Nutrient resorption in tropical savanna forests and woodlands of central Brazil

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Abstract Nutrient limitation in Brazilian savanna (known as cerrado) presumably causes trees to maximize nutrient resorption from senesced leaves to reduce their dependence on nutrient availability. To assess patterns between nutrient resorption and soil fertility, we measured community-level nitrogen (N), phosphorus (P), and potassium (K) concentrations in mature and senesced leaves and soil fertility in the upper 50 cm soil layer in structurally diverse cerrado ecosystems in the Cuiaba Basin (CB) and Pantanal (PAN) of Mato Grosso, Brazil. Foliar nutrient concentration data were used to estimate resorption efficiency and proficiency, and correlation was used to determine whether resorption efficiency and proficiency varied across soil fertility gradients. We found that N and P resorption proficiency (NRP and PRP, respectively) and P resorption efficiency (PRE) increased significantly as total soil N (NRP) and extractable P (PRP and PRE) declined. In contrast, K resorption efficiency (KRE) declined as soil sand content and bulk density increased, which was likely due to a reduction in soil water-holding capacity. Leaf N/P ratios indicate potential N limitation and/or N + P co-limitation for ecosystems in the PAN and P limitation and/or N + P co-limitation for ecosystems in the CB, while trends in leaf N/K ratios indicate possible K or K + P co-limitation for the CB only. Our results illustrate that cerrado forests and woodlands have highly variable nutrient resorption capacities that vary predictably across soil fertility or textural gradients and indicate that cerrado communities have flexible nutrient resorption that can reduce their dependence on soil nutrient availability.

Keywords Cerrado · Nitrogen · Nutrient cycling · Phosphorus · Plant–soil relationships ·← Potassium

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Introduction

Nutrient availability is a well-known limiting factor for tropical forest and savanna structure and function (Goodland and Pollard 1973; Lopes and Cox 1977; Jordan and Herrera 1981; Laurance et al. 1999; Lloyd et al. 2008; Paoli et al. 2008; Viani et al. 2011;

Vourlitis et al. 2013). As a result, tropical trees have developed numerous strategies to reduce nutrient limitation, including the development of extensive surface root mats that rapidly cycle available nutrients into plant biomass, sclerophyllous leaves that minimize nutrient losses from leaching, and efficient nutrient resorption that minimizes the loss of nutrients that are currently in plant biomass (Jordan and Herrera 1981; Vitousek and Sanford 1986).

Effective nutrient resorption is a key nutrient conservation strategy that allows plants to reduce their dependence on soil nutrient availability (Aerts 1996; Killingbeck 1996; van Heerwaarden et al. 2003; Covelo et al. 2008; Reed et al. 2012; Vergutz et al. 2012). Thus, it is reasonable to assume that resorption efficiency should be high in infertile sites and low in fertile sites (Killingbeck 1996; Davidson et al. 2007; Reed et al. 2012). However, predictable patterns of nutrient resorption efficiency, or the percent reduction in the nutrient pool between mature and senescing leaves, across environmental gradients have been elusive because resorption can vary over seasonal and interannual scales and can be influenced environmental variables such as light and water availability (Aerts 1996; Killingbeck 1996; Covelo et al. 2008). In addition, there are difficulties in estimating resorption efficiency because leaf area and mass decline during senescence as carbon and nutrients are translocated to more physiologically active leaves (van Heerwaarden et al. 2003). While there are ways to correct for these changes (van Heerwaarden et al. 2003; Reed et al. 2012; Vergutz et al. 2012), widely varying measurement techniques lead to additional uncertainty in estimating nutrient resorption efficiency (Cai and Bongers 2007). Nutrient resorption proficiency, estimated as the minimum nutrient concentration in senescing leaves, is perhaps a more objective approach for quantifying nutrient resorption because it measures the physiological limit that a species can resorb nutrients and does not rely on mature leaf nutrient concentrations that vary considerably more over space and time (Killingbeck 1996; Covelo et al. 2008). Even so, isolated measurements may not adequately characterize the minimum nutrient concentration of senescent leaves (Killingbeck 1996).

Despite these problems, there are examples where variations in resorption proficiency have been linked to soil fertility gradients, especially when community-scale resorption proficiency is considered. For example, N and P concentrations of recently fallen litter in temperate rainforests along the Franz Josef chronosequence in New Zealand declined significantly as soil N and P declined, indicating that N and P resorption proficiency was significantly higher in more infertile soils (Richardson et al. 2005, 2008). Wright and Westoby (2003) found that the resorption proficiency of Australian evergreen trees and shrubs was substantially higher in sites with low N and P availability. Similarly, Lu et al. (2012) found that grasses of the Chinese steppe had substantially higher N resorption proficiency as soil extractable N declined; however, the response in N resorption efficiency across the N availability gradient was species specific.

Building on these examples, we describe variations in the community-level N, P, and K resorption efficiency and proficiency of Brazilian savanna (locally known as cerrado) within and between two regions, the Cuiaba Basin and Pantanal of southern Mato Grosso, Brazil, that differ substantially in soil physical and chemical properties and hydrology (Wantzen et al. 2012; Vourlitis et al. 2013). Because cerrado trees and shrubs are known to be nutrient (especially P and cation) limited (Goodland and Pollard 1973; Lopes and Cox 1977; Lloyd et al. 2008; Viani et al. 2011; Vourlitis et al. 2013), we predicted that N, P, and K resorption efficiency and proficiency would increase as soil N, P, and K declined.

