Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil

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Abstract

Several studies pointed out soil properties as the prime determinant of cerrado (the Brazilian savanna) physiognomies, and a gradient from "campo cerrado" (a shrub savanna) to "cerradão" (a tall woodland) has been correlated with a soil fertility gradient. Based on this hypothesis, we investigated soil-vegetation relationships in the Pé-de-Gigante Reserve (São Paulo State, Southeastern Brazil). We randomly distributed 10 quadrats (10 × 10 m) on each of the following physiognomies: "campo cerrado", "cerrado *sensu stricto*", "cerradão", and seasonal semideciduous forest, previously defined by the analysis of satellite images (LANDSAT-5). We sampled the woody individuals with stem diameter > 3 cm at soil level, identifying their species. In each quadrat, we collected soil samples at the depths of 0–5, 5–25, 40–60, and 80–100 cm, and determined pH, K, Ca, Mg, P, Al, H + Al, base saturation, aluminium saturation, cation exchange capacity, and percentage of sand, clay and loam. Obtained data were submitted to a canonical correspondence analysis (CCA) and to a detrended correspondence analysis (DCA). Our results showed a clear distinction between semideciduous forest and the cerrado physiognomies, based in soil parameters. The former was related to higher concentrations of cations and clay in the soil, while the latter was related to higher concentrations of exchangeable aluminium in the soil surface. The three cerrado physiognomies – "campo cerrado", "cerrado *sensu stricto*", and "cerradão" – could not be distinguished considering plant density and the analysed soil features.

Introduction

The Cerrado (Brazilian savanna) biome originally covered about 23% of the Brazilian territory and more than 90% of the Central Brazilian Plateau (Rizzini 1997). The Cerrado biome comprises a vegetation type associated to special ecological conditions where "savanna vegetation dominates, but it is not necessarily exclusive", being interspersed with riparian or gallery forests, patches of semideciduous forest, swamp and/or marshes (Bourlière and Hadley 1983). However, the "cerrado *sensu lato*" includes a variety of physiognomies from "campo limpo" (a grassland formation), through "campo sujo", "campo cerrado", and "cerrado *sensu stricto*" (savannic intermediary formations), to "cerradão" (a forest formation) (Coutinho

1978) (Figure 1), in which the density of woody individuals (trees and shrubs) is one of the most evident variables (Goodland 1971; Ribeiro et al. 1985).

The causes of the existence of savanna physiognomies and semideciduous forest under the same climate have been debated since the very first ecological investigations in cerrado environments, carried out by Warming (1892). The availability of nutrients in the soil has been pointed out by many authors as one of the most important determinants of cerrado vegetation. Working in Minas Gerais State (Brazilian Central Plateau), Goodland and Pollard (1973) showed a positive correlation between the gradient of cerrado physiognomies (as shown in Figure 1), expressed quantitatively by arboreal basal area per hectare, and edaphic variables such as the amounts of ni-
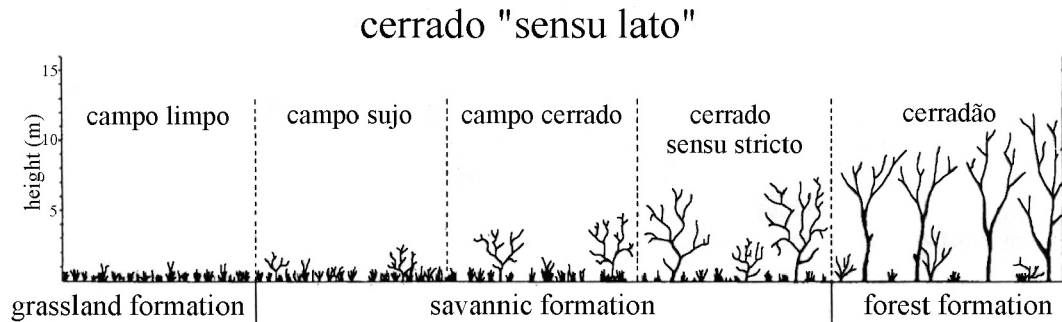
cerrado "sensu lato"

Figure 1. The cerrado physiognomic gradient (according to Coutinho (1978), modified).

trogen, phosphorus, and potassium. However, other researchers did not find similar relationships (Askew et al. 1971; Gibbs et al. 1983; Ribeiro 1983; Haridasan 1992).

