The length of the dry season may be associated with leaf scleromorphism in cerrado plants

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ABSTRACT

Despite limitations of low fertility and high acidity of the soils, the cerrado flora is the richest amongst savannas. Many cerrado woody species show sclerophyllous leaves, which might be related to the availability of water and nutrients in the soil. To better understand the function and structure of cerrado vegetation within its own variations, we compared two cerrado communities: one in its core region in central Brazil (Brasília, DF) and the other on its southern periphery (Itirapina, SP). We contrasted the length of the dry season, soil fertility rates, leaf concentrations of N, P, K, Ca and Mg and the specific leaf area (SLA) between these communities. The dry season was shorter on the periphery, where the soil was more fertile although more acidic. Plants from the periphery showed higher SLA and higher leaf concentrations of N, P, Ca and Mg. We propose that the higher SLA of plants from the periphery is related to the shorter dry season, which allows better conditions for nutrient uptake.

Key words: savanna, mineral nutrition, rainfall seasonality, specific leaf area.

INTRODUCTION

Savannas occupy 20% of emerged lands (Sankaran et al. 2005), covering 21% of the Brazilian territory (Souza and Habermann 2012), 25% of the Australian

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territory (Williams et al. 2005) and 40% of Africa's land area (Okitsu 2005). Savannas are composed of grasses, shrubs and trees, and the function and structure of species are strongly influenced by ecological filters (Gottsberger and Silberbauer-Gottsberger 2006). For instance, fire frequency,

soil fertility, water availability and herbivory have been recognized as important ecological filters in savannas (Sankaran et al. 2005).

Soil nutrient uptake and leaf development are water-dependent (Kreuzwieser and Gessler 2010). In fact, leaf traits such as nutritional status and the specific leaf area (SLA, e.g. proportion of leaf area unit of leaf mass) have been regularly used to explain responses of savanna species to variations in ecological filters. In Australian savannas, species growing on poor soils and subjected to high frequency of fire and droughts possess decreased concentrations of nutrients in their leaves, which tend to be more sclerophyllous (low SLA). In contrast, species growing on fertile soils with low frequency of drought and fire show nutrient-rich and less sclerophyllous leaves (Wright et al. 2001, Prior et al. 2005). Although there are some indications that changes in nutrient availability affects leaf nutrient status and SLA of cerrado species (Bucci et al. 2006, Delgado et al. 2013), detailed studies at the community level are lacking.

The Cerrado domain is very large (~2 millions km^2), and similar vegetation physiognomies occur in areas with distinct water availability (Gottsberger and Silberbauer-Gottsberger 2006) and may grow on soils from different geological formations (Motta et al. 2002). Thus, the structure and functioning of different cerrado plant communities could vary considerably due to variations in water and nutrient availability in these soils.

Considering that cerrado *sensu stricto* communities located in the core and on the southern periphery of its domain are subjected to soils with different geological formations and fertility, and to different seasonalities, we tested the hypothesis that variations in SLA and leaf nutritional status between both communities are connected to the length of the dry season and soil fertility. After all, these are important differences empirically noted between such locations and there is some evidence that the length of the dry season might affect leaf nutritional

status of cerrado species (Bustamante et al. 2012). We expect the plants on the southern periphery to be less sclerophyllous and retain more nutrients in their leaves in comparison to plants from the core, where soils appear to be poorer and the dry season, longer.

MATERIALS AND METHODS

SITE AND STUDY DESCRIPTION

The study was conducted in two cerrado *sensu stricto* fragments, one in the core region and the other on the southern periphery of the Cerrado domain. In the core of the Cerrado, the plant community was located at the Ecological Reserve of IBGE (15°57'S 47°52'W) in Brasília, the Brazilian Federal District. On the periphery, the plant community was growing on the São José da Conquista farm (22°13'S 47°53'W), in Itirapina, São Paulo state. Both sites present rainy summers and dry winters.

A 30-year-dataset was used to estimate the mean annual rainfall, length of the dry and wet seasons and air temperature, from 1980 to 2010 (Walter 1986). The climatic data were provided by the National Institute of Meteorology (INMET 2013). Total annual rainfall in the core is about 1452 mm and the mean annual temperature, about 21°C. On the periphery, total annual rainfall is 1512 mm and mean annual temperature near 20°C (Fig. 1).

