



Nutrient cycling between soil and leaf litter in the Cerrado (Brazilian savanna) on eutrophic and dystrophic Neosols

Vinícius Nunes Alves¹, José Luiz Rodrigues Torres², Regina Maria Quintão Lana³,
and Marcelo Henrique Ongaro Pinheiro⁴

Received: October 18, 2017

Accepted: October 30, 2017

ABSTRACT

We evaluated nutrient cycling by measuring leaf litter production and decomposition in the Brazilian savanna (cerrado *sensu stricto*) on eutrophic (calcareous) and dystrophic (arenitic) Neosols over the same spatiotemporal scale. We installed three transects in the Cerrado with plots in each Neosol type. Areas along the transects were randomly chosen for determining soil chemical properties, and accumulated leaf litter was collected monthly for a year for analysis. We used litter bags to test for a correlation between loss of dry mass and nutrient release. The calcareous cerrado had higher levels of macronutrients, higher pH, and lower Al compared to the arenitic cerrado. The estimated annual release of leaf litter nutrients in kg ha⁻¹ yr⁻¹ was higher in the calcareous cerrado. Nutrient concentration was significantly higher in different months in the calcareous cerrado, except for S and N. In general, the loss of dry mass was not correlated with nutrient release. Calcareous Neosol is unique to the cerrado *sensu stricto*, and retains more nutrients and facilitates higher leaf litter chemical quality than cerrado of the same physiognomy on dystrophic soils. Nutrient release is not always related to loss of dry mass, regardless of the amount of leaf litter.

Keywords: calcareous, calcium, nutrient dynamics, shallow soil, soil fertility

Introduction

Some of the most important scientific questions in terrestrial ecosystem ecology have been concerned with understanding nutrient cycling dynamics in the atmosphere, vegetation biomass, and soil (D'Odorico & Porporato 2006; Sutherland *et al.* 2006). Nutrient release occurs through various mechanisms that depend on the type of litter (Berg & McClaugherty 2008). Chemical elements, especially macronutrients such as nitrogen, sulfur, and phosphorus, sustain trophic chains (Moss 2010) and ecosystem function (Raffaelli & Frid 2010).

Nutrient cycling is a process that occurs primarily in the edaphic environment, and involves litter accumulation and

subsequent decomposition (Berg & McClaugherty 2008), followed by the transfer of nutrients to the soil (Schulze *et al.* 2002; Raffaelli & Frid 2010). When soil fertility is high, this can be reflected in the concentrations of foliar nutrients (Rossatto *et al.* 2015), and consequently, litter with higher chemical quality may stimulate greater performance by decomposing microorganisms (Seastadt 1984). The Brazilian savanna, known as cerrado *sensu stricto* (Paiva *et al.* 2015), predominantly occurs on dystrophic, alic and deep soils (Latosols) (Eiten 1972; Gottsberger & Silberbauer-Gottsberger 2006). Several authors partially attribute these dystrophic soils to high aluminum saturation (Goodland 1971; Larcher 2000; Gottsberger & Silberbauer-Gottsberger 2006), which contributes to lower soil pH, decreasing

¹ Programa de Pós-graduação em Ecologia e Conservação de Recursos Naturais, Instituto de Biologia, Universidade Federal de Uberlândia, 38405-320, Uberlândia, MG, Brazil

² Instituto Federal do Triângulo Mineiro, 38064-790, Uberaba, MG, Brazil

³ Instituto de Ciências Agrárias, Universidade Federal de Uberlândia, 38400-902, Uberlândia, MG, Brazil

⁴ Laboratório de Botânica e Ecologia no Domínio Cerrado, Universidade Federal de Uberlândia, 38304-402, Ituiutaba, MG, Brazil

* Corresponding author: mpinheiro@ufu.br



nutrient solubility for plants (Eiten 1972). However, there is currently some debate on whether nutritional disorders in plants are directly or indirectly affected by Al (Souza *et al.* 2017).

Most of the studies involving aspects of nutrient cycling in the cerrado have been conducted in areas comprised entirely of Latosols (Peres *et al.* 1983; Schiavini 1983; Nardoto *et al.* 2006; Kozovits *et al.* 2007; Valenti *et al.* 2008; Villalobos-Vega *et al.* 2011; Paiva *et al.* 2015; Valadao *et al.* 2016). There is also a smaller portion of the Cerrado with shallow soils on rocky outcrops (Neosols), which can be mineral-rich (e.g., basalt, diabase and gabbro) or mineral-poor (e.g., arenite, quartz and shale) (Eiten 1972; Reatto *et al.* 1998). This portion of the Cerrado (~7.3 %) is dominated by *campos rupestres*, and there is no description to date of cerrado *sensu stricto* on calcareous outcrops. Instead, calcareous descriptions are limited to forest formations of the Cerrado, mainly dry deciduous forests (Reatto *et al.* 1998). However, the occurrence of calcareous soil was identified in cerrado *sensu stricto* vegetation in the municipality of Ituiutaba, Minas Gerais State, Brazil, (Souza *et al.* 2017). In addition, our field observations (white coloration) combined with chemical analysis (excess calcium) indicate specifically the occurrence of Neosol with rocky calcareous outcrop in the cerrado *sensu stricto*. Since plants extract nutrients mainly from soils, (Cianciaruso *et al.* 2006) and the storage of these nutrients occurs in the litter (Campos *et al.* 2008), it is expected that nutrient concentration in the soil reflects, to some degree, nutrient concentrations in the litter.

The calcareous presence in soil increases the pH and cation exchange capacity in the edaphic milieu (Vitti *et al.* 2015), increasing nutrient availability for plants, which is a factor that may favor biomass productivity (Haridasan 2000; 2008), except with calcifuge species, which may suffer impairment in nutrient uptake (e.g., P and K) (Lee 1998) and growth (Haridasan & Araújo 1988; Lee 1998). In Neotropical ecosystems, such as the Cerrado, higher soil fertility is also associated with higher leaf litter nutrient concentration (Rossatto *et al.* 2015), which enables greater performance by decomposing microorganisms (Seastadt 1984). In addition to the potential differences in decomposition rate due to differences in leaf chemical quality, the proportion of leaf mass also declines exponentially over time (Villalobos-Vega *et al.* 2011), and the loss of leaf dry mass is directly related to the release of leaf nutrients through the action of decomposers (Berg & McClaugherty 2008).

In this context of nutrient dynamics between soil and vegetation, there is a shortage of experimental approaches on the same spatiotemporal scale, which allows a reasonable control of climatic variables, such as moisture, that may modulate nutrient dynamics between soil and plants (Goodland 1971; Peres *et al.* 1983; Coutinho 2002). Thus, we evaluated whether nutrient cycling differs in the same physiognomy of savanna in an apparently different

soil (calcareous influence) and in an apparently typical soil (dystrophic - arenite influence) in the same region. Since the edaphic differences between areas have been confirmed experimentally, we expected higher soil fertility and lower acidity on calcareous soil. Also, considering that leaf nutrients would respond to soil fertility (Fyllas *et al.* 2009), we expected (1) a greater contribution of nutrients (especially Ca, Mg, N and S) in both leaf litter deposited and leaf litter undergoing decomposition in the cerrado with calcareous influence and (2) a decrease in nutrient content in the leaf litter with decomposition time in the cerrado, regardless of whether the soil was eutrophic or dystrophic.

Materials and methods

Study areas

We conducted the study on two contiguous remnants of cerrado *sensu stricto* (s.s) on a mountain range within the limits of Ituiutaba, Minas Gerais (Fig. 1). The range hosts areas of seasonal forest or cerrado on the slopes, in addition to springs of streams (Pinheiro, pers. obs.). Ituiutaba is located in the mesoregion of the Triângulo Mineiro and Alto Paranaíba regions, where the predominant edaphic class is Red Latosol (Martins & Costa 2014). The total area encompassing both remnants is approximately 50 ha, and it is situated along a cuesta plateau (IBGE 1995). The regional climate is characterized as tropical savanna climate (Aw), with rainy summers and dry winters (Alvares *et al.* 2014), where dystrophic Red Latosol is the primary soil type (IBGE 2001).

