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Soil and leaf nutrient content of tree species support deciduous forests on limestone outcrops as a eutrophic ecosystem

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ABSTRACT

The leaf and soil nutrient status of plants has been used to infer structural and functional aspects at the ecosystem level. Such data are available for tropical and savanna systems growing on poor and acidic soils; however, information for species growing on eutrophic and basic soils is lacking. Deciduous tropical forest is one of the most endangered types of tropical forest, and despite the high level of attention aimed at it, little is known about the nutritional composition of its leaves. Here, we provided information on leaf nutrient content ratios and relationships for deciduous tree species growing on a limestone outcrop in Central Brazil. We compared our data on soil and leaf macronutrient concentration with previously published data from savannas and humid forests in the Neotropics. We found that deciduous forest tree species possessed elevated concentrations of N, K, and Ca compared with those of other forest and seasonal systems. The higher leaf Ca and P is due to the elevated Ca and P content in soils of deciduous forest. We discussed these findings in the light of soil aspects, functional adaptations, and priorities that should be given to the conservation and management of deciduous forest.

Keywords: calcium, deciduous forest, leaf nutrient, limestone outcrops, nitrogen

Introduction

Foliar nutrient concentration has been used as an important parameter to recognize critical processes of community assembly and species coexistence (Aerts & Chapin III 2000). It has been used to understand leaf structure and function at the ecosystem level, which act as regulators of plant productivity, biomass accumulation, and decomposition (McLaughlin & Wimmer 1999; Vitousek & Sanford 1986; Bustamante *et al.* 2006; Wright *et al.* 2007). These processes are supposed to differ drastically between different vegetation types such as forests and savannas because these systems may be conditioned to different periods of seasonal drought, edaphic aspects, and even fire frequency (Pennington *et al.* 2006; Furley 2007; Haridasan 2008; Gotsch *et al.* 2010). Data on leaf nutrient concentration for tropical forests and savannas are available in the literature (Klinge *et al.* 1983; Vitousek & Sanford 1986; Haridasan 2008), particularly for growing vegetation on poor and acidic soils. However, such information is lacking for mesotrophic forest areas, which appear scattered within the poor

acid oxisols throughout the Brazilian territory (Haridasan & Araújo 2005).

Seasonal deciduous tropical forests (SDTF or simply deciduous forest) occur in small areas in Central and South America (Miles *et al.* 2006), and they are commonly associated with the scattered distribution of calcareous rock outcrops in the Neotropics (eutrophic rocks) (Sanchez-Azofeifa *et al.* 2013). Because of this scattered pattern, deciduous forests are dispersed among other vegetation types, possessing boundaries with humid forests and seasonal savannas (Pennington *et al.* 2009). The majority of deciduous forests in Brazil appear in seasonal areas, which are subjected to a low amount of annual rainfall (less than 1000 mm/year). This seasonal pattern exposes the vegetation to a large period of drought, thus resulting in the selection of species in which the deciduous phenological pattern is dominant (Mooney *et al.* 1995; Oliveira-Filho *et al.* 2006). In addition to seasonal aspects, such forests occupy areas where the not well-developed and incipient soils hold elevated levels of macronutrients, particularly Ca and Mg (Furley & Ratter 1988; Mooney *et al.* 1995; Haridasan

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2008; Pennington *et al.* 2006). Soil conditions must be reflected in leaf nutrient concentrations (Kimmins 2003), which implies that the knowledge of such information can elucidate the characteristics of these systems accurately, as generally being composed of an exclusive flora (Furley & Newey 1979; Felfili *et al.* 2007).

Somavilla *et al.* (2014), described the morpho-anatomical leaf structure of deciduous forests species as mesomorphic because these species have thinner leaves at elevated values of specific leaf area (80–270 cm²·g⁻¹). Based on this information and taking into account the leaf economic spectrum (Wright *et al.* 2004) and the edaphic aspects of such systems (Pennington *et al.* 2006), one may expect elevated concentrations of macronutrients in leaves of deciduous forest species.

