

Variations in Stand Structure and Diversity along a Soil Fertility Gradient in a Brazilian Savanna (Cerrado) in Southern Mato Grosso

George Louis Vourlitis*

Department of Biological Sciences
California State University
San Marcos, CA 92096

Francisco de Almeida Lobo

Faculdade de Agronomia
Medicina Veterinária e Zootecnia
Departamento de Solos e
Engenharia Rural
Universidade Federal de Mato Grosso
Mato Grosso, Brazil

Shelley Lawrence

Department of Biological Sciences
California State University
San Marcos, CA 92096

Isabela Codolo de Lucena

Programa de Pós-Graduação em
Ecologia e Recursos Naturais-PPGERN
Universidade Federal de São Carlos
São Carlos, Brazil

Oswaldo Borges Pinto Jr.

Higo José Dalmagro

Programa de Pós-Graduação em Física
Ambiental- PGFA
Instituto de Física
Universidade Federal de Mato Grosso
Mato Grosso, Brazil

Carmen Eugenia

Rodriguez Ortiz

Departamento Botânica e Ecologia-
Instituto de Biociencias
Universidade Federal de Mato Grosso
Mato Grosso, Brazil

Jose de Souza Nogueira

Programa de Pós-Graduação em Física
Ambiental- PGFA
Instituto de Física
Universidade Federal de Mato Grosso
Mato Grosso, Brazil

Brazilian savanna (cerrado) is composed of vegetation and soil types that are spatially variable, and links between cerrado physiognomy and soil properties are poorly understood. To reduce this uncertainty, we measured the plant community structure within cerrado vegetation types located near Cuiaba, Mato Grosso, Brazil, that varied in soil physical and chemical properties. We hypothesized that vegetation composition, including tree density, leaf area index (LAI), grass cover, and tree species diversity would be highly correlated with soil C content and fertility. Our results indicate that soil organic matter content (SOM) was significantly ($p < 0.05$) correlated with tree density and LAI but negatively correlated with grass cover. Moreover, SOM content explained almost all of the spatial variation in cation exchange capacity (CEC) and soil N content (Pearson $r > 0.90$), and tree species diversity and richness increased significantly with soil fertility. These data suggest that cerrado species richness and diversity is coincident with more fertile soils, which is qualitatively similar to results reported for tropical forests across regional fertility gradients in the Amazon Basin. These results have implications for the maintenance of soil C storage and fertility and tree species diversity in cerrado.

Abbreviations: CEC, cation exchange capacity; IRI, index of relative importance; LAI, leaf area index; PCA, principal components analysis; SOM, soil organic matter.

Brazilian savanna, locally known as cerrado, covers approximately 20 to 25% of the total land cover of Brazil and is the second largest vegetation type following Amazonian forest (Furley and Ratter, 1988). Cerrado is composed of distinctive physiognomies that vary as a function of height, cover, and/or density of trees (Goodland, 1971; Eiten, 1972; Furley and Ratter, 1988). The factors that affect the physiognomy and distribution of cerrado remain a subject of debate; however, seasonal variation in rainfall, soil fertility and drainage, and fire are considered the most important (Eiten, 1972; Furley and Ratter, 1988; Lopes and Cox, 1977).

In terms of soil properties, variations in soil texture, water holding capacity, and chemical properties, such as pH and Al^{3+} concentration, have been found to be important variables affecting cerrado physiognomy and tree species distribution (Lopes and Cox, 1977; Furley and Ratter, 1988; de Souza et al., 2007; de Assis et al., 2011). Nutrient limitation has been implicated as a primary factor inhibiting the development of forests in tropical savanna, and across large-scale fertility gradients, an increase in soil fertility can lead to an increase in the production of woody vegetation, and the density and cover of trees (Goodland and Pollard, 1973; Lopes

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*Corresponding author (georgev@csusm.edu).

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and Cox, 1977; Lloyd et al., 2008; Bond 2010). Similar patterns have been observed across regional fertility gradients in tropical forests, where rates of biomass production have been found to increase with soil fertility (ter Steege et al., 2006; Malhi et al., 2009; Quesada et al., 2009). There is also evidence that plant species richness increases along soil fertility gradients (Tuomisto et al., 2003; Long et al., 2012), presumably because an increase in richness leads to an increase in ecosystem nutrient retention (Hooper and Vitousek 1997, 1998). However, while soil fertility may control forest distribution and growth, trees also affect soil fertility through nutrient uptake and retention (Hooper and Vitousek, 1997), resource use efficiency (ter Steege et al., 2006), and litter production (Vitousek and Sanford, 1986; Malhi et al., 2009). Trees have a greater capacity than grasses to access leached nutrients deep within the soil profile because of their more extensive root systems, and re-distribute these nutrients to the soil surface through the input of nutrient-rich litter and/or hydraulic redistribution (Kellman, 1979; Mordelet et al., 1993; Troxler-Gann et al., 2005; Wetzel et al., 2005; Saha et al., 2010; Vourlitis et al., 2011).

Unfortunately, much of what is known about tropical plant–soil relationships is from regional-scale studies where factors such as climate variability, plant dispersal ability, and disturbance history can obscure relationships between soil physical and chemical properties and forest structure (Clark et al., 1998; Hall et al., 2004; John et al., 2007). However, tropical soils exhibit high variability in soil physical and chemical properties over small spatial scales (<1 ha), due to variations in topography, substrate and parent material, and plant species influences on litter quantity and quality, and this high subhectare variability is useful for determining how vegetation structure varies across soil physical and chemical gradients (Richter and Babbar, 1991; de Souza et al., 2007). Thus, our objective was to determine if regional-scale relationships between soil fertility and stand structure were qualitatively similar at the subhectare scale. To fulfill this objective we exploited small scale (1–10,000 m²) spatial variation in edaphic properties to quantify relationships between soil properties and cerrado physiognomy. We hypothesized that cerrado tree density, LAI, and species richness and diversity would be positively related to soil fertility.