Among the study areas are dispersed rocky outcrops that can be defined as Neosols (Benedetti *et al.* 2011; IBGE 2007), originating from the Bauru Group, Marília Formation, which correspond to entisol according to the American classification (USDA 1999) and leptosol according to the international classification (FAO 1998). The rock types were identified by observations *in loco* (the analysis being performed by Dr. Alice Bosco). From rock coloration (whitish) and effervescence reaction with dilute hydrochloric acid, we identified the mineral calcite in calcareous rocky outcrop, sparsely present in area 1, in accordance with Souza *et al.* (2017), who conducted their study close to this outcrop. While in Area 2, we identified the scattered occurrence of arenitic rocky outcrop (brownish). In theory, these two rock types would provide different soil fertility between sites. For simplification purposes, we referred the cerrado of Area 1 with calcareous Neosol as “calcareous cerrado” and the cerrado of Area 2 with arenitic Neosol as “arenite cerrado.” The calcareous cerrado has an altitude ranging between 680 and 700 m, and it is referenced by a calcite point with the coordinates 19°03'438"S 49°26'422"W. The arenitic cerrado has an altitude ranging from 705 to 710 m, and it is referenced by an arenite point with the coordinates 19°03'633"S 49°26'075"W.



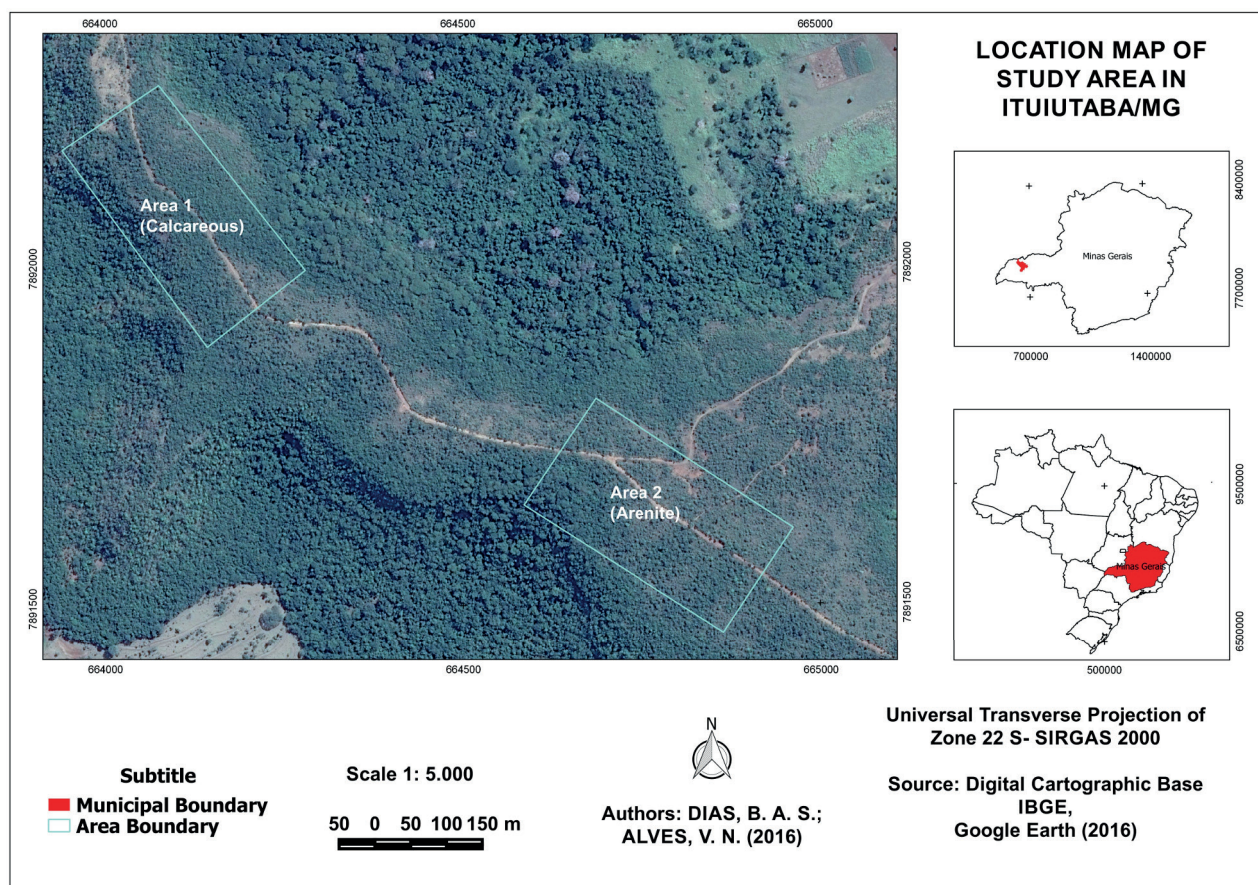


Figure 1. Map indicating study area locations. Area 1 is composed of calcareous cerrado, and Area 2 is composed of arenite cerrado in Ituiutaba municipality, situated in Minas Gerais State, Brazil. We used ArcGIS to adapt an image obtained from Google Earth.

Both areas contain abundant herbaceous stratum, and according to a phytosociological survey in progress, the shrub-tree community frequently includes cerrado species. To date, the most common plant species in the calcareous cerrado are *Callisthene fasciculata* Mart. (Vochysiaceae), *Luehea paniculata* Mart. (Malvaceae) and *Terminalia argentea* Mart. & Zucc (Combretaceae). In the arenite cerrado, the most common species are *Miconia albicans* (Sw.) Steud. (Melastomataceae), *Ouatea hexasperma* (A. St.-Hil.) Baill (Ochnaceae) and *Roupala montana* Aubl. (Proteaceae). The two areas do not form a closed canopy, but the apparent thickening of the shrubby-arboreal stratum differs between them; the calcareous cerrado is a dense cerrado s.s. with predominantly arboreal stratum, especially near the first transect, while the arenite cerrado area is a typical cerrado s.s. with shrubby-arboreal stratum that is less predominant (see Fig. S1A-B in supplementary material for general appearance of the vegetations).

Soil collection and analysis

We installed three 100-m transects per area (i.e., calcareous cerrado and arenite cerrado), with a minimum distance of 50 m in between. Twenty contiguous plots

(10 m²) were marked along each transect, for a total of 60 plots per area. We then randomly chose 20 plots for soil collection and chemical characterization. We obtained soil (depth = 0.2 m) from 15 different sample points, which were randomly determined. Each sample was placed in an individual, labeled plastic bag, and the chemical analysis was later performed in the laboratory.

Soil layers from the 15 collection points within a single plot were combined and homogenized (N= 20 plots in each area). Soil pH was determined in water using a soil-liquid ratio of 1:2.5. Exchangeable divalent cations (Ca²⁺ and Mg²⁺) and exchangeable acidity (Al³⁺) were extracted with 1 mol L⁻¹ KCl, and concentrations were determined by titration (Embrapa 1997). Exchangeable potassium was determined using the photometric method directly in the soil stratum, obtained using Mellich-1 solution according to Raji *et al.* (2001). Organic matter (OM) content was determined using a colorimetric method with 5 mol L⁻¹ sulfuric acid (Cantarella *et al.* 2001). P was determined by spectrophotometry using the reaction of molybdate with ascorbic acid (Embrapa 2009). We also calculated the base saturation (V%) of all samples according to the following formula: $V\% = 100.S/T$, where S = sum of bases and T = cation exchange capacity at pH 7. With the mean values obtained from base saturation

(V%) of all samples of each area, we determined whether soils were eutrophic ($\geq 50\%$) or dystrophic ($<50\%$) according to Embrapa criteria (2006).