Soils under cerrado are usually poor, acid, well-drained, deep, and show high levels of exchangeable aluminium (Queiroz-Neto 1982; Lopes 1984; Reatto et al. 1998). Aluminium can compete with other elements for the same chemical sites on the soil particles. Therefore, it was suggested that contents of exchangeable aluminium could be related to vegetation structure and composition (Arens 1963). Goodland and Pollard (1973) also showed a negative relationship between the basal area of cerrado trees and the content of exchangeable aluminium in the soil. Conversely, Haridasan (1992) suggested that aluminium concentration in the soil solution was probably not determining the occurrence of cerrado instead of forest, when comparing two cerrados in the Brazilian Federal District and another in Goiás State. Therefore, results are usually conflicting and inconclusive.

Vegetation and soil are so intimately related that it is difficult to identify cause-and-effect relationships. For instance, vegetation can aggregate and protect soil surface against water and wind erosion, and influence the transfer of nutrients to the soil solution, especially iron and aluminium, adding organic components to the soil (Ellis and Mellor 1995). Some species from Neotropical savannas, as *Byrsonima crassifolia* (L.) Kunth, *Clethra hondurensis* Britton, *Quercus shipii* Standl., *Q. oleoides* Cham. & Schlcht-ndl., and *Miconia albicans* (Sw.) Triana, are able to promote surface soil enrichment to levels as high as in the nearby forests (Kellman 1979). On the other hand, several authors highlighted the importance of soil resources in the establishment of plant communities, suggesting that competition between plant species occur mainly in the substrate (Tilman 1985; Fitter 1987).

More recently, other environmental features such as geomorphology, soil drainage, and water regime have been studied in order to explain the cerrado-forest gradient (Sherpherd et al. 1989; Furley 1996; Oliveira-Filho et al. 1997).

Our aim was to investigate soil-vegetation relationships in a gradient of three cerrado physiognomies and a contiguous seasonal forest patch, at a local scale, and based on the woody individuals. We confronted the density of woody species and some chemical and physical soil properties, trying to answer the following questions: Are vegetation physiognomies related to soil properties? Are soil fertility and the content of exchangeable aluminium related to vegetation structure and/or floristic variation, as proposed by other authors? At what depth are soil variables best correlated with the vegetation physiognomy?

Methods

We carried out this study in the Pé-de-Gigante Reserve (21°36–47′ S; 47°34–41′ W), which is part of the Vassununga State Park, in Santa Rita do Passa Quatro Municipality, São Paulo State, Brazil. The Reserve comprises 1,225 ha, in altitudes ranging from 590 to 740 m (Pivello et al. 1999) (Figure 2).

Regional climate is Cwa (according to Köppen (1948)) or type II (following Walter (1986)), which is the typical savanna climate with wet summers (October to March) and dry winters (May to August) (Figure 3).