MATERIALS AND METHODS

Site Description

Research was conducted in the Cuiaba Basin at the Fazenda Miranda, located 15 km south southeast of Cuiaba, Mato Grosso, Brazil (15°43'51" S, 56°04'17" W). Mean annual rainfall and temperature are 1420 mm and 26.5°C, respectively, and rainfall is strongly seasonal with a dry season extending from May to September (Vourlitis and da Rocha, 2011). The research area is on flat terrain at an elevation of 181 m above sea level. The regional soil type is a rocky, dystrophic red–yellow latosol locally known as a Solo Concrecionário Distrófico (RadamBrasil, 1982).

Cerrado vegetation in this region is highly fragmented because of widespread land cover change to support cattle

(*Bos taurus*) and soybean [*Glycine max* (L.) Merr.] production (Jasinski et al., 2005). We located five fragments that varied in area and landform type, and within each fragment, a permanent 100-m long transect was randomly established (Table 1). Transect 1 was located within an upland forest dominated by tall (8–10 m) trees including *Astronium fraxinifolium* Schott., *Aspidosperma subincanum* Mart., *Rhamnidium elaeocarpum* Reiss., and *Curatella americana* L. This type of forest is locally recognized as cerradão (“big cerrado”), which is generally found on well-drained soils of intermediate and low fertility (Goodland, 1971; Eiten, 1972; Furley and Ratter, 1988). Transect 2 was a mixed tree–shrub woodland characteristic of cerrado sensu stricto, which has a shorter, more open canopy than cerradão (Goodland, 1971; Eiten, 1972; Furley and Ratter, 1988). Common tree species include *C. americana*, *Qualea grandiflora* Mart., *Q. parvifolia* Mart., *Caryocar brasiliense* Cambess., and *Terminalia argentea* Mart. & Zucc that reached a height of about 5 to 8 m. Transect 3 was a mixed forest–grassland that was dominated by grasses and the tree species *C. americana* and *Diospyros hispida* A. DC. This type of cerrado is referred to as *campo sujo* (dirty field), where woody cover is usually <30 to 40% reflecting the higher importance of grasses (Goodland, 1971; Eiten, 1972; Furley and Ratter, 1988). Transect 4 had patches of dense scrub that were composed of short (4–6 m), densely packed trees, primarily *Tabebuia roseo alba* (Ridl.) Sand. and *Matayba guianensis* Radlk., with occasional open areas dominated by grasses and *C. americana*. Transect 5 was in a seasonally flooded forest referred to as a “Cambarazal” owing to the dominance of the tree species, *Vochysia divergens* Pohl (Cambará). *Vochysia divergens* is a 15- to 20-m tall tree native to the Amazonian riparian forest (Lorenzi, 2002), but has been vigorously spreading into seasonally flooded campo cerrado of the Pantanal for over four decades (da Cunha and Junk, 2004).

Field Measurements and Laboratory Analyses

Field sampling was conducted over a 3-wk period during the dry season in June 2011. The density and basal area of trees ≥ 3 cm in diameter was measured every 5 m on each 100-m transect using the point-quarter method (Goldsmith and Harrison, 1976). Briefly, each measurement point was divided into four quadrants, and within each quadrant, the distance to the nearest tree and its circumference at diameter breast height (1.3 m aboveground) were measured. Leaf area index was measured every 5 m along each transect using a photosynthetically active radiation (PAR)-ceptometer (AccuPAR LP-80, Decagon Devices, Inc., Pullman, WA). The LAI was calculated from the ceptometer software assuming a spherical leaf angle distribution.

The dry mass of the surface organic matter (litter) pool was measured every 10 m along each transect within 25-cm diam. quadrats (except Transect 5 [Cambarazal] which was flooded during the time of field sampling). Litter samples were dried at 70°C for 1 wk and weighed to the nearest 0.01 g using a digital balance.

Surface (0–20 cm) soil core samples were obtained every 10 m along each transect using a 761.4 cm³ (18.7-cm deep \times 7.2 cm

Table 1. Summary of vegetation structural characteristics for the cerrado vegetation types at the Fazenda Miranda. All data are mean (\pm se; $n = 20$ /transect) values except species diversity which is a mean (\pm 95% confidence interval) calculated from bootstrap resampling. Also shown are the results of a one-way ANOVA including the F statistic, factor (transect) and error degrees of freedom (subscript associated with the F statistic), and p value. Values within each row with a different letter are significantly different ($p < 0.05$) according to a Tukey–Kramer test except species diversity, where different letters indicate that the 95% confidence intervals do not overlap.

Variable, units	Upland forest (Transect 1)	Woodland (Transect 2)	Mixed grassland (Transect 3)	Dense scrub (Transect 4)	Flooded forest (Transect 5)	$F_{4,95}$	p
LAI, m ² /m ²	3.6 \pm 0.4 ^{ab}	4.3 \pm 0.3 ^b	1.3 \pm 0.3 ^c	4.3 \pm 0.5 ^b	2.2 \pm 0.3 ^{ac}	13.6	<0.001
Diameter, cm	9.2 \pm 1.0 ^{ab}	8.7 \pm 0.6 ^{ab}	9.8 \pm 0.6 ^{ab}	7.3 \pm 0.5 ^b	10.5 \pm 0.8 ^c	2.8	<0.05
Density, no. ha	2114 \pm 400 ^a	2281 \pm 267 ^a	533 \pm 62 ^b	2557 \pm 531 ^a	767 \pm 143 ^b	8.1	<0.001
Basal area, m ² /ha	18.6 \pm 5.0 ^a	18.5 \pm 3.5 ^a	4.5 \pm 0.6 ^b	18.3 \pm 5.7 ^a	9.8 \pm 3.2 ^b	2.6	<0.05
Graminoid cover, %	32.7 \pm 8.3 ^a	16.7 \pm 4.3 ^b	64.0 \pm 5.1 ^c	41.1 \pm 7.9 ^a	64.8 \pm 8.8 ^c	8.5	<0.001
Diversity (H')	2.8 \pm 0.7 ^a	2.1 \pm 0.7 ^a	0.8 \pm 0.2 ^b	1.9 \pm 0.4 ^{ab}	1.0 \pm 0.3 ^b	–	–
Richness, no. species	28	20	8	26	6	–	–