Here, we studied the concentrations and ratios of leaf nutrients in common tree species growing in a deciduous forest on limestone outcrops in Central Brazil. We also utilized previously published data on leaf nutrients for humid forests and savannas that occur among deciduous forests in Central Brazil (Furley 2007) to compare our data with the nutrient content of other types of humid forests in Brazil (Atlantic and Amazon forest). Our approach relies on comparisons of species exclusive for each environment only, which allows a fine comparison of nutritionally distinct groups of plants that should be formed exclusively by differences in edaphic conditions (Araújo & Haridasan 1988). Because deciduous forests grow on limestone outcrops, we expect to find that deciduous forests show an elevated concentration of macronutrients in their leaves compared with that of other tropical ecosystems. Based on the analysis of distinct tropical forest and savanna ecosystems, we also hypothesized that nutrient concentrations in soils will be positively related with their concentrations in leaves of species at the community level (Kimmins 2003; Hardtle *et al.* 2005).

Materials and Methods

Study site and species

This study was performed in a patch of deciduous forest occurring in the northeastern region of Goiás State, Brazil, at "Fazenda Sabonete," municipality of Iaciara in the Paranã valley (14°03'53.2"S, 46°29'15.2"W). The dominant vegetation type of this region is the savannas; however, deciduous, semi-deciduous, and evergreen gallery forests are also present (Silva *et al.* 2006). Savannas occur mainly on poor oxisols, whereas semi-deciduous and deciduous forests are restricted to shallow soils and limestone patches, respectively (Felfili *et al.* 2007). We sampled individuals from the more common and dominant species in the studied deciduous forest (Felfili *et al.* 2007). The selection was based on the availability of individuals and leaves at the studied site, taking into account the important value index obtained in the same study area by a previous phytosociological study

(Tab. 1) (Felfili *et al.* 2007). The selected species represent almost 70% of the total tree individuals with DBH >5 cm (Felfili *et al.* 2007)

Sample collection and nutrient analysis

Soil data for deciduous forests were retrieved from Carvalho (2009), where 25 soil samples were collected in the studied forest (twenty-five 20 × 20 m plots, covering 1 ha). Data for soil samples were analyzed following EMBRAPA (1997) standard procedures. Leaves were collected in February 2009 from the boundaries of the crown in all studied trees, comprising three chosen individuals per species. We sampled completely expanded sunlit leaves, without any sign of senescence or herbivory damage, located at the second or third node from the branch tip. Three leaves were collected for each individual and were dried at 70°C for 3 days. The dried leaves were finely ground and a subsample was taken for macronutrient determinations (N, P, K, Ca, and Mg). Total leaf N was determined in diluted acid digests using the micro-Kjeldahl procedure (Allen *et al.* 1974). Total extractable P was determined colorimetrically by complex formation with molibdovanadate according to Allen *et al.* (1974). K, Ca, and Mg were determined by atomic absorption after wet digestion with a tri-acid mixture of nitric, sulphuric, and perchloric acids (10:1:2).

Data compilation and statistical analysis

For comparisons of deciduous forest with other vegetation types, we assessed previously collected data for each type of vegetation that normally surrounds deciduous forest formations and also for other forest types appearing in the Atlantic and Amazon rainforests (Tab. 2). We selected studies reporting leaf and soil macronutrient concentrations for

Table 1. List of the studied tree species in a deciduous forest under limestone outcrops in Central Brazil. Data compiled from Felfili *et al.* (2007)

Species	Family
Dilodendron bipinnatum Radlk.	Sapindaceae
Pseudobombax tomentosum (Mart. & Zucc.) A.Robyns	Malvaceae
Myracrodruon urundeuva Allemão	Anacardiaceae
Cavanillesia arborea (Willd.) K.Schum.	Malvaceae
Acacia tenuifolia (L.) Willd.	Fabaceae
Combretum duarteanum Cambess.	Combretaceae
Tabebuia impetiginosa (Mart. ex A.DC.) Standley	Bignoniaceae
Sterculia striata A.St.-Hil. & Naudin	Malvaceae
Aspidosperma subincanum Mart. ex A.DC.	Apocynaceae
Guazuma ulmifolia Lam. var. ulmifolia	Malvaceae
Commiphora leptophloeos (Mart.) J.B.Gillett	Burseraceae
Bauhinia ungulata L.	Fabaceae
Cnidoscolus vitifolius (Mill.) Pohl A.	Euphorbiaceae

Table 2. List of the studied vegetation types in the Neotropics. Data for leaf and soil nutrient content were compiled from the following references.