Soils in the study area are mainly Neossolos (sandy soils) and Latossolos, according to the Brazilian Classification System (EMBRAPA Empresa
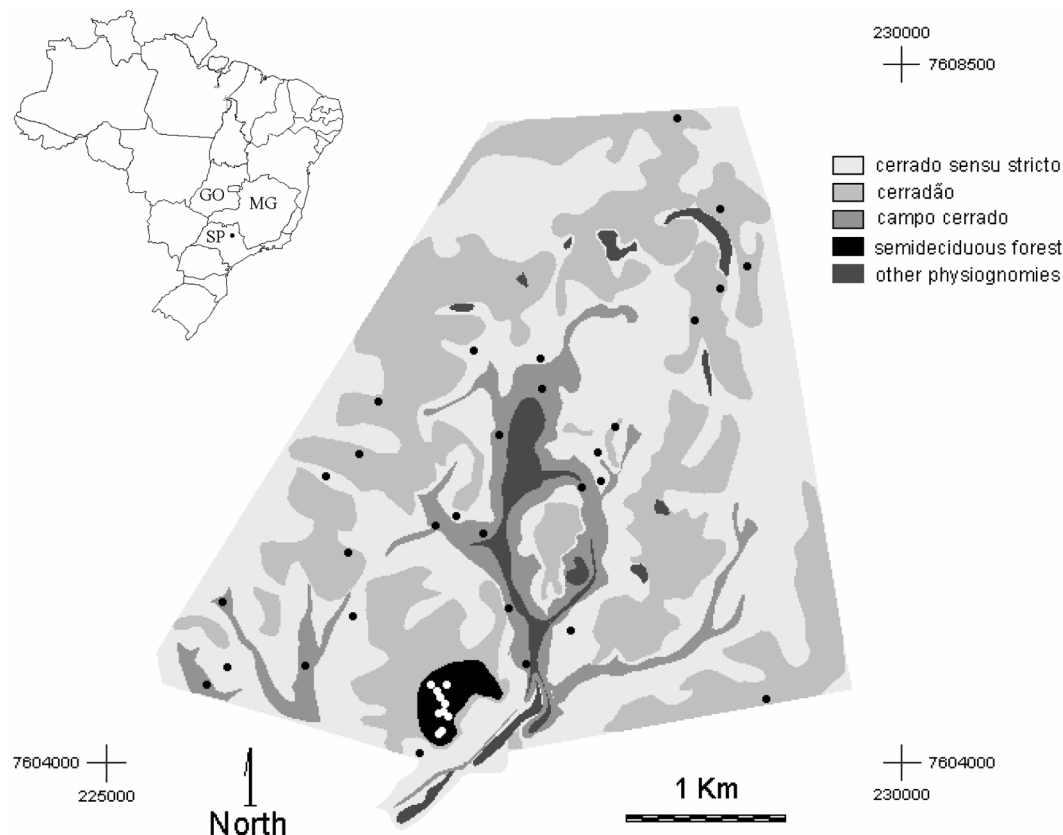
Figure 2. Location of Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, São Paulo State, Brazil) (SP = São Paulo State, MG = Minas Gerais State and GO = Goiás State) and its vegetation, based on LANDSAT satellite image (modified from Pivello et al. (1999)). Points represent approximate location of sample quadrats.

Brasileira de Pesquisa Agropecuária 1999), or Entisols and Oxisols (SOIL SURVEY STAFF 1990).

The Pé-de-Gigante Reserve includes several savanna physiognomies as well as riparian forest and floodplain marsh – which appear along the Paulicéia stream, in the centre of the Reserve – and a small patch of seasonal semideciduous forest. The cerrado ecosystems ("cerrado *sensu lato*") comprise "campo cerrado", "cerrado *sensu stricto*" and "cerradão".

We studied four of the vegetation physiognomies found in the Pé-de-Gigante Reserve: "cerradão", "cerrado *sensu stricto*" and "campo cerrado" which together occupy almost all the study area (96.6%), and the seasonal semideciduous forest patch (1.3% of the Reserve), comparing their soil properties and woody flora.