Methods

Site descriptions

Cerrado forests and woodlands in the Cuiaba Basin (CB) and Pantanal (PAN) were sampled in July 2012 and 2013, which is during the climatological dry season (Vourlitis and da Rocha 2011) when deciduous and semi-deciduous trees in both regions are shedding leaves and leaf nutrient concentrations reach a seasonal minimum (Dalmagro et al. 2013). Cerrado in this region is structurally diverse because of widely varying soil parent material (Radambrasil 1982) and hydrological regimes (Nunes da Cunha and Junk 2001; Wantzen et al. 2012; Vourlitis et al. 2011, 2013; Dalmagro et al. 2013). The PAN and CB sites are separated by approximately 90 km; however, both

Table 1 Mean (±SE; $n = 10$) structural characteristics, including tree diameter and density, leaf area index (LAI), grass cover, and dominant tree species for the forest and woodland stands of the Cuiaba Basin (CB) and Pantanal (PAN)

Ecosystem type	Site	Diameter (cm)	Density (trees/ha)	LAI (m^2/m^2)	Grasses (%)	Primary tree species[a]
Upland forest (cerradão)	CB	8.6 ± 0.9	1,407 ± 379	4.5 ± 0.2	32.7 ± 8.3	*Af; Ca, Tau, Re*
	PAN	13.7 ± 2.0	1,441 ± 292	5.8 ± 0.1	5.1 ± 2.5	*Cf, Ef, Me, Vd*
Mixed forest	CB	9.2 ± 1.3	1,717 ± 438	2.5 ± 0.6	41.1 ± 7.9	*Af; Ca, Mg*
	PAN	26.6 ± 3.9	1,479 ± 332	7.4 ± 0.3	2.4 ± 0.9	*Ac, Cc, Me, Sp*
Gallery forest (cambarazal)	CB	11.9 ± 1.5	519 ± 132	2.1 ± 0.4	64.8 ± 8.8	*Ad, Hg, Vd*
	PAN	23.6 ± 1.9	1,020 ± 142	6.3 ± 0.2	0.6 ± 0.3	*Lp, Me, Vd*
Woodland (sensu stricto)	CB	9.4 ± 0.8	2,556 ± 368	3.1 ± 0.2	16.7 ± 4.3	*Ca, Qg, Qp, Tar*
	PAN	13.1 ± 1.3	1,656 ± 296	3.7 ± 0.1	18.9 ± 4.1	*Af, Ca, Tau, Th*
Mixed grassland (campo sujo)	CB	6.8 + 0.6	533 + 62	1.3 + 0.3	64.0 + 5.1	*Ca, Dh*
	PAN	ND	ND	ND	ND	ND

Brazilian names for the vegetation types are indicated in parentheses. *ND* no data

[a] (*Ad*) *Alchornea discolor* Poepp. & Endl.; (*Ac*) *Aspidosperma cylindrocarpon* M. Arg.; (*Af*) *Astronium fraxinifolium*; (*Cf*) *Callisthene fasciculata*; (*Cc*) *Cupania castaneifolia* Mart.; (*Ca*) *Curatela americana*; (*Dh*) *Diospyros hispida* A. DC. (*Ef*) *Eugenia florida* DC. (*Hg*) *Hirtella glandulosa* Spreng.; (*Lp*) *Licania parvifolia* Huber.; (*Mg*) *Matayba guianensis* Radlk.; (*Me*) *Mouriri elliptica* Mart.; (*Qg*) *Qualea grandiflora* Mart.; (*Qp*) *Qualea parviflora* Mart.; (*Re*) *Rhamnidium elaeocarpum* Reiss.; (*Sp*) *Scheelea phalerata* (Mart.) Bur.; (*Tau*) *Tabebuia aurea*; (*Th*) *Tabebuia heptaphylla*; (*Tar*) *Terminalia argentea* Mart. & Zucc.; (*Vd*) *Vochysia divergens*

regions have a mean annual rainfall of 1,420 mm, nearly all of which occurs during the months of October–April, and a mean annual temperature of 26.5 °C (Nunes da Cunha and Junk 2001; Vourlitis and da Rocha 2011).

In the CB, research was conducted at Fazenda Miranda, which is 15 km SSE of Cuiaba, Mato Grosso, Brazil (15°43′51″S: 56°04′17″W). Sites were approximately 180 m above sea and on level to slightly sloping (<5 %) terrain. The regional soil type is a shallow (30–50 cm), rocky, dystrophic red-yellow latosol locally known as a Solo Concrecionário Distrófico (Radambrasil 1982; Vourlitis et al. 2013). In the PAN, research was conducted at Bahia das Pedras (16°29′53″S; 56°24′46″W), which is located 130 km SSW from Cuiabá, Mato Grosso, Brazil. Study sites were located 120–130 m above sea level on level terrain. Many forests and woodlands experience 0.5–2 m of flooding for 2–5 months during the wet season (Nunes da Cunha and Junk 2004). The regional soil type is classified as a Gleyic Solonetz (Zeilhofer 2006).

We located different forest and woodland stands at each site that varied in physiognomy and species composition and have not experienced fire for over 35 years (Table 1). In the PAN, four different sites consisting of upland forests and mixed forests, which

experience little or no flooding, and seasonally flooded gallery forests and woodlands were selected, while in the CB, five different sites consisting of upland and mixed forests, woodlands, mixed grasslands, and seasonally flooded gallery forests were selected for study (Table 1).

Upland forest (locally recognized as cerradão) consists of trees that are approximately 15 m tall with a density of 1,500 trees/ha and a leaf area index (LAI) that typically exceeds 5 m^2/m^2 (Vourlitis and da Rocha 2011; Vourlitis et al. 2013). Dominant tree species varied between the CB and PAN, but in particular, *Astronium fraxinifolium* and *Callisthene fasciculata* were common to the CB and PAN, respectively (Table 1), and both species are thought to be indicators nutrient-rich (mesotrophic) cerradão (Eiten 1972; Furley and Ratter 1988). Cerrado woodlands (locally known as cerrado sensu stricto) were mixed tree–shrub woodlands that have a shorter canopy than cerradão (Goodland 1971; Eiten 1972; Furley and Ratter 1988). Common tree species in the CB include *A. fraxinifolium*, *Curatella americana*, *Qualea grandiflora* Mart., *Q. parvifolia* Mart., *Terminalia argentea* Mart., and Zucc, while common tree species in the PAN include *A. fraxinifolium*, *C. americana*, *Tabebuia aurea*, and *T. heptaphylla* (Table 1). Gallery forests (locally known as

cambarazais) are seasonally flooded forests that are dominated by the tree species *Vochysia divergens* Pohl (Nunes da Cunha and Junk 2004; Vourlitis et al. 2011). Gallery forest structure varied considerably between the CB and PAN (Table 1) and is typically a function of age since invasion (Schöngart et al. 2011), with the youngest stands having the smallest tree diameter, basal area, and LAI. Mixed forests share characteristics with upland and woodland vegetation types (Table 1); however, their floristic composition is different enough where they cannot be classified as either cerradão or sensu stricto, and often, these forests are thought to be successional (Eiten 1972). Our mixed forest stands differed substantially in their structural characteristics and species composition, with the PAN forest dominated by a palm, *Scheelea phalerata* (Mart.) Bur. and the CB stand dominated by *A. fraxinifolium*, *C. americana*, and *Matayba guianensis* Radlk. The mixed grassland site in the CB (locally known as campo sujo) was dominated by grasses and the tree species *C. americana* and *Diospyros hispida* A. DC (Table 1). Woody cover is usually <30–40 % reflecting the higher importance of grasses (Goodland 1971; Eiten 1972; Furley and Ratter 1988).