The differences in natural fertility between the two cerrado areas were confirmed as assumptions for choosing the sites and proceeding with the comparisons. The calcareous cerrado showed eutrophic characteristics, while the arenite cerrado displayed dystrophic characteristics. The mean base saturation values (V%) of all samples were 77 V% in the calcareous cerrado and 29 V% in arenite cerrado. The P, K, Ca and Mg contents were significantly higher in the calcareous cerrado, as were OM and pH. Al was very low (0.0) in calcareous cerrado Neosol according to the quantitative method used, while mean Al content in the arenite cerrado was $1.28 \text{ cmol dm}^{-3}$ (Tab. 1). The calcareous and arenite cerrado areas were then characterized as eutrophic and dystrophic, respectively, according to the mean base saturation values (V%) and Embrapa criteria (2006).

Leaf litter collection and macronutrient analysis of accumulated and decomposed leaf litter

From July 2015 to June 2016, we collected monthly-accumulated litter in 20 litter traps (50 x 50 cm) for evaluation of production, since twenty was considered a sufficient number for sample significance (Proctor 1983). Litter traps were composed of 2 mm nylon screens situated 20 cm above the ground. We separated only the leaf component for chemical analysis in the laboratory.

To evaluate leaf litter decomposition in the two areas, we randomly selected 10 litter traps to place in litter bags on the soil, totaling 100 litter bags per area. In each litter bag, 10 g of leaf litter were allocated. We removed 20 litter bags per area, at approximately 15, 30, 60, 90 and 120 days after the beginning of the rainy season (between October and April) (Bustamante *et al.* 2012). The plant material with both methods was placed in individual plastic bags for sorting, drying, and weighing. Chemical analysis was performed to quantify the nutritional condition of the leaf litter produced (accumulation in litter traps) and decomposed (fixed quantity in the litter bags). When possible, we compared the mean values obtained in our

chemical analysis with the mean values obtained in other cerrado areas and in deciduous forest remnants. Such forest formations in Brazil typically occur on shallow soils with calcareous concretions (Silva *et al.* 2013a).

For both areas, the monthly-accumulated leaf litter (representing production) and the litter bag content (representing decomposition) were ground, dried (at 85 °C for 48 h), and subjected to chemical analysis for quantification of macronutrient content. Nitrogen was determined using the Kjeldahl method (Tedesco *et al.* 1985), while P and K were determined by nitric-perchloric acid digestion (Bataglia *et al.* 1983), and P also colorimetrically (Embrapa 1997). Ca and Mg were determined by atomic absorption spectrophotometry (Bataglia *et al.* 1983), and S by turbidimetry (Tedesco *et al.* 1985). The mean macronutrient contents of accumulated leaf litter were multiplied by the corresponding dry mass and presented in kg ha^{-1} at annual and monthly levels. The mean macronutrient content of leaf litter from decomposition bags was related to the dry mass of the samples over the chosen time intervals (sampling months).

Statistical analyses

When evaluating differences in macronutrient content of leaf litter between the two areas, we were not able to group data for all months in a temporal analysis due to field incidents (e.g., seasonal interference by wild animals or by severe rain and wind), and the subsequent lack of sampling balance between the areas. Thus, to determine whether the leaf litter nutrient content differed between the areas, we performed independent t-tests from month to month. For months in which the data (original or transformed) did not show a normal distribution and/or homoscedastic variance, we performed Mann-Whitney tests.

We also determined whether there were correlations between the amount of dry mass in leaf litter (in litter bags) and concentrations of each macronutrient over the course of decomposition. Therefore, we performed a Spearman's correlation test for all macronutrients, since the data were not parametric (normal distribution and homoscedastic variance).

Normality and homoscedasticity in the data distribution were tested by the Kolmogorov-Smirnov and Levene tests,

Table 1. Soil chemical attributes in the edaphic layer of calcareous and arenite cerrado. Minimum, median and maximum values are presented for Mann-Whitney test. Means \pm S.E. are presented for independent t-test. Degrees of freedom (d.f.) = 38. Notation: standard error (S.E.).

Soil chemical attributes	"calcareous cerrado"	"arenite cerrado"	T-value	U-value	P-value
P ($\text{mg} \cdot \text{dm}^{-3}$)	1.10 < 2.55 < 6.90	0 < 0.55 < 0.90	-	0.000	< 0.001
K ($\text{cmolc} \cdot \text{dm}^{-3}$)	0.37 \pm 0.01	0.14 \pm 0.01	13.61	-	< 0.001
Ca ($\text{cmolc} \cdot \text{dm}^{-3}$)	5.71 \pm 0.47	0.89 \pm 0.14	12.96	-	< 0.001
Mg ($\text{cmolc} \cdot \text{dm}^{-3}$)	2.16 \pm 0.12	0.61 \pm 0.11	9.40	-	< 0.001
OM ($\text{dag} \cdot \text{kg}^{-1}$)	6.52 \pm 0.34	2.71 \pm 0.16	11.40	-	< 0.001
pH	6.29 \pm 0.05	5.17 \pm 0.04	17.15	-	< 0.001
Al ($\text{cmolc} \cdot \text{dm}^{-3}$)	0	1.28 \pm 0.10	-	-	-

respectively, using $P < 0.05$ as threshold criterion. For all analysis, we adopted $\alpha = 0.05$ as our threshold for statistical significance.

Results

Macronutrients in accumulated leaf litter

Over the year, macronutrients stored by leaf litter in the calcareous cerrado (Area 1) followed the descending order: $\text{Ca} > \text{N} > \text{K} > \text{Mg} > \text{P} > \text{S}$, while in the arenite cerrado (area 2), macronutrients stored by leaf litter followed almost the same descending order: $\text{N} > \text{Ca} > \text{K} > \text{Mg} > \text{P} > \text{S}$ (Tab. 2). The contents of all macronutrients oscillated over the year, following the leaf litter production seasonality in both areas, which was concentrated in the dry season. From comparisons between areas, the efficient use of most macronutrients (except N and S) was inversely proportional to their return in the areas' leaf litter (Tab. 2).

Throughout the year, leaf litter in the calcareous cerrado displayed significantly higher Ca content than in the arenite cerrado (Fig. 2), with values proportionally ranging from 0.5 to 29 % of mean available dry mass in the areas. During most of the year, K, Mg, and P contents were also significantly higher in the calcareous cerrado (Figs. 3-5), with values ranging from 0.3 to 22 % for K, from 0.1 to 5 % for Mg and from 0.01 to 2 % for P. In contrast, the S content was significantly higher in leaf litter of the arenite cerrado in the dry season (Fig. 6), with values ranging from 0.02 to 1 %. N content was significantly higher in the calcareous cerrado leaf litter in two of the rainy season months, but higher in leaf litter in the arenite cerrado in one of the dry season months (Fig. 7), with values ranging from 0.9 to 20 %.

Macronutrients in leaf litter with decomposition

Among macronutrients, only variation in K correlated significantly and positively with the amount of leaf litter in both areas. That is, its concentration decreased as the dry mass decreased with decomposition (Fig. 8A-B) in the two areas, showing 70 to 75 % variation over the months. This effect did not occur with the other macronutrients - N, P, Ca, Mg and S - which oscillated irregularly during decomposition in the two areas, showing no significant correlation over months.

Discussion

Soil fertility

From comparison between areas in relation to surface soil layers, where nutrient uptake mostly occurs (Cramer *et al.* 2009), we found that calcareous cerrado soil was less acidic, with negligible Al saturation, and retained higher contents of most macronutrients compared to arenite cerrado soil, probably due to alkaline calcareous rock and mineral richness (Reatto *et al.* 1998; Felfili *et al.* 2007). These differences between calcareous and typical (more acidic) soils are in accordance with other cerrado areas (Haridasan 1988; Souza *et al.* 2017) and forest communities of the Cerrado (Haridasan & Araújo 1988). Moreover, OM, which also was higher in Area 1, may be even important in providing nutrients for plants in the cerrado (Goodland & Ferri 1979), riparian forests of the Cerrado (Moreno & Schiavini 2001) and Australian savannas (Holt & Coventry 1990). Even in experiential situations of OM addition, the results usually indicate pH increase and decrease in Al saturation (Wong &

Table 2. Leaf litter dry weight, macronutrient content (g kg^{-1}) in leaf litter dry mass and macronutrient use efficiency estimated in $\text{kg ha}^{-1}\text{yr}^{-1}$ in each study area. Notation: standard error (S.E.).