To sample the woody vegetation and soil, we randomly distributed 10 quadrats (10 × 10 m) on each physiognomy by taking out ten pairs of geographical coordinates for each physiognomy from a table of randomic numbers and locating them on a vegetation
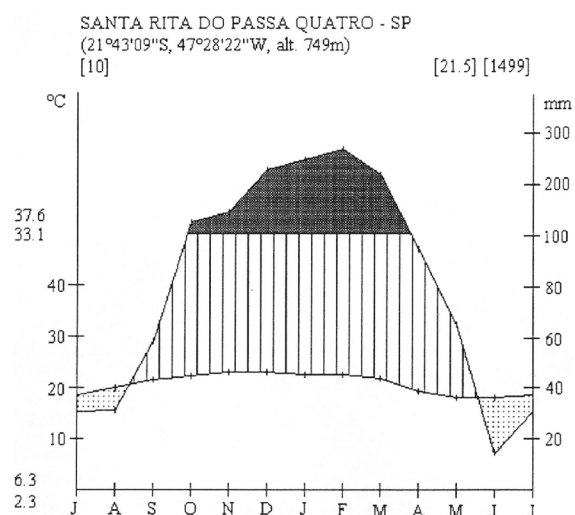

Figure 3. Climate diagram following Walter and Lieth (Walter 1986) for the Pé-de-Gigante Reserve region. Data from DAEE – Departamento de Águas e Energia Elétrica do Estado de São Paulo meteorological station, in Santa Rita do Passa Quatro (21°43′09″ S; 47°28′22″ W, for the period of 1985 to 1994 (Pivello et al. 1998).

map (1:50.000), previously produced (Pivello et al. 1999). The vegetation map and the proposed vegetation classes were based on the classification of LANDSAT-5 satellite images (from 05/7/1995, 22/8/ 1995, 29/01/1996, 23/7/1996 and 08/6/1997), according to the normalised difference vegetation index (NDVI) (Rouse et al. 1973). In the field, each quadrat was located and geo-referred with a GPS (Global Positioning System) (Figure 2).

We sampled every woody individual (stem diameter > 3 cm at soil level, following SMA (Secretaria do Meio Ambiente) (1997)) found in each quadrat and identified them to species level, using an identification key based on vegetative characters (Batalha and Mantovani 1999). We calculated the species absolute density, according to Mueller-Dombois and Ellenberg (1974).

In each quadrat, we collected randomly soil samples in four depths (0–5, 5–25, 40–60, and 80–100 cm) for chemical and granulometric analyses. Air dried soil samples were sieved (2.0 mm) and analysed for total organic carbon (OM) by spectrophotometry after oxidation with sodium dichromate in presence of sulfuric acid and a subsequent titration with ammonic ferrous sulfate; phosphorus (P) was determined by spectrophotometry after anion exchange resin extraction; exchangeable Al, basic cations (K, Ca, Mg) and H+Al were extracted with 1 mol_c L^{-1} KCl, cation exchange resin and buffer SMP, respectively; cation exchange capacity (CEC) was determined based on the sum of K, Ca and Mg; base saturation (V) was calculated as a percentage of total CEC; aluminium saturation (m) was calculated based on effective cation exchange capacity; sum of bases (SB) represents Ca + Mg + K (procedures described by van Raij et al. (1987) and Camargo et al. (1986)). Soil pH was determined in $CaCl_2$ (0.01 M) solution. Soil particles were analysed following the Boyoucus's method (described by Camargo et al. (1986)).

Soil features and the absolute density of plant species were ordinated by direct analysis of gradient. We used canonical correspondence analyses (CCA) (ter Braak 1986) to investigate relationships between environmental variables and species abundance in sample plots. The original matrix considered the absolute density of all sampled species, as the density of woody species is a robust parameter to distinguish cerrado physiognomies (Goodland 1971; Ribeiro et al. 1985). The matrix of environmental variables comprised the soil attributes (pH, organic matter, P, K, Ca, Mg, Al, H + Al, CEC, V, m, sand, loam and

clay), and separate matrices were made for each soil depth (0–5, 5–25, 40–60, and 80–100 cm).

After a preliminary analysis, we eliminated variables with high multicollinearity, detected by high inflation values, and variables poorly correlated with ordination axes, indicated by low intraset correlation coefficients and non-significant canonical coefficients (t values < 2.1). Significance of the overall CCA ordination was tested using a Monte Carlo permutation procedure (ter Braak 1986).