Vegetation and soil sampling

Foliar and soil samples were obtained every 10 m along a permanent 100 m transect that was randomly located in each ecosystem. Foliage was collected from all trees (at least 2–3 individuals) within a 2–3 m radius circle every 10 m on each transect. The sampling radius varied from point to point because of spatial variations in tree density and to obtain enough mature and senesced leaf material from a variety of different species the sampling radius expanded when tree density was low and contracted when tree density was higher. Foliage was sampled using a pole saw from branches exposed to full sun, and approximately, the same amount of leaf material was collected from each individual sampled (ca. 4–6 leaves). For each individual, foliage was separated into mature, fully expanded, and old, senesced (chlorotic, brown) foliage. Mature foliage was defined as the first set of green, fully expanded leaves, while senesced leaves were defined as those that readily fell off the branch as it was removed from the individual tree. All of the leaf material collected at each sampling point was pooled by age (i.e., mature or senesced), and no attempt was made to adjust leaf nutrient

concentrations based on species abundance. Because leaves were sampled from many of the same trees used to estimate species abundance, the average mature and senesced leaf nutrient concentrations for each transect are thought to be proportional to the overall community nutrient composition of each stand.

Soil samples were obtained from the soil surface (0–10 cm) every 10 m on each transect and from the subsurface (10–50 cm) every 20 m on each transect using a 761.4 cm^3 bucket auger or a 100 cm^3 impact auger (Models 300.07 and 404.60, respectively; AMS Inc., American Falls, ID, USA). In 2012, only surface samples were obtained, but in 2013, soil samples were obtained at 10 cm depth increments in the soil profile to a maximum depth of 50 cm (except in the CB mixed forest and grassland).

Plant and soil sample analysis

Foliage samples were oven-dried at 70 °C for 1 week and weighed to the nearest 0.01 g using a digital balance. Mature and senesced foliage was analyzed for N, P, and K concentrations from micro-Kjeldahl (N), nitric acid (P), and perchloric acid (K) digests. N and P digests were analyzed using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil), and K digests were analyzed using a flame photometer (DN-61, Digimed, São Paulo, Brazil).

Soil samples were analyzed for bulk density, particle size distribution (texture), percent rockiness, pH, total N, extractable P and K concentrations, and soil organic matter (SOM) content as described by in detail by Vourlitis et al. (2013). Particle size distribution was measured for surface soil only using the Bouyoucos hydrometer method. Soil pH was analyzed from 1:2.5 soil/distilled water extracts using a pH meter (PMPH-1, Digimed, São Paulo, Brazil). Total soil N was measured from micro-Kjeldahl digests that were analyzed using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil). Soil extractable P and K was analyzed from Mehlich-I (0.05 M HCl + 0.025 M H_2SO_4) extracts using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil) and a flame photometer (DN-61, Digimed, São Paulo, Brazil), respectively. Soil organic matter content was analyzed by the Walkley–Black method using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil). Soil collected from the impact auger, which minimizes the potential for soil compaction and deformation, was

used to calculate surface soil bulk density. Bulk density was calculated as the dry soil mass per unit sampling volume after drying soil cores at 105 °C for 5 days (Blake and Hartge 1986).

Data analysis

Nutrient resorption efficiency (RE) was calculated as $[(N_M - N_S)/N_M] \times 100$, where N_M is the nutrient concentration of mature leaves and N_S is the nutrient concentration of senesced leaves (Reed et al. 2012). Resorption efficiency derived from mass-based concentrations may underestimate the actual RE because they ignore changes in leaf mass during senescence (Aerts 1996; van Heerwaarden et al. 2003; Vergutz et al. 2012). However, Aerts (1996) suggested that this bias is likely to be small because leaf mass decline during senescence due to the withdrawal of soluble compounds is <10 %. Nutrient resorption proficiency (RP) is the minimum nutrient concentration of senesced leaves (Killingbeck 1996; Aerts 1996). We assumed that RP was equal to N_S at the time of field sampling because leaves were collected during the dry season, which is typically when deciduous and semi-deciduous cerrado trees in the CB and PAN are shedding leaves (Dalmagro et al. 2013).

Differences in mean nutrient concentrations and ratios (N/P and N/K) between mature and senesced leaves were analyzed using a two-way ANOVA with ecosystem type (E) and leaf age (A) as main effects. Differences in RE for N, P, and K between ecosystems were assessed by comparing mean ±95 % confidence intervals. Linear correlation or regression analysis was used to assess relationships between soil surface and/or profile average properties (independent variables) and foliar nutrient concentrations (N_M and N_S), RE, and RP (dependent variables). Soil profile averages were calculated for total N and extractable P and K where subsurface soil data were obtained; however, for the mixed forest and grassland stands in the CB, data were only collected for the surface soil layer. Thus, profile averages for these sites were estimated using logarithmic regression of surface (independent variable) and profile average nutrient concentrations (dependent variable) from the sites where both variables were available (Total N: $0.92 \times LN(x) + 0.73$, $r^2 = 0.88$, $p < 0.005$: extractable P: $2.91 \times LN(x) - 2.91$, $r^2 = 0.78$, $p < 0.01$; extractable K: $32.3 \times LN(x) - 93.5$, $r^2 = 0.61$, $p < 0.05$, $n = 7$ for each

equation). All statistical analyses were conducted using NCSS statistical software (version 7, NCSS, LLC, Kaysville, UT, USA).

Results

Variations in soil fertility and texture

Surface (0–10 cm) soils in woodlands and mixed grasslands were significantly ($p < 0.05$) sandier than forests in the Cuiaba Basin (CB), and in general, soils of the CB were sandier than those of the Pantanal (PAN), while in the PAN, woodlands and gallery forests had a higher sand content, and lower silt and clay content, than upland and mixed forests (Table 2). Soil organic matter (SOM) content in the CB was highest in the upland forest and lowest in gallery forest, while SOM content in the PAN was highest in the mixed forest and lowest in gallery forest. Ecosystem differences in surface soil pH depended on the research site, and in the CB upland and mixed forests and woodlands had the highest pH, while in the PAN, mixed and gallery forests had the highest pH (Table 2). In general, soil pH was higher in the CB than in the PAN except in gallery forests (Table 2).