diam.) bucket auger (Model 300.07; AMS Inc., American Falls, ID). Soil samples were analyzed for physical properties, such as percent stoniness, soil moisture, SOM content, and particle-size distribution (percent sand, silt, and clay), and chemical properties, such as pH, total N, extractable P, and cation (K⁺, Ca²⁺, Mg²⁺, Al³⁺, and H⁺) content, using a commercial soil analysis laboratory (ArgoAnálise, Inc., Cuiaba, Mato Grosso, Brazil). The soil chemical parameters were chosen because they are typically reported for cerrado soils (Lopes and Cox, 1977; Furley and Ratter, 1988; Haase, 1999; Lilienfein et al., 2003; de Souza et al., 2007; Vourlitis et al., 2011; Wantzen et al., 2012), making comparisons between our work, and that of other groups, easily comparable. Furthermore, many of these variables (pH, P, Al³⁺, and Ca²⁺ content) are reportedly important for limiting the distribution of tropical savanna trees (Goodland and Pollard, 1973; Ruggiero et al., 2002; Paoli et al., 2008), and soil physical properties, such as clay, sand, and organic matter content are important for the water and nutrient retention of tropical soils (de Souza et al., 2007; de Assis et al., 2011).

Soil moisture was determined gravimetrically, while percent stoniness was measured as the mass of rocks ≥ 2 mm in size divided by the total dry mass of soil sample ($\times 100$). Particle size distribution was measured using the Bouyoucos hydrometer method following chemical dispersion in NaOH. Soil pH was analyzed in distilled water extracts from 1:2.5 soil/extract proportions using a standard pH meter (PMPH-1, Digimed, São Paulo, Brazil). Total N was analyzed using the micro-Kjeldahl method. Soil extractable P and K⁺ was analyzed colorimetrically from Mehlich (0.05 M HCl + 0.025 M H₂SO₄) extracts using a spectrophotometer (Q1-108D, Quimis, São Paulo, Brazil) and a flame photometer (DN-61, Digimed, São Paulo, Brazil), respectively. Soil extractable Ca²⁺ and Mg²⁺ were analyzed from 1 M KCl extracts using a flame-Atomic Absorption spectrometer (AA-275; Varian, Inc., Palo Alto, CA). Soil-extractable Al³⁺ and H⁺ were analyzed by titration using a digital burette (Model 236-080, Jencons, Leicestershire, UK) from 1 M KCl extracts. Soil organic matter was analyzed colorimetrically using the Walkley–Black method (Nelson and Sommers, 1996). Soil CEC was calculated as the sum of all measured cations (Robertson et al., 1999).

Litter samples were analyzed for N, P, K⁺, Ca²⁺, and Mg²⁺ by the same commercial analytical laboratory used for the soil analyses. Litter samples were digested using micro-Kjeldahl methods (N) and 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).

Data Analysis

Point-quarter and line intercept data were used to quantify tree species and graminoid (grasses + sedges) abundance, respectively. Following Dahdouh-Guebas and Koedam (2006), tree density was calculated for each sampling point and species as a function of the mean distance. Basal area of each tree species at each sampling point was calculated by converting the trunk circumference into area (m²/tree) and multiplying by the density (trees/m²). Tree species frequency of occurrence was calculated by counting the number of sampling points per transect that a given tree species was observed. Relative estimates of tree density, cover, and frequency of occurrence per transect were calculated for each tree species by dividing the absolute estimates by their respective totals. The index of relative importance (IRI) for each species per transect was calculated as the sum of relative density, cover, and frequency of occurrence (Goldsmith and Harrison, 1976). Graminoid cover was measured along each transect using the line-intercept method, where plant cover was calculated as the proportion of each transect intercepted by each plant species (Goldsmith and Harrison, 1976).

Tree species richness within each cerrado stand was calculated as the number of species encountered per transect, and tree species diversity was calculated using the Shannon–Weiner (H') index (Magurran, 1998). Estimates of the IRI for each species per transect were used to calculate H', and confidence intervals ($\pm 95\%$) were calculated for H' by bootstrapping estimates of H' over 1000 iterations by randomly sampling (with replacement) the IRI values for each species per transect (Efron and Tibshirani, 1993).

Differences in soil physical and chemical properties, vegetation structure (tree density and basal area, graminoid cover, and LAI), and litter mass and chemistry between cerrado stands were quantified using one-way ANOVA. Correlations between soil physical and chemical properties were determined by Pearson-product moment correlation. Because of significant correlation between many soil physical and chemical variables (described below), principal components analysis (PCA) was used to derive uncorrelated variables that could be used to assess the dependence between soil and vegetation properties. Factors were generated using the Varimax orthogonal rotation technique and only factors with an eigenvalue >1 were retained (Kaiser, 1960). Relationships between PCA factors, vegetation properties, and surface litter biomass and chemistry were examined using linear regression. Statistical analyses were conducted using NCSS statistical software (Version 7, NCSS, LLC, Kaysville, UT).

RESULTS

Vegetation structure

Vegetation structure varied substantially within and between the cerrado vegetation types, with the upland forest (Transect 1), woodland (Transect 2), and the dense scrub (Transect 4) having the most similar vegetation structure (Table 1). Within-stand variations in tree density (Fig. 1a) and grass cover (Fig. 1b) were highest in the dense-scrub and lowest in the flooded forest (Transect 5). Leaf area index varied between 4.3 and 3.6 m²/m² for the upland-forest, woodland, and dense scrub, while the flooded forest and mixed grassland (Transect 3) had a LAI of 2.2 and 1.3 m²/m², respectively. Differences in tree diameter were smaller between the cerrado vegetation types, and the largest trees were found in the flooded forest. Tree density and basal area followed similar patterns, with the upland-forest, woodland, and the dense-scrub stands having a significantly higher density and basal area than the mixed-grassland and flooded-forest stands. In contrast, the mixed grassland and flooded forest had significantly higher graminoid (grasses + sedges) cover. Mean ($\pm 95\%$ confidence interval) tree species diversity ranged between 2.8 \pm 0.7 for the upland forest and 0.8 \pm 0.2 for the mixed grassland, and these trends were highly correlated (Pearson's $r = 0.93$; $p < 0.05$; $n = 5$ transects) with species richness.