Area	Dry weight (Mean ± SE)	Macronutrient stock (Mean ± SE)		Macronutrient use efficiency*
		Kg ha ⁻¹ a ⁻¹		
“calcareous cerrado”	3647 ± 49	Ca	45.08 ± 0.43	80.90
		N	31.56 ± 0.17	115.55
		K	23.71 ± 0.14	153.81
		Mg	9.36 ± 0.03	389.63
		P	2.29 ± 00	1592.57
		S	1.27 ± 00	2871.65
“arenitic cerrado”	2014 ± 42	N	19.32 ± 0.25	104.24
		Ca	15.91 ± 0.27	126.58
		K	8.93 ± 0.13	225.53
		Mg	4.25 ± 0.03	473.88
		P	1.12 ± 00	1798.21
		S	0.89 ± 00	2262.92

* This attribute was estimated as the mean dry mass of leaf litter divided by the mean amount of the macronutrient in leaf litter during the year. In this estimate it is assumed that nutrient use efficiency does not vary with the amount of macronutrient circulated, according Vitousek (1982).



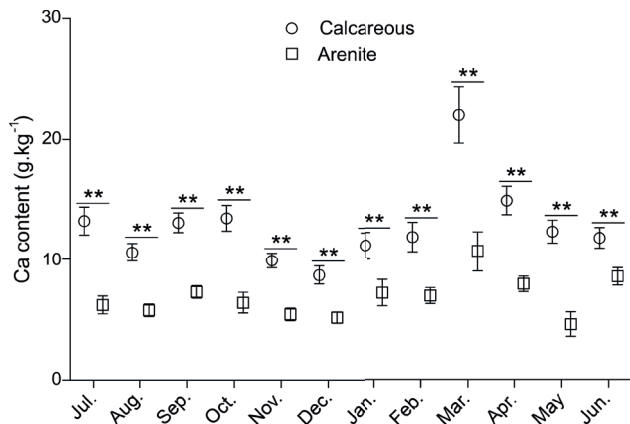


Figure 2. Calcium content (Ca) in the leaf litter of calcareous and arenite cerrado over one year (mean \pm S.E.). **indicates significant differences between areas with $\alpha < 0.01$. We show the raw data for all months. The data of the months July, August, December, March, April, May and June were parametric (independent t-test; T values varied from 2.81 to 5.76; significant p values varied from 0.00001 to 0.007). The data for the months of September, October, November, January and February were parametric after log transformation (independent t-test; T values varied from 2.81 to 6.52; significant p values varied from 0.00001 to 0.008).

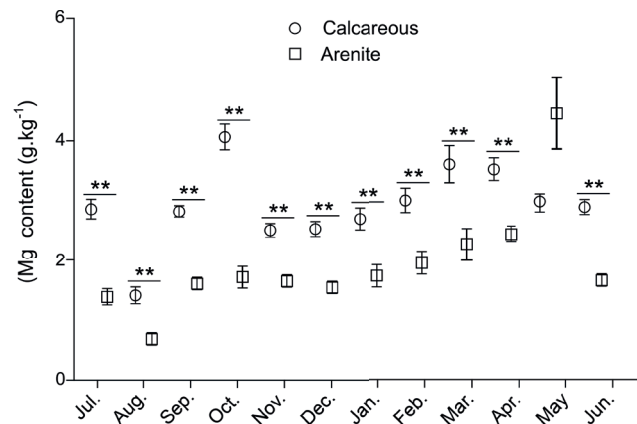


Figure 4. Magnesium content (Mg) in the leaf litter of calcareous and arenite cerrado over one year (mean \pm S.E.). **indicates significant differences between areas with $\alpha < 0.01$. We show the raw data for all months. The data for the months of July, September, October, November, December, January, February, March, April and June were parametric (independent t-test; T values varied from 2.96 to 7.62; significant p values varied from 0.00001 to 0.007). The data for August were parametric after log+1 transformation (independent t-test; T = 4.12 and p = 0.0002). The data for May were non-parametric (Mann-Whitney test; U = 179.50 and p = 0.772).

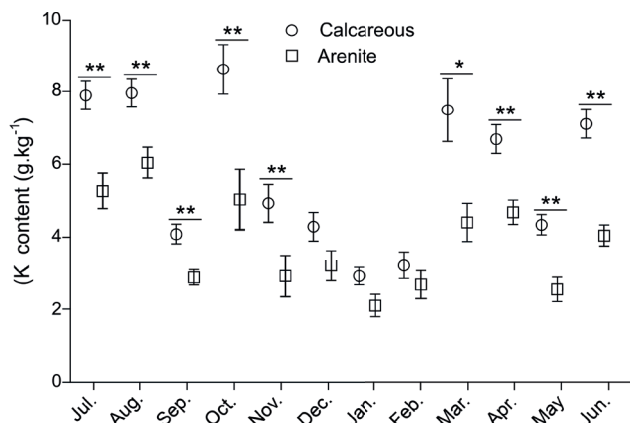


Figure 3. Potassium content (K) in the leaf litter of calcareous and arenite cerrado over one year (mean \pm S.E.). *indicates significant differences between areas with $\alpha < 0.05$ and **indicates significant differences between areas with $\alpha < 0.01$. We show the raw data for all months. The data for all months were parametric (independent t-test; T values varied from 0.87 to 6.07; significant p values varied from 0.00001 to 0.015; non-significant p values varied from 0.089 to 0.392).

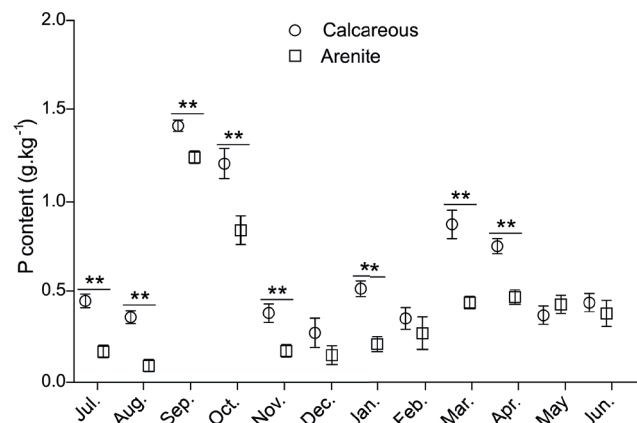


Figure 5. Phosphorus content (P) in the leaf litter of calcareous and arenite cerrado over one year (mean \pm S.E.). **indicates significant differences between areas with $\alpha < 0.01$. We show the raw data for all months. The data for the months of July, September and November were non-parametric (Mann-Whitney test; U values varied from 17.00 to 67.50; significant p values varied from 0.0001 to 0.005). The data for the months of August, October, December, January, February, March, April, May and June were parametric (independent t-test; T values varied from -0.81 to 7.74; significant p values varied from 0.0001 to 0.003; non-significant p values varied from 0.204 to 0.503).

Swift 2003), probably due to precipitation of soluble Al and the formation of Al-OM complexes (Bessho & Bell 1992). Thus, OM may play an important role in Al alleviation in acidic soils, where there are species non-tolerant to Al toxicity, mainly cultivated plants (Haridasan 2008). However, such role is not important for native plant species, which are adapted to high levels of acidity and Al (Watanabe

& Osaki 2002), especially Al-accumulating species present in the families Rubiaceae, Melastomaceae and Vochysiaceae (Jansen *et al.* 2002a; b).