Detrended correspondence analysis (DCA) (ter Braak et al. 1995) was also carried out for the most abundant species – in our case, those with 10 or more individuals – using density data. As the DCA results indicated internal variability in the semideciduous forest, a canonical correspondence analysis (CCA) was done using only soil surface (0–5cm) data related to this vegetation physiognomy. In this case, the vegetation matrix had 54 species and the environmental matrix had percentage of clay, sum of bases and aluminium content values. All multivariate analyses used the CANOCO package (ter Braak 1988).

Since aluminium appears to be an important element in cerrado soils and many authors (Arens 1963; Goodland and Pollard 1973) have discussed its relationship with the vegetation and with other soil properties, especially pH and the content of bases, we plotted the mean and standard deviation values of exchangeable aluminium, aluminium saturation, pH and base saturation along soil depth in the four studied physiognomies to observe the patterns. Spearman correlation test was carried out relating aluminium content with pH evidence relationships among such variables.

Results

We sampled 123 species of woody plants, belonging to 45 families (Table 1). The richest families were Fabaceae (15 species), Myrtaceae (12 species), Caesalpiniaceae (7 species) and Asteraceae, Bignoniaceae, Mimosaceae, Rubiaceae and Vochysiaceae, with 5 species each, which together accounted for 48% of the total number of species.

Soil properties according to the sampled vegetation physiognomies and soil depth are shown in Table 2. These values against species density in the canonical correspondence analysis (CCA) revealed significant correlation at the first three soil depths (0–5, 5–25, and 40–60 cm) in the first axis (F = 3.18, p <

Table 1. Woody plant species surveyed in the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, São Paulo State), according to families.

Anacardiaceae
  Astronium graveolens Jacq.
  Tapirira guianensis Aubl.
Annonaceae
  Annona coriacea Mart.
  Annona crassiflora Mart.
  Guatteria australis A. St-Hil.
  Xylopia aromatica A. St-Hil.
Apocynaceae
  Aspidosperma cuspa (Kunth) S. F. Blake
  Aspidosperma cylindrocarpon Müll. Arg.
  Aspidosperma tomentosum Mart.
Araliaceae
  Didymopanax vinosum (Cham. & Schltdl.) Seem
Asteraceae
  Eremanthus erythropappus Sch. Bip.
  Eremanthus sphaerocephalus Baker
  Gochnatia pulchra Cabrera
  Piptocarpha rotundifolia (Less.) Baker
  Vernonia rubriramea Mart.
Bignoniaceae
  Jacaranda caroba (Vell.) A. DC.
  Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S. Moore.
  Tabebuia ochracea (Cham.) Standl.
  Tabebuia serratifolia (Vahl.) Nicholson
  Zeyhera tuberculosa (Vell.) Bur.
Bombaceae
  Eriotheca gracilipes (K. Schum.) A. Robyns
  Pseudobombax grandiflorum (Mart. & Zucc.) A. Robyns
Boraginaceae
  Cordia sellowiana Cham.
Burseraceae
  Protium heptaphyllum (Aubl.) March
Caesalpiniaceae
  Bauhinia forficata Link
  Bauhinia rufa (Bong.) Steud.
  Copaifera langsdorffii Desf.
  Dyptichandra aurantiaca Tul.
  Hymenaea courbaril L.
  Hymenaea stigonocarpa Mart.
  Sclerolobium paniculatum Vogel
Caryocaraceae
  Caryocar brasiliense Cambess.
Celastraceae
  Plenckia populnea Reissek
Chrysobalanaceae
  Couepia grandiflora (Mart. & Zucc.) Benth. ex Hook. f.
  Licania humilis Cham. & Schltdl.
Clusiaceae
  Kielmeyera rubriflora Cambess.

Table 1. Continued.

