

Variations in aboveground vegetation structure along a nutrient availability gradient in the Brazilian pantanal

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Abstract

Background and aims Forest expansion into seasonally flooded (hyperseasonal) savanna of the Brazilian Pantanal has been occurring for decades. Our goal was to evaluate how ecosystem physiognomy varied across a nutrient availability gradient and if hyperseasonal savanna had adequate nutrient stocks to support forest expansion.

Methods We quantified soil properties, aboveground ecosystem structure, and nutrient stocks of three savanna and three forest stands in the Pantanal of Mato Grosso, Brazil, and used correlation analysis to assess

how aboveground vegetation structure varied across a soil nutrient availability gradient.

Results Wood and foliage carbon storage and leaf area index were positively correlated with soil extractable phosphorus (P), calcium (Ca^{2+}), and magnesium (Mg^{2+}) concentrations but not soil organic matter or texture. Soil profiles indicated that vegetation enriched surface P and K^+ availability but not Ca^{2+} and Mg^{2+} . Savanna ecosystems had adequate K^+ , Ca^{2+} , and Mg^{2+} to support gallery and riparian forests but not palm forest, while the savanna P stock was inadequate to support forest expansion.

Conclusions Hyperseasonal savanna has adequate nutrients (except P) to support forest expansion. Forest trees likely invade P-deficient savanna by surviving in P-rich microsites. Over time, biotic enrichment of soil may accelerate forest expansion into P-poor savanna.

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Introduction

The productivity of tropical forests and savanna is thought to be nutrient limited, particularly by phosphorus (P) (Goodland and Pollard 1973; Lopes and Cox 1977; Jordan and Herrera 1981; Laurance et al. 1999; Paoli et al. 2008; Ostertag 2010; Wright et al. 2011;

Pasquini and Santiago 2012; Silva et al. 2013). Evidence for nutrient limitation is best assessed through field manipulative experiments (Ostertag 2010; Wright et al. 2011; Pasquini and Santiago 2012), but studies along soil nutrient availability gradients have also shown that net primary production, standing crop, leaf area index (LAI), and/or specific leaf area (SLA) are positively correlated with nutrient availability (Laurance et al. 1999; Harrington et al. 2001; Malhi et al. 2009; Paoli et al. 2008; Lloyd et al. 2008; Quesada et al. 2009; Viani et al. 2011; Vourlitis et al. 2013).

Some authors suggest that soil nutrient availability precludes forest physiognomies from tropical savannas (Goodland and Pollard 1973; Lopes and Cox 1977; Lloyd et al. 2008; Silva et al. 2008). Others suggest that soil nutrient stocks are adequate to support wood production (Bond 2010; Silva et al. 2010) but forests may not expand into these areas because rates of tree growth are too slow to compensate for the loss of woody biomass to fire (Hoffmann et al. 2012; Silva et al. 2013). However, in areas where fire is suppressed trees may be able to invade and persist in richer microsites within nutrient-poor savanna (Ruggiero et al. 2002; Durigan and Ratter 2006; Silva et al. 2013). Over time, trees can enrich soil nutrient availability through a variety of processes, such as the redistribution and accumulation of leached nutrients from litter inputs (Jobbagy and Jackson 2001; Bond 2010; Vourlitis et al. 2011; Wigley et al. 2013), an increase in nutrient inputs from throughfall (Kellman 1979), a decline in nutrient retention and resorption (Richardson et al. 2005; Vourlitis et al. 2014), and the accumulation of dissolved nutrients under tree canopies through mass-flow and/or diffusion (Hanan and Ross 2010; Saha et al. 2010). With an increase in tree cover, shading can eventually eliminate savanna understory grasses and/or shrubs, greatly reducing flammability and the potential for tree mortality from fire (Hoffmann et al. 2012; Silva et al. 2013).

These processes are thought to be important for the forest expansion that has been observed in savanna-forest ecotones throughout South America (Silva et al. 2008, 2010, 2013). Presumably, similar processes are important for forest expansion into the seasonally flooded grasslands and savanna of the Pantanal, which has been observed for several decades (Nunes da Cunha and Junk 2004; Santos et al. 2006). The Pantanal is the largest wetland in the world (Haase 1999), and is a mosaic of vegetation types that are arrayed along a gradient of flood duration and/or intensity (Junk et al.

2006; Nunes da Cunha and Junk 2009). Plant species diversity is high (Pott and Pott 1994); however, few plant species are endemic, and for example, all of the over 500 tree species are immigrants from the surrounding upland savanna (Cerrado) biome (Junk et al. 2006). The similarities in ecosystem physiognomy and plant species composition between the Pantanal and Cerrado has led many authors to consider the Pantanal as a part of the Cerrado biome (Junk et al. 2006; Ribeiro and Walter 2008; Nunes da Cunha and Junk 2009), referred to as “hyperseasonal savanna,” or a savanna that is subjected to both wet season flooding and dry season drought (*sensu* Eiten 1972).

The lack of endemism presumably facilitates the invasion of trees into hyperseasonal savanna grasslands and woodlands, provided that environmental conditions are suitable for tree survival and upland species can tolerate seasonal flooding. Persistent flooding during the rainy season can cause declines in tree growth and/or physiological performance due to soil anoxia or hypoxia (Parolin et al. 2010; Dalmolin et al. 2012; Dalmagro et al. 2013). However, many upland species have physiological and/or morphological adaptations that allow them to tolerate seasonal flooding, such as physiological plasticity that minimizes variation in gas exchange over seasonal flooding cycles (Parolin et al. 2010; Dalmolin et al. 2012; Dalmagro et al. 2013) and the development of hypertrophied lenticels and adventitious roots that help aerate roots under anoxic or hypoxic conditions (Colmer and Greenway 2010; Shimamura et al. 2010).

Forest expansion into seasonally flooded grasslands of the Pantanal is intimately linked to flooding cycles and land use history, and historically, fire has been used as a tool to reduce woody encroachment and promote savanna grasslands (Nunes da Cunha and Junk 2004; Junk and Nunes da Cunha 2012). Generally, forest trees have a lower resistance to fire than savanna trees (Hoffmann et al. 2003), and forest expansion into grasslands that are frequently burned is restricted because trees cannot grow fast or long enough to reach the “fire-resistance threshold,” where the possibility of fire-induced mortality is greatly reduced (Hoffmann et al. 2012). While wildfires and human-induced fires still occasionally occur (Junk and Nunes da Cunha 2005), the use of fire as a management tool is prohibited within the portion of the Pantanal that is part of the Brazilian National Park System (Couto et al. 2006). Thus, assuming a similar scenario for upland forest-

savanna transitions (Durigan and Ratter 2006; Silva et al. 2013), trees could invade hyperseasonal savanna during low-water periods when seeds can germinate and seedlings can become established (Nunes da Cunha and Junk 2004), and persist in nutrient-rich microsites provided that fire is infrequent. Over time, trees could establish, modify soil nutrient availability, expand to the point that understory plants are excluded and the potential for fire damage is diminished, and persist (Durigan and Ratter 2006; Vourlitis et al. 2011; Silva et al. 2008, 2013), thus accelerating rates of forest expansion into hyperseasonal savanna.