The calcareous cerrado showed higher mean values for all soil chemical attributes except for acidity, compared to cerrado areas on Oxisols and a deciduous forest area on Basaltic Eutrophic Neosol (Tab. 3). Unlike the calcareous

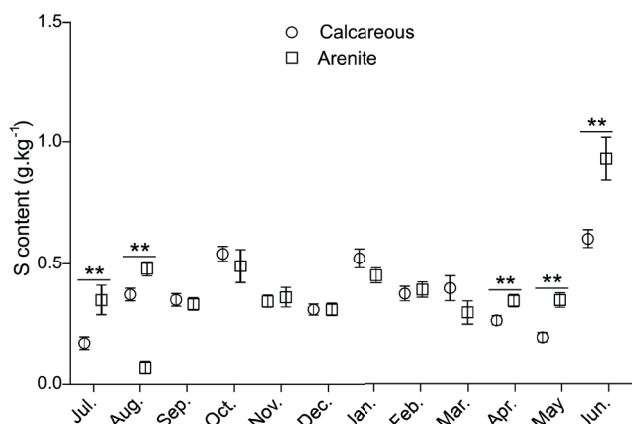


Figure 6. Sulfur content (S) in the leaf litter of calcareous and arenite cerrado over one year (mean \pm S.E.). **indicates significant differences between areas with $\alpha < 0.01$. We show the raw data for all months. The data for the months of July, August, October, January, February, March, April and May were parametric (independent t-test; T values varied from -4.88 to 1.37; significant p values varied from 0.0001 to 0.13; non-significant p values varied from 0.186 to 0.943). The data for the months of September, November, December and June were non-parametric (Mann-Whitney test; U values varied from 94.00 to 289.00; significant p value of indicated month was 0.001; non-significant p values varied from 0.186 to 0.943).

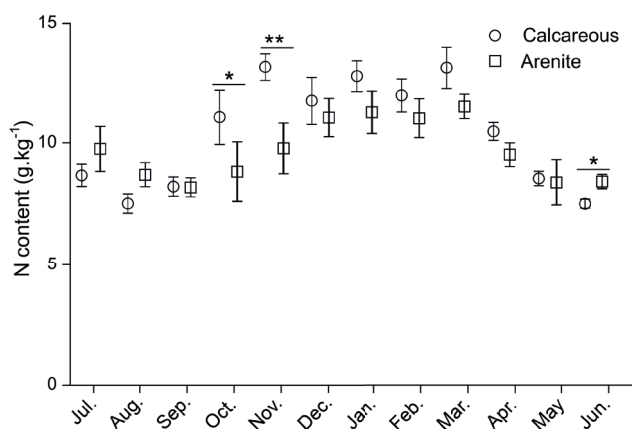


Figure 7. Nitrogen content (N) in the leaf litter of calcareous and arenite cerrado over one year (mean \pm S.E.). *indicates significant differences between areas with $\alpha < 0.05$ and **indicates significant differences between areas with $\alpha < 0.01$. We show the raw data for all months. The data for the months of July, September, November, December, January, February and April were parametric (independent t-test; T values varied from -1.11 to 2.98; significant p values varied from 0.005 to 0.032; non-significant p values varied from 0.123 to 0.986). The data for October were parametric after log transformation (independent t-test; T = 2.22 and p = 0.032). The data for the months of August, March, May and June were non-parametric (Mann-Whitney test; U values varied from 109.00 to 277.50; significant p value for indicated month was 0.035; non-significant p values varied from 0.241 to 0.282).

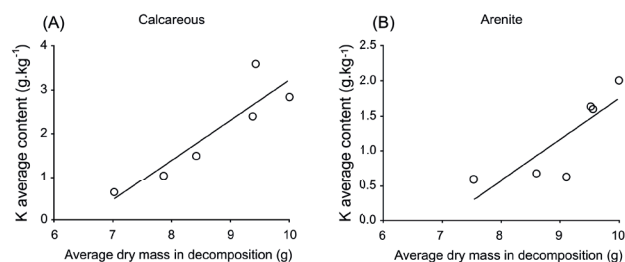


Figure 8. Correlation analysis for the relationship between loss of dry mass in leaf litter from decomposition bags and potassium (K) content in (A) calcareous cerrado (Spearman's correlation, p=0.01, d.g.=6, r = 0.94) and in (B) arenite cerrado (Spearman's correlation, p=0.03, d.g.=6, r = 0.88).

cerrado area, these other areas are not influenced by calcareous rock, and according to Reatto *et al.* (1998), young soils with calcareous rock in rough reliefs (such as Area 1) tend to be differentially rich in bases. However, when compared to calcareous cerrado and a deciduous forest with the same edaphic classification (i.e., calcareous Neosol), the former showed higher proportions of most of the chemical attributes present in the forest (Tab. 3). These differences may be due to the calcareous rocky outcrops of this forest that are very developed, forming extensive and thick blocks along the area (Rossatto *et al.* 2015).

The dystrophic arenite cerrado showed intermediate mean macronutrient values compared to areas of dystrophic cerrado (Latosols) and deciduous eutrophic forests (Tab. 3). The highest nutrient content of the arenite cerrado compared to cerrado on Oxisols can be attributed to drainage differences between more or less developed soils. At least in Atlantic forests, shallow soils are generally less leached and less acidic than well-developed soils (Guilherme *et al.* 2012), which may favor nutrient retention in the surface layer. In addition, Rossatto *et al.* (2015) assert that young soils are rich in macronutrients, particularly Ca, Mg, and P, showing higher base saturation. In addition, the finding that our study areas, savannas, contained higher mean values of nutrients than a deciduous eutrophic forest partially refutes the hypothesis of Bond (2010) that savannas do not contain sufficient nutrients to sustain forests.

Macronutrient concentration in accumulated leaf litter

Throughout the year, the patterns for estimated macronutrient content in dry leaf mass were similar between areas, since the macronutrients were measured in the seasonal leaf fall, which in both areas were concentrated in the dry season (especially July to October), according to others studies in the cerrado (Nardoto *et al.* 2006;

Table 3. Soil chemical attributes in the two study areas compared to other areas of cerrado *sensu stricto* (s.s.) and deciduous seasonal forest (d.s.).

Reference	Vegetation	Soil	P mg.dm ⁻³	K cmolc.dm ⁻³	Ca cmolc.dm ⁻³	Mg cmolc.dm ⁻³	O.M. dag.kg ⁻¹	pH H ₂ O
Rossatto <i>et al.</i> 2015	'cerrado' s.s.	Red Latosol	0.46	0.30	0.11	0.06	1.20	4.67
Rossatto <i>et al.</i> 2015	forest d.s.	Calcareous Neosol	2.14	0.43	14.65	5.86	5.80	6.64
Valadão <i>et al.</i> 2016	'cerrado' s.s.	Red Latosol	-	0.07	0.03	0.20	1.23	4.86
Viera <i>et al.</i> 2010	forest d.s.	Basaltic Neosol	2.20	0.13	4.70	2.00	-	5.5
Present study	'cerrado' s.s.	Calcareous Neosol	3.01	0.36	5.71	2.16	6.52	6.29
Present study	'cerrado' s.s.	Arenitic Neosol	0.53	0.15	0.88	0.61	2.71	5.17

Kozovits *et al.* 2007). The similarity between the two areas concerning the decreasing order of mean macronutrient returned by leaf litter indicated that the proportionality of leaf macronutrients in the cerrado does not depend solely on soil fertility. The fact that Ca in leaf litter of Area 1 was the macronutrient returned in greatest magnitude was probably due to the influence of high Ca levels in the calcareous rock, which may consist of about 99 % calcium carbonate (Braun-Blanquet *et al.* 1983). In Area 2, the decreasing order in annual mean macronutrients returned by leaf litter was similar to that of a cerrado on Latosol (Nardoto *et al.* 2006), which also began with N and only differed in sequence from the arenite cerrado due to inversion of S and P in the last position. The return of all macronutrients was higher in calcareous cerrado leaf litter, and it may be explained by the fact that areas with higher natural fertility reflect higher nutrient contents in leaves (Haridasan 2000).

