten im Ökonomiespektrum der Blätter in Einklang steht. Wir analysierten SLA, N und P von 125 Gehölzarten aus unterschiedlichen Blattwurftypen (laubwerfend, halblaubwerfend, kurzlaubwerfend oder immergrün). Wir berücksichtigten auch LLS-Daten (33 Arten), sowie die maximale Netto-Photosynthese je Blattfläche ( $A_{area}$ , 56 Arten) und je Blattmasse ( $A_{mass}$ , 31 Arten). Unterschiede zwischen den Blattwurftypen wurden mit GLMM und ANOVA getestet. Wir fanden keine

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Unterschiede hinsichtlich SLA und N zwischen den Blattwurfstypen, aber die Blätter blattwerfender Arten hatten eine höhere P-Konzentration als die von immergrünen Arten. Es gab keine Unterschiede hinsichtlich LLS und  $A_{\text{mass}}$ , aber  $A_{\text{area}}$  variierte zwischen den Blattwurfstypen. Halblaubwerfende Arten wiesen höhere  $A_{\text{area}}$ -Werte als laubwerfende und kurzlaubwerfende Arten, aber alle anderen paarweisen Unterschiede waren nicht signifikant. Angesichts der geringen Unterschiede hinsichtlich LLS, SLA, N, P und Netto-Photosynthese postulieren wir, dass laubwerfende, halblaubwerfende, kurzlaubwerfende und immergrüne Arten keine funktionellen Gruppen von neotropischen Savannengehölzen begründen.

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**Keywords:** Cerrado; Deciduousness; Leaf life span; Seasonality; Specific leaf area; Trade-offs

## Introduction

The relationship between specific leaf area (SLA, i.e. light intercepting area deployed per leaf dry mass) and both leaf nitrogen concentration (N) and leaf phosphorous concentration (P) is well known for angiosperms in several ecosystems, from tundras to tropical forests (Reich, Walters, & Ellsworth 1997; Reich, Ellsworth, Walters, Vose, et al. 1999). SLA captures the fundamental trade-off between resource acquisition and conservation in plants; therefore species with a high SLA typically have high leaf N and P, and consequently a higher photosynthetic capacity (Westoby, Falster, Moles, Vesk, & Wright 2002). Leaf N and P are also positively related to stomatal conductance and relative growth rate (Reich, Walters, & Ellsworth 1992; Westoby et al. 2002).

SLA, N and P also decrease in similar proportions with increasing leaf life span (LLS): species with high LLS commonly have low SLA, N and P (thick leaves), whereas species with low LLS have high SLA, N, and P (soft leaves; Reich et al. 1992; Westoby et al. 2002; Pringle et al. 2010). The high investment in N and P leaf concentration in species with low LLS is linked to the construction of leaves with more photosynthetic structures (chlorophyll content), which improve carbon gain. On the other hand, species with high LLS produce leaves with more non-photosynthetic structures (less investment in N and P content), which results in thick leaves. In general, the cost of producing leaves with high life spans is greater than that of leaves with low life spans (Villar & Merino 2001). Usually, species with high LLS have leaves with a lower photosynthetic capacity than species with low LLS (Chabot & Hicks 1982; Westoby et al. 2002). However, species with high LLS display the leaves for a long time and have more time to pay off the costs of leaf construction than do species with low LLS. In addition, because species with high LLS are exposed for a long period of time to the action of herbivores and environmental factors, such as water, light and temperature fluctuations, they are more vulnerable than species with low LLS (Chabot & Hicks 1982; Westoby et al. 2002). As a consequence, leaves of species with high LLS tend to be more resistant (thick leaves) and have a greater investment in defence and maintenance (Wright & Westoby 2002; Pringle et al. 2010). In short, the SLA–LLS spectrum is a trade-off between the potential rate of return per leaf area per unit time and the duration of return. Thus, SLA, N and P are important traits to assess leaf ecological strategies.

In South America, the cerrado is the largest savanna region, originally occupying about 20% of the Brazilian territory (Ratter, Ribeiro, & Bridgewater 1997). The cerrado presents a wide physiognomic range, from grassland to tall woodlands, and a high richness of woody species (Ratter et al. 1997). The soils are poor in nutrients and acidic, with a low cation exchange capacity and high levels of aluminium saturation (Haridasan 2008). Like other savannas, the cerrado is characterized by a sharp seasonality, with a pronounced rainless season ranging from May to October (Ratter et al. 1997). In response to the seasonality, cerrado woody species generally present two contrasting ecological strategies, concerning timing of leaf production and loss, which encapsulate the whole range of the LLS, from deciduousness to evergreenness (Franco et al. 2005; Lenza & Klink 2006; Araújo & Haridasan 2007). In other plant communities, such as temperate forest, LLS seems to be the main trait influencing the range of leaf physiological and morphological attributes of woody species (Reich, Walters, & Ellsworth 1997; Reich, Ellsworth, Walters, Vose, et al. 1999). In cerrado, however, the difference in LLS between deciduous and evergreen woody species is quite small when compared to other plant communities under the same regional climate (Damascos, Prado, & Ronquim 2005; Souza, Prado, Damascos, & Albino 2009). In general, the LLS of cerrado woody species is around 12 months; deciduous species drop leaves at the end of the dry season and remain leafless for a short period of time (around one month; Damascos et al. 2005). As a result, deciduous and evergreen woody species may not present large differences in leaf traits, such as in SLA, N and P, and they may not comprise discrete leaf functional groups.