Biome	Type of Vegetation	Nº Species	References
Neotropical savanna	Savanna	10	Rossatto *et al.* (2013)
Neotropical savanna	Gallery Forest	15	Rossatto *et al.* (2010); Nogueira and Haridasan (1997)
Neotropical savanna	Semi-deciduous forest	10	Moreno (2005); Haridasan and Araujo (2005)
Neotropical savanna	Deciduous forest	13	This study
Atlantic rainforest	Primary rainforest	11	Boeger *et al.* (2005)
Atlantic rainforest	Secondary rainforest	14	Sambuichi (2003)
Amazon forest	"Terra Firme" forest	12	Klinge *et al.* (1983)
Amazon forest	"Várzea" forest	15	Klinge *et al.* (1983)
Amazon forest	"Igapó" forest	14	Klinge *et al.* (1983)

gallery forest (a humid forest appearing near small streams), semi-deciduous forest (seasonal vegetation growing on not well-developed soils), and savanna (seasonal vegetation growing on deep and well-drained soils). All the previously selected vegetation types appear in a climate similar to that where deciduous forest is found (Ribeiro & Walter 2008) but differing in soil conditions. For the Atlantic rainforest (humid forest on deep and drained soils) (Morellato & Haddad 2000), we selected one study dealing with two situations: in a primary Atlantic rainforest and in an agroforested system (Sambuichi 2003). Our samples of the Amazon rainforest included a "Terra firme" forest (humid tropical forest on deep and drained soils), an "Igapó" forest (seasonally flooded forest, poor in nutrients), and a "Várzea Forest" (seasonally flooded forest, rich in nutrients) (Pires & Prance 1985). To make our data comparable, we selected studies that used a similar methodology to ours to estimate macronutrient concentrations in leaves and soils.

To compare average leaf macronutrient (N, P, K, Ca, and Mg) concentrations at the community level between distinct vegetation types, we performed a multivariate analysis of variance (MANOVA) followed by Tukey's test because there is a strong correlation between leaf nutrients, particularly between N and P and Ca and Mg (Zar 2010). Values of leaf macronutrient concentrations for each species were used as replicates because we were interested in testing for differences between vegetation types. The number of replicates analyzed per vegetation varied from 10 to 15 (see Tab. 2). We performed a linear regression to test the relationships between soil nutrient content and leaf nutrient content at the community level. We used linear regression analysis to assess the position of each vegetation on a single axis of variation in an ecosystemic relationship between N and P and Ca and Mg. In all cases, α was taken as 5%.

Results

Soil properties of studied ecosystems

The incipient soils of deciduous forest had a pH value around six and elevated values of exchangeable Ca and Mg (Tab. 3) as well as higher values of exchangeable P (Tab. 3).

Deciduous forest soils were comparable to semi-deciduous forest soils in terms of P content. However, their elevated potential of Ca and Mg exchange is comparable only to "Várzea" forest soils (Tab. 3). Savanna and the other studied forest soils possessed higher iron and aluminum concentrations (Tab. 3).

Leaf nutrient content in tree species of deciduous forest and other ecosystems

Leaf macronutrient concentrations for deciduous forest tree species are shown in Table 4. Eight species showed N:P ratios higher than 16 (Tab. 4), whereas two had values near 30 (25 for *Guazuma ulmifolia* and 30 for *Cavanillesia arborea*). None of the species studied had values lower than 14, and four of them had values between 14 and 16.

We found significant differences in the concentration of leaf nutrients and N:P ratio in the evaluated vegetation types (MANOVA: Wilks $\lambda = 0.056$, df = 48, $F = 110.79$, $P < 0.01$). Compared to trees in other forest and savanna types, the deciduous tree species studied here showed higher values for almost all nutrients studied. N concentration for deciduous forest was around 2.4% and only semi-deciduous and "Várzea" forests had similar values for this and some other nutrients (Tab. 5). Ca concentration was elevated in deciduous forests compared with that of other systems because the leaf concentration reached 1.7% (also similar with the value found for "Várzea" forest), which is far from the values found for other types of forest (less than 0.8%) (Tab. 5). In contrast, P and Mg concentrations were higher for "Várzea" and secondary Atlantic rainforest than for deciduous forest (Tab. 5). N:P ratios were higher than 16 for all studied vegetations (Tab. 5).