Other information at the annual level about areas includes nutrient concentration stoichiometry, especially Ca:Mg and N:P, which have intrinsic relationships that may be unbalanced due to small changes in soil conditions (Rossatto *et al.* 2015). The annual mean Ca:Mg ratio was higher in Area 1 (4.38 g kg⁻¹) than in Area 2 (3.57 g kg⁻¹), probably due to an antagonistic relationship between them (Baker & Pilbeam 2006), which can increase with very abundant Ca in the system. In relation to mean ratio of N:P, Aerts & Chapin (2000) defined values above 16 as a limitation of P. The annual mean N:P ratio was higher in Area 2 (23.06 g kg⁻¹) than in Area 1 (17.00 g kg⁻¹), which was associated with low P availability in soil analyses. Such P limitation is in accordance with that commonly expected for a large number of Neotropical systems (Bustamante *et al.* 2006; Araújo & Haridasan 2007; Rossatto *et al.* 2015).

The higher estimated annual return of Ca, K, Mg and P in the calcareous cerrado compared to arenite cerrado reflected concentrations of these macronutrients, which were significantly higher in Area 1 than Area 2 during the whole year or most months. Such results suggested that cerrado species on eutrophic soils show a less conservative strategy for most macronutrients. Additionally, the use efficiency of Ca, K, Mg and P between the areas was also the inverse of their concentrations in leaf litter, in accordance with Vitousek (1982). According to Parron *et al.* (2011),

cerrado plants in soils with higher natural fertility tend to deposit more nutrients per unit of leaf litter biomass compared to plants in soils with lower natural fertility. We can then deduce from this that calcareous cerrado plants on eutrophic soils lose more nutrients, while plants on dystrophic arenitic soils are able to re-absorb and conserve nutrients. This is in accordance with the hypothesis that nutrient resorption efficiency increases as soil fertility decreases (Vourlitis *et al.* 2014).

Despite that the estimated annual return of S was higher in Area 1, this was not reflected in the S concentrations nor in S use efficiency. In the dry months, the S concentrations in leaf litter were significantly higher in Area 2, where Ca content was much lower. It is known that high Ca content may cause a decrease in other minerals, such as S (Ferri 1979). Additionally, about 90 % of S occurs in the organic form (Ferri 1979) and it can be drained along with water to other sites, or exported from the soil milieu by transformation into the gas phase (Begon *et al.* 2007). These factors can lower S content in leaf litter, making it difficult to determine differences in concentrations between areas during the rainy season.

The monthly N concentrations in accumulated litter leaf showed high variability between the areas, besides S use efficiency being relatively close between the areas. On the one hand, eutrophic soil conditions with presence of calcareous outcrops contributed to a significantly higher N concentration in Area 1 for a few months. In addition, such differences may arise from the fertility effect on the increase in species richness (Gentry 1988), which increases the likelihood of finding nitrogen-fixing species (Silva *et al.* 2013b). Such relation may be supported at the end of the phytosociological survey in progress, in which the proportion of Fabaceae species and individuals in the areas will be recorded and analyzed. On the other hand, N is a primary food source for decomposers, being present in proteins and vitamin compounds (Ferri 1979), and is one of the main elements that determines decomposition rate (i.e., based on the C:N ratio) (Larcher 2000). Considering that some decomposers can access the leaves accumulated in the litter traps throughout the month, and that decomposition of nutrients renders them unavailable to leaves (Schiavini 1983), this may have contributed to the lack of difference

in leaf N content between the areas. Additionally, one of the litter traps in the arenite cerrado showed much higher N concentrations in some months. This particular litter trap contained mostly leaves of *Ouratea hexasperma* as there was one plant near the litter trap with branches located directly above. However, the association of a high N content with leaf litter of this species is in contrast to a study by Araújo & Haridasan (2007), who demonstrated that this typical cerrado species is an evergreen and has relatively low N content in mature leaves. Thus, such process in the current study deserves further investigation.

Comparisons between study areas and cerrado areas on Oxisols showed that, with the exception of S, leaf macronutrient concentrations (Tab. 4) suggested that calcareous soil increases the nutritional quality of cerrado leaf litter, which tends to accelerate decomposition rates (Dahlgren *et al.* 2003) with subsequent mineralization. When comparing concentrations of leaf macronutrients of the arenite cerrado with areas of cerrado on Oxisols, results were highly variable (Tab. 4). Since cerrado soil is also dystrophic, it may be that the differences between soils are due to phytosociological differences between areas, for example, by one area having higher abundance of leguminous species.

When comparing dystrophic cerrado to deciduous forests, we found that foliar concentrations of N, Ca, Mg, and P were invariably higher in the latter (Tab. 4), in agreement with Paiva *et al.* (2015) who showed that forest litter has higher nutrients than savanna litter. However, foliar K concentrations were higher in most cerrado areas compared to deciduous forest areas (Tab. 4), possibly due to differences in soil leaching rates. Considering only the comparison between the calcareous cerrado and eutrophic deciduous forests, we noted that Mg concentration was higher in Area 1. A plausible explanation for this difference is that excess Ca may exert an antagonistic effect on Mg uptake, competing for binding sites on plant cell membranes (Baker & Pilbeam 2006) and reducing Mg content. We noticed that results from other studies of deciduous seasonal forests may be due to differences in the methods used. For example, in a study by Rossato *et al.* (2015), nutrient concentrations were measured in photosynthetically active mature leaves that were mechanically extracted, which

probably have more nutrients than dry naturally fallen leaves (Miranda *et al.* 2002); in a study by Viera *et al.* (2010), the litter used for the analysis was not only composed of the leaf component but also of twigs.

Decomposition of macronutrients in leaf litter

The loss of dry leaf mass is directly related, among other factors, to the loss (release) of nutrients during the decomposition process (Schiavini 1983; Berg & McLaugherty 2008). This relation was found only for K, in which its concentration decreased as a function of the loss of dry mass of the leaf litter, according a significant positive relationship between percent weight remaining and K concentration in residual material, as observed in the leaf litter of some dry deciduous forest species (Bargali *et al.* 2015). These results indicate that K is subject to extensive leaching from decomposing leaf litter; however, K is not the only mobile macronutrient, and explanations for the absence of significant correlations between dry mass loss and release of other macronutrients are needed with further investigations.

Regardless of the significance of the correlations, the similarity of the results between the areas showed that the relationship between the loss of dry mass and macronutrient release is not only altered due differences in the chemical quality of the leaf litter. The absence of correlations between leaf dry mass and most of the macronutrients measured suggests that other factors also modulate decomposition, such as lignin content of the species in the litter bags (Gholz *et al.* 2000), the diversity of decomposers between sample points or areas (Seastadt 1984; Berg & McLaugherty 2008), surface water availability for decomposers, which varies with soil texture (Coleman *et al.* 2004), microclimatic conditions (Gholz *et al.* 2000), or even external sources of macronutrients in the natural environment.

Conclusions

We confirmed that the cerrado in the study area occurs under eutrophic and dystrophic conditions on the same spatiotemporal scale. The cerrado under calcareous influence has a higher content of most macronutrients in accumulated

Table 4. Mean total macronutrient content of leaf litter in calcareous vs. arenite cerrado in the current study compared with other areas of cerrado *sensu stricto* (s.s.) and deciduous forest.