Recently, Franco et al. (2005) and Araújo and Haridasan (2007) investigated the relationship between SLA, N and P in evergreen and deciduous tree species in cerrado and found (1) a positive relationship between SLA and both N and P, and (2) higher values of SLA, N and P in deciduous than in evergreen trees. However, the number of species studied was small (11 species, Franco et al. 2005; 15 species, Araújo & Haridasan 2007) and restricted to a single site. In the present study, we analyzed the SLA, N and P of 125 woody species with distinct patterns of LLS in four cerrado sites with different physiognomies. We investigated possible differences among deciduous, semideciduous, brevideciduous, and evergreen species. We also included published data on LLS for 33 woody species and on maximum net

photosynthesis per leaf area ( $A_{\text{area}}$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and per leaf mass ( $A_{\text{mass}}$ ,  $\mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ) for 56 and 31 species, respectively. LLS and maximum net photosynthesis are related to leaf morphophysiological traits (Reich et al. 1999). Nevertheless, differences in the LLS among plants with distinct leaf deciduousness are small in the cerrado (Damascos et al. 2005; Souza et al. 2009), and cerrado woody species with a distinct leaf habit overlap considerably in their ecophysiological features (Goldstein et al. 2008). In view of this we expect that cerrado woody species with different leaf habits have similar values of SLA, N and P. In summary, we asked: (1) Do species with a distinct leaf habit have distinct values of specific leaf area, leaf nitrogen and phosphorus concentrations, leaf life span, maximum net photosynthesis per leaf area and maximum net photosynthesis per leaf mass?

## Materials and methods

### Ecological data

We compiled data on SLA, leaf N and P concentrations of woody species occurring across four cerrado sites (Appendix A). Our data comprised information on woody species from two different cerrado physiognomies: an open savanna (campo cerrado) and three dense savanna types (cerrado sensu stricto). The open savanna site is located in Emas National Park, central Brazil (approximately at 18°17' S, 52°53' W; Silva & Batalha 2010; Batalha, Silva, Cianciaruso, & Carvalho 2011). The dense savanna sites are located at the Ecological Reserve of IBGE (approximately at 15°56' S, 47°52' W; Franco et al. 2005), the Federal University of São Carlos reserve, south-eastern Brazil (approximately at 21°59' S, 47°51' W; Paula 2002; Damascos et al. 2005), and at the Itirapina Experimental Station (approximately at 22°13' S, 47°51' W; Silva & Batalha 2009). The areas have a seasonal climate with a rainy summer and dry winter. The soils are deep, well-drained, strongly acid dystrophic latosols or oxisols, with a high aluminium concentration (Franco et al. 2005; Silva & Batalha 2008; Silva & Batalha 2009; Dantas & Batalha 2011), and the vegetation had not been burnt for 3 to 12 years when the measurements were made (see Appendix B for more detail on the environmental characteristics of each site).

We gathered information on SLA ( $\text{mm}^2/\text{mg}$ ), N and P (mg/g) from 125 woody species that we could classify unambiguously as deciduous, semideciduous, brevideciduous and evergreen (Appendix A). These traits were measured following a protocol for plant functional trait measurement (Cornelissen et al. 2003), according to which between five and ten fully expanded leaves, without symptoms of herbivore and pathogen attack, were sampled from five to ten individuals during the rainy season. In addition, we gathered information on LLS for 33 woody species (Paula 2002; Damascos et al. 2005; Franco et al. 2005;

Peixoto 2007; Souza et al. 2009; Noleto 2010), and on  $A_{\text{area}}$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and  $A_{\text{mass}}$  ( $\mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ) for 56 and 31 species, respectively (Prado & Moraes 1997; Franco 2002; Franco et al. 2005; Peixoto 2007). Data on LLS were obtained from three sites (IBGE, São Carlos and Itirapina) and maximum net photosynthesis per leaf area ( $A_{\text{area}}$ ) and leaf mass ( $A_{\text{mass}}$ ) were obtained from only two sites (IBGE and São Carlos).

We grouped the species according to leaf habit using data on LLS (Damascos et al. 2005; Franco et al. 2005; Noleto 2010; Paula 2002; Peixoto 2007; Prado, Wenhui, Rojas, & Souza 2004; Souza et al. 2009) and references in the literature (Lenza & Klink 2006; Pirani, Sanchez, & Pedroni 2009; Silvério & Lenza 2010). We considered as deciduous those species that shed all the leaves on their crown at the end of the dry season, remaining leafless for about four to five weeks. Brevideciduous species have a similar behaviour but remain leafless for no more than three weeks. Semideciduous species are those that shed approximately half of their leaves at the end of the dry season, and evergreens are those that retain their leaves throughout the year. Evergreen leaf-exchangers (species that shed and produce leaves throughout the year) and perennial evergreens (species that retain leaves on shoots for more than one growth season) were not considered as separate groups, due to the lack of data or confidence in classifying them all as such.