Variations in surface soil fertility were somewhat more predictable in the CB, with the highest concentrations of total N and extractable P in upland forest, intermediate concentrations in mixed forests, and the lowest concentrations in gallery forest, woodlands, and mixed grasslands (Table 2). In the PAN, total N was highest in the upland forest, intermediate in the mixed and gallery forests, and lowest in the woodlands, while extractable P was similar in the forested ecosystems and lowest in the woodland (Table 2). There were no significant differences in extractable K between ecosystems of the PAN, but in the CB extractable K concentrations were higher in the upland and mixed forests and mixed grasslands and lowest in the gallery forest and woodlands (Table 2). In general, PAN soils, with the exception of upland forests, had higher total N and extractable K than CB soils, while gallery forests and woodlands of the PAN had higher extractable P than similar ecosystems of the CB (Table 2). As mentioned above (see "Data analysis"), average total N and extractable P and K for the entire soil profile (0–50 cm) were significantly correlated with surface soil concentrations.

Table 2 Mean [±95 % confidence intervals (CI); $n = 10$] soil surface (0–10 cm) sand, silt, clay, soil organic matter (SOM), total N, and extractable P and K concentrations and soil pH for the cerrado ecosystems of the Cuiabá Basin (CB) and the Pantanal (PAN)

Variable	Upland forest (cerradão)		Mixed forest		Gallery forest (cambarazal)		Woodland (sensu stricto)		Mixed grassland (campo sujo)	
	CB	PAN	CB	PAN	CB	PAN	CB	PAN	CB	PAN
Sand (g/kg)	610 ± 66^{ad}	117 ± 33^A	513 ± 67^{ab}	161 ± 20^A	484 ± 34^b	414 ± 27^B	800 ± 26^c	429 ± 62^B	700 ± 54^d	ND
Silt (g/kg)	153 ± 25^{ad}	371 ± 30^A	202 ± 29^{ab}	334 ± 13^A	234 ± 19^b	259 ± 20^B	70 ± 11^c	254 ± 24^B	116 ± 19^d	ND
Clay (g/kg)	238 ± 41^{ad}	512 ± 32^A	285 ± 38^a	506 ± 15^A	282 ± 17^a	327 ± 22^B	130 ± 15^b	317 ± 42^B	184 ± 35^d	ND
SOM (g/kg)	37 ± 7^a	20 ± 2^{AC}	27 ± 7^{ac}	21 ± 2^A	13 ± 2^b	16 ± 3^{AC}	17 ± 6^{bc}	17 ± 1^C	19 ± 2^c	ND
pH	5.7 ± 0.3^a	4.8 ± 0.1^A	5.7 ± 0.2^a	5.2 ± 0.1^B	4.9 ± 0.1^b	5.2 ± 0.1^B	5.4 ± 0.2^a	4.7 ± 0.1^A	4.9 ± 0.1^b	ND
Total N (g/kg)	2.2 ± 0.4^a	2.7 ± 0.4^A	1.5 ± 0.4^{ab}	2.3 ± 0.4^{AB}	1.1 ± 0.1^b	2.0 ± 0.4^{AB}	1.0 ± 0.2^b	1.7 ± 0.2^B	1.0 ± 0.2^b	ND
P (mg/kg)	6.2 ± 1.9^a	7.1 ± 1.6^{AB}	3.5 ± 1.2^a	10.4 ± 6.2^{AB}	2.9 ± 0.6^b	11.1 ± 2.8^A	2.5 ± 0.4^b	5.4 ± 0.7^B	2.3 ± 0.4^b	ND
K ± (mg/kg)	94 ± 32^a	95 ± 19^A	96 ± 28^a	97 ± 19^A	25 ± 6^b	87 ± 23^A	29 ± 12^b	74 ± 12^A	63 ± 10^a	ND

Brazilian names for the ecosystem types are indicated in parentheses. *ND* no data. For the CB, values within a row with different lowercase letters are significantly different ($p < 0.05$) according to the 95 % CI, while for the PAN values within a row with different uppercase letters are significantly different according to the 95 % CI

Variations in leaf nutrient concentration

Mature leaf N was on average 1.5 times higher than senesced leaf N in the PAN (Fig. 1a) and CB (Fig. 1b), but there were statistically significant differences between ecosystems types. In the PAN, gallery forests had the highest N concentration for mature and senesced leaves and mixed forests had the lowest (Fig. 1a). In the CB, upland forests had the highest leaf N for mature and senesced leaves followed by mixed grasslands and woodlands (Fig. 1b). While not statistically analyzed, leaf N was generally lower in the CB than in the PAN, especially for mature leaves.

There were no significant differences in leaf P concentration between ecosystems of the PAN (Fig. 1c) and CB (Fig. 1d), but mature leaf P concentration was significantly higher than senesced leaf P concentration. Leaf P concentrations were between 1.2 (mixed forest) and 1.8 (upland forest) times higher in mature leaves for stands in the PAN (Fig. 1c), but relative differences in P between mature and senesced leaves were larger in the CB and ranged between 1.5 (upland) and 2.8 (gallery forest; Fig. 1d). While not statistically analyzed, ecosystems of the CB had foliar P concentrations that were less than half of that observed for the PAN.

Foliar K concentration was significantly higher in mature leaves than in senesced leaves, and there were significant differences in foliar K between ecosystems of the CB but not the PAN (Fig. 1e, f). Mature leaf K concentration in the PAN was on average 2–4 times higher than senesced leaf K (Fig. 1e), while in the CB, mature leaves had between 1.7 and 2.2 times higher K concentration than senesced leaves (Fig. 1f). Woodlands and mixed grasslands in the CB had highest K concentration, especially for mature leaves, while gallery forests had the lowest (Fig. 1f).

N/P ratios for forests and woodlands of the PAN ranged between 7.1 and 10.2 and were similar between ecosystems types and leaf ages (Fig. 2a). In the CB, N/P ratios for mature leaves ranged between 16 (upland forest) and 22 (mixed forest), while N/P ratios for senesced leaves ranged between 19 (woodlands) and 34 (gallery forests); however, there were no statistically significant differences in the N/P ratio between ecosystems and leaf ages Fig. 2b).