Reference	Vegetation	Soil	N g.kg ⁻¹	K g.kg ⁻¹	Ca g.kg ⁻¹	Mg g.kg ⁻¹	P g.kg ⁻¹	S g.kg ⁻¹
Kozovits <i>et al.</i> 2007	'cerrado' s.s.	Red Latosol	8.48	-	-	-	-	-
Nardoto <i>et al.</i> 2006	'cerrado' s.s.	Red Latosol	7.30	1.30	2.70	1.10	0.20	0.40
Paiva <i>et al.</i> 2015	'cerrado' s.s.	Red Latosol	10.24	4.97	5.92	1.58	0.38	-
Rossatto <i>et al.</i> 2015	deciduous forest	Calcareous Neosol	23.49	1.30	17.11	2.17	1.30	-
Viera <i>et al.</i> 2010	deciduous forest	Basaltic Neosol	20.50	1.70	19.50	2.40	0.70	1.10
Present study	'cerrado' s.s.	Calcareous Neosol	10.41	5.78	12.75	2.90	0.61	0.37
Present study	'cerrado' s.s.	Arenitic Neosol	9.74	3.82	6.89	1.93	0.40	0.42



leaf litter, in comparison with cerrado under the influence of arenitic outcrops or on Oxisols. This demonstrates that Brazilian savannas on eutrophic soils usually exert a less conservative strategy with nutrients. In relation to decomposing leaf litter, the release of macronutrients in the cerrado does not differ according to leaf litter nutritional quality. Moreover, heterogeneity of the difference in macronutrients between distinct calcareous cerrado and some forests reinforces the notion that nutrient availability does not always act as one of the driving factors for savanna formation.

Acknowledgements

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the financial support. We thank the Universidade Federal de Uberlândia (UFU) for their logistic support. We thank Mr. Claudinei (Escala farm) for allowing us to use their natural areas of cerrado. We thank Dr. Alice Bosco Santos for field visit and rocks identification. We thank Olivia Maria Lima and Marcela Freitas for proofreading of the English. We thank Hygor Pepe Hailer for support with figures edition.

References

- Aerts R, Chapin FS. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* 30: 1-67.
- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. 2014. Koppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711-728.
- Araújo JF, Haridasan M. 2007. Relação entre deciduidade e concentrações foliares de nutrientes em espécies lenhosas do cerrado. *Brazilian Journal of Botany* 30: 533-542.
- Baker AV, Pilbeam DJ. 2006. *Handbook of plant nutrition*. Boca Raton-Londres-Nova York, CRC Press.
- Bargali SS, Shukla K, Singh L, Ghosh L, Lakhera ML. 2015. Leaf litter decomposition and nutrient dynamics in four tree species of dry deciduous forest. *Tropical Ecology* 56: 191-200.
- Bataglia OC, Furlani AMC, Teixeira JPF, Gallo JR. 1983. Métodos de análises químicas de plantas. *Boletim* 78. Campinas, IAC.
- Begon M, Harper JL, Townsend CR. 2007. *Ecologia - de indivíduos a ecossistemas*. Porto Alegre, Artmed.
- Benedetti MM, Curi N, Sparovek G, Carvalho Filho A, Silva SHG. 2011. Updated Brazilian's georeferenced soil database: an improvement for international scientific information exchanging. In: Gungor ROE. (ed.) *Principles, application and assessment in soil science*. Rio de Janeiro, Embrapa Solos. p. 307-330.
- Berg B, McClaugherty C. 2008. *Plant litter: decomposition, humus formation, carbon sequestration*. Berlin, Springer.
- Bessho T, Bell LC. 1992. Soil solid and solution phase changes and mung bean response during amelioration of aluminum toxicity with organic matter. *Plant and Soil* 140: 183-196.
- Bond W. 2010. Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. *Plant and Soil* 334: 47-60.
- Braun-Blanquet J, Fuller GD, Conard HS. 1983. *Plant sociology: the study of plant communities*. Londres-Nova York, McGraw-Hill.
- Bustamante MMC, Medina E, Asner GP, Nardoto GB, Garcia-Montiel DC. 2006. Nitrogen cycling in tropical and temperate savannas. *Biogeochemistry* 79: 209-237.
- Bustamante MMC, Nardoto GB, Pinto AS, Resende JCF, Takahashi FSC, Vieira LCG. 2012. Potential impacts of climate change on biogeochemical functioning of Cerrado ecosystems. *Brazilian Journal of Biology* 72: 655-671.
- Campos EH, Alves RR, Serato DS, Rodrigues GSSC, Rodrigues SC. 2008. Acúmulo de serrapilheira em fragmentos de mata mesofítica e cerrado stricto sensu em Uberlândia-MG. *Sociedade & Natureza* 20: 189-203.
- Cantarella H, Quaggio JA, Raij B. 2001. Determinação da matéria orgânica. In: Raij B, Andrade JC, Cantarella H, Quaggio JA. (eds.) *Análise química para avaliação da fertilidade de solos tropicais*. Campinas, IAC. p. 189-199.
- Cianciaruso MV, Pires JSR, Delitti WBC, Silva EFLP. 2006. Produção de serrapilheira e decomposição do material foliar em um cerrado na Estação Ecológica de Jataí, município de Luiz Antônio, SP, Brasil. *Acta Botanica Brasílica* 20: 49-59.
- Coleman DC, Crossley Jr DA, Hendrix PF. 2004. *Fundamentals of Soil Ecology*. San Diego, Elsevier Academic Press.
- Coutinho LM. 2002. O bioma cerrado. In: Klein AL. (ed.) *Eugen Warming e o cerrado brasileiro: um século depois*. São Paulo, Editora UNESP. p. 77-91.
- Cramer MD, Hawkins HJ, Verboom GA. 2009. The importance of nutritional regulation of plant water flux. *Oecologia* 161: 15-24.
- Dahlgren RA, Horwath WR, Tate KW, Camping TJ. 2003. Blue oak enhance soil quality in California oak woodlands. *California Agriculture* 57: 42-47.
- D'Oroico P, Porporato A. 2006. *Dryland ecohydrology*. Dordrecht, Springer.
- Eiten G. 1972. The Cerrado vegetation of Brazil. *Botanical Review* 38: 201-341.
- Embrapa. 1997. *Manual de métodos de análise de solo*. 2nd. edn. Rio de Janeiro, Fundação Embrapa.
- Embrapa. 2009. *Manual de análises químicas de solos, plantas e fertilizantes*. 2nd. edn. Brasília, Fundação Embrapa.
- Embrapa criteria. 2006. *Sistema brasileiro de classificação de solos*. 2nd. edn. Brasília, Fundação Embrapa.
- FAO. 1998. *World reference base for soil resources*. World soil resources report. Rome, FAO/ISRIC/ISSS.
- Felfili JM, Nascimento ART, Fagg CW, Meirelles EM. 2007. Floristic composition and community structure of a seasonally deciduous forest on limestone outcrops in Central Brazil. *Brazilian Journal of Botany* 30: 611-621.
- Ferri MG. 1979. *Fisiologia vegetal*. Vol. 1. São Paulo, Epu/Edusp.
- Fyllas NM, Patiño S, Baker TR, et al. 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* 6: 2677-2708.
- Gentry AH. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1-34.
- Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology* 6: 750-65.
- Goodland R. 1971. Oligotrofismo e alumínio no cerrado. In: Ferri MG. (ed.) *III Simpósio sobre o cerrado*. São Paulo, Edgard Blücher. p. 44-60.
- Goodland R, Ferri MG. 1979. *Ecologia do Cerrado*. São Paulo, Universidade de São Paulo.
- Gottsberger G, Silberbauer-Gottsberger I. 2006. *Life in the cerrado: A South American tropical seasonal vegetation. Origin, structure, dynamics and plant use*. Vol. 1. Ulm, Reta Verlag.
- Guilherme FAG, Ferreira TO, Assis MA, Torrado PV, Morellato LPC. 2012. Soil profile, relief features and their relation to structure and distribution of Brazilian Atlantic rain forest trees. *Scientia Agricola* 69: 61-69.
- Haridasan M. 1988. Performance of *Miconia albicans* (sw.) triana, an aluminum-accumulating species, in acidic and calcareous soils. *Communications in Soil Science and Plant Analysis* 19: 7-12.
- Haridasan M. 2000. Nutrição mineral de plantas nativas do cerrado. *Revista Brasileira de Fisiologia Vegetal* 12: 54-64.
- Haridasan M. 2008. Nutritional adaptations of native plants of the cerrado biome in acid soils. *Brazilian Journal of Plant Physiology* 20: 183-195.