Spatial Patterns in Soil and Litter Properties

Within transect variations in SOM content were highest in the upland forest and dense scrub and lowest in the flooded forest (Fig. 1c), while sand content was more variable in upland forest, dense scrub, and mixed grassland and least variable in the woodland (Fig. 1d). Total soil N varied by more than twofold in the upland forest and dense scrub, while the other cerrado stands exhibited lower spatial variation (Fig. 1e). Extractable P varied by twofold in upland forest and mixed grassland, threefold in the flooded forest, and over sixfold in dense scrub (Fig. 1f).

Upland-forest and mixed-grassland soils had the highest percentage (>60%) of rocks, followed by woodland and dense

scrub (16.8–31.4%), while the flooded forest had no rocks in the upper 20-cm soil layer (Table 2). Spatial differences in soil-textural properties were complex, but in general, all stands had a higher proportion of sand than silt or clay. Sand content was highest in the woodland and lowest in the flooded forest, while silt and clay content were highest in the flooded forest and lowest in woodland (Table 2). Soil moisture was highest in the flooded forest, which had standing water at the time of the field sampling, upland forest and dense scrub had intermediate soil moisture (8.5–8.8%), while the mixed-forest transects had the lowest soil moisture (5.2–5.5%; Table 2). Soil organic matter content was highest in the upland forest and dense scrub and lowest in the flooded forest. The upland-forest, dense-scrub, and woodland stands had a significantly ($p < 0.05$) higher pH (5.72–5.94) than the mixed grassland and flooded forest (4.94–4.95). In general, upland forest had higher total N, extractable P and cations (except Al³⁺), and CEC than the other vegetation types, and for many of the soil nutrient variables, dense scrub was more similar to upland forest than the other cerrado types (Table 2).

All of the soil chemical properties were highly correlated with SOM content, and with the exception of Al³⁺, as SOM content increased so did soil fertility (Table 3). The positive correlation between SOM and CEC was striking ($r = 0.99$), and not surprisingly, soil pH was significantly negatively correlated with extractable Al³⁺ content ($r = -0.91$; Table 3). Other soil physical properties had lower correlations with soil chemical variables; however, total soil N was positively correlated with clay content and negatively correlated with sand content, while total N, extractable cations (except Al³⁺), and CEC were positively correlated with percent stoniness (Table 3).

Litter pool mass was significantly lower in mixed grassland (Table 4), and was positively correlated with LAI ($r = 0.48$; $p < 0.05$; $n = 40$), tree density ($r = 0.48$; $p < 0.05$; $n = 40$), and basal area ($r = 0.48$; $p < 0.05$; $n = 40$), and negatively correlated with graminoid cover ($r = -0.39$; $p < 0.05$; $n = 40$). Litter N concentration was similar across all vegetation types, but P concentration was highest in the upland forest, K⁺ concentration was highest in the dense scrub and lowest in the woodland, and litter Ca²⁺ concentration was significantly lower in the mixed grassland (Table 4).

Relationships between Soil Properties and Vegetation Structure

Principal components analysis was used to simplify the soil data into uncorrelated factors that could be used to assess relationships between soil properties, vegetation structure (LAI, tree density, basal area and diameter, graminoid cover), and species richness and diversity (H'). The PCA results revealed three uncorrelated factors with eigenvalues > 1 that explained 91% of the variance in the soil physical and chemical variables. The first factor (PCA-1) explained 42% of the variance in soil properties, and was primarily a soil fertility factor that was composed of SOM, pH, total N, extractable P, K⁺, Ca²⁺, Mg²⁺, Al³⁺, and CEC (Table 5). All of the variables, with the exception of