N/K ratios varied significantly as a function of leaf age for the PAN (Fig. 2c) and CB (Fig. 2d), and there were also significant differences between ecosystems in the CB. In the PAN, N/K ratios for senesced leaves
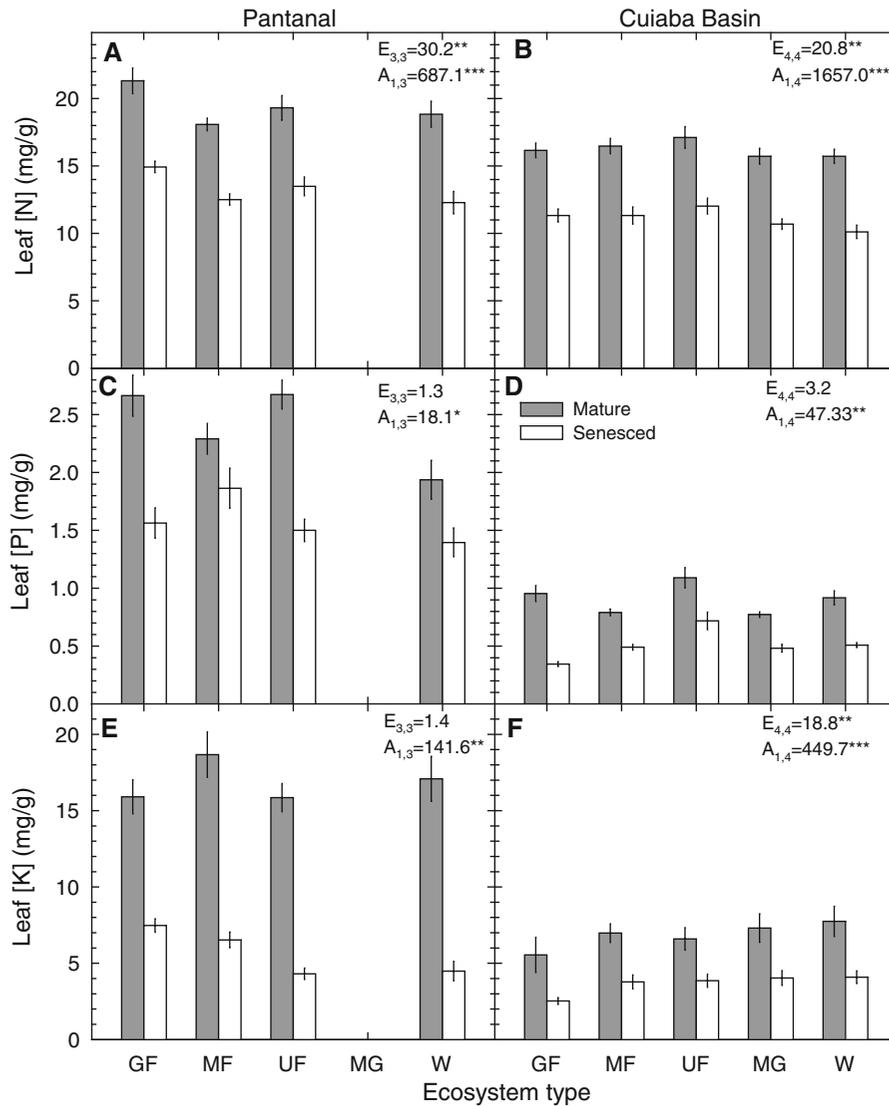
Fig. 1 Mean (±SE; $n = 10$) nitrogen (**a**, **b**), phosphorus (**c**, **d**), and potassium (**e**, **f**) concentrations for mature (*gray bars*) and senesced (*white bars*) leaves for gallery forests (GF), mixed forests (MF), upland forests (UF), mixed grasslands (MG), and woodlands (W) of the Cuiaba Basin (right-hand panels) and the Pantanal (left-hand panels). Also shown are the results of a two-way ANOVA (*F* statistic and degrees of freedom) for ecosystem type (**e**) and leaf age (**a**). *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

were on average 2 times higher than mature leaves for gallery and mixed forests and 3 times higher for upland forests and woodlands (Fig. 2c). Similarly, N/K ratios were higher for senesced leaves for all forests and woodlands of the CB, but differences were smaller compared to the PAN (Fig. 2d). Gallery forests in the CB had significantly higher N/K ratios for both mature and senesced leaves than other forests and woodlands, and in general, CB stands had higher N/K ratios than PAN stands for both mature and senesced leaves.

Variations in nutrient resorption efficiency

The mean N resorption efficiency (NRE) was similar for ecosystems of the PAN and CB and varied between 28 and 36 % for PAN gallery forests and CB woodlands, respectively (Fig. 3a). In contrast, P resorption efficiency (PRE) varied significantly for forests and woodlands of the CB, with the highest values (61.2 %) in the gallery forest (Fig. 3b). Phosphorus resorption efficiency was on average 38 % for other ecosystems of the CB, while in the PAN, PRE varied between 16.1
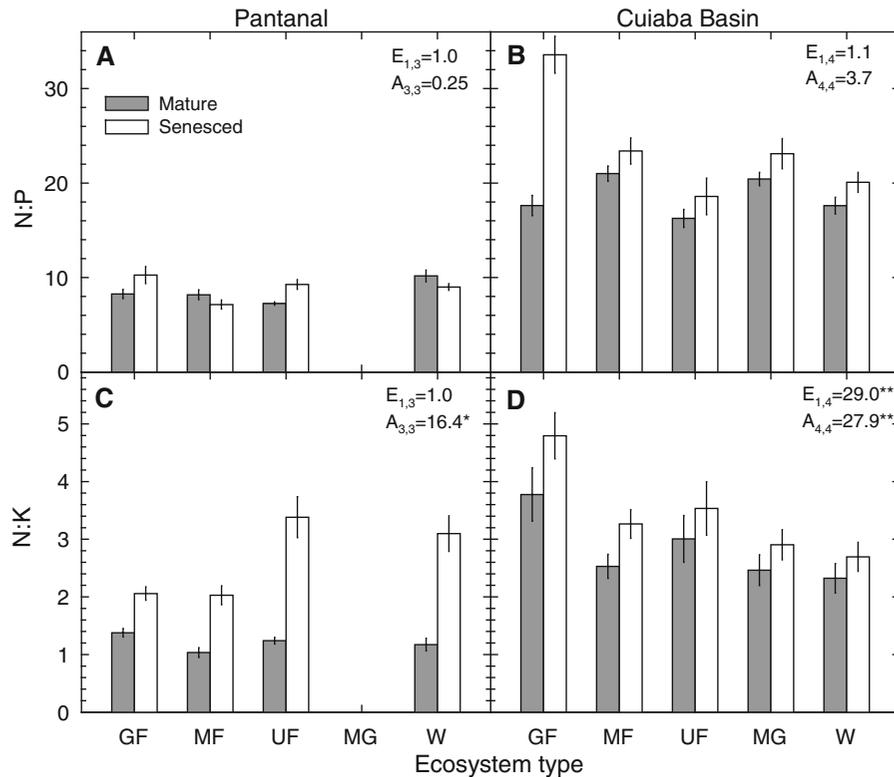
Fig. 2 Mean ($\pm$SE; $n = 10$) mass-based nitrogen/phosphorus (**a**, **b**) and nitrogen/potassium (**c**, **d**), ratios for mature (*gray bars*) and senesced (*white bars*) leaves for gallery forests (GF), mixed forests (MF), upland forests (UF), mixed grasslands (MG), and woodlands (W) of the Cuiaba Basin (right-hand panels) and the Pantanal (left-hand panels). Also shown are the results of a two-way ANOVA (*F* statistic and degrees of freedom) for ecosystem type (**e**) and leaf age (**a**). *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