Here we explore links between soil nutrient availability and aboveground ecosystem physiognomy in seasonally flooded forests, savannas, and grasslands of the Brazilian Pantanal. Given that soil nutrient availability may limit tree growth and forest development in upland savanna, we predicted that forest physiognomy characteristics such as tree density, wood C storage, and leaf area index (LAI) would be positively related to soil nutrient availability. We also predicted that soil nutrient stocks in hyperseasonal savanna would be sufficient to support the high wood biomass and LAI associated with forests.

Materials and methods

Site descriptions

We sampled forest and hyperseasonal grassland and savanna ecosystems in the Pantanal of southern Mato Grosso, Brazil in June–August of 2009–2013. Research was conducted near Espirito Santo (16°39'50"S; 56°47'50"W) and Bahia das Pedras (16°29'53"S; 56°24'46"W), which are located within a protected nature reserve where the use of fire has been prohibited since 2001 (Couto et al. 2006). The sites are located on flat, level terrain, 120–130 m above sea level, and all of the ecosystems are subjected to seasonal flooding that occurs during the wet season between December and June (Nunes da Cunha and Junk 2001). The long-term (30 year) mean annual rainfall is estimated to be 1400 mm and the average annual temperature is approximately 26 °C, and all sites experience a dry season that occurs between May and September (Nunes da Cunha and Junk 2001).

Three forest ecosystems were studied consisting of a gallery forest, a palm forest, and a riparian forest. The

gallery forest is approximately 8 m tall and is situated on a broad flat floodplain that lacks a main stream that is typical of a riparian forest (Ribeiro and Walter 2008). Dominant tree species include *Mouriri elliptica* Mart., *Vochysia divergens* Pohl, and *Eugenia florida* DC, and most of the tree species are coincident with those reported for gallery (Mata Galeria) and riparian (Mata Ciliar) forests as well as upland Cerrado and Cerradão (Supplementary data; Table S1). During the wet seasons of 2009–2013, this forest experienced a 0.3–0.5 m seasonal flood pulse that lasted approximately 6–8 weeks. The riparian forest is approximately 10–12 m tall, and is situated along a stream that often has standing water well into the dry season. Dominant tree species include *V. divergens* and *M. elliptica*, which were also the primary species observed in the gallery forest; however, the gallery forest is much more species rich than the riparian forest (Table S1). The flood pulse in the riparian forest was slightly larger (0.5–1.0 m) and of longer duration (12–16 weeks) than the flood pulse observed in the gallery forest. The palm forest is approximately 8 m tall and is dominated by the palm *Scheelea phalerata* (Mart.), and to a lesser extent *M. elliptica* and *Aspidosperma cylindrocarpon* M. Arg. (Table S1). The palm forest was intermittently flooded during the peak of the flood period; however, soils were saturated and the water table was at the soil surface for at least 6–8 weeks.

Three hyperseasonal savanna ecosystems were studied, a grassland, mixed-grassland, and a woodland. While grasslands may not be universally considered as “savanna,” we follow the nomenclature of Eiten (1972) and Ribeiro and Walter (2008) who define savanna as a gradient of physiognomies ranging from woodlands dominated by trees and shrubs (i.e., Cerrado sensu stricto) to grasslands lacking trees (i.e. Campo limpo). Thus, hereafter we refer to the hyperseasonal woodland, mixed-grassland, and grassland collectively as hyperseasonal savanna. During the wet seasons of 2009–2013, all the hyperseasonal savanna ecosystems experienced a flood pulse of approximately 0.5–1.0 m that lasted 12–16 weeks. The savanna woodland has a maximum height of approximately 6–7 m and includes the tree species *Astronium fraxinifolium*, *Curatella americana*, and *Tabebuia aurea*, which are associated with typical upland Cerrado (Table S1). The mixed-grassland is composed of bunchgrasses, small shrubs, and trees (principally *V. divergens* and *C. americana*) that are <3 cm in diameter, and is similar in

physiognomy to Campo Sujo Cerrado. The grassland is composed entirely of bunchgrasses, and is similar to Campo Limpo Cerrado (Ribeiro and Walter 2008).

Vegetation and soil sampling

Ecosystems were sampled during the dry season because that is when seasonally flooded forests and savannas are accessible and variations in trunk water-storage, which can lead to errors in estimating above-ground woody biomass, are minimal (Breitsprecher and Bethel 1990). This is also the period when deciduous and semi-deciduous trees shed their leaves and leaf nutrient concentrations reach a seasonal minimum (Dalmagro et al. 2013).

Vegetation and soil sampling were conducted along a 100 m long permanent transect that was randomly installed in each stand (Silva et al. 2008; Vourlitis et al. 2011, 2013). Tree diameter and density were measured every 5–10 m along each transect using the point-quarter method (Goldsmith and Harrison 1976). Each sample point was divided into four quadrants, and the distance and diameter of the closest tree in each quadrant ≥ 3 cm in diameter at breast height (DBH=1.3 m aboveground level) was measured. Tree density was calculated for each sampling point as a function of the mean distance of the closest tree in each quadrant (Goldsmith and Harrison 1976; Vourlitis et al. 2011, 2013). Wood density was measured from tree cores obtained at breast height using an increment borer (approximately 65 trees/site in 2012 and 240 trees/site in 2013). Leaf area index (LAI) was measured every 5 m along each transect using a photosynthetically active radiation (PAR)-ceptometer (AccuPAR LP-80, Decagon Devices, Inc., Pullman, WA, USA). Tree foliage in the forest and woodland ecosystems was collected from branches exposed to full sun every 10 m along each transect using a pole-saw, and separated into young fully expanded and old senescent (chlorotic, brown) foliage (Vourlitis et al. 2014), while grass foliage was not sampled at any of the sites.