  Kielmeyera variabilis Mart.
Combretaceae
  Terminalia brasiliensis Cambess.
Connaraceae
  Connarus suberosus Planch.
Ebenaceae
  Dyospiros hispida A. DC.
Erythroxylaceae
  Erythroxylum suberosum A. St-Hil.
Euphorbiaceae
  Actinostemon communis Müll. Arg.
  Croton floribundus Spr.
Fabaceae
  Acosmium dasycarpum (Vogel) Yakovlev
  Acosmium subelegans (Mohl) Yakovlev
  Andira anthelmia (Vell.) J. Macbr.
  Andira cuiabensis Benth.
  Bowdichia virgilioides Kunth.
  Dalbergia frutescens (Vell.) Britton
  Dalbergia miscolobium Benth.
  Machaerium aculeatum Raddi.
  Machaerium acutifolium Vogel
  Machaerium stiptatum Vogel
  Machaerium villosum Vogel
  Platyciamus regnellii Benth.
  Platypodium elegans Vogel
  Pterodon pubescens Benth.
  Vatairea macrocarpa (Benth.) Ducke
Flacourtiaceae
  Casearia sylvestris Sw.
Lacistemaceae
  Lacistema aggregatum (O. Berg) Rusby
Lauraceae
  Nectandra megapotamica (Spr.) Mez
  Ocotea corymbosa (Meiss.) Mez
  Ocotea pulchella Mart.
Loganiaceae
  Strychnos pseudoquina A. St-Hil.
Lythraceae
  Lafoensia pacari A. St-Hil.
Malpighiaceae
  Byrsonima coccolobifolia A. Juss.
  Byrsonima crassa Nied.
  Byrsonima intermedia A. Juss.
Melastomataceae
  Miconia albicans Triana
  Miconia ligustroides Naudin
  Miconia rubiginosa (Bonpl.) A. DC.
  Tibouchina stenocarpa (A. DC.) Cogn.
Meliaceae
  Cedrela fissilis Vell.

Table 1. Continued.

Mimosaceae
   Anadenanthera falcata (Benth.) Speg.
   Anadenanthera macrocarpa (Benth.) Brenan
   Dimorphandra mollis Benth.
   Plathymenia reticulata Benth.
   Stryphnodendron obovatum Mart.
Monimiaceae
   Siparuna guianensis Aubl.
Myristicaceae
   Virola sebifera Aubl.
Myrtaceae
   Campomanesia pubescens (A. DC.) O. Berg
   Eugenia aurata O. Berg
   Eugenia florida A. DC.
   Eugenia punicifolia (Kunth) A. DC.
   Myrcia bella Cambess.
   Myrcia lasiantha A. DC.
   Myrcia guianensis O. Berg
   Myrcia tomentosa (Aubl.) A. DC.
   Myrcia uberavensis O. Berg
   Myrciaria floribunda (West & Willd.) O. Berg
   Psidium laruotteanum Cambess.
   Siphoneugenia regnelliana (Kiaesrk.) Mattos
Nyctaginaceae
   Guapira noxia (Netto) Lund
   Guapira opposita (Vell.) Reitz.
   Neea theifera Oerst.
Ochnaceae
   Ouratea semiserrata (Mart. & Nees) Engl.
   Ouratea spectabilis (Mart.) Engl.
Polygalaceae
   Bredemeyera floribunda Willd.
Proteaceae
   Roupala montana Aubl.
Rubiaceae
   Amaioua guianensis Aubl.
   Coussarea hydrangeaefolia (Benth.) Benth. & Hook. ex Müll.
   Arg.
   Guettarda virbunoides Cham. & Schltdl.
   Palicourea rigida Kunth
   Tocoyena formosa (Cham. & Schltdl.) K. Schum.
Rutaceae
   Esenbeckia febrifuga (A. St-Hil.) A. Juss. ex Mart.
   Zanthoxylum rhoifolium Lam.
Sapindaceae
   Cupania oblongifolia Mart.
   Cupania vernalis Cambess.
   Matayba elaegnoides Radlk.
Sapotaceae
   Pouteria ramiflora (Mart.) Radlk.
   Pouteria torta (Mart.) Radlk.

Table 1. Continued.