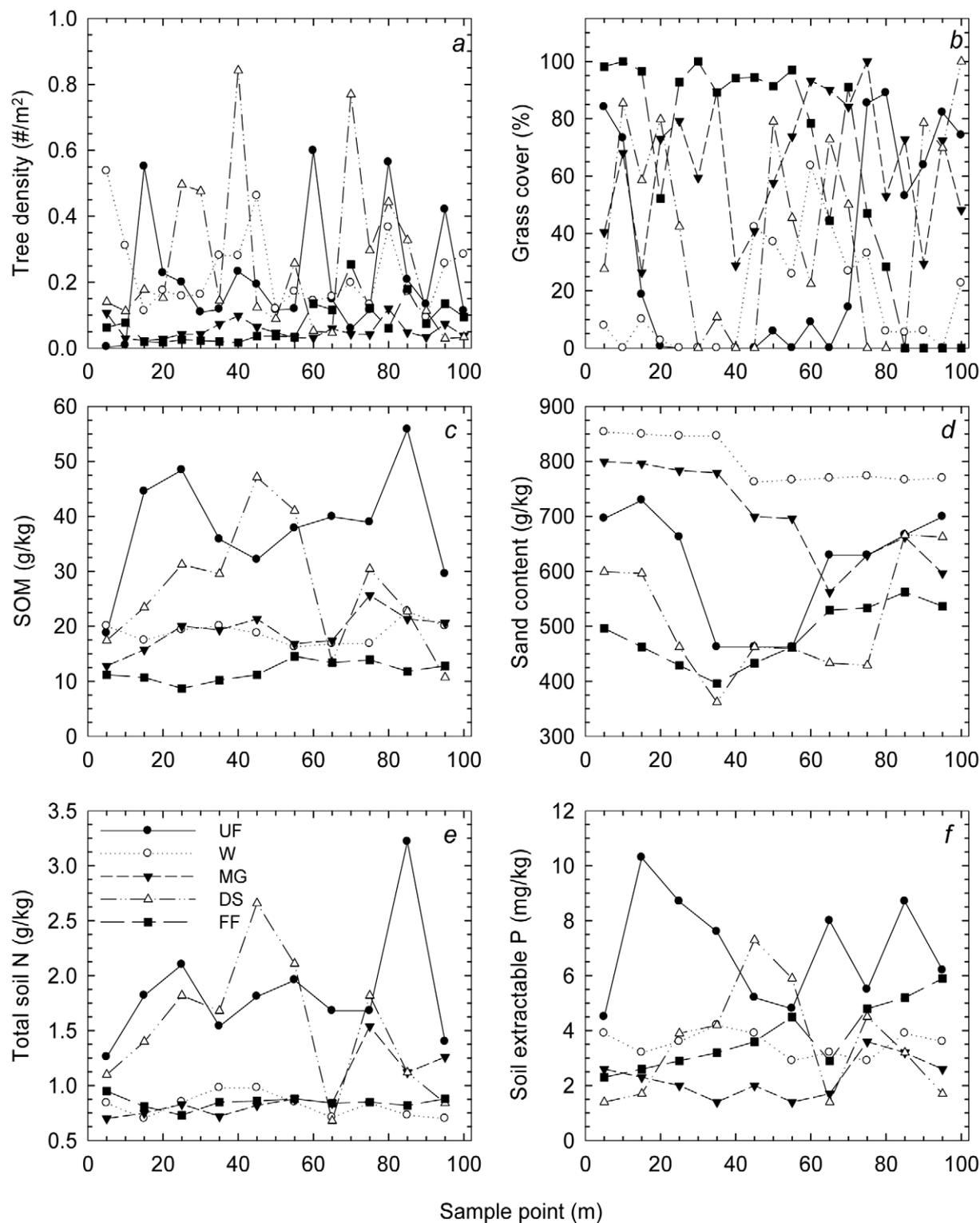


Fig. 1. Spatial variation in (a) tree density, (b) grass cover, (c) soil organic matter content, (d) sand content, (e) total soil N, and (f) extractable P along a 100-m long transect within upland forest (Transect 1; closed-circles, solid-line), woodland (Transect 2; open circles, dotted line), mixed grassland (inverted closed triangles; dashed lines), dense scrub (Transect 4; open triangles, dotted dashed line), and flooded forest (closed squares, long dashed lines). Soil samples were obtained every 10 m along each transect from the upper 0- to 20-cm soil layer.

Al^{3+} , were negatively correlated with PCA-1, indicating that soil fertility increased as PCA-1 declined. The PCA-2 was a soil texture factor that explained 21% of the variance in the soil variables (Table 5), and was positively correlated with sand content and negatively correlated with silt and clay content. The

PCA-3 explained 28% of the variance in the soil variables, and was a mix of soil physical variables (rocks) and fertility variables (Table 5).

Many of the vegetation structural characteristics were significantly correlated with PCA-1 but not with the other PCA factors (Table 6). Leaf area index was significantly negatively

Table 2. Summary of mean (\pm se; $n = 10$ /transect) soil physical and chemical properties for the cerrado vegetation types at the Fazenda Miranda. Also shown are the results of a one-way ANOVA including the F statistic, factor (transect) and error degrees of freedom (subscript associated with the F statistic), and p value. Values within each row with a different letter are significantly different ($p < 0.05$) according to a Tukey–Kramer test.

Variable	Upland forest (Transect 1)	Mixed-forest shrubland (Transect 2)	Mixed-forest grassland (Transect 3)	Dense scrub (Transect 4)	Flooded forest (Transect 5)	$F_{4,45}$	p
Rocks, %	63.2 \pm 5.3 ^a	16.8 \pm 3.8 ^b	67.1 \pm 5.6 ^a	31.4 \pm 8.4 ^b	0.0 \pm 0.0 ^c	29.4	<0.001
Soil moisture, %	8.5 \pm 0.9 ^a	5.2 \pm 0.1 ^b	5.4 \pm 0.5 ^b	8.8 \pm 0.7 ^a	28.1 \pm 1.0 ^c	176.8	<0.001
Sand, g/kg	610 \pm 33 ^a	800 \pm 13 ^b	700 \pm 28 ^{ab}	513 \pm 34 ^{ac}	484 \pm 18 ^c	24.4	<0.001
Silt, g/kg	153 \pm 13 ^a	70 \pm 4 ^b	116 \pm 10 ^a	202 \pm 15 ^c	234 \pm 9 ^c	35.3	<0.001
Clay, g/kg	237 \pm 21 ^a	130 \pm 8 ^b	184 \pm 18 ^c	285 \pm 19 ^a	282 \pm 9 ^a	17.7	<0.001
SOM†, g/kg	38.1 \pm 3.3 ^a	18.8 \pm 0.6 ^b	19.1 \pm 1.1 ^b	26.7 \pm 3.7 ^c	11.8 \pm 0.6 ^d	19.2	<0.001
pH	5.98 \pm 0.15 ^a	5.76 \pm 0.06 ^a	4.94 \pm 0.06 ^b	5.72 \pm 0.13 ^a	4.95 \pm 0.04 ^b	24.8	<0.001
Total N, g/kg	1.85 \pm 0.17 ^a	0.82 \pm 0.03 ^b	0.95 \pm 0.09 ^b	1.52 \pm 0.19 ^a	0.85 \pm 0.02 ^b	14.1	<0.001
P, mg/kg	6.95 \pm 0.63 ^a	3.53 \pm 0.14 ^b	2.28 \pm 0.23 ^b	3.52 \pm 0.64 ^b	3.79 \pm 0.39 ^b	14.7	<0.001
K ⁺ , mg/kg	127.9 \pm 12.8 ^a	54.0 \pm 5.9 ^b	62.6 \pm 5.2 ^b	95.8 \pm 14.3 ^a	31.1 \pm 1.5 ^c	16.6	<0.001
Ca ²⁺ , cmol _c /dm ³	3.36 \pm 0.50 ^a	1.60 \pm 0.11 ^b	0.52 \pm 0.07 ^c	2.17 \pm 0.44 ^a	0.57 \pm 0.02 ^c	15.2	<0.001
Mg ²⁺ , cmol _c /dm ³	1.12 \pm 0.17 ^a	0.58 \pm 0.04 ^b	0.26 \pm 0.03 ^c	0.82 \pm 0.16 ^a	0.22 \pm 0.01 ^c	13.0	<0.001
Al ³⁺ , cmol _c /dm ³	0.10 \pm 0.07 ^a	0.00 \pm 0.00 ^a	0.64 \pm 0.05 ^b	0.11 \pm 0.07 ^a	0.56 \pm 0.02 ^b	35.6	<0.001
H ⁺ , cmol _c /dm ³	4.11 \pm 0.34 ^a	2.78 \pm 0.06 ^b	3.55 \pm 0.20 ^{ab}	3.43 \pm 0.33 ^{ab}	2.85 \pm 0.11 ^b	5.5	<0.005
CEC, cmol _c /dm ³	9.02 \pm 0.77 ^a	5.08 \pm 0.14 ^{bc}	5.12 \pm 0.20 ^{bc}	6.78 \pm 0.82 ^b	4.27 \pm 0.11 ^c	13.5	<0.001