The dry mass of the surface organic matter (litter) pool was measured every 10 m along each transect within 25 cm diameter quadrats. Soil samples were obtained for all sites from the soil surface (0–10 cm) every 10 m along each transect, while for the forest and savanna woodland sites, subsurface soil samples were also obtained every 20 m along each transect at 10 cm increments to a maximum depth of 50 cm. Soil samples

were collected using either a 761.4 cm³ bucket auger (Model 300.07, AMS Inc., American Falls, ID, USA) or a 100 cm³ impact auger for bulk density (Model 404.60, AMS Inc., American Falls, ID, USA).

Plant, litter, and soil sample analysis

Litter, foliage, and wood samples were oven-dried at 70 °C for 1 week and weighed using a digital balance. Trunk wood density was calculated as the dry wood mass divided by core volume (Chave et al. 2005). Specific leaf area (SLA=one-sided leaf area/leaf dry weight) of trees was calculated for young and senescent foliage from leaf disks of a known area obtained in the field. Leaf disks were oven-dried and weighed, and SLA was calculated for young and senescent leaves by dividing the fresh leaf area by the leaf dry mass.

Soil pH was analyzed from distilled water slurries using a pH meter (PMPH-1, Digimed, São Paulo, Brazil). Extractable P and K⁺ were analyzed from Mehlich-I extracts using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil) and a flame photometer (DN-61, Digimed, São Paulo, Brazil), respectively. Extractable Ca²⁺ and Mg²⁺ were analyzed from 1M KCl extracts using a flame-atomic absorption spectrometer (AA-275; Varian, Inc., Palo Alto, CA, USA). Extractable Al³⁺ and H⁺ were analyzed from 1M KCl extracts by titration using a digital burette (Model 236–080, Jencons, Leicestershire, UK). Soil cation exchange capacity (CEC) was calculated as the sum of all measured cations (Robertson et al. 1999). Soil organic matter (SOM) content and litter, foliage, and wood organic C concentrations were analyzed by the Walkley-Black method (Nelson and Sommers 1996) using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil).

Tree foliage and wood samples were digested using nitric and perchloric acid for P and cations. Digests were analyzed for P and K⁺ using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil) and a flame photometer (DN-61, Digimed, São Paulo, Brazil), respectively, and Ca²⁺ and Mg²⁺ using an atomic absorption spectrometer (AA-275; Varian, Inc., Palo Alto, CA, USA).

Data analysis

Total aboveground wood biomass for trees ≥ 3 cm DBH was calculated as a function of tree density, DBH, and wood density using equations for tropical forest and cerrado trees (Chave et al. 2005; Schöngart et al. 2011).

Wood C or nutrient content was calculated as the product of total aboveground wood biomass and the wood C or nutrient content, respectively. Litter C was calculated as the C concentration (gC/kg dry weight) multiplied by the surface dry litter mass (kg dry weight/ha). Tree foliage C or nutrient content was calculated from LAI (m^2 leaf area/ m^2 ground area) and the mean C or nutrient concentration (gC or nutrient/g dry leaf mass) and SLA (cm^2 leaf area/g dry leaf mass) of young and old leaves. Grass C and nutrient concentrations and SLA were not measured and assumed to be comparable to tree foliage (Lilienfein et al. 2001). Total soil nutrient stocks for the upper 50 cm soil layer of the forest and woodland stands were estimated from the soil nutrient concentration data and surface (0–10 cm) soil bulk density measurements. These calculations assume that bulk density does not vary significantly with depth up to 50 cm, and while this is unknown for our sample sites, previous research in Brazilian savanna suggests that variations in bulk density to depths as great as 2 m are not significant (Lilienfein et al. 2003). Subsurface soil samples for grass-dominated savanna were not collected, and relative variations in soil nutrient concentrations with depth were assumed to be proportional to the average change in nutrient concentration observed for the woodland savanna stand.

Differences in vegetation structure and soil properties between ecosystems were analyzed using a one-way ANOVA. Differences in soil extractable nutrients and SOM as a function of ecosystem and depth were analyzed using a two-way ANOVA. In the event of a statistically significant F-statistic, differences in means were assessed using a Tukey-Kramer test. Comparisons between savanna and forest nutrient stocks were made using a one-tailed *t*-test that tested the hypothesis that savanna nutrient stocks were significantly lower than forest nutrient stocks (Sokal and Rohlf 1995). Relationships between soil properties and vegetation structure were examined using linear correlation and/or regression. All statistical analyses were conducted using NCSS statistical software (Version 7, NCSS, LLC, Kaysville, UT, USA).

Results

Variations in ecosystem structure and soil characteristics

Wood C storage in trees ≥ 3 cm DBH ranged from 0 to 38 MgC ha^{-1} in hyperseasonal savanna and from 56 to

103 MgC ha^{-1} in forests (Fig. 1a). Within forests, the palm and riparian forests had significantly higher wood C storage than the gallery forest, which in turn had slightly, but not significantly, higher wood C storage than the savanna woodland (Fig. 1a). Variations in foliage C storage (Fig. 1b) and LAI (Fig. 1d) between savanna and forest were similar and more consistent than variations in wood C, with savanna having significantly lower foliage C storage and LAI than forest. Foliage C storage was on average 0.8–0.9 MgC ha^{-1} for savanna and 1.4–1.5 MgC ha^{-1} for forests (Fig. 1b), while LAI ranged from 3.4 to 3.8 $\text{m}^2 \text{m}^{-2}$ for savanna and 5.8–7.4 $\text{m}^2 \text{m}^{-2}$ for forests, with the palm forest having significantly higher LAI than the gallery and riparian forests (Fig. 1d). Variations in litter C storage were substantially more complex, with grassland, mixed-grassland, gallery forest, and riparian forest having significantly higher surface litter C pools than savanna woodland and palm forest (Fig. 1c).

All of the measured soil surface (0–10 cm) physical and chemical properties varied significantly between the research sites; however, differences depended on the soil variable (Fig. 2). Grassland and mixed-grassland savanna had the lowest extractable P concentrations while palm and riparian forests had the highest (Fig. 2a). The mixed-grassland had the lowest extractable K^+ while the forests had the highest (Fig. 2b). Mixed grasslands also had significantly lower extractable Ca^{2+} (Fig. 2c) and Mg^{2+} (data not shown) than the other savanna ecosystems, but forests had significantly higher extractable Ca^{2+} and Mg^{2+} than savanna. Extractable Al^{3+} was lowest in mixed grassland and highest in the savanna woodland and gallery forest (Fig. 2d), while soil organic matter content was highest in the grassland and lowest in the mixed-grassland (Fig. 2e). Soil textural properties also varied considerably between sites, and the mixed grassland had the highest sand and lowest clay content while the palm and gallery forests had the highest clay and lowest sand content (Fig. 2f).