Relationships between soil and leaf nutrient content and between leaf nutrients in the studied systems

We found significant positive relationships between soil P and plant leaf P concentration ($r^2 = 0.289$, $P = 0.034$) as well as between soil Ca and plant leaf Ca concentration ($r^2 = 0.76$, $P = 0.003$) (Fig. 1). However, these relationships were not significant for K ($r^2 = 0.033$, $P = 0.308$) or Mg ($r^2 = 0.00$, $P = 0.589$) concentration.

Table 3. Average soil properties in the deciduous forest on limestone outcrops in Central Brazil and other vegetation types (see Table 2). Data presented here comprise only surface layer of soil profile (between 0-20 cm). na = not available.

Vegetation	Soil properties								
	pH	O.M.	P	Al	K	Ca	Mg	Fe	H+Al
		%	mg.dm^{-3}			cmol.dm^{-3}			
Deciduous forest	6.64	5.80	2.14	na	0.43	14.65	5.86	30.45	4.38
Semi-deciduous Forest	5.70	2.30	2.70	0.10	0.54	8.09	1.45	na	4.00
Gallery forest	5.12	12.4	1.98	0.36	0.70	2.30	0.65	70.67	5.45
Savanna	4.67	1.20	0.46	0.45	0.30	0.11	0.06	89.00	6.94
Primary rainforest	na	na	na	na	na	na	na	na	na
Secondary rainforest	5.00	1.80	1.70	0.25	0.25	4.03	3.04	70.54	na
"Várzea" forest	4.91	1.12	0.84	0.23	0.18	22.60	1.80	54.60	na
"Terra Firme" forest	4.30	1.80	0.70	0.45	0.23	0.11	0.11	45.43	na
"Igapó" forest	4.01	3.62	0.75	0.80	0.17	1.90	0.09	47.43	na

Table 4. Leaf nutrient concentrations on a dry mass basis (g.kg^{-1}, mean (±S.E.)) and N:P ratio in leaves of deciduous forest tree species in Central Brazil.

Species	N	P	K	Ca	Mg	N:P
D. bipinnatum	22.64 (0.30)	1.24 (0.04)	7.88 (0.21)	14.44 (2.9)	1.38 (0.01)	15.74 (0.80)
P. tomentosum	23.54 (0.28)	1.71 (0.26)	12.59 (0.20)	13.17 (1.42)	2.74 (0.01)	20.97 (0.70)
M. urundeuva	20.90 (0.28)	1.38 (0.35)	7.47 (0.12)	15.95 (3.5)	2.05 (0.05)	19.67 (0.51)
C.arborea	24.13 (0.10)	1.67 (0.21)	12.47 (0.77)	16.11 (2.4)	1.88 (0.06)	30.83 (1.06)
A. tenuifolia	29.34 (0.02)	1.07 (0.07)	8.63 (0.28)	16.78 (2.1)	1.48 (0.08)	15.19 (1.63)
C. duarteanum	24.10 (0.23)	2.41 (0.12)	6.41 (0.33)	15.48 (3.4)	2.00 (0.12)	17.95 (1.53)
T. impetiginosa	22.84 (0.06)	1.29 (0.19)	12.13 (0.37)	19.07 (6.9)	1.78 (0.04)	18.25 (2.28)
S. striata	23.84 (0.23)	1.57 (0.07)	9.69 (0.04)	7.63 (0.45)	3.60 (0.01)	17.60 (0.97)
A. subincanum	17.84 (0.03)	1.02 (0.15)	14.01 (0.74)	22.66 (3.4)	2.26 (0.04)	13.92 (1.44)
G. ulmifolia	22.45 (0.12)	1.14 (0.07)	12.27 (0.02)	19.55 (1.9)	1.95 (0.01)	24.39 (2.59)
C. leleptophloes	18.44 (0.37)	0.76 (0.08)	12.37 (0.19)	14.41 (3.0)	2.18 (0.02)	14.13 (0.82)
B. ungulata	30.50 (0.06)	1.45 (0.04)	8.31 (0.10)	18.30 (1.6)	1.92 (0.03)	14.73 (1.05)
C. vitifolius	25.11 (0.11)	1.81 (0.11)	24.48 (0.53)	8.91 (0.28)	3.05 (0.04)	27.44 (0.56)

Table 5. Average leaf nutrient concentration (g.kg^{-1}) and N:P ratio for deciduous forest and other vegetation types.