- Haridasan M, Araújo GM. 1988. Aluminium-accumulating species in two forest communities in the Cerrado Region of Central Brazil. *Forest Ecology and Management* 24: 15-26.
- Holt JA, Coventry RJ. 1990. Nutrient cycling in Australian Savannas. *Journal of Biogeography* 17: 427-432.
- IBGE – Instituto Brasileiro de Geografia e Estatística. 1995. Manual técnico de geomorfologia. Rio de Janeiro, Fundação IBGE.
- IBGE – Instituto Brasileiro de Geografia e Estatística. 2001. Mapa de solos do Brasil. Escala 1:5.000.000. Rio de Janeiro, Fundação IBGE.
- IBGE – Instituto Brasileiro de Geografia e Estatística. 2007. Manual técnico de pedologia. Rio de Janeiro, Fundação IBGE.
- Jansen S, Broadley M, Robbrecht E, Smets E. 2002a. Aluminum hyperaccumulation in angiosperms: a review of its phylogenetic significance. *Botanical Review* 68: 235-269.
- Jansen S, Watanabe T, Smets E. 2002b. Aluminium accumulation in leaves of 127 species in Melastomataceae with comments on the order Myrtales. *Annals of Botany* 90: 53-64.
- Kozovits AR, Bustamante MMC, Garofalo CR, *et al.* 2007. Nutrient resorption and patterns of litter production and decomposition in a neotropical savanna. *Functional Ecology* 21: 1034-1043.
- Larcher W. 2000. *Ecofisiologia vegetal*. São Carlos, Rima.
- Lee JA. 1998. The calcicole-calcifuge problem revisited. *Advances in Botanical Research* 29: 1-30.
- Martins FP, Costa RA. 2014. A compartimentação do relevo como subsídio aos estudos ambientais no município de Ituiutaba-MG. *Sociedade & Natureza* 26: 317-331.
- Miranda HS, Bustamante MMC, Miranda AC. 2002. The fire fator. In: Oliveira PS, Marquis RJ. (eds.) *The cerrados of Brazil: ecology and natural history of a neotropical savanna*. New York, Columbia University Press. p. 51-68.
- Moreno MIC, Schiavini I. 2001. Relação entre vegetação e solo em um gradiente florestal na Estação Ecológica do Panga, Uberlândia (MG). *Revista Brasileira de Botânica* 24: 537-544.
- Moss B. 2010. *Ecology of freshwaters: a view for the twenty-first century*. Oxford, John Wiley & Sons.
- Nardoto GB, Bustamante MMC, Pinto AS, Klink CA. 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.
- Paiva AO, Silva LCR, Haridasan M. 2015. Productivity-efficiency tradeoffs in tropical gallery forest-savanna transitions: linking Plant Soil processes through litter input and composition. *Plant Ecology* 216: 775-787.
- Parron LM, Bustamante MMC, Markewitz D. 2011. Fluxes of nitrogen and phosphorus in a gallery forest in the Cerrado of central Brazil. *Biogeochemistry* 105: 89-104.
- Peres JRR, Suhel AR, Vargas MAT, Drozdowicz A. 1983. Litter production in areas of Brazilian cerrados. *Pesquisa Agropecuária Brasileira* 18: 1037-1043.
- Proctor J. 1983. Tropical forest litterfall. I. Problems of data comparison. In: Sutton SL, Whitmore TC, Chadwick AC. (eds.) *Tropical rain forest: ecology and management*. Oxford, Blackwell. p. 267-273.
- Raffaelli DG, Frid CLJ. 2010. The evolution of ecosystem ecology. In: Raffaelli DG, Frid CLJ. (eds.) *Ecosystem ecology: a new synthesis*. Cambridge, Cambridge University Press. p. 1-18.
- Raij B, Andrade JC, Cantarella H, Quaggio JA. 2001. *Análise química para avaliação da fertilidade de solos tropicais*. Campinas, IAC.
- Reatto A, Correia JR, Spera ST. 1998. Solos do Bioma Cerrado: aspectos pedológicos. In: Sano SM, Almeida SP. (eds.) *Cerrado: ambiente e flora*. Planaltina, Embrapa-CPAC. p. 47-86.
- Rossatto DR, Carvalho FA, Haridasan M. 2015. Soil and leaf nutrient content of tree species support deciduous forests on limestone outcrops as a eutrophic ecosystem. *Acta Botanica Brasílica* 29: 231-238.
- Schiavini I. 1983. Alguns aspectos da ciclagem de nutrientes em uma área de cerrado (Brasília, DF): chuva, produção e decomposição de litter. MSc Thesis, Universidade de Brasília, Brasília.
- Schulze ED, Beck E, Müller-Hohenstein K. 2002. *Plant Ecology*. Berlin, Springer.
- Seastadt TR. 1984. The role of microarthropods in decomposition and mineralisation process. *Annual Review of Entomology* 29: 25-46.
- Silva LCR, Hoffmann WA, Rossatto DR, Haridasan M, Franco AC, Horwath WR. 2013a. Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil. *Plant and Soil* 373: 829-842.
- Silva DM, Batalha MA, Cianciaruso MV. 2013b. Influence of fire history and soil properties on plant species richness and functional diversity in a neotropical savanna. *Acta Botanica Brasílica* 27: 490-497.
- Souza MC, Habermann G, Amaral CL, Rosa AL, Pinheiro MHO, Costa FB. 2017. *Vochysia tucanorum* Mart.: an aluminum-accumulating species evidencing calcifuge behavior. *Plant and Soil* 419: 377-389.
- Sutherland WJ, Armstrong-Brown S, Armsworth PR, *et al.* 2006. The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology* 43: 617-627.
- Tedesco MJ, Volkweiss SJ, Bohnen H. 1985. *Análise de solo, plantas e outros materiais*. Boletim técnico de solos n.º 5. Porto Alegre, Faculdade de Agronomia, UFRGS.
- USDA – U.S. Department of Agriculture. 1999. *Soil taxonomy - a basic system of soil classification for making and interpreting soil surveys*. 2nd. edn. Washington, Soil Survey Staff.
- Valadão MBX, Marimon-Junior BH, Oliveira B, Lúcio NW, Souza MGR, Marimon BS. 2016. Biomass hyperdynamics as a key modulator of forest self-maintenance in a dystrophic soil in the Amazonia-Cerrado transition. *Scientia Forestalis* 44: 475-485.
- Valenti MW, Cianciaruso MV, Batalha MA. 2008. Seasonality of litterfall and leaf decomposition in a cerrado site. *Brazilian Journal of Biology* 68: 459-465.
- Viera M, Caldato SL, Rosa SF, *et al.* 2010. Nutrientes na serapilheira em um fragmento de floresta estacional decidual, Itaara, RS. *Ciência Florestal* 20: 611-619.
- Villalobos-Vega R, Goldstein G, Haridasan M, *et al.* 2011. Leaf litter manipulations alter soil physicochemical properties and tree growth in a Neotropical savanna. *Plant and Soil* 346: 385-397.
- Vitousek P. 1982. Nutrient cycling and nutrient use efficiency. *The American Naturalist* 119: 553-572.
- Vitti GC, Otto R, Saviato J. 2015. Manejo do enxofre na agricultura, n.º 152. Piracicaba, International Plant Nutrition Institute.
- Vourlitis GL, Lobo FA, Lawrence S, *et al.* 2014. Nutrient resorption in tropical savanna forests and woodlands of central Brazil. *Plant Ecology* 215: 963-975.
- Watanabe T, Osaki M. 2002. Mechanisms of adaptation to high aluminum condition in native plant species growing in acid soils: a review. *Communications in Soil Science and Plant Analysis* 33: 1247-1260.
- Wong MTF, Swift RS. 2003. Role of organic matter in alleviating soil acidity. In: Rengel Z. (ed.) *Handbook of soil acidity*. New York, Marcel Dekker Inc. p. 337-358.