(mixed forests) and 43.1 % (upland forests), but because of large within ecosystem variation, these differences were not statistically significant. Potassium resorption efficiency (KRE) varied significantly between forests and woodlands of the PAN but not in the CB (Fig. 3c). Potassium resorption efficiency was highest in upland forests (72.6 %) and woodlands (62.8 %) of the PAN and lowest in gallery forest (49.9 %), while forests and woodlands of the CB had a KRE of approximately 41 %.

Relationships between foliar nutrient concentrations, resorption efficiency, and soil properties

The N concentration of mature and senesced leaves increased significantly as a function of total N of the surface soil (Fig. 4a), while only senesced leaves had a

statistically significant increase in leaf N concentration when the average total soil N concentration of the 0–50 cm soil profile was considered (Fig. 4b). The P concentration for mature and senesced leaves increased significantly as a function of surface (Fig. 4c) and profile average (Fig. 4d) extractable P concentration. There was no statistically significant relationship between mature and senesced leaf K concentrations as a function of surface (Fig. 4e) or profile average (Fig. 4f) extractable K concentration.

Nitrogen resorption efficiency was not significantly correlated with any soil physical or chemical variables (Table 3). However, PRE was significantly negatively correlated with the average extractable P concentration of the 0–50 cm soil profile (Table 3). Potassium resorption efficiency was not significantly correlated with surface or profile average soil extractable K but was correlated with soil bulk density (-0.80) and
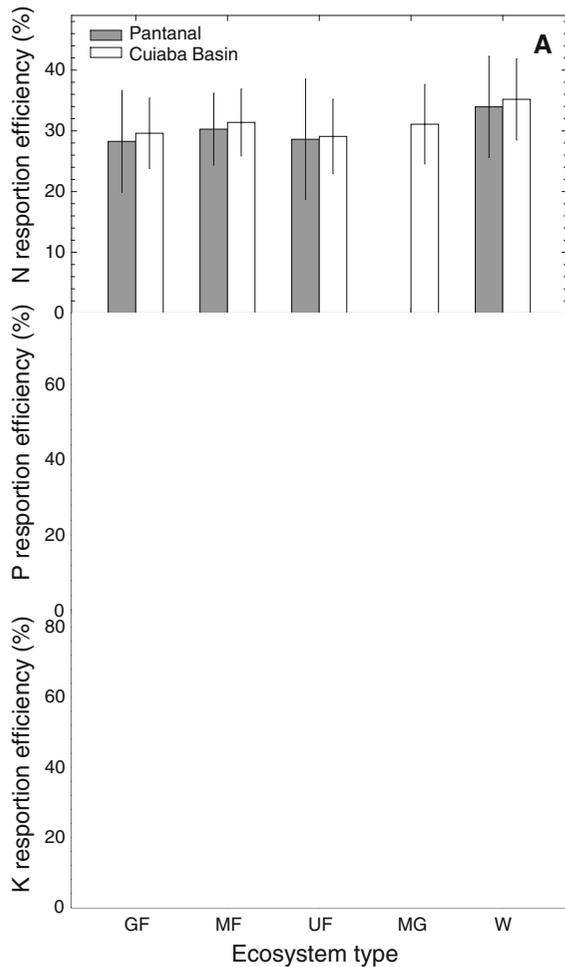
Fig. 3 Mean (±95 % confidence interval; $n = 10$) nitrogen (**a**), phosphorus (**b**), and potassium (**c**) resorption efficiency for gallery forests (GF), mixed forests (MF), upland forests (UF), mixed grasslands (MG), and woodlands (W) of the Pantanal (*gray bars*) and the Cuiaba Basin (*white bars*)

textural variables such as sand (−0.80), silt (0.80), and clay (0.78) content (Table 3).

Discussion

Nutrient availability is thought to be an important limiting factor for savanna primary production (Goodland and Pollard 1973; Lopes and Cox 1977; Lloyd et al. 2008; Viani et al. 2011; Vourlitis et al. 2013), and effective nutrient resorption is presumably a critical conservation strategy that allows plants to reduce their dependence on soil nutrient availability (Aerts 1996; Killingbeck 1996; van Heerwaarden et al. 2003;

Covelo et al. 2008; Hayes et al. 2014; Vergutz et al. 2012). Thus, we predicted that N, P, and K resorption efficiency and proficiency would increase as soil N, P, and K declined in cerrado forests and woodlands of southern Mato Gorsso, Brazil. Our data partially support this prediction, as PRE increased significantly as soil extractable P declined and NRP and PRP increased as soil extractable N and P, respectively, declined (Fig. 4).