| Vegetation type	N	P	K	Ca	Mg	N:P
Deciduous forest	23.49	1.30	11.44	17.11	2.17	19.12
Savanna	14.55	0.51	3.61	4.42	1.41	30.36
Gallery forest	18.88	1.02	4.22	5.17	2.79	20.01
Semi-deciduous forest	21.38	1.19	8.44	7.61	3.41	18.68
Primary rainforest	14.00	0.24	5.23	7.41	2.81	58.98
Secondary rainforest	20.77	1.57	9.63	11.50	2.93	13.23
"Terra Firme" forest	17.50	0.76	8.15	2.84	1.16	23.03
"Igapó" forest	17.30	0.62	8.88	8.72	2.3	27.90
"Várzea" forest	25.40	1.31	10.90	17.70	4.00	19.39
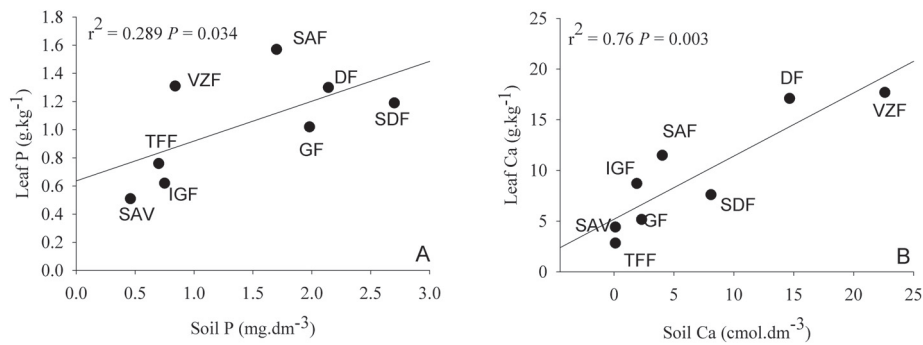
Figure 1. Relationships between soil P and leaf P concentration (A) and soil Ca and leaf Ca concentration (B) for systems studied. DF: deciduous forest; GF: gallery forest; IGF: "Igapó" forest; PAF: primary Atlantic rainforest; SAF: secondary Atlantic rainforest; SDF: semi-deciduous forest; SAV: savanna, TFF: "Terra Firme" forest; and VZF: "Várzea" forest.

Concerning the relationships between leaf nutrients of the evaluated systems, a common linear axis of variation was found in the relationship between Ca and Mg ($r^2 = 0.476$, $P = 0.041$) (Fig. 2A) and between N and P ($r^2 = 0.693$, $P = 0.001$) (Fig. 2B). The relationship between Ca and Mg was significant only when deciduous and "Várzea" forests were dropped out of the analysis (Fig. 2A); otherwise, the relationship was not significant ($r^2 = 0.322$, $P = 0.105$).

Discussion

Edaphic aspects and leaf nutrient concentration

We confirmed our hypothesis because deciduous forest had the higher leaf concentration of N, K, and Ca (Tab. 5) among the studied ecosystems. Secondary Atlantic rainforest is used for cacao plantations, which are fertilized (Sambuichi 2003); therefore, deciduous forests also had the highest P concentration of the systems studied (Tab. 5). The traditional assumption that plant nutritional status normally represents site fertility (Kimmins 2003) was confirmed at the community level for the studied Neotropical systems, at least for Ca and P (Fig. 1).

The limestone outcrops at the studied site belong to the Old Mesozoic/New Proterozoic era and are fundamentally formed by a parent material that has an elevated Ca and Mg content (Fernandes et al. 1982; Finatec 2001). These rocks occur scattered along the study site forming large blocks; however, small pieces of weathered limestone can be found together with an incipient black and highly fertile soil at some sites, which normally does not surpass 20 cm in depth (Felfili et al. 2007). As compared to the soil of other vegetations, these incipient soils are richer in macronutrients, particularly in terms of Ca, Mg, and P and also showed elevated values for organic matter and base saturation (Tab. 3).

The present soil condition of deciduous forest can explain the richer nutritional contents of the leaves of its species, at least for P and Ca, because we found a positive and significant relationship between soil and leaf nutrient concentration (Fig. 1). The soil under deciduous forests is not well-developed and the parent materials are constantly suffering from physical (due to the strong seasonal aspect of the system) and biological weathering (roots of tree species grow between the rocks, breaking it) (Felfili et al. 2007). These factors allow the deciduous forests to receive a high annual input of macronutrients to be used in forest productivity and biomass accumulation (particularly, Ca and Mg).