Extractable P and K^+ concentrations varied significantly between the savanna woodland and forest ecosystems and as a function of depth (Fig. 3a, b, and c). Both variables declined significantly with depth, with the surface 0–20 cm layer being significantly enriched relative to the subsurface layers. The palm forest had the highest extractable P and K^+ regardless of depth, while the woodland had the lowest (Fig. 3a, b). Concentrations of SOM varied significantly as a function of depth but

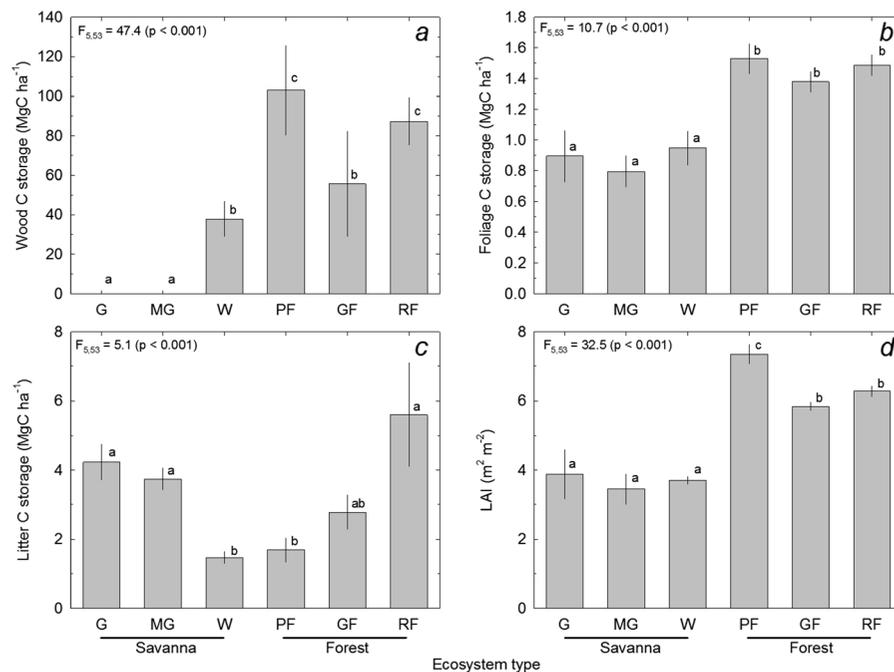


Fig. 1 Mean (\pm se; $n=10$) wood (a), foliage (b), and litter (c) carbon storage and leaf area index (d) for grass-dominated (G), mixed grassland-woodland (MG), and woodland (W) hyperseasonal savanna ecosystems and the palm (PF), gallery (GF), and riparian (RF) forests of the Brazilian Pantanal. Also shown are the results of a one-way ANOVA (F-statistic, degrees of

freedom, and p-value). In the event of a significant ANOVA, a Tukey-Kramer test was performed to test for significant differences between means. Means with a different lower-cased letter are statistically different ($p < 0.05$). Analyses for wood and litter C storage were LN-transformed prior to ANOVA to achieve normality

not by ecosystem, and surface (0–20 cm) soil layers were significantly enriched in SOM relative to the sub-surface. Palm and riparian forests had higher SOM in the upper 30 cm surface layers, while gallery forest had the highest SOM in the deeper soil layers, which accounted for the significant ecosystem by depth (ExD) interaction (Fig. 3c). Extractable Ca^{2+} varied significantly as a function of ecosystem and depth, with the highest values found in palm forest and the lowest values found in the savanna woodland (Fig. 3d). In contrast to extractable P, K, and SOM, Ca^{2+} became significantly enriched in the 40–50 cm soil layers. Similar patterns were observed for extractable Mg^{2+} ; however, the palm forest exhibited a larger increase in extractable Mg^{2+} with depth compared to the other ecosystems, presumably accounting for the significant ExD interaction (Fig. 3e). Extractable Al^{3+} concentration varied significantly between ecosystems and with depth, and there was a significant ExD interaction (Fig. 3f). However, Al^{3+} exhibited clear zones of accumulation at 20–30 cm for the palm and gallery forests, a slightly deeper layer of accumulation in the riparian forest, but no obvious zone of accumulation in the

savanna woodland (Fig. 3f). In general, woodland and gallery forest had the highest extractable Al^{3+} in the surface 0–20 cm layers, while woodland and riparian forest had the highest Al^{3+} in the deeper (40–50 cm) soil layers. The palm forest had consistently lower extractable Al^{3+} at all depths, except the soil surface, than the other ecosystems (Fig. 3f).

Variations in a variety of the aboveground ecosystem structural components were positively correlated with soil pH and nutrient availability but not soil textural properties such as SOM, sand, and clay content (Table 1). Ecosystem variations in LAI, wood C storage, and foliage C storage were significantly positively correlated with soil pH, extractable P, and extractable Ca^{2+} and Mg^{2+} , while tree wood density was positively related with extractable K^+ . In contrast, tree density and litter C storage were not significantly correlated with any of the measured soil variables (Table 1).

Estimates of aboveground and soil nutrient pools

Total aboveground (wood+foliage) and soil (0–50 cm) nutrient pools were significantly higher in forests than in