We studied 15 woody species in the core and 21 species on the southern periphery (Table I). In both communities, three plots of 15 x 15 m were established and only species that were common among plots were selected. The plants were sampled between February and March 2005 (in the core; Araújo 2006) and 2011 (on the periphery). Soil sampling was also performed in the three plots.

SPECIFIC LEAF AREA AND NUTRITIONAL STATUS

Fully expanded mature leaves were sampled from 4-6 plants per species, according to the availability. The leaves were washed with deionized water and oven-dried at 60°C until constant mass to avoid N losses (Souza et al. 2015).

(a) Core (1100 m)
1980-2010   21.2C   1452 mm

(b) Periphery (610 m)
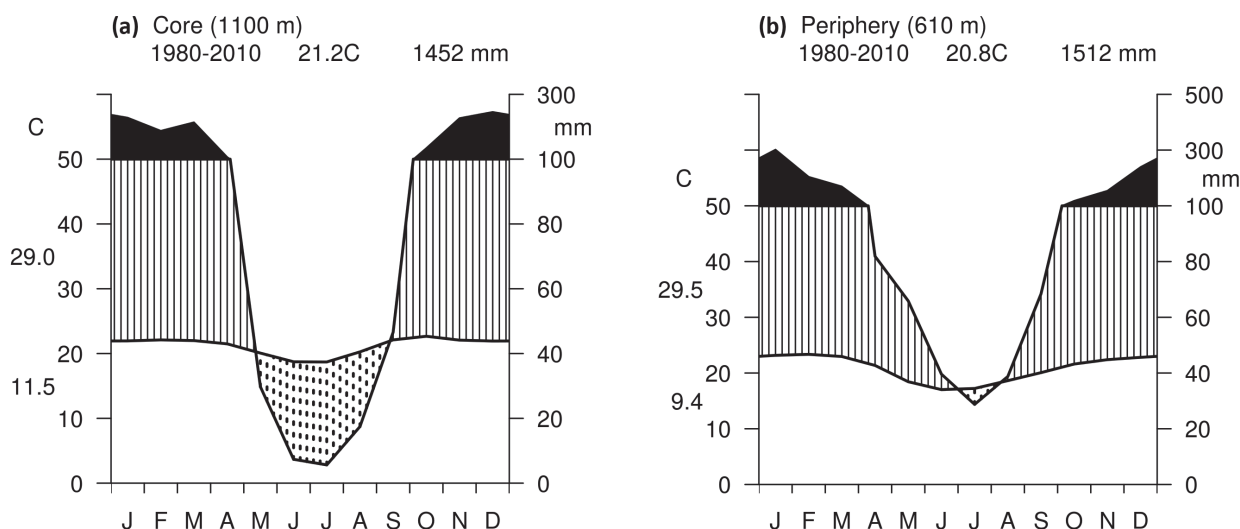1980-2010   20.8C   1512 mm

Figure 1 - Walter climatic diagram displaying the length of the dry and wet seasons, elevation, annual rainfall and air temperature and monthly averages for a period of 30 years (1980–2010) in the core **(a)** and southern periphery **(b)** of the Cerrado.

To determine the specific leaf area (SLA), six leaves per plant of each species were used for obtaining 40 leaf discs of pre-determined area (1 cm of diameter). The SLA was calculated as the ratio between leaf area (cm^2) and leaf dry mass (g) (Habermann and Bressan 2011). Leaves from both communities were digested in an acid solution (nitric:percloric) and leaf N concentration was determined by the micro-Kjeldahl method. For the core's community, the concentration of Ca, Mg and K were determined by atomic absorption spectrophotometry and P was measured colorimetrically (Allen 1989). For the periphery's community, leaf concentrations of Ca and Mg were determined by atomic absorption spectrophotometry, K was determined using a flame photometer, and P was determined colorimetrically (Sarruge and Haag 1974, Dantas and Batalha 2011). SLA and nutrient leaf status was measured and computed as per species. However, to test our hypothesis and for statistical reasons we combined every species from each plant community and analyzed them together.