### Data analysis

The biological traits displayed by a species are at the same time a product of its particular evolutionary history and the result of specialization to the environment that it inhabits. Thus, an important step in comparative analysis, especially when seeking to correlate species traits with functional groups, is to verify how much of the trait similarity among species is due to shared ancestry (Diniz-Filho, Sant'Ana, & Bini 1998; Staggemeier, Diniz-Filho, & Morellato 2010). To verify the importance of the species evolutionary history for trait variability, we quantified phylogenetic signals in SLA, N, P, LLS,  $A_{\text{area}}$  and  $A_{\text{mass}}$  using phylogenetic eigenvector regression analyses (PVR; Diniz-Filho et al. 1998). PVR estimates the phylogenetic signal on traits by extracting a series of vectors that describe the phylogeny from a double-centred phylogenetic distance matrix among species. These vectors can then be used as predictor variables in multiple regressions, and the adjusted  $R^2$  value can be interpreted as an estimate of the degree of the phylogenetic signal (Diniz-Filho et al. 1998; Staggemeier et al., 2010). We log-transformed the traits and regressed them against the phylogenetic eigenvectors so that the estimated values expressed phylogenetic trends in the data, whereas residuals expressed independent evolutionary paths for each species. The phylogenetic information was obtained from a phylogenetic tree constructed for all sampled species using Phylomatic software, a phylogenetic toolkit for the

assembly of phylogenetic trees (Webb & Donoghue 2005). The age of the nodes of the families were estimated from the dated angiosperm super-tree of Davies et al. (2004). Since the Fabaceae present polytomies, we distributed the genera into their subfamilies following the latest understanding of these relationships (Angiosperm Phylogeny Website; Stevens 2001). We assigned branch lengths of these genera by spacing undated nodes evenly above the family node. We computed the PVR with the *vegan* (Oksanen et al. 2008) and *picante* (Kembel et al. 2010) packages within the R environment (R Development Core Team 2011). We did not find any significant phylogenetic signal in the traits analyzed (Appendix C). Therefore, we undertook all the analyses with the raw data because we had confidence that the species relatedness was not a source of bias (lack of independence) in our results.

To test for differences in SLA, N and P among deciduous, semideciduous, brevideciduous and evergreen species, we fitted generalized linear mixed-effects models (GLMM) for each response variable, including species identity nested within sites (IBGE, Emas, São Carlos and Itirapina) as a random effect to account for repeated measures of species. We included sites and the interaction between sites and leaf habit as additional fixed factors to control for possible effects due to sampling site characteristics. We fitted models using restricted maximum likelihood, with a Gaussian distribution and identity link function using the “lmer” function in the “lme4” R package (R Development Core Team 2011). We compared the full model (with all terms and interactions) and the reduced model (with the term of interest excluded) using a likelihood ratio test, whereby the change in deviance between models follows a Chi-square distribution and the degrees of freedom represent the difference in the number of parameters between the full and reduced models (Quinn & Keough 2002). Parameter estimates were obtained from models including only significant terms and estimates of full models are presented in Appendix D.

We tested differences in LLS,  $A_{\text{area}}$  and  $A_{\text{mass}}$  among leaf habit groups using ANOVA, including sites, and the interaction between sites and leaf habit groups, as additional explanatory variables to test for possible dependency on the sampling site. We did not use GLMM here because for these data we do not have variability within species (i.e., each species appeared only in a single site). All measures of  $A_{\text{area}}$  for semideciduous species were exclusive to São Carlos, and therefore we could not include them in this analysis. We also had a low sample size of  $A_{\text{mass}}$  measurements for semideciduous species ( $n=2$ ), so they were excluded from the analyses. Post hoc multiple comparisons were applied in order to test for differences among levels of leaf habit or sites, when statistically significant in GLMM or ANOVA, using the “glth” function in the “multicomp” R package (R Development Core Team 2011) and applying Bonferroni’s correction for critical  $P$  values.

For all analyses, we tested for homoscedasticity and the normality distribution of residuals by using standardized residuals versus fitted values scatter plots and Shapiro–Wilk

**Table 1.** Estimated parameters for significant predictor terms of GLMM of SLA, N and P (all variables logarithm transformed) in relation to leaf habit group and sampling site.

Model	Predictor term	Estimate $\pm$ SE <sup>a</sup>
SLA <sup>a</sup>	Intercept	0.80 $\pm$ 0.03
	Site	
	Emas	0.01 $\pm$ 0.03
	São Carlos	0.34 $\pm$ 0.03
	Itirapina	0.24 $\pm$ 0.03
N <sup>a</sup>	Intercept	1.10 $\pm$ 0.03
	Site	
	Emas	0.13 $\pm$ 0.03
	São Carlos	0.16 $\pm$ 0.04
	Itirapina	0.25 $\pm$ 0.04
P <sup>b</sup>	Intercept	−0.17 $\pm$ 0.03
	Leaf habit	
	Brevideciduous	0.03 $\pm$ 0.02
	Semideciduous	0.07 $\pm$ 0.03
	Deciduous	0.08 $\pm$ 0.02
	Site	
	Emas	0.12 $\pm$ 0.04
São Carlos	0.00 $\pm$ 0.04	
	Itirapina	0.16 $\pm$ 0.05

<sup>a</sup>Estimates are relative to the IBGE site (intercept).