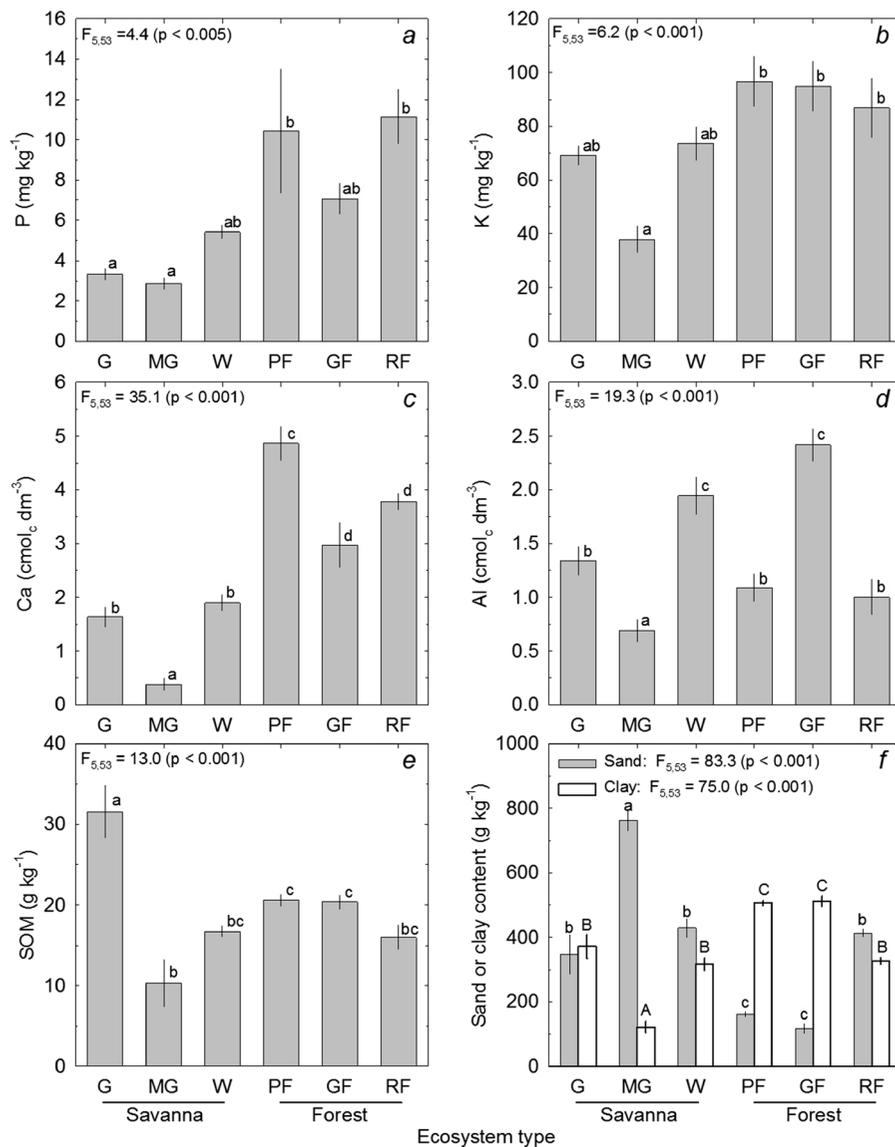


Fig. 2 Mean (\pm se; $n=10$) surface (0–10 cm) soil extractable phosphorus (a), potassium (b), calcium (c), aluminum (d), and soil organic matter (e) concentration and sand (grey bars) and clay (white-bars) content (f) for grass-dominated (G), mixed grassland-woodland (MG), and woodland (W) hyperseasonal savanna ecosystems and the palm, (PF), gallery (GF), and riparian (RF) forests of the Brazilian Pantanal. Also shown are the results of a one-way

ANOVA (F-statistic, degrees of freedom, and p-value). In the event of a significant ANOVA, a Tukey-Kramer test was performed to test for significant differences between means. Means with a different lower-cased letter are statistically different ($p < 0.05$) except for clay content where upper-case letters were used to differentiate significantly different mean values

savanna ecosystems (Fig. 4). Aboveground P storage in forests ranged from 90 to 200 kgP ha⁻¹ and were over 5-times higher than in savanna ($t_4=2.7$; $p < 0.05$), while soil P storage in forests ranged from 18 to 35 kgP ha⁻¹ and was over 2-times higher than in savanna ($t_4=2.4$; $p < 0.05$; Fig. 4a). Similar trends were observed for K⁺; however, soil K⁺ storage exceeded aboveground K⁺

storage in savanna but not in forest (Fig. 4b). Forests stored on average 287 kgK ha⁻¹ in aboveground biomass, which was over 5-times higher than observed for savanna ($t_4=2.4$; $p < 0.05$), while forests stored on average 235 kgK ha⁻¹ in the upper 50 cm soil layer, which was 1.5-times higher than observed for savanna ($t_4=2.5$; $p < 0.05$); Fig. 4b). Soil Ca²⁺ and Mg²⁺ pools were 5–7