SOIL CHARACTERIZATION

Soil samples were randomly collected (0-30 cm in depth) from each of the three plots. Chemical parameters [pH, N, organic matter (OM), P, K, Ca, Mg and Al] and physical properties (percentage of clay, silt and total sand) were determined according to Raij et al. (1987). Procedures are described in English in Dantas and Batalha (2011).

DATA ANALYSIS

The variations in pH, OM, P, K, Ca, Mg and Al in the soils and the variations in leaf concentrations of N, P, K, Ca and Mg, and also in SLA between both communities were analyzed using a multivariate analysis of variance MANOVA at 5% level. We used a standardized major axis (SMA) regression to test for significant differences in slopes and intercepts between leaf concentrations of N x P, Ca x Mg, SLA x N, and SLA x P (Warton et al. 2006) for both communities. We performed the statistical procedures in R (R Development Core Team 2012).

RESULTS

CLIMATE AND SOIL CHARACTERIZATION

Both regions exhibited similar total annual rainfall and average temperature, but the dry season on the peripheral community was not

TABLE I

**List of species selected from two cerrado *sensu stricto* communities
located in the core and on the southern periphery of the Cerrado.**

Family	Specie	Site	Leaf deciduousness*
Annonaceae	*Annona coriacea* Mart.	Periphery	EG
Annonaceae	*Xylopia aromatica* (Lam.) Mart.	Periphery	EG
Apocynaceae	*Aspidosperma tomentosum* Mart.	Periphery	D
Araliaceae	*Schefflera paniculata* Elmer	Core	EG
Calophyllaceae	*Kielmeyera coriacea* Mart.	Core	D
Caryocaraceae	*Caryocar brasiliensis* A.St.-Hil.	Core/Periphery	BD/D
Erythroxylaceae	*Erythroxylum suberosum* A.St.-Hil.	Periphery	BD
Erythroxylaceae	*Erythroxylum tortuosum* Mart.	Periphery	BD
Erythroxylaceae	*Erythroxylum pelleterianum* A.St.-Hil.	Periphery	D
Fabaceae	*Sclerolobium paniculatum* Vogel	Core	EG
Fabaceae	*Dalbergia miscolobium* Benth.	Core	BD
Fabaceae	*Stryphnodendron adstringens* (Mart.) Coville	Core	BD
Malpighiaceae	*Byrsonima crassa* Nied.	Core	BD
Malpighiaceae	*Byrsonima basiloba* A.Juss.	Periphery	EG
Malpighiaceae	*Byrsonima intermedia* A.Juss.	Periphery	EG
Malpighiaceae	*Banisteriopsis variabilis* B.Gates	Periphery	D
Malvaceae	*Eriotheca gracilipes* (K.Schum.) A.Robyns	Periphery	D
Melastomataceae	*Miconia pohliana* Cogn.	Core	EG
Melastomataceae	*Miconia rubiginosa* (Bonpl.) A.DC.	Periphery	EG
Melastomataceae	*Miconia fallax* DC.	Periphery	EG
Myrsinaceae	*Rapanea umbellata* Mart.	Periphery	EG
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O.Berg	Core	BD
Myrtaceae	*Myrcia bella* Cambess.	Periphery	BD
Nyctaginaceae	*Guapira noxia* (Netto) Lundell	Core	D
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	Periphery	BD
Ochnaceae	*Ouratea hexasperma* Baill.	Core	EG
Rubiaceae	*Tocoyena formosa* (Cham. & Schltdl.) *K.Schum.*	Periphery	D
Salicaceae	*Casearia sylvestris* Swartz	Periphery	BD
Sapotaceae	*Pouteria torta* (Mart.) Radlk.	Periphery	EG
Styracaceae	*Styrax ferrugineus* Nees & Mart.	Periphery	BD
Vochysiaceae	*Vochysia elliptica* Mart.	Core	EG
Vochysiaceae	*Vochysia thyrsoidea* Pohl	Core	EG
Vochysiaceae	*Qualea grandiflora* Mart.	Core/Periphery	D/BD
Vochysiaceae	*Qualea parviflora* Mart.	Core	D

*Leaf deciduousness of cerrado *senso stricto* species from plant communities in the core (Araújo 2006) and on the southern periphery (Souza et al. 2015) of the Cerrado. EG – evergreen, BD – brevideciduous, D – deciduous.

only shorter (July-August) but also milder, while in the core the dry season was longer (May – September) and more severe (Fig. 1).