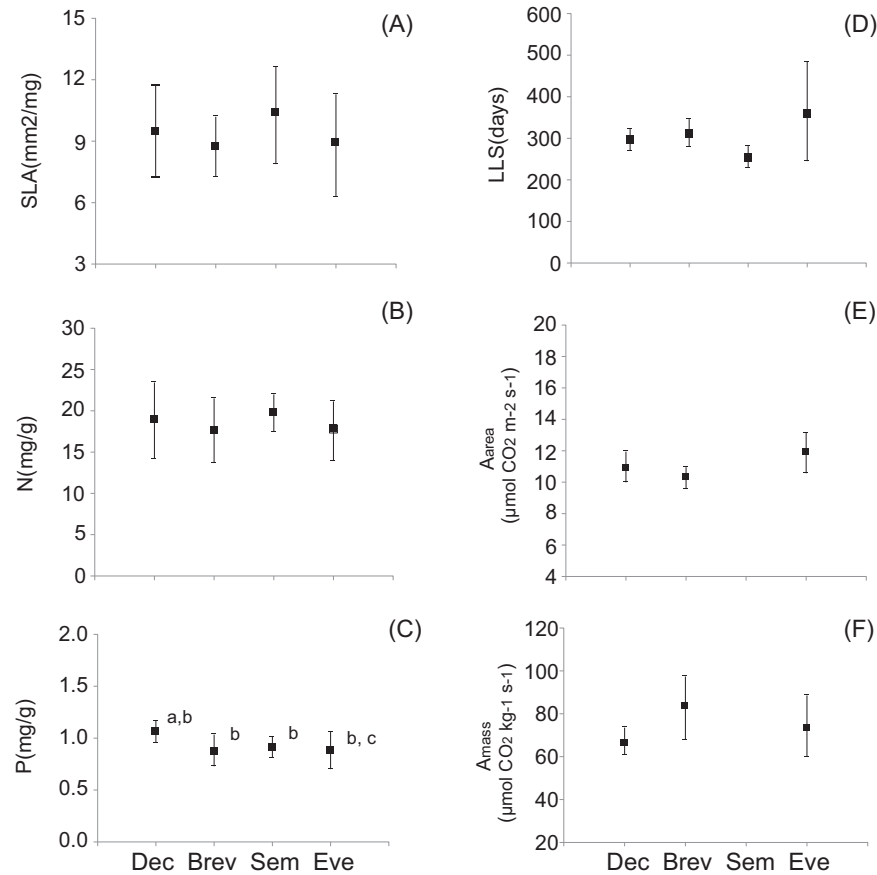
<sup>b</sup>Estimates are relative to evergreen species at the IBGE site (intercept).

tests, respectively (Legendre & Legendre 1998). When normality could not be accessed, log-transformed response variables were used.

## Results

We analyzed the SLA, N and P of 125 species belonging to 45 families and the LLS of 33 species belonging to 21 families (Appendix A).

We did not find significant differences in SLA and N among any of the leaf habit groups ( $\chi^2=17.06$ ,  $df=12$ ,  $P=0.15$ ;  $\chi^2=10.59$ ,  $df=12$ ,  $P=0.56$ , respectively) (Appendix D), but P differed among them ( $\chi^2=31.14$ ,  $df=12$ ,  $P=0.002$ ) (Table 1, Fig. 1). Deciduous species had a higher mean leaf P concentration than evergreen species ( $z=-4.20$ ,  $P<0.001$ , Table 1, Fig. 1), but all other pairs of leaf habit groups had a similar P concentration value (deciduous–brevideciduous:  $P=0.18$ ; evergreen–brevideciduous:  $P=0.48$ ; semideciduous–brevideciduous:  $P=0.54$ ; semideciduous–deciduous:  $P=0.99$ ; semideciduous–evergreen:  $P=0.04$ ; paired comparisons with adjusted critical  $P=0.008$ ). All response variables, SLA, N and P, differed among sites ( $\chi^2=30.62$ ,  $df=12$ ,  $P=0.002$ ;  $\chi^2=25.78$ ,  $df=12$ ,  $P=0.01$ ; and  $\chi^2=27.32$ ,  $df=12$ ,  $P=0.007$ , respectively) (Table 1). We did not find, however, any significant effects of interaction



**Fig. 1.** Leaf traits of cerrado woody species with distinct leaf habit. (A) Specific leaf area (mm<sup>2</sup>/mg), (B) leaf nitrogen concentration (mg/g), (C) leaf phosphorus concentration (mg/g), (D) leaf-life-span (days) (E) Aarea, and (F) Amass. Values are averages  $\pm$  standard error. Dec = deciduous, Brev = brevidciduous, Sem = semideciduous, and Eve = evergreen. Different letters indicate significant differences ( $\alpha = 5\%$ ).

between sites and leaf habit for SLA, N or P ( $\chi^2 = 9.02$ ,  $df = 9$ ,  $P = 0.44$ ;  $\chi^2 = 7.81$ ,  $df = 9$ ,  $P = 0.55$ ; and  $\chi^2 = 11.75$ ,  $df = 9$ ,  $P = 0.23$ , respectively), indicating that differences among groups based on leaf habit do not depend on the site in which the species were sampled (see Appendix D).