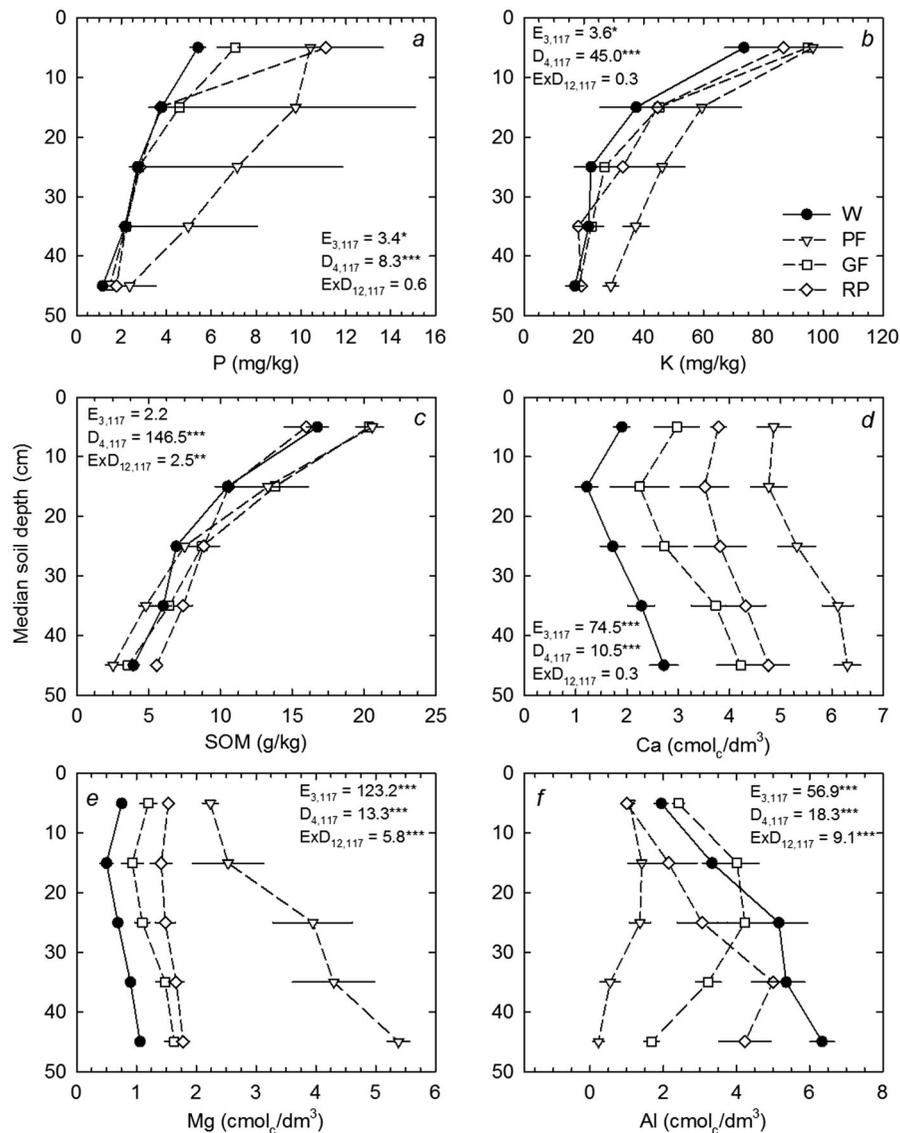


Fig. 3 Mean (\pm se; $n=10$ for surface and 6 for the subsurface soil layers) soil extractable phosphorus (a), potassium (b), soil organic matter (c), calcium (d), magnesium (e), and aluminum (f) concentration as a function of depth in 10 cm increments for hyperseasonal woodland (black-circles, solid-lines), palm forest (inverted-triangles, dashed-lines), gallery forest (squares, dashed-

lines), and riparian forest (diamonds, dashed-lines) in the Brazilian Pantanal. Depth from the soil surface is displayed as the median value for each 10 cm depth interval. Also shown are the results of a two-way ANOVA (F-statistic, degrees of freedom, and p-value) showing the main effects of ecosystem (E) and soil depth (D) and the ecosystem \times depth (ExD) interaction

times higher than aboveground pools regardless of ecosystem. Forests stored on average 725 kgCa ha^{-1} in aboveground biomass compared to 145 kgCa ha^{-1} for savanna ($t_4=3.7$; $p<0.01$), while forests stored approximately $4,231 \text{ kgCa ha}^{-1}$ in the upper 50 cm soil layer compared to $1,010 \text{ kgCa ha}^{-1}$ estimated for savanna ($t_4=3.9$; $p<0.01$; Fig. 4c). Aboveground Mg^{2+} storage was nearly 7-times higher in forests (260 kgMg ha^{-1})

than in savanna (39 kgMg ha^{-1}), while average soil Mg^{2+} storage in forests was $1,321 \text{ kgMg ha}^{-1}$ vs. 264 kgMg ha^{-1} for savanna, amounting to a 5-fold higher soil Mg^{2+} storage in forests (Fig. 4d).

Based on the estimated aboveground and soil nutrient pool sizes (Fig. 4), we calculated the potential for forest expansion into hyperseasonal savanna using the approach of Silva et al. (2013). We assumed that the sum

Table 1 Linear correlation coefficients for relationships between selected ecosystem and surface soil variables. Bold values are statistically significant ($p < 0.05$; $n = 6$)

Soil variable	LAI ($\text{m}^2 \text{ m}^{-2}$)	Wood density (g cm^{-3})	Tree density (Trees ha^{-1})	Wood C (Mg ha^{-1})	Foliage C (Mg ha^{-1})	Litter C (Mg ha^{-1})
pH	0.86	0.60	0.51	0.93	0.86	0.07
Extractable P (kg ha^{-1})	0.83	0.75	0.60	0.93	0.89	0.16
Extractable K (kg ha^{-1})	0.70	0.84	0.77	0.77	0.79	-0.12
Extractable Ca (kg ha^{-1})	0.96	0.68	0.66	0.96	0.95	-0.13
Extractable Mg (kg ha^{-1})	0.96	0.62	0.63	0.95	0.93	-0.19
Extractable Al (kg ha^{-1})	0.01	0.54	0.59	0.05	0.13	-0.45
Organic matter content (g kg^{-1})	0.06	-0.21	-0.15	-0.12	0.02	0.03
Sand content (g kg^{-1})	-0.70	-0.56	-0.62	-0.60	-0.71	0.33
Clay content (g kg^{-1})	0.72	0.54	0.61	0.61	0.72	-0.35

of the total aboveground (wood+foliage) and soil (0–50 cm) nutrient stocks for savanna would be indicative of the total available nutrients in savanna while the total aboveground nutrient stocks in forests would be indicative of the forest demand for nutrients. For each nutrient we subtracted the forest aboveground stock from the total savanna stock to determine if there was a nutrient surplus or deficit after building a forest in savanna (Silva

et al. 2013). Our results indicate that savanna P stocks are insufficient for the expansion of any of the forests studied here (Fig. 5). Potassium deficiency would also limit the expansion of palm forest into savanna, but other forests were only limited by K^+ in the most K-poor savanna ecosystems, such as the mixed-grassland (Fig. 4). Average Ca^{2+} availability appears to be adequate in savanna for forest expansion, while average

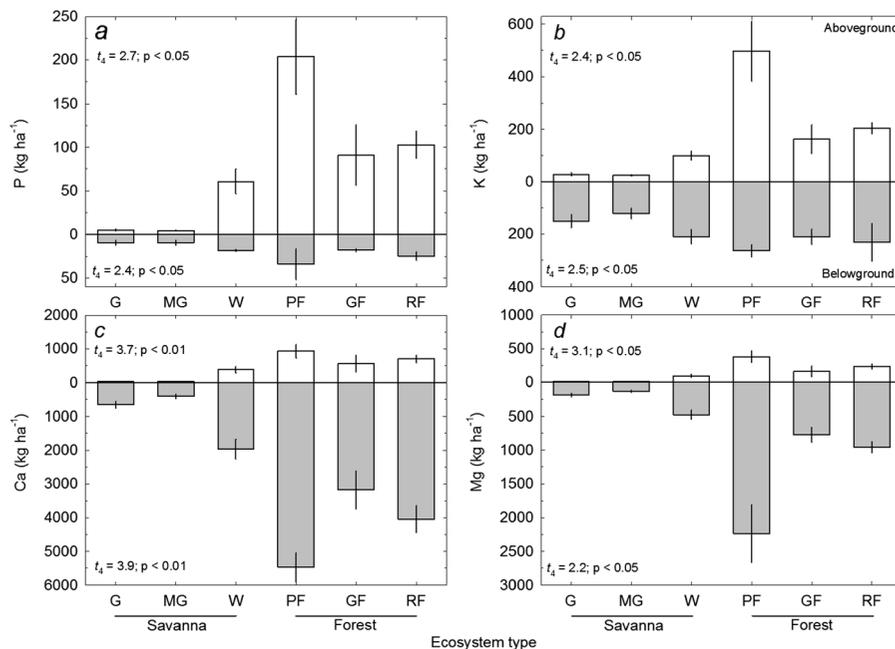


Fig. 4 Mean (\pm se; $n = 10$ for aboveground and 6 for soil variables) aboveground (wood+foliage; white-bars) and soil (0–50 cm; grey-bars) phosphorus (a), potassium (b), calcium (c), and magnesium (d) stocks for grass-dominated (G), mixed grassland-woodland (MG), and woodland (W) hyperseasonal savanna, and

palm (PF), gallery (GF), and riparian (RF) forests of the Brazilian Pantanal. Also shown are the results of a one-tailed t -test (t -statistic, degrees of freedom, and p -value) that tested the hypothesis that forest nutrient stocks were significantly larger than savanna nutrient stocks