The soil from the periphery was more acidic (pH < 4.0) although richer in N, P, Ca and Mg in comparison to the soil from the core (Table II). In addition, the soil from the core showed higher percentages of clay and silt. The Al saturation (m%) and K and OM concentrations did not differ between the sites (Table II).

Leaf Traits

The plant community located on the southern periphery of the Cerrado domain showed higher

leaf concentrations (g kg^{-1}) of N (18.22 ± 8.05), P (1.06 ± 0.34), Ca (5.33 ± 1.97), and Mg (1.96 ± 0.72) in comparison to the plant community in the core region: N (14.36 ± 7.46), P (0.64 ± 0.24), Ca (3.71 ± 2.78), and Mg (1.34 ± 0.66) (Fig. 2).
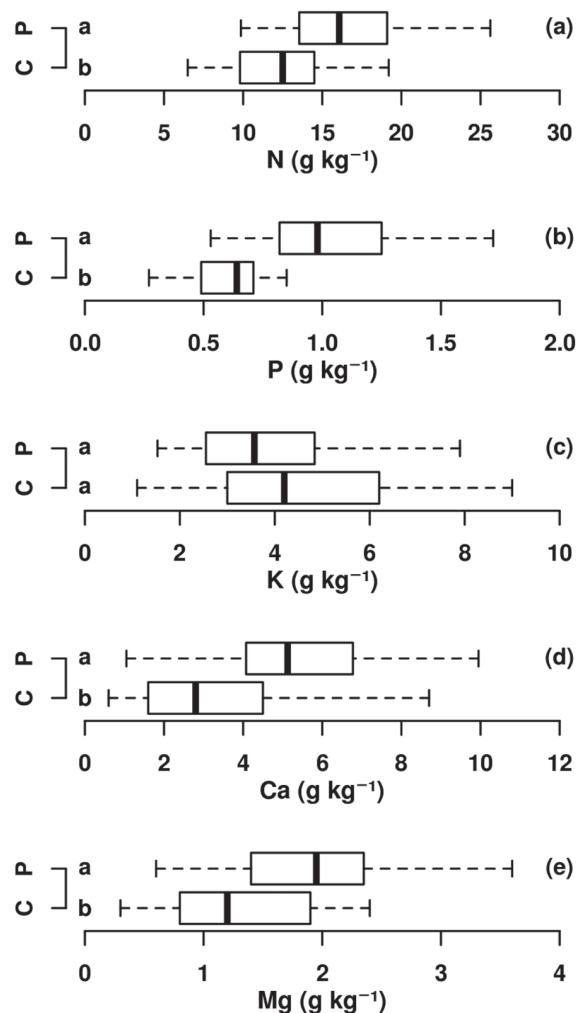

Figure 2 - Box plots showing leaf nutrient concentration [nitrogen **(a)**, phosphorus **(b)**, potassium **(c)**, calcium **(d)** and magnesium **(e)**] in two cerrado *sensu stricto* communities located in the core and southern periphery of the Cerrado. The line in the middle of each box indicates the 50th percentile of the observed distribution; the left and right parts of each box represent the 25th and 75th percentiles, respectively; the left and right error bars of each box are the 5th and the 95th percentiles of the observed distribution. Different letters indicate significant difference (p < 0.05) using a multivariate analysis of variance (MANOVA) at 5% level between the core (C) and the southern periphery (P) of the Cerrado.

TABLE II
Soil properties of two cerrado *sensu stricto* communities in the core and on the southern periphery of the Cerrado.