Leaf habit groups did not differ in LLS,  $A_{mass}$  and  $A_{area}$  ( $F_{3,24} = 1.07$ ,  $P = 0.38$ ;  $F_{2,23} = 1.27$ ,  $P = 0.30$ ; and  $F_{2,41} = 2.13$ ,  $P = 0.13$ , respectively) (Fig. 1). Also, there was no interaction between leaf habit groups and sites ( $F_{3,24} = 0.94$ ,  $P = 0.44$ ;  $F_{2,23} = 2.02$ ,  $P = 0.16$ ; and  $F_{2,41} = 0.005$ ,  $P = 0.99$ , respectively). Leaf life span differed among sites ( $F_{2,24} = 6.37$ ,  $P = 0.006$ ), whereas  $A_{mass}$  and  $A_{area}$  did not ( $F_{1,23} = 0.18$ ,  $P = 0.67$ ; and  $F_{1,41} = 1.19$ ,  $P = 0.28$ , respectively) (Fig. 1 in Appendix D). Details about the differences in species traits between sites are presented in Appendix D, but we have refrained from discussing these variations since it is beyond the scope of this paper and also because trait differences among leaf habit groups did not depend on the sampling site (all interaction terms were non-significant).

## Discussion

In general for the savanna woody species studied here, deciduous, brevidciduous, semideciduous and evergreen species did not exhibit distinct leaf functional trait values. The absence of a significant difference in LLS that we observed between species with distinct leaf habits highlight the fact that deciduous and evergreen species in these savannas show little difference in LLS (Damascos et al. 2005; Souza et al. 2009), and may explain the similar values of SLA, N, P,  $A_{area}$  and  $A_{mass}$ . Although independent studies have found that deciduous species in cerrado may produce leaves with higher SLA than evergreen species (Franco et al. 2005; Araújo & Haridasan 2007; Carvalho, Bustamante, Kozovits, & Aasner 2007) and that evergreen species may have higher (Carvalho et al. 2007) or lower (Franco et al. 2005; Nardoto, Bustamante, Pinto, & Klink 2006) leaf N and P concentrations, we found that deciduous, brevidciduous, semideciduous and evergreen species do not constitute discrete leaf functional groups. This adds evidence in favour of

the postulate of Goldstein et al. (2008), who state that leaf trait variation in cerrado woody species can be better understood by representing them as a continuum of functional differences rather than by assigning them to arbitrary functional groups. However, we did not observe any directionality in our data. In fact, there was a high trait variability within each leaf habit, especially for SLA, N, LLS (evergreens) and  $A_{\text{mass}}$  (Fig. 1).

The plants inhabiting the cerrado have to face three major environmental filters: seasonal droughts, nutrient-poor soils, and natural fires (Ratter et al. 1997). Thus, cerrado plants exhibit an array of physiological and morphological traits to cope with these pressures (Franco 2002). These three filters should alter plant trade-offs hindering our ability to detect functional groups based on leaf habit using leaf traits. Consequently, as we found here, clear differences in leaf functional traits may not emerge between evergreen, brevideciduous and deciduous species in cerrado. In the next paragraphs we offer some potential explanations on how these environmental filters may be related to our findings.

The period of drought in the cerrado induces a partial stomatal closure in woody plants, decreasing the stomatal conductance and photosynthetic rate (Perez & Moraes 1991; Prado et al. 2004). Under this seasonal water limitation, differences in root traits are expected to arise between deciduous and evergreen species, as long as deciduousness has evolved as a drought-avoidance mechanism (Chabot & Hicks 1982). Deciduous and evergreen cerrado woody species have marked differences in water uptake, with deciduous species using water from deeper soil layers than evergreen species (Jackson et al. 1999). Also, there is a clear interdependence between the degree of leaf deciduousness and the crown structural traits in cerrado woody species (Souza, Prado, Albino, Damascos, & Souza 2011). Thus, in these plants, root depth and crown architectural properties seem to be much more linked to water relations and leaf habit than to leaf traits.

SLA, N and P are largely associated with carbon gain in plants, so that evergreen species generally exhibit a photosynthetic capacity that is lower than in deciduous species (Chabot & Hicks 1982; Westoby et al. 2002). Nevertheless, we found that woody species in cerrado exhibit similar values for photosynthetic rate independently of their leaf habit. Indeed, similar maximum photosynthetic rates have already been observed for deciduous and evergreen cerrado woody species, with values ranging from 12 to 20  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$  (see Franco 2002 for references). These similar photosynthetic rates may be due to the conversion of plant resources in non-photosynthetic tissues, larger leaf construction and maintenance costs, the degree and duration of crown deciduousness or the combined effects of herbivory and partial leaf loss in deciduous species, all of which could potentially counteract the benefits to evergreen species of maintaining a photosynthetically active crown in the dry season (see references in Franco 2002).