Mg²⁺ availability may be deficient for the expansion of palm forest but is sufficient for the expansion of gallery and riparian forests into savanna (Fig. 5).

Discussion

Variations in ecosystem structure and soil characteristics

Low soil nutrient availability can limit tree growth and forest expansion into savanna because nutrient availability may be insufficient for wood production, or tree growth may be too slow to compensate for biomass lost from fire (Bond 2010; Hoffmann et al. 2012; Silva et al. 2013). However, in areas where fire is suppressed or infrequent, trees growing in more nutrient rich microsites can grow large enough where they become resistant to fire (Hoffmann et al. 2012), and over time,

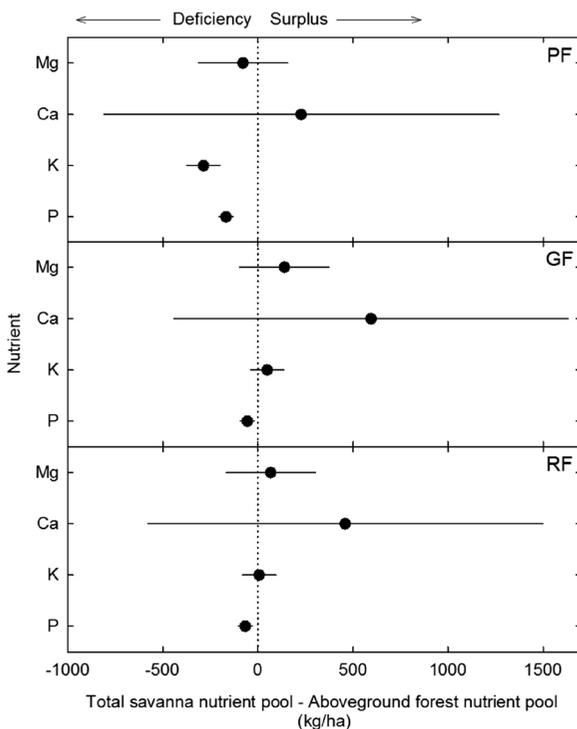


Fig. 5 The mean (± 1 sd; $n=3$ savanna vegetation types) difference (savanna-forest) between total savanna nutrient pools (soil+aboveground) and aboveground (wood+foliage) forest nutrient pools for palm forest (*top-panel*), gallery forest (*middle-panel*), and riparian forest (*bottom-panel*). Positive values indicate an excess in available nutrients for the construction of a forest in savanna while negative values indicate a deficit in available nutrients for the construction of a forest in savanna

modify soil nutrient availability (Durigan and Ratter 2006; Silva et al. 2013). We hypothesized that these processes may also explain the forest expansion into hyperseasonal savanna that has been observed for decades in the Brazilian Pantanal (Junk et al. 2006; Nunes da Cunha and Junk 2001; 2004; 2009). Specifically, we tested the hypotheses that variations in ecosystem physiognomy such as tree density, wood C storage, and leaf area index (LAI) would be positively related to soil nutrient availability and that nutrient stocks in hyperseasonal savanna would be sufficient to support the high wood biomass and LAI associated with forests.

Our data partially support these hypotheses. Forests had significantly higher wood and leaf C storage and LAI, but not litter C storage, than hyperseasonal savanna. Ecosystem variations in LAI and wood and foliage C storage were positively correlated with soil extractable P, Ca²⁺, and Mg²⁺, while wood density was positively related to soil extractable K⁺. These trends were likely due to both variations in inherent soil fertility and vegetation effects on nutrient availability. For example, trends in extractable P and K⁺ with depth indicate surface enrichment, which was presumably due to the redistribution of leached P and K⁺ from plant litter inputs (Jobbágy and Jackson 2001; Bond 2010; Vourlitis et al. 2011; Wigley et al. 2013). Litter inputs from forests growing on nutrient-rich soil also tend to be enriched with nutrients because vegetation is not as proficient at retaining nutrients (Richardson et al. 2005; Hayes et al. 2014; Vourlitis et al. 2014). In contrast, profiles of extractable Ca²⁺ and Mg²⁺ did not exhibit surface enrichment from vegetation, but instead increased with depth indicating surface leaching of Ca²⁺ and Mg²⁺ and accumulation with depth (Couto et al. 2006; Silva et al. 2010). Thus, the differences in extractable Ca²⁺ and Mg²⁺ between forest and savanna were presumably due in part to variations in substrate properties (Jobbágy and Jackson 2001; Wigley et al. 2013). With the exception of the riparian forest, higher clay content presumably caused an increase in extractable cation content in forest soils due to higher cation exchange capacity and lower rates of leaching (McDonald et al. 2005; Wantzen et al. 2012).

Comparisons between the pantanal C storage to other studies

Aboveground C storage estimated for the forests studied here was approximately 50 % lower than upland humid

tropical forests of the Amazon Basin (Malhi et al. 2009) but was comparable to other seasonal forests. For example, *V. divergens* dominated riparian forests of the Pantanal reportedly store between 8 MgC ha⁻¹ for young (67 year old) and 100 MgC ha⁻¹ for older (124 year old) stands (Schöngart et al. 2010, 2011), while floodplain forests of the Amazon Basin reportedly store between 115 and 140 MgC ha⁻¹ (Worbes 1997; Schöngart et al. 2010). Estimates for aboveground C storage for seasonal forests range between 40 and 100 MgC ha⁻¹ in central Brazil (Silva et al. 2013) and 65–130 MgC ha⁻¹ in the Yucatan Peninsula of Mexico (Vargas et al. 2008).