Similar to other studies (e.g., Wright and Westoby 2003; Richardson et al. 2005; Lu et al. 2012), correlations with soil fertility were stronger for RP than for RE. This is probably because RE varies considerably in space and time, and since we only sampled during the dry season, the actual potential RE may differ considerably than our measured RE because of the phenological and physiological state of the vegetation in these communities and extant environmental characteristics such as soil water content (Aerts 1996; Killingbeck 1996; Covelo et al. 2008). During the dry season, mature and senesced leaf N and P concentrations for dominant tree species in the PAN and CB are at a seasonal minimum because of soil water limitation (Dalmagro et al. 2013), thus, while N_S was probably at a seasonal minimum so was N_M, which undoubtedly affected our estimates of RE. In addition, our estimates of RE relied on differences in mass-based nutrient concentrations between mature and senesced leaves, which fail to consider declines in leaf area and/or mass as carbon and nutrients are removed during senescence (van Heerwaarden et al. 2003; Vergutz et al. 2012). Thus, our estimates of RE may underestimate the actual potential RE (van Heerwaarden et al. 2003; Cai and Bongers 2007).

Our estimates for NRE ranged between 28 and 35 % compared to 30–55 % reported for other tropical trees (Cai and Bongers 2007; Chatain et al. 2009; Gomes and Luizão 2012; Reed et al. 2012; Vergutz et al. 2012). Our estimates of PRE were much more variable and ranged between 15 and 62 %, with the highest value being comparable to PRE estimates reported for other tropical tree species (Cai and Bongers 2007; Chatain et al. 2009; Gomes and Luizão 2012; Reed et al. 2012; Vergutz et al. 2012). Variations in KRE were site specific, with ecosystems of the CB having an average KRE of 45 %, while ecosystems of the PAN had a range of KREs between 55 and 75 %, all of which are similar to (ca. 40–78 %) those reported for other tropical forests (Cai and Bongers
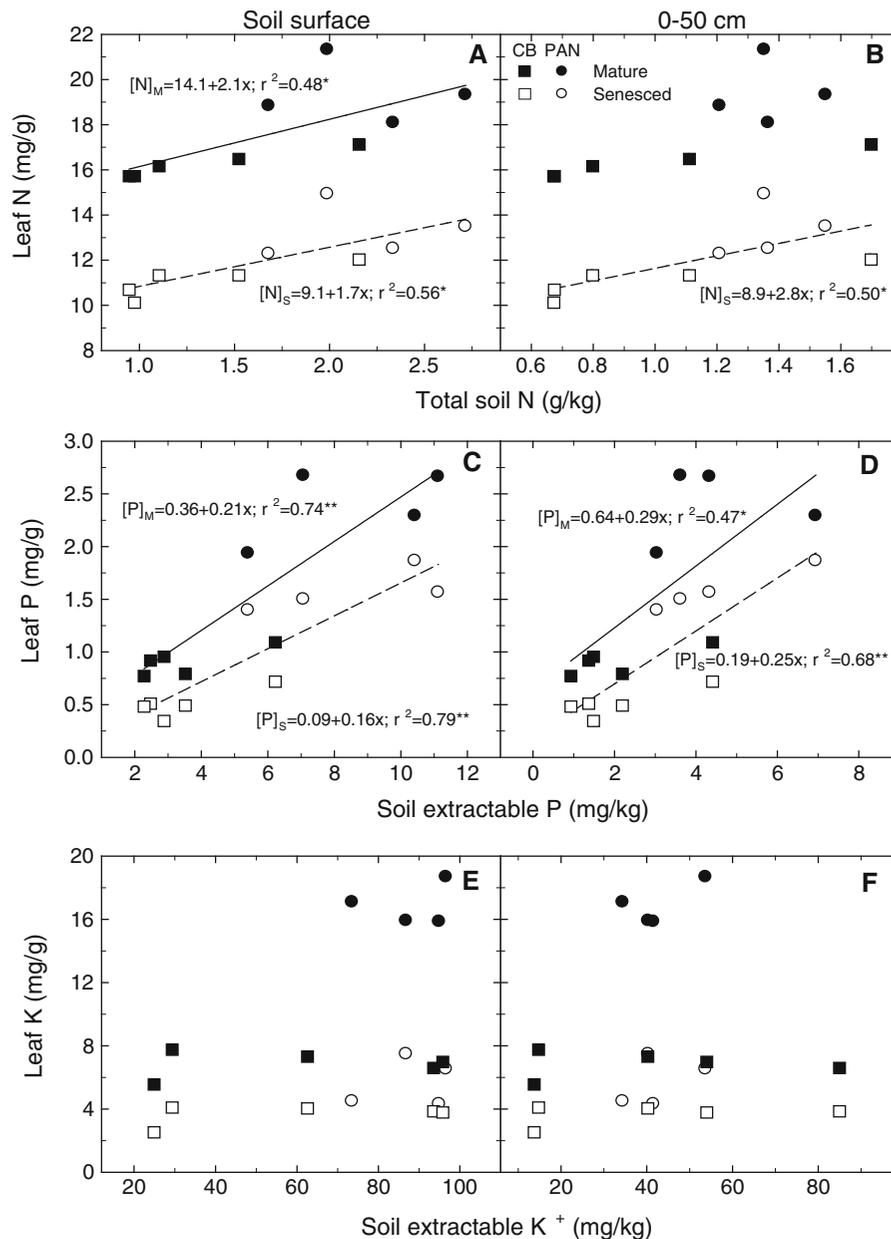
Fig. 4 Scatter plots for **a** and **b** leaf nitrogen concentration versus total soil nitrogen, **c** and **d** leaf phosphorus concentration versus extractable soil phosphorus, and **e** and **f** leaf potassium concentration versus extractable soil potassium for mature (*black symbols*) and senesced leaves (*white symbols*) of forests and woodlands of the Cuiaba Basin (*squares*) and the Pantanal

(*circles*). **a**, **c**, and **e** The surface 0–10 cm soil layer and **b**, **d**, **f** the average 0–50 cm soil profile. Linear regression lines and equations indicate a statistically significant (*$p < 0.05$; **$p < 0.01$) trend between mature (*solid lines*) or senesced (*dashed lines*) leaves and soil nutrient concentration

2007; Chatain et al. 2009; Gomes and Luizão 2012; Vergutz et al. 2012). In spite of the potential biases in estimating RE, PRE was found to be negatively correlated with the average extractable P of the soil

profile (0–50 cm) and PRE was typically lower in the PAN where soil extractable P was generally higher (Table 2), indicating that P availability explained some of the variance in PRE.