Cerrado species with a distinct leaf habit showed no differences in SLA, so investment in the production of photosynthetic leaf tissues is similar. This finding, and the fact that

species with a distinct leaf habit have similar LLS, indicates that the “payback time” (the time that a leaf needs to compensate its cost in terms of carbon investment) may be similar for deciduous, brevideciduous, semideciduous and evergreen species in these savannas. Moreover, the nutrient-poor soils in cerrado may also contribute to the similar SLA, N and P values between deciduous and evergreen plants (Goldstein et al. 2008). Most of the cerrado soils have extremely low nitrogen and phosphorous availability (e.g. phosphorous levels are generally below 1 ppm; Montgomery & Askew 1983; Ruggiero, Batalha, Pivello, & Meirelles 2002), which could hinder overall photosynthetic rates in woody plants. Because cerrado soils are highly weathered, economic use of nutrients is a crucial prerequisite for the persistence of these species (Meinzer et al. 1999). Given that LLS tends to be longer in species growing in low-nutrient soils, soil conditions in these savannas may act as a filter, selecting species with relatively higher “payback time” among the leaf habit groups. Thus, trade-offs among these groups may be present in other plant structures. Indeed, as we already pointed out, plants with a distinct leaf habit in these savannas do have different root systems and resource exploration strategies (Scholz et al. 2008).

We cannot ignore the role that fire may play in determining similar leaf trait values despite species having a distinct leaf habit. Fire frequency in the studied savannas is high (see references in Cianciaruso, Silva, Gaston, Batalha, & Petchev 2012; Dantas, Pausas, Batalha, Loiola, & Cianciaruso 2013), which, for example, could select against long leaf lifespans among the evergreen species. Also, in addition to the fact that these species occur in poor-soils, fire could select species with a similar leaf nutrient concentration. In fact, recent studies conducted in the cerrado show that frequent fires predominantly assemble species with similar leaf functional traits (Cianciaruso et al. 2012) and that fires may increase intraspecific, but not interspecific, variability in functional traits, including leaf traits (Dantas et al. 2013). Dantas et al. (2013) showed that recurrent fires select plant individuals with lower N and P contents and lower SLA, which suggests the existence of a nutrient stress. In the cerrado, fires promote nutrient loss from the system (Pivello & Coutinho 1992) and, because cerrado soils are nutrient-poor (Ruggiero et al. 2002; Dantas & Batalha 2011), individuals under high fire frequency could be facing a significant nutrient limitation. In addition, such nutrient stress may also be a consequence of the indirect effects of increased herbivory after fire (Lopes & Vasconcelos 2011). Therefore, these abiotic and biotic filters are another possible explanation for the similar leaf traits we observed to the studied species.

In some cerrado sites, where seasonality is more pronounced, differences in leaf traits may be larger than we found (see Franco et al. 2005; Araújo & Haridasan 2007). If this were the case, then deciduous and evergreen species represent close states of a spectrum of LLS in cerrado, which may occasionally be recognized as discrete functional groups. The plasticity of traits in response to environmental changes has

largely been ignored from analyses of plant functional groups (Lavorel et al. 2007), though it may contribute considerably to the different findings of studies investigating plant communities under highly variable environments (Pornon, Marty, Winterton, & Lamaze 2011), such as the cerrado (Cianciaruso et al. 2012; Dantas et al. 2013) and other savannas. Yet, although investigating the variability in leaf traits among sites was not our objective here, we did find trait variability across sites (Appendix D). This indicates that the environment plays a role in the variability of these species independently of leaf habit and should be investigated in more detail in the future.

In conclusion, our results diverge from those previously found in the cerrado (Franco et al. 2005; Araújo & Haridasan 2007) as well in other plant communities (Reich et al. 1997, 1999). Deciduous, brevideciduous, semideciduous and evergreen species may not constitute different functional groups in cerrado because they cannot be distinguished on the basis of LLS, SLA, leaf N and P, and the photosynthetic rates between them. As a consequence, deciduous and evergreen species may to a certain extent respond similarly to the environmental pressures of the cerrado (e.g., seasonal drought, nutrient-poor soils, fire). We postulated that this is due to the high plasticity of leaf traits and life spans in cerrado plant species or that differences in leaf habit should be related to other plant traits, such as root depth and crown architecture. Nevertheless, wherever the seasonality is more pronounced, differences in leaf traits are expected to emerge; this is however still a question to be answered.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2013.05.002>.

## References

Araújo, J. F., & Haridasan, M. (2007). Relação entre deciduidade e concentrações foliares de nutrientes em espécies lenhosas do cerrado. *Revista Brasileira de Botânica*, 30, 533–542.