In contrast, the grass-dominated hyperseasonal savanna stands stored slightly lower aboveground C than comparable upland savanna stands (i.e., campo sujo and campo limpo), because the woody stems encountered in our grass-dominated stands were smaller than our 3 cm DBH measurement threshold. However, estimates of the foliar and litter C storage for our sites are nearly identical to those reported for upland savanna (de Castro and Kauffman 1998; Barbosa and Fearnside 2005; Grace et al. 2006; Vourlitis and da Rocha 2011). Estimates of woody C storage for the hyperseasonal woodland are nearly 4-times higher than comparable upland savanna woodlands (i.e., cerrado denso and sensu stricto), which may have been due to the species composition of our seasonally flooded woodland. For example, while many of the species encountered in the woodland stand are common cerrado species (Table S1), the four dominant tree species (*Astronium fraxinifolium*, *Curatella americana*, *Tabebuia aurea*, and *T. heptaphylla*) are also common gallery and riparian forest species, which tend to be larger than savanna woodland trees (Rossatto et al. 2009).

Potential limitations to forest expansion into hyperseasonal savanna

We hypothesized that nutrient stocks in hyperseasonal savanna would be sufficient to support high wood biomass and LAI associated with forests. Our results indicate that the hyperseasonal savanna ecosystems studied here had adequate Ca²⁺ availability, and with the exception of the palm forest, adequate Mg²⁺ and K⁺ availability to support forest expansion. The higher nutrient stocks, and therefore, presumed requirements of the palm forest were striking, and it is clear that these forests have substantially higher nutrient sequestration in

biomass and soil than the other forests (see Fig. 4). According to Pott and Pott (1994) and Lorenzi (2002), palm forests dominated by *Scheelea phalerata* are found in clay-rich soils that are high in nutrients, especially Ca²⁺, and local habitants of the Pantanal often use the distribution of *S. phalerata* as an indicator of high soil fertility. Only P availability appeared to be universally limiting to the forests studied here, but it is important to note that only extractable P was measured from the upper 50 cm soil layer and it is likely that trees with deeper root systems would be able to obtain additional P from deeper soil layers (Bond 2010; Wigley et al. 2013). However, P deficiency is consistent with leaf chemistry data (i.e., N:P and P:K ratios) from forest and woodland trees in the Pantanal that suggest P limitation (Vourlitis et al. 2014).

While hyperseasonal savanna appeared to be P deficient there are several mechanisms in which forest expansion may occur in these habitats. First, spatial variations in nutrient availability within a given ecosystem can be large (Vourlitis et al. 2013), and there are likely microsites that have adequate P to support tree recruitment (Silva et al. 2008). Many forest tree species have higher growth rates than woody savanna species (Rossatto et al. 2009) and many forest trees are able to grow in nutrient-poor savanna soils, although their growth rates may be reduced (Viani et al. 2011). Thus, forests trees can likely survive in these nutrient-rich microsites, provided that the fire return interval is long enough for trees to reach the fire resistance threshold (Hoffmann et al. 2012), especially within the protected areas of the Pantanal where the use of fire is prohibited. Secondly, nutrient inputs from seasonal flooding may provide a temporary pulse of nutrients (Hanan and Ross 2010; Saha et al. 2010), which may increase the potential for survival and recruitment of forest trees in nutrient-poor hyperseasonal savanna substrates.

Plant nutrient enrichment is an important driver of the spatial variation in surface soil nutrient availability (Wood et al. 2009; Hanan and Ross 2010; Saha et al. 2010; Vourlitis et al. 2011; Holdo et al. 2012). As trees become established they can increase soil nutrient availability and expand in savanna through a variety of mechanisms (Durigan and Ratter 2006; Silva et al. 2008; Vourlitis et al. 2011). Forest tree roots can capture nutrients leached from the topsoil and redistribute these nutrients to the soil surface with the accumulation of surface litter (Jobbágy and Jackson 2001; Richardson et al. 2005; Bond 2010; Vourlitis et al. 2011; 2014;

Wigley et al. 2013). The higher LAI of forests also increases the potential for accumulation of dry atmospheric nutrient deposition and subsequent throughfall (Kellman 1979; Silva et al. 2008), which is likely to be substantial in this region due to periodic biomass burning that occurs in the surrounding savanna (Eck et al. 2000). Forest trees also have higher rates of transpiration during the dry season than savanna grasses (Santos et al. 2003; Oliveira et al. 2005; Vourlitis and da Rocha 2011; Dalmagro et al. 2014), which can cause accumulation of dissolved nutrients under tree canopies through mass-flow and/or the development of concentration gradients (Hanan and Ross 2010; Saha et al. 2010). Thus, in the absence of frequent fire, which can both increase tree mortality and losses of aboveground and soil surface nutrient stocks (Kauffman et al. 1994; Hoffmann et al. 2012), biotic enrichment of soil nutrient availability by invading trees may be a key process that promotes forest expansion into hyperseasonal savanna (Durigan and Ratter 2006; Silva et al. 2013). While speculative, this model is consistent with observations along upland savanna-forest transitions throughout South America (Durigan and Ratter 2006; Silva et al. 2008, 2013).

Conclusions

Our results are qualitatively similar to those reported for upland savanna, and add to our knowledge of plant-soil interactions in tropical ecosystems. In terms of the Pantanal, our results indicate that forest expansion into hyperseasonal savanna is possible given the available nutrient stocks, except for P, and the potential for vegetation to locally modify nutrient availability. Integrating our results with others, we propose the following model of forest expansion into hyperseasonal savanna. Variations in the duration and intensity of the flood pulse will disperse tree seeds into savanna and affect the survival and recruitment of germinating seeds. These flood pulses will also transport nutrients into savanna, which may increase surface nutrient availability in microsites where they accumulate. Because the use of fire is prohibited within the Pantanal, forest tree seedlings that are germinating and recruiting into savanna can grow in these nutrient-rich microsites to a size where they become more resistant to infrequent wildfires or fires that are started outside the Pantanal. As these trees grow, they can enrich surface nutrient availability through nutrient redistribution in litter,

throughfall, and/or accumulation from mass flow and diffusion, and facilitate the invasion of other forest trees into hyperseasonal savanna. Over time, increases in tree cover can eliminate savanna grasses and understory vegetation and reduce flammability, and at this stage, the potential for fire to damage and/or kill trees is substantially lower. While more research is needed to test this model, it is consistent with observations along upland savanna-forest ecotones throughout South America.

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