Soil parameter	Site		P value
	Core	Periphery	
pH (CaCl$_2$)	4.6 ± 0.2	3.9 ± 0.1	<0.001
Organic matter (g dm^{-3})	28.3 ± 0.4	20.7 ± 2.4	0.138
N (%)	0.14 ± 0.2	0.17 ± 0.3	<0.001
P (mg dm^{-3})	1.6 ± 0.4	2.2 ± 0.3	0.031
K (mmol$_c$ dm^{-3})	1.0 ± 0.5	1.3 ± 0.2	0.298
Ca (mmol$_c$ dm^{-3})	0.2 ± 0.2	1.9 ± 0.5	0.001
Mg (mmol$_c$ dm^{-3})	0.3 ± 0.4	1.1 ± 0.2	0.011
Al (mmol$_c$ dm^{-3})	8.5 ± 2.4	13.4 ± 1.5	0.013
Al saturation (m %)	85.4 ± 8.1	75.9 ± 3.3	0.07
Clay %	65.4 ± 6.9	13.2 ± 0.8	<0.001
Sand %	19.7 ± 4.3	84.5 ± 1,2	<0.001
Silt %	14.2 ± 2.8	2.3 ± 0.6	0.001

The plant community on the periphery exhibited higher SLA values (125.56 ± 38.14 cm^2 g^{-1}) than those exhibited by plants in the core (69.01 ± 20.41) (Fig. 3). There were positive correlations between leaf concentration of N and P (Fig. 4a), and between Ca and Mg (Fig. 4b) for both communities. Significant differences between plant communities were observed in the N x P relationship due to the significant variation in the intercepts (Fig. 4a).
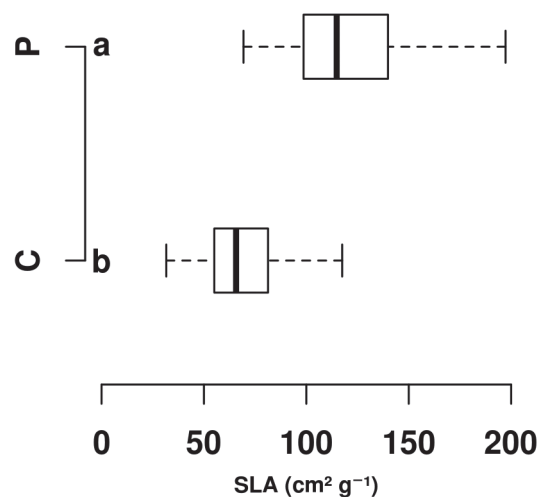

Figure 3 - Box plots of specific leaf area (SLA) in cerrado *sensu stricto* communities located in the core (C) and on the southern periphery (P) of the Cerrado. Box plot characteristics are as described in Figure 2.
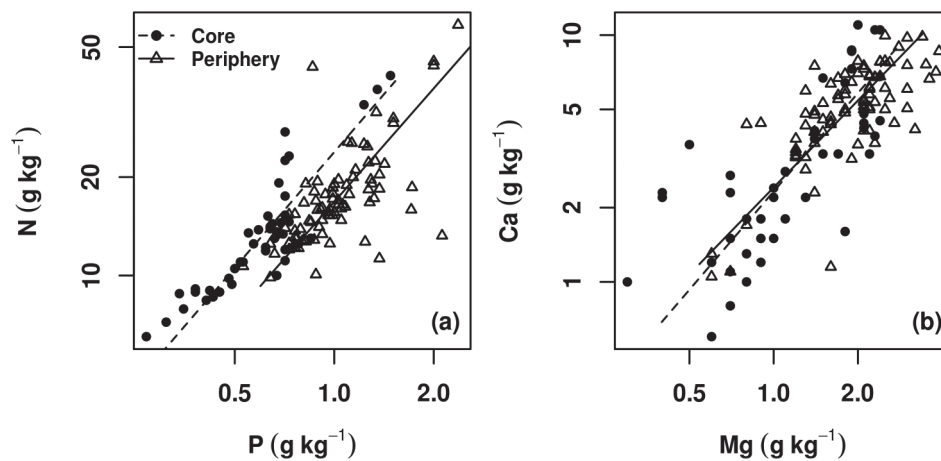
Figure 4 - Standardized major axis (SMA) relationships between leaf concentrations of N *versus* P (core – p<0.001, R^2 = 0.772, intercept = 1.378, slope = 1.776; periphery – p<0.001, R^2 = 0.451, intercept = 1.225, slope = 1.153) **(a)** and Ca *versus* Mg (core – p<0.001, R^2 = 0.549, intercept = 0.367, slope = 1.324; periphery – p<0.001, R^2 = 0.535, intercept = 0.383, slope = 1.170) **(b)** for two cerrado *sensu stricto* communities in the core and on the southern periphery of the Cerrado. Axes are log10 scaled.