- Batalha, M. A., Silva, I. A., Cianciaruso, M. V., & Carvalho, G. H. (2011). Trait diversity on the phylogeny of cerrado woody species. *Oikos*, 120, 1741–1751.
- Carvalho, A. P., Bustamante, M. M. C., Kozovits, A. R., & Aasner, G. P. (2007). Variações sazonais nas concentrações de pigmentos e nutrientes em folhas de espécies de cerrado com diferentes estratégias fenológicas. *Revista Brasileira de Botânica*, 30, 19–27.
- Chabot, B. F., & Hicks, D. J. (1982). The ecology of leaf life spans. *Annual Review of Ecology, Evolution, and Systematics*, 13, 229–259.
- Cianciaruso, M. V., Silva, I. A., Gaston, K. J., Batalha, M. A., & Petchey, O. L. (2012). The influence of fire on phylogenetic and functional structure of woody savannas: Moving from species to individuals. *Perspectives in Plant Ecology, Evolution and Systematics*, 14, 205–216.
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., et al. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335–380.
- Damascos, M. A., Prado, C. H. B. A., & Ronquim, C. C. (2005). Bud composition branching patterns and leaf phenology in cerrado woody species. *Annals of Botany*, 96, 1075–1084.
- Dantas, V. L., & Batalha, M. A. (2011). Vegetation structure: Fine scale relationships with soil in a cerrado site. *Flora*, 206, 341–346.
- Dantas, V., Pausas, J., Batalha, M., Loiola, P., & Cianciaruso, M. V. (2013). The role of fire in structuring trait variability in Neotropical savannas. *Oecologia*, 171, 487–494.
- Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E., & Savolainen, V. (2004). Darwin's abominable mystery: Insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 1904–1909.
- Diniz-Filho, J. A. F., Sant'Ana, C. E. R., & Bini, L. M. (1998). An eigenvector method for estimating phylogenetic inertia. *Evolution*, 52, 1247–1262.
- Franco, A. C. (2002). Ecophysiology of woody plants. In P. S. Oliveira, & R. J. Marquis (Eds.), *The cerrados of Brazil: Ecology and natural history of a Neotropical savanna* (pp. 178–197). New York: Columbia University Press.
- Franco, A. C., Bustamante, M., Caldas, L. S., Goldstein, G., Meinzer, F. C., Kozovits, A. R., et al. (2005). Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees Structure and Function*, 19, 326–335.
- Goldstein, G., Meinzer, F. C., Bucci, S. J., Scholz, F. G., Franco, A. C., & Hoffmann, W. A. (2008). Water economy of Neotropical savanna trees: Six paradigms revisited. *Tree Physiology*, 28, 395–404.
- Haridasan, M. (2008). Nutritional adaptations of native plants of the cerrado biome in acid soils. *Brazilian Journal of Plant Physiology*, 20, 183–195.
- Jackson, P. C., Meinzer, F. C., Bustamante, M., Goldstein, G., Franco, A., Rundel, P. W., et al. (1999). Partitioning of soil water among tree species in a Brazilian cerrado ecosystem. *Tree Physiology*, 19, 717–724.
- Kemmel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., et al. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.

- Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., et al. (2007). Plant functional types: Are we getting any closer to the Holy Grail? In J. G. Canadell, D. Pataki, & L. Pitelka (Eds.), *Terrestrial ecosystems in a changing world* (pp. 149–160). Berlin: Springer-Verlag.
- Legendre, P., & Legendre, L. (1998). *Numerical ecology*. Amsterdam: Elsevier.
- Lenza, A. E., & Klink, C. A. (2006). Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília DF. *Revista Brasileira de Botânica*, 29, 627–638.
- Lopes, C. T., & Vasconcelos, H. L. (2011). Fire increases insect herbivory in a neotropical savanna. *Biotropica*, 43, 612–618.
- Meinzer, F. C., Goldstein, G., Franco, A. C., Bustamante, M., Iglar, E., Jackson, P., et al. (1999). Atmospheric and hydraulic limitations on transpiration in Brazilian cerrado woody species. *Functional Ecology*, 13, 273–282.
- Montgomery, R. F., & Askew, G. P. (1983). Soils of tropical savannas. In D. W. Goodall (Ed.), *Ecosystems of the world – Tropical savannas* (pp. 63–77). Berlin: Elsevier.
- Nardoto, G. B., Bustamante, M. M. C., Pinto, A. S., & Klink, C. A. (2006). Nutrient use efficiency at ecosystem and species level in savanna areas of Central Brazil and impacts of fire. *Journal of Tropical Ecology*, 22, 191–201.
- Noletto, L. G. (2010). *Longevidade foliar, compostos fenólicos e nitrogenados em lianas e árvores suporte em um fragmento de Cerrado na estação experimental de Itirapina-SP*. Universidade Estadual de Campinas (PhD thesis)
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, D. L., Stevens, M. H. H., & Wagner, H. (2008). *vegan: Community ecology package. R package version 1.13-1*. <http://vegan.r-forge.r-project.org>
- Paula, N. F. (2002). *Capacidade fotossintética, deciduidade e teor de nitrogênio e fósforo em espécies lenhosas do cerrado*. Universidade Federal de São Carlos (PhD thesis).
- Peixoto, M. M. (2007). *Variações sazonais no metabolismo de carbono e relações hídricas em espécies lenhosas do Cerrado de diferentes grupos funcionais*. Universidade de Brasília (MSc thesis).
- Perez, S. C. J. G. A., & Moraes, J. A. P. V. (1991). Determinação do potencial hídrico, condutância estomática e potencial osmótico em espécies dos estratos arbóreo arbustivo e herbáceo de um cerrado. *Revista Brasileira de Fisiologia Vegetal*, 3, 27–37.
- Pirani, F. R., Sanchez, M., & Pedroni, F. (2009). Fenologia de uma comunidade arbórea em cerrado sentido restrito, Barra do Garças MT. *Acta Botanica Brasílica*, 23, 1096–1109.
- Pivello, V. R., & Coutinho, L. M. (1992). Transfer of macronutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). *Journal of Tropical Ecology*, 8, 487–497.
- Pornon, A., Marty, C., Winterton, P., & Lamaze, T. (2011). The intriguing paradox of leaf lifespan responses to nitrogen availability. *Functional Ecology*, 25, 796–801.
- Prado, C. H. B. A., & Moraes, J. A. P. V. (1997). Photosynthetic capacity on mass and on area basis and leaf specific mass in twenty woody species of cerrado vegetation under field conditions. *Photosynthetica*, 33, 103–112.
- Prado, C. H. B. A., Wenhui, Z., Rojas, M. H. C., & Souza, G. M. (2004). Seasonal leaf gas exchange and water potential in a woody cerrado species community. *Brazilian Journal of Plant Physiology*, 16, 7–16.
- Pringle, E. G., Adams, R. I., Broadbent, E., Busby, P. E., Donnatti, C. I., Kurten, E. L., et al. (2010). Distinct leaf-trait syndromes of evergreen and deciduous trees in a seasonally dry tropical forest. *Biotropica*, 43, 299–308.
- Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. New York: Cambridge University Press.
- R Development Core Team. (2011). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org>
- Ratter, J. A., Ribeiro, J. F., & Bridgewater, S. (1997). The Brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany*, 80, 223–230.
- Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., et al. (1999). Generality of leaf trait relationships: A test across six biomes. *Ecology*, 80, 1955–1969.
- Reich, P., Walters, M. B., & Ellsworth, D. S. (1992). Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs*, 62, 365–392.
- Reich, P., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 13730–13734.
- Ruggiero, P. G. C., Batalha, M. A., Pivello, V. R., & Meirelles, V. R. (2002). Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. *Plant Ecology*, 160, 1–16.
- Scholz, F. G., Bucci, S. J., Goldstein, G., Moreira, M. Z., Meinzer, F. C., Domec, J. C., et al. (2008). Biophysical and life-history determinants of hydraulic lift in Neotropical savanna trees. *Functional Ecology*, 22, 773–786.
- Silva, D. M., & Batalha, M. A. (2008). Soil-vegetation relationships in cerrados under different fire frequencies. *Plant and Soil*, 311, 87–96.
- Silva, I. A., & Batalha, M. A. (2009). Co-occurrence of tree species at fine spatial scale in a woodland cerrado southeastern Brazil. *Plant Ecology*, 200, 277–286.
- Silva, I. A., & Batalha, M. A. (2010). Woody plant species co-occurrence in Brazilian savannas under different fire frequencies. *Acta Oecologica*, 36, 85–91.
- Silvério, D. V., & Lenza, E. (2010). Fenologia de espécies lenhosas em um cerrado típico no Parque Municipal do Bacaba, Nova Xavantina, Mato Grosso, Brasil. *Biota Neotropica*, 10, 205–216.
- Souza, J. P., Prado, C. H. B. A., Albino, A. L., Damascos, M. A., & Souza, G. M. (2011). Network analysis of tree crowns distinguishes functional groups of Cerrado species. *Plant Ecology*, 212, 11–19.
- Souza, J. P., Prado, C. H. B. A., Damascos, M. A., & Albino, A. L. S. (2009). Influence of shoot inclination on irradiance and morphophysiological leaf traits along shoots in cerrado trees with distinct leaf deciduousness. *Brazilian Journal of Plant Physiology*, 21, 281–289.
- Staggemeier, V. G., Diniz-Filho, J. A. F., & Morellato, L. P. C. (2010). The shared influence of phylogeny and ecology on the reproductive patterns of Myrteae (Myrtaceae). *Journal of Ecology*, 98, 1409–1421.
- Stevens, P. F. (2001). *Angiosperm phylogeny website. Ver. 9*. <http://www.mobot.org/MOBOT/research/APweb/>



- Villar, R., & Merino, J. (2001). Comparison of leaf construction costs in woody species with differing leaf lifespans in contrasting ecosystems. *New Phytologist*, *151*, 213–226.
- Webb, C. O., & Donoghue, M. J. (2005). Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes*, *5*, 181–183.
- Westoby, M., Falster, D., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, *33*, 125–159.
- Wright, I. J., & Westoby, M. (2002). Leaves at low versus high rainfall: Coordination of structure lifespan and physiology. *New Phytologist*, *155*, 403–416.

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