Table 3 Linear correlation coefficients between N, P, and K resorption efficiency and soil variables measured for the cerrado stands of the Cuiaba Basin and Pantanal

	N resorption efficiency	P resorption efficiency	K resorption efficiency
Total N (surface)	−0.57	−0.42	0.64
Extractable P (surface)	−0.54	−0.53	0.48
Extractable K (surface)	−0.47	−0.64	0.39
Total N (0–50 cm)	−0.57	−0.41	0.45
Extractable P (0–50 cm)	−0.43	**−0.68**	0.47
Extractable K (0–50 cm)	−0.43	−0.51	−0.06
Bulk density (surface)	0.40	0.52	**−0.80**
pH (surface)	0.00	−0.07	−0.61
Soil organic matter (surface)	−0.24	−0.29	−0.25
Sand content (surface)	0.52	0.30	**−0.80**
Silt content (surface)	−0.52	−0.23	**0.80**
Clay content (surface)	−0.51	−0.35	**0.78**

Bold values are statistically significant ($p < 0.05$)

In contrast, KRE was found to be strongly correlated with soil physical properties such as bulk density and texture (Table 3). These relationships reflect the regional differences in soil type between the PAN and the CB and are probably indicative of differences in water-holding capacity and availability in the PAN and CB soils (Sardans et al. 2012). Mature leaf K concentrations are positively correlated, and N/K ratios are negatively correlated, with mean annual precipitation across a variety of forests (Sardans et al. 2012). Average annual rainfall is similar between the CB and PAN (Nunes da Cunha and Junk 2001; Vourlitis and da Rocha 2011); however, soils of the CB are rocky, high in sand content, and have limited water-holding capacity, while soils of the PAN have high clay content, few rocks, lower bulk density, and a high water-holding capacity (Rabambrasil 1982; Zeilhofer 2006; Vourlitis et al. 2011 and 2013; Wantzen et al. 2012; Rodrigues et al. 2014). Our data on mature

leaf K concentration and N/K ratios reflect these soil textural and structural differences, as mature leaf K concentrations (Fig. 1e, f) were three times higher, and N/K ratios were lower (Fig. 2c, d), in the PAN than the CB. Thus, given the link between leaf K and water availability (Sardans et al. 2012), regional differences in soil water-holding capacity presumably explain the statistically significant correlation between KRE and soil physical properties and the large differences in mature leaf K concentration observed here.

The variations in mature and senesced leaf N and P concentrations along the soil fertility gradient (Fig. 4) indicate a strong control of soil N and P availability on leaf N and P nutrition and NRP and PRP (Richardson et al. 2005, 2008; Davidson et al. 2007; Reed et al. 2012; Hayes et al. 2014). Relationships between leaf and soil N and P concentrations were typically stronger for the surface soil, which reflects tightly coupled plant–soil N and P recycling (Jordan and Herrera 1981; Vitousek and Sanford 1986; Davidson et al. 2007). Patterns between leaf and soil N and P concentrations also reflected the large regional differences between the CB and the PAN soils. As mentioned above, soils of the CB tend to be very shallow, sandy, rocky, and low in N, P, and base cations, while soils of the PAN are deeper, more clay-rich, and higher in N, P, and base cations (Rabambrasil 1982; Zeilhofer 2006; Vourlitis et al. 2011, 2013; Wantzen et al. 2012). In turn, the higher soil N and P fertility in the PAN (Table 2) resulted in higher mature and senesced leaf N and P concentrations (Fig. 4a–d).

Senesced leaf concentrations of <0.7 % for N and <0.05 and 0.03 % for P in evergreen and deciduous species, respectively, are thought to be indicative of complete resorption (Killingbeck 1996); however, highly P limited systems may have senesced leaf concentrations as low as 0.01 % (Hayes et al. 2014). Based on these values and the fact that the forests and woodlands studied here are composed of a mixture of evergreen, deciduous, and semi-deciduous trees and shrubs (Lorenzi 2002), none of the forests of the CB or PAN had complete N resorption (minimum value = 1 % for the CB woodland), while most of the forests and woodlands of the CB had senesced leaf P concentrations approaching complete resorption (0.03–0.05 %; Fig. 1). These data suggest relatively stronger P limitation than N, especially for the CB stands; however, N/P ratios may be a better tool for

assessing the potential for N and P limitation for these stands. Although leaf nutrient ratios of tropical trees may vary seasonally and between species (Townsend et al. 2007), Koerselman and Meuleman (1996) and Güsewell (2004) suggested that a N/P ratio <10–14 is indicative of N limitation and a N/P >16–21 is indicative of P limitation. By these criteria, mature leaves in the PAN ecosystems appear to be N limited with the potential for N + P co-limitation (Fig. 2a), while the CB ecosystems appear to be more P limited, but also may experience N + P co-limitation, especially in upland forests (Fig. 2b). The potential for N limitation is somewhat surprising given the relatively low NRP; however, N limitation of cerrado is not unprecedented (Bustamante et al. 2006). Similarly, Olde Venterink et al. (2003) suggested that N/K ratios <2.1 and K/P ratios >3.4 of mature leaves would exclude K limitation. By these criteria, mature leaves in the PAN ecosystems had N/K ratios <2.1 (Fig. 2c) and K/P ratios >3.4 (data not shown), indicating little potential for K limitation, while mature leaves of the CB forests and woodlands had N/K ratios >2.1 (Fig. 2d) and K/P ratios >3.4 (data not shown), suggesting possible K or K + P co-limitation (Olde Venterink et al. 2003).

In conclusion, we hypothesized that nutrient resorption efficiency and proficiency would increase as soil fertility declined, and our results in part supported this hypothesis. Resorption efficiency for P and resorption proficiency for N and P increased significantly as soil N or P declined, while no trends in K resorption proficiency and soil extractable K were evident. Resorption proficiency for N was not complete, while PRP was nearly complete for forests and woodlands of the CB. Trends in leaf N/P ratios indicate potential N limitation and/or N + P co-limitation for ecosystems in the PAN and P limitation and/or N + P co-limitation for ecosystems in the CB, while trends in leaf N/K ratios indicate possible K or K + P co-limitation for CB forests and woodlands only. Our results illustrate that cerrado forests and woodlands have highly variable nutrient resorption capacities that vary predictably across soil fertility or textural gradients and indicate that whole communities can increase nutrient resorption in infertile sites and reduce their dependence on soil nutrient availability.

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