† SOM = soil organic matter, CEC = cation exchange capacity.

correlated with PCA-1 indicating that LAI increased with soil fertility. Tree density, basal area, and species diversity and richness were also negatively correlated with PCA-1, indicating that tree abundance, species richness, and diversity coincided with an increase in soil fertility. Graminoid cover was positively correlated with PCA-1, indicating that graminoids were more abundant in lower fertility stands. Litter mass and chemistry (except K⁺) were significantly negatively correlated with PCA-1 (Table 6), indicating that litter pool mass and litter N, P, and Ca²⁺ concentration increased with soil fertility. Litter K⁺ and Ca²⁺ were also significantly negatively correlated with PCA-2, indicating that K⁺ and Ca²⁺ concentration increased as sand content declined (Table 6).

DISCUSSION

Vegetation Structural Characteristics

Tree density reportedly ranges between 2360 and 2911 trees/ha for cerradão (upland forest) and cerrado sensu stricto (woodland) and 764 trees/ha for campo sujo (mixed grassland) (Goodland, 1971; de Castro and Kauffman, 1998; Felfili et al., 2004; Vourlitis and da Rocha, 2011), which is similar to what was found at the Fazenda Miranda. Reported estimates of basal area range from 3.0 to 4.3 m²/ha for campo sujo to 9.7 to 121.2 m²/ha for cerradão and sensu-stricto (Goodland, 1971; de Castro and Kauffman, 1998; Felfili et al., 2004; Vourlitis and da Rocha, 2011), which are highly variable but encompass values measured for our stands (Table 1). All of the stands at the Fazenda Miranda had a higher LAI than other cerrado stands, especially

Table 3. Results from a Pearson-product moment linear correlation analysis of the soil physical and chemical properties of the cerrado vegetation types at the Fazenda Miranda. Bold values indicate statistically significant linear correlations between variables ($p < 0.05$; $n = 10$ /transect).

Properties	Rocks	Sand	Silt	Clay	SOM	pH	N	P	K ⁺	Ca ²⁺	Mg ²⁺	Al ³⁺	H ⁺	CEC
Rocks	–													
Sand	0.21	–												
Silt	–0.27	-0.99	–											
Clay	–0.15	-0.99	0.95	–										
SOM†	0.59	–0.08	0.00	0.15	–									
pH	0.13	0.06	–0.13	0.00	0.71	–								
N	0.49	-0.31	0.24	0.36	0.92	0.61	–							
P	0.29	–0.12	0.09	0.14	0.78	0.57	0.71	–						
K ⁺	0.53	–0.17	0.08	0.25	0.88	0.75	0.81	0.68	–					
Ca ²⁺	0.35	–0.09	0.02	0.14	0.91	0.88	0.85	0.78	0.82	–				
Mg ²⁺	0.35	–0.07	0.01	0.13	0.90	0.88	0.83	0.73	0.83	0.99	–			
Al ³⁺	0.02	–0.16	0.20	0.11	-0.56	-0.91	-0.46	-0.45	-0.57	-0.73	-0.73	–		
H ⁺	0.65	–0.07	0.03	0.11	0.73	0.13	0.72	0.53	0.50	0.45	0.41	–0.10	–	
CEC	0.56	–0.13	0.06	0.18	0.99	0.68	0.94	0.80	0.83	0.92	0.91	-0.53	0.74	–

† SOM = soil organic matter, CEC = cation exchange capacity.

Table 4. Summary of mean (\pm se; $n = 10$ /transect) surface litter pool mass and chemistry for the cerrado vegetation types at the Fazenda Miranda. Also shown are the results of a one-way ANOVA including the F statistic, factor (transect) and error degrees of freedom (subscript associated with the F statistic), and p value. Values within each row with a different letter are significantly different ($p < 0.05$) according to a Tukey-Kramer test.

Variable	Upland forest (Transect 1)	Woodland (Transect 2)	Mixed grassland (Transect 3)	Dense scrub (Transect 4)	Flooded forest (Transect 5)	$F_{3,36}$	p
Litter mass, kg/m ²	7.6 \pm 1.7 ^a	10.2 \pm 1.6 ^a	2.2 \pm 1.0 ^b	10.6 \pm 2.4 ^a	ND†	4.9	<0.01
N, g/kg	11.2 \pm 0.8	9.5 \pm 0.3	10.1 \pm 0.3	10.1 \pm 0.7	ND	1.6	NS‡
P, g/kg	0.57 \pm 0.04 ^a	0.34 \pm 0.03 ^b	0.29 \pm 0.03 ^b	0.31 \pm 0.04 ^b	ND	13.1	<0.001
K ⁺ , g/kg	1.9 \pm 0.2 ^a	0.8 \pm 0.1 ^b	2.0 \pm 0.7 ^{ac}	2.5 \pm 0.4 ^c	ND	2.4	<0.05
Ca ²⁺ , g/kg	9.9 \pm 1.1 ^a	8.9 \pm 0.7 ^a	4.9 \pm 0.4 ^b	9.6 \pm 0.9 ^a	ND	8.2	<0.001

† ND = not determined.