However, for the Ca x Mg relationship, there was no significant variation either for intercept or for elevation between both communities. In addition, we found no clear relationship between SLA x N (Fig. 5a) or between SLA x P (Fig. 5b).

DISCUSSION

The total annual rainfall in the core (~1450 mm) was nearly the same as the periphery (~1500 mm) and these rainfall values are enough to support forest vegetation in the tropics (Gottsberger and
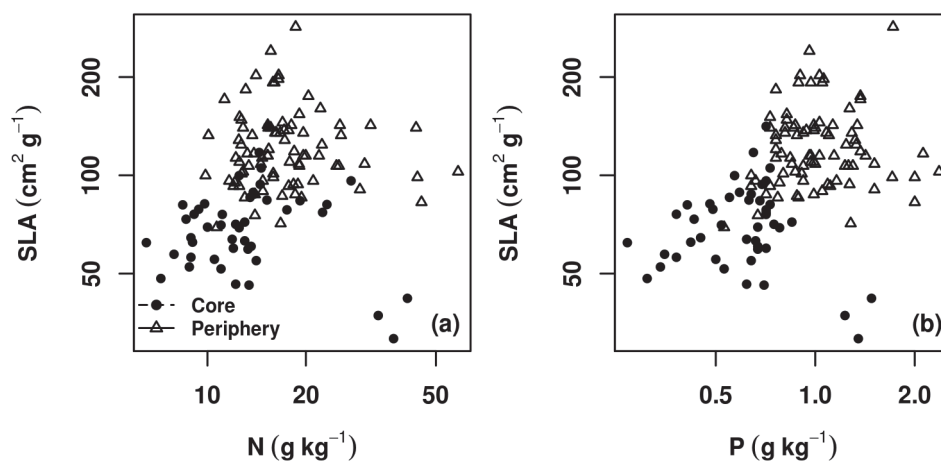

Figure 5 - Standardized major axis (SMA) relationships between leaf concentrations of N x SLA (p>0.05) and P x SLA (p>0.05) for two cerrado *sensu stricto* communities in the core (C) and on the southern periphery (P) of the Cerrado. Axes are log10 scaled.

Silberbauer-Gottsberger 2006, Silva et al. 2013). Rather than similar annual rainfall between the sites, we observed and highlight a significant difference in the length of the dry season between the communities (2 months on the periphery and approximately 5 months in the core).

Savanna species from wet regions are less sclerophyllous (show high SLA) than species from dry regions, which tend to have low SLA (Wright et al. 2001, Prior et al. 2005). Indeed, this is true only for savannas where the total annual rainfall and the length of the dry season are negatively correlated (M.C. Souza et al., unpublished data). For example, in the Australian savanna, rainfall decreases from the north of the country toward the center, while the length of the dry season shows the opposite pattern. In this scenario, SLA gets higher as going to the north region (Prior et al. 2005 for references). For Neotropical savannas, such as the cerrado, there is no clear relationship between annual rainfall and the length of the dry season (Gottsberger and Silberbauer-Gottsberger 2006). In fact, the length and severity of the dry season is much more variable than the total annual rainfall, which is similar across most of the Cerrado region (Gottsberger and Silberbauer-Gottsberger 2006).