Soil nutrient content of deciduous forests was only comparable to that found for "Várzea" soils (Klinge et al. 1995), a vegetation type constantly affected by flooding. In the "Várzea" forest, the elevated nutrient content can be explained by an annual input derived from nutrient-rich sediments coming from the weathering of Andean rocks (Prance 1979; Junk 1993). Concerning the other forest types, the present soil nutrient availability is low; this can be explained by the fact that most of the soil nutrient content existing in the past is now stored in the forest biomass (Vitousek & Sanford 1986; Haridasan 2000, 2001; Lilienfein et al. 2001). For savannas, the weathering in the past (Eiten 1972) and the frequent fires (which consume plant and litter biomass, releasing nutrients as ashes and smoke) (Coutinho 1979) may explain the low nutrient concentration found in its soil.

There was a strong and positive relationship between leaf Ca and leaf Mg; a single axis of variation encompassed the studied vegetation types only when deciduous and "Várzea" forests were removed from the analysis (Fig. 2A). This result suggests that deciduous and "Várzea" forests possess unique stoichiometric relationships for these elements (McGroddy et al. 2004). This may be caused by elevated annual inputs of Ca and Mg from their weathering sources: the Andes for "Várzea" and limestone rocks for deciduous forests, while there is a lack of weathering sources providing Ca and Mg in the other systems studied (Vitousek & Sanford 1986; Whitmore 1998). For the leaf N:P relationship, a single axis of variation encompassed all studied vegetations, with deciduous forests and the Atlantic rainforests being at opposite ends of the spectrum (Fig. 2B). The P supply for deciduous forests is continuous because of the supply stored in their soils (Table 3), whereas there is no weathering source and
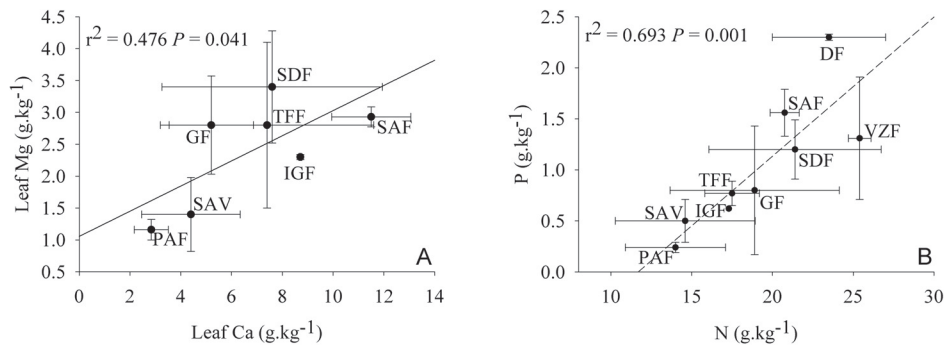
Figure 2. Relationships between leaf Ca and Mg concentration for systems studied (A) and relationship between leaf N and P concentration (B) for systems studied. DF: deciduous forest; GF: gallery forest; IGF: "Igapó" forest; PAF: primary Atlantic rainforest; SAF: secondary Atlantic rainforest; SDF: semi-deciduous forest; SAV: savanna, TFF: "Terra Firme" forest; and VZF: "Várzea" forest.

continuous loss of dissolved organic P for the Atlantic forests because of the elevated rainfall (Hedin *et al.* 1995).

The unique similarity found between deciduous forests and all the other systems studied is their similar N:P ratio; all of the studied systems suffered from P limitation because of their N:P ratios above 16 (Güsewell 2004). The exception is the secondary Atlantic rainforest, in which the N:P ratio is lower than 16. These results are in accordance with the expected commonly reported P limitation for a high number of Neotropical vegetation systems (Vitousek 1984; Bustamante *et al.* 2006). We found a certain degree of variability in the N:P ratio of deciduous trees species; however, most species show values higher than 16. Interestingly, five species in this system, of which four (*Tabebuia, Pseudobombax, Sterculia,* and *Myracruodon*) are the major common and phytosociologically dominant species (Felfili *et al.* 2007), showed no limitation for P or for N (N:P ratios around 15). This finding points to a high spatial variability in local P limitation because the sampled soils soil have higher values of P availability (Tab. 3).