‡ NS = not significant.

during the dry season (Miranda et al., 1997; Vourlitis and da Rocha, 2011). Estimates of tree species diversity (H') for cerrado woodlands reportedly range from 3.0 to 3.7 (Felfili et al., 2004), which is higher than the values observed at Fazenda Miranda, but estimates of species richness are similar to those reported here (Batalha et al., 2001; Ribeiro and Tabarelli, 2002). These data suggest that certain tree species at Fazenda Miranda had a higher relative abundance than others. One such tree species, *Curatella americana*, had high importance values (0.62–2.47) in all of the fragments except the cambarazal (flooded forest), where *Vochysia divergens* was dominant (IRI = 2.24). Compared to similar forests in the Pantanal, the flooded forest at Fazenda Miranda had a lower tree basal area and LAI but a higher tree density (Haase, 1999; Vourlitis et al., 2011), which likely reflects a younger, aggrading forest at the Fazenda Miranda. However, estimates of tree species richness and diversity were similar for the Pantanal and Fazenda Miranda reflecting the mono-specific nature of these forests (da Cunha and Junk, 2004).

Soil Physical and Chemical Properties

Soil physical and chemical properties reported for cerrado vary substantially, but in general, the soil properties reported for the cerrado stands at Fazenda Miranda appear to be typical of cerrado soils (Lopes and Cox, 1977; Furley and Ratter, 1988; Haase, 1999; Lilienfein et al., 2003; de Souza et al., 2007; Vourlitis et al., 2011; Wantzen et al., 2012). Soil pH is reported to be on average 5 for cerrado; however, well-drained arboreal forms of cerrado, such as upland forest, may have pH values as high as 6.5 (Lopes and Cox, 1977; Furley and Ratter, 1988; Haase, 1999; Lilienfein et al., 2003; de Souza et al., 2007). Similar trends were observed for surface (0–20 cm) soils collected at Fazenda Miranda, with the upland forest and woodland having higher pH than mixed grassland and flooded forest. Much of the variation in soil chemistry was associated with SOM content. In particular, variations in pH, total N, extractable P, and cations (except Al³⁺), and CEC were positively correlated with SOM content, illustrating the central role of SOM in nutrient storage and cycling, especially for N and P (Lopes and Cox, 1977; Fernandes et al., 1997; Bustamante et al., 2006). For example, SOM may account for 25 to 90% of the CEC in many tropical soils; however, the impact of SOM on CEC is dependent on pH (Oorts et al., 2000). The CEC may be positively correlated with

Table 5. Factor loadings for three factors generated from principal components analysis (PCA). Bold values indicate significant correlations between a given variable and factor.

Variable	PCA Factors		
	PCA-1	PCA-2	PCA-3
Rocks	0.009	0.252	-0.855
SOM†	-0.662	-0.068	-0.736
Sand	-0.005	0.997	0.021
Silt	0.060	-0.989	0.030
Clay	-0.044	-0.983	-0.065
pH	-0.982	0.063	-0.093
Total N	-0.578	-0.305	-0.707
P	-0.593	-0.132	-0.530
K	-0.696	-0.154	-0.560
Ca	-0.868	-0.085	-0.451
Mg	-0.873	-0.071	-0.428
Al	0.924	-0.160	-0.052
H	-0.061	-0.060	-0.916
CEC	-0.644	-0.119	-0.741

† SOM = soil organic matter, CEC = cation exchange capacity.

SOM content in soils with a pH > 5.5 because the dissociation of carbonyl and phenol groups and hydrolysis of bound metals in SOM lead to an increase in the number of negatively charged sites (Lopes and Cox, 1977; Oorts et al., 2000). Such a pH-dependent increase in the number of negatively charged sites on

Table 6. Results from a Pearson-product moment linear correlation analysis of the soil factors generated from principal components analysis (PCA), vegetation characteristics, and litter pool biomass and chemistry of the cerrado stands at the Fazenda Miranda. Bold values indicate statistically significant linear correlations between variables ($p < 0.05$).

Variable	n	PCA-1	PCA-2	PCA-3
LAI	50	-0.75	-0.04	0.23
Diameter	50	-0.15	0.07	0.14
Density	50	-0.53	-0.04	0.01
Basal area	50	-0.55	-0.14	0.10
Graminoid	50	0.63	-0.19	0.01
Diversity	5	-0.96	0.14	-0.26
Richness	5	-0.94	0.03	-0.31
Litter mass	40	-0.56	-0.20	-0.01
Litter N	40	-0.39	-0.22	0.03
Litter P	40	-0.61	-0.17	-0.24
Litter K ⁺	40	0.09	-0.40	-0.10
Litter Ca ²⁺	40	-0.80	-0.31	0.04

SOM would also explain the negative correlation between SOM content and extractable Al^{3+} that was observed in these soils (Oorts et al., 2000).

Relationships between Soil Properties and Vegetation Structure

We predicted that tree density and species diversity would increase with soil fertility, and spatial variations in soil fertility, expressed as PCA-1, were highly correlated with tree density, basal area, LAI, and tree species richness and diversity, indicating that tree abundance was closely related to soil fertility. These results are qualitatively similar to those reported from other tropical forests and savannas across global, regional, and local spatial scales, and in most of these studies, low P and/or cation (K^+ , Ca^{2+} , Mg^{2+}) availability are thought to be one of the most important controls on forest structure (Goodland and Pollard, 1973; Lopes and Cox, 1977; Laurance et al., 1999; Paoli et al., 2008; Lloyd et al., 2008; Quesada et al., 2009). For example, in tropical forests, forest biomass, stem density, and/or wood productivity are positively associated with P and cation availability across regional (i.e., Amazon Basin), landscape (1000 km²), and local (15 km²) spatial scales (Laurance et al., 1999; Malhi et al., 2009; Paoli et al., 2008; Quesada et al., 2009). Similar results have been reported from savanna over global (Lloyd et al., 2008) and regional (Lopes and Cox, 1977; Goodland and Pollard, 1973; Fölster et al., 2001; Moreno et al., 2008) scales, and typically, woody plant abundance reportedly decreases and grass abundance increases as soil fertility declines. Our data suggest that these patterns hold at the local scale as well. In general, PCA-1 was most closely correlated with soil pH (−0.98), Al^{3+} (0.92), Ca^{2+} and Mg^{2+} (−0.87), K^+ (−0.70), and to a lesser extent P (−0.59) and N (−0.58) content (Table 5), indicating that tree abundance may have been more sensitive to Al^{3+} availability, low pH, and/or non- Al^{3+} cation deficiency than by P or N deficiency. High levels of exchangeable Al^{3+} can lead to competition with other nutrients on cation exchange sites, enhancing nutrient deficiency (Ruggiero et al., 2002).