For plants, in general, water deficit not only affects leaf structure, but may also impair plant growth and development by restricting plant transpiration and thus soil nutrient uptake (Chaves et al. 2002). For cerrado plants it may also occur (Prado et al. 2004), and the dry season reduces soil nutrient uptake and, consequently, the amount of soil-derived nutrients available to be deployed in new leaves (Kreuzwieser and Gessler 2010). We observed that the peripheral plant community showed higher leaf N concentration and SLA in comparison to the plant community from the core, suggesting low scleromorphism on the southern peripheral community. Association between high soil N availability and low leaf scleromorphism was already observed for some cerrado species (Delgado et al. 2013). A significant correlation

between SLA and N was observed in studies comparing Australian savannas under different soil fertilities and rainfall regimes (Wright et al. 2001), and when comparing congeneric species from savanna and forest environments in Brazil (Hoffmann et al. 2005). In the present study, we did not observe significant SLA x N correlations for any of the two communities, suggesting that this relationship is not conserved for all savanna physiognomies.

Leaf scleromorphism has also been used to discriminate between forest and savanna species. Forest species are less sclerophyllous (have high SLA) than savanna species (Hoffmann et al. 2005) since the main limitation in forests is the capture of sunlight (Givnish 1988, Habermann and Bressan 2011), while in savannas the main challenge is surviving the dry season (Prado et al. 2004, Bucci et al. 2008). Less sclerophyllous species invest more in photosynthetic tissues, have higher ratios of mesophyll to epidermis, and mesophyll to leaf thicknesses (Delgado et al. 2013, Somavilla et al. 2014); moreover, these species accumulate more N, P, Ca and Mg in their leaves on a leaf mass basis (Hoffmann et al. 2005).

Low pH, high Al concentration and low fertility are typical characteristics of cerrado soils (Haridasan 2008), but within cerrado areas, soils may vary regarding pH and fertility rates (Cianciaruso et al. 2013). In the core, the soil is less fertile and less acidic although it presents similar Al saturation (m%) in relation to the soil from the southern periphery. Soil Ca concentration was ten times greater on the periphery in relation to the core, and plants from the periphery retained more nutrients in their leaves, including Ca.

On the periphery, soils are younger and less leached than soils from the core (Motta et al. 2002), and we noted that the dry season is shorter on the southern periphery. Therefore, the annual rainfall seems to be better distributed on the periphery, providing better conditions for nutrient uptake and accumulation in leaves. In contrast, the long

dry season in the core (Fig. 1) may impair plant growth, nutrient uptake and accumulation. These associations support the hypothesis that leaf scleromorphism and the nutritional status of the cerrado *sensu stricto* plant communities may not reflect solely the soil fertility where these plants grow, but also that the length of the dry season may play an important role on the structure and functioning of these communities.

CONCLUSIONS

Our results support the hypothesis that plants on the southern periphery are less sclerophyllous and retain more nutrients in their leaves in comparison to the core region. This illustrates that similar vegetation physiognomies within the Cerrado domain can differ in leaf functional traits. Based on 30-year data sets of climatic data, and on measurements of soil fertility and leaf traits, we propose that rather than total rainfall, the length of the dry season may be an important cause of variation of leaf traits, determining structural differences between plant communities of the same physiognomies.

RESUMO

Apesar das limitações nutricionais e elevada acidez dos solos, a flora do cerrado é a mais rica entre as savanas. Muitas espécies lenhosas do cerrado possuem folhas escleromórficas e o nível de escleromorfismo foliar parece depender da disponibilidade de água e nutrientes no solo. Visando um melhor entendimento sobre a estrutura e funcionalidade da vegetação do cerrado, foram comparadas duas comunidades de cerrado *sensu stricto*: uma na região central do Brasil (Brasília, DF) e a outra na periferia sul (Itirapina, SP). Para tal, comparamos a duração da estação seca, a fertilidade do solo, as concentrações foliares de N, P, K, Ca e Mg e a área foliar específica (AFE) entre as duas comunidades do cerrado. A estação seca na periferia foi menor em relação à região central, e seu solo foi considerado mais fértil e mais ácido. A vegetação periférica apresentou maior AFE e apresentou maiores concentrações foliares de N, P, Ca e Mg. Baseado nestes resultados, propomos que a maior AFE observada na comunidade periférica se deve à menor duração da estação seca, a qual possibilita melhores condições para absorção de nutrientes do solo.

Palavras-chave: savana, nutrição mineral, precipitação, área foliar específica.

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