The role of nutrients on the ecophysiology of deciduous forest species

Ca plays an important role in forest productivity, particularly in plant growth (McLaughlin & Wimmer 1999), because plants in environments limited in Ca can respond to its addition (Villela & Haridasan 1994). Because of their higher leaf Ca concentration, deciduous forest species are able to accumulate it in leaf tissues, thus forming diverse types of Ca crystals (Somavilla *et al.* 2014). This accumulation of Ca may serve as a source of Ca during the process of water regulation, particularly for osmotic purposes (Ghanem *et al.* 2010).

Foliar N and P concentration are related to the content of chlorophyll and carboxilation enzymes, which are intrinsically linked to photosynthetic demand (Duursma & Marshall 2006) and, therefore, influenced by light availability. The higher N concentration found in deciduous forest trees coupled with the high values of specific leaf area (Somavilla

et al. 2014) may indicate elevated carbon assimilation and productivity because these systems are not limited by light (Baker *et al.* 2003; Poorter 2008; Somavilla *et al.* 2014). Deciduous forest trees on these limestone outcrops maintain their canopy without leaves for a period of 5–6 months during the dry period (Carvalho 2009). This situation shows that productivity may be restricted to the few months when water is available. The coupling of higher values of specific leaf area (Somavilla *et al.* 2014) and elevated N and P concentrations may be a strategy to perform substantial carbon assimilation and growth in this short period (Hoffmann *et al.* 2005; Poorter 2008; Gotsch *et al.* 2010).

K achieves the highest values among the studied vegetations in dry forest trees (Tab. 5). Its concentration in deciduous forest tree species can be three times higher than that found in savannas (which are constantly prone to fire and may lose significant amounts of K) and two times higher than in wet forests (Tab. 5). This suggests that K is playing an important role in water level regulation in these species, particularly in stomata control, because these plants keep their leaves active during the first 2–3 months in the dry season. In addition, all of the studied species possess mucilaginous substances in their leaf cells (Somavilla *et al.* 2014), including in some guard cells of stomata. Mucilaginous substances in cells can serve as means of water storage, thus demanding high amounts of K ions to produce the expected control (Ghanem *et al.* 2010). The foliar K concentration can also play an important role in osmotic regulation in the trunks of some species: *C. arborea,* for example, is a tree with low wood density that can store water in its trunk as an adaptive strategy to low water availability (Rojas-Jiménez *et al.* 2007).

Leaf nutrients and their implication for dry forest management and conservation

The assessment of leaf nutritional status can bring important and essential information for direct actions in the conservation of species (Sariyildsz & Anderson 2005). In deciduous forests on limestone outcrops, special attention has to be given to Ca because it is very abundant in soils and

in the leaves of tree species. Ca is proposed as an important nutrient for biomass accumulation and plant growth, thus acting in important steps in the metabolism of cells, including carbon fixation. Based on Ca leaf content, Hou & Merkle (1950) classified plants into two groups: the calcicole (leaf concentration between 15.7 and 22.7 g·kg) and the calcifugous (with leaf concentration between 4.8 and 10.8 g·kg). Based on this criterion, 8 of the 12 studied species can be considered calcicole. This fact deserves special attention, particularly in the production of seedlings with the purpose of forest restoration, because these species may not be able to establish and grow under low Ca availability in the soil.

The selective extraction of rocks to produce cement for urban constructions and calcarium to correct soil pH for crop production (Felfili 2003) could bring significant changes in this type of forest not only because it demands heavy machinery but also because it can bring significant changes in nutrient cycles and rock weathering patterns. Because of the intrinsic relationships between Ca and Mg and N and P, small changes in soil conditions could lead to an imbalance in nutrient relationships for tree species in this type of forest. The most affected should be species showing balanced N:P ratios (ratio around 15, as *Myracrodruon urundeuva*, *Pseudobombax tomentosum* and *Sterculia striata*).

Conclusions

Among the ecosystems studied, deciduous forests have the highest nutrient content of elements such as Ca and Mg either in soils or leaves. This demonstrates that eutrophic soils, associated with severe seasonal aspects such as long drought, could have filtered species able to store nutrients and use these available resources (before losing their leaves) to resist the drought, thus supporting a eutrophic ecosystem even in harsh abiotic conditions.

Acknowledgments

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