However, it is unclear whether an increase in tree density leads to an increase in soil fertility or whether an increase in soil fertility leads to an increase in tree density. Many authors argue that forests and woodlands can only persist in areas of high soil fertility, and that savanna grasslands typically have soil fertility levels too low to support trees and shrubs (Goodland and Pollard, 1973; Lloyd et al., 2008). Such patterns appear to be important in limiting the development of tropical forests along the forest–savanna boundary, where rainfall is adequate to support the development of forest (Ruggiero et al., 2002). But within the cerrado domain, Bond (2010) argues that most savanna soils contain enough nutrients in the upper 2 m soil layer to support trees. However, nearly 60% of the total root biomass and 75% of the fine root biomass of tropical savanna plants is reportedly in the upper 30- to 50-cm soil layer (Jackson et al., 1996; Lilienfein et al., 2001), and most nutrients are enriched in the surface soil layers (Kellman, 1979; Jobbágy and Jackson,

2001; Ruggiero et al., 2002). Together, these data suggest that surface soil layers play an important role in the nutrient uptake of savanna plants, and that nutrient-poor surface soils may limit the establishment of trees in cerrado.

Clearly, plants can affect soil fertility through nutrient uptake and retention (Hooper and Vitousek, 1997), resource use efficiency (ter Steege et al., 2006), and litter production (Vitousek and Sanford, 1986; Malhi et al., 2009). Trees have a greater capacity than grasses to access leached nutrients deep within the soil profile because of their more extensive root systems, and redistribute these nutrients to the soil surface through the input of nutrient-rich litter and/or hydraulic redistribution (Troxler-Gann et al., 2005; Wetzel et al., 2005; Saha et al., 2010), which has been reported from a variety of savanna ecosystems worldwide (Kellman, 1979; Mordelet et al., 1993; Vourlitis et al., 2011). While incomplete, our data are consistent with these results as litter mass was significantly higher in the forest, woodland, and dense-scrub fragments (Table 4) and soil fertility (PCA-1) was significantly correlated with litter mass and litter N, P, and Ca^{2+} concentration (Table 6).

Our data also suggest a close link between soil fertility and cerrado tree species richness and diversity at the Fazenda Miranda, which is consistent with the results from some studies (Gentry, 1988; Tuomisto et al., 2003; Long et al., 2012) but not others (Clinebell et al., 1995; de Souza et al., 2007). These divergent results may be due to other factors, such as precipitation, that can obscure relationships between soil fertility and species diversity across large spatial scales, the degree of spatial variability in soil properties, and/or an asymptotic response in plant species richness as soil fertility increases (Tuomisto et al., 2003; de Souza et al., 2007; Long et al., 2012). At our small spatial scale, variations in climate were not likely to be important, thus, high spatial variability in soil fertility (see Fig. 1 and Table 2) was presumably the driving force behind the correspondingly high spatial variability in tree species diversity and richness. This result was demonstrated both between fragments (Table 6), and within fragments, where using the coefficient of variation ($|\text{standard deviation}/\text{mean}| \times 100$) to quantify the spatial variation in soil fertility within each fragment (Schlesinger et al., 1996), tree species richness was found to increase asymptotically as within-fragment spatial variability (CV) in soil fertility (PCA-1) increased ($\text{Richness} = 32.24(1 - e^{-1.31 \times \text{CV}})$; $r^2 = 0.81$; $F_{1,3} = 15.84$; $p = 0.03$). Similar patterns were not observed with the other PCA factors, indicating that variation in soil fertility was the primary driver in spatial patterns of tree species richness across a variety of spatial scales. In turn, species rich communities tend to have high variability in growth form and patterns of resource use, partitioning, and allocation, which can enhance ecosystem nutrient retention, soil fertility, and spatial variation in soil resource use (Hooper and Vitousek, 1997).

There is also broad consensus that soil fertility is important for controlling the distributions of many tropical tree species (Clark et al., 1998; Hall et al., 2004; ter Steege et al., 2006; John et al., 2007; de Souza et al., 2007), and there are undoubtedly tree

species at the Fazenda Miranda that are restricted to particular soils. Preliminary analysis indicates that the abundance of some species, such as *Aspidosperma subincanum* Mart., *Chrysophyllum marginatum* (Hook. & Am.) Radlk., *Matayba guianensis* Radlk., and *Rhamnidium elaeocarpum* Reiss. was positively related to soil fertility, while the abundance of other species, such as *Caryocar brasiliense* Cambess., *Qualea grandiflora* Mart., *Q. parviflora* Mart., and *Terminalia argentea* Mart. & Zucc. were positively related to sand content. The extent to which soil chemical and physical properties control species distributions is the subject of continuing research.

In conclusion, we exploited small scale (1–10,000 m²) spatial variations in edaphic properties to quantify relationships between soil properties and cerrado physiognomy, and predicted that tree density, LAI, and species diversity would increase with soil fertility. Our data largely supported this hypothesis, as variations in cerrado stand structure and tree species diversity were significantly correlated with soil fertility but not soil physical properties measured here, even though these physical properties, in particular SOM and clay content, are undoubtedly important in maintaining soil fertility. How soil fertility interacts with spatial and temporal variations in soil moisture in these cerrado stands is currently unknown and is the subject of continuing research, but these interactions are undoubtedly important in affecting cerrado stand structure (de Assis et al., 2011). The high correlation between stand structure and soil fertility appeared to be due to in part variations in litter input, suggesting that vegetation modification of soil fertility was an important factor in maintaining spatial variations in soil fertility.

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