Styracaceae
   Styrax ferrugineus Nees & Mart.
Symplocaceae
   Symplocos pubescens Klotz
Tiliaceae
   Luehea divaricata Mart.
Verbenaceae
   Aegiphila lhotzkiana Cham.
   Aegiphila sellowiana Cham.
   Aloysia virgata (Ruiz & Pav.) A. Juss.
   Lippia salviaefolia Cham.
Vochysiaceae
   Qualea dichotoma Warm.
   Qualea grandiflora Mart.
   Qualea parviflora Mart.
   Vochysia cinammomea Pohl
   Vochysia tucanorum Mart.

0.01, for 0–5 cm; F = 2.82, p < 0.01, for 5–25 cm; F = 2.99, p < 0.01, for 40–60 cm) but it was not significant at 80–100 cm. The first two soil depths also showed overall significance (F = 1.35, p = 0.01; F = 1.10, p = 0.01, respectively at 0–5 cm and 5–25 cm). The best correlation in the CCA came from surface soils (0–5 cm), represented in the ordination diagram (Figure 4).

The canonical coefficients, the intraset correlation coefficients, and the correlation between environmental variables (of 0–5cm soil depth) and ordination axes are presented in Table 3, where the most significant variables for the first two axes according to t values for soil surface can also be distinguished. Considering both the canonical coefficient and intraset correlation coefficient, the soil variable most related to vegetation physiognomies was the percentage of clay. Potassium, pH, calcium, phosphorous and base saturation (V) were also important according to one or another coefficient. Analysing the results in Figure 4Table 2 we can also notice a tendency of decreasing contents of clay following the gradient from semideciduous forest to campo cerrado.

The sum of all unconstrained eigenvalues was 6.21; the sum of canonical eigenvalues using soil surface data (0–5cm) was 1.79. In this CCA analysis, species cumulative percentages of variance in the four first axes were respectively 9.6%, 13.4%, 16.7% and 19.4%. For the species-environment correlation this proportion was 33.2%, 46.4%, 57.9%, and 67.5%. Soil data at 5–25 cm depth showed, for the first four

Table 2. Soil physical and chemical properties (mean, standard deviation, median, and the first and the third quartiles [25% and 75%]) of cerrado physiognomies and semideciduous forest in the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, São Paulo State) at four different depths (0–5, 5–25, 40–60 and 80–100 cm). (OM = organic matter, P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = exchangeable aluminium, V = base saturation, m = aluminium saturation, clay = percentage of clay).

Depth cm	Vegetation		pH CaCl2	OM g/kg	P mg/kg	K mmolc/kg	Ca mmolc/kg	Mg mmolc/kg	Al mmolc/kg	V %	m %	clay %
0–5	campo cerrado	mean	3.48	31.10	7.70	0.45	1.50	1.70	10.60	5.20	74.40	7.80
		standard deviation	0.18	10.54	5.21	0.26	0.97	0.67	3.13	2.04	4.27	2.20
		median	3.40	28.00	6.50	0.45	1.00	2.00	11.00	5.00	73.50	7.00
		25%	3.40	23.25	4.25	0.20	1.00	1.00	8.25	4.25	71.50	6.00
		75%	3.58	38.50	8.75	0.58	1.75	2.00	12.00	5.75	75.75	9.50
	cerrado *sensu stricto*	mean	3.52	35.30	4.90	0.76	1.20	1.70	11.30	4.70	75.30	9.00
		standard deviation	0.20	8.45	1.66	0.43	0.63	0.67	2.71	1.77	8.62	2.54
		median	3.45	35.50	4.50	0.65	1.00	2.00	11.00	4.00	77.00	8.00
		25%	3.40	32.50	4.00	0.45	1.00	1.00	9.25	3.25	70.25	8.00
		75%	3.68	38.50	5.00	0.90	1.75	2.00	13.50	5.75	81.75	10.00
	cerradão	mean	3.35	53.40	6.10	0.63	2.30	1.80	18.40	3.70	81.20	14.20
		standard deviation	0.17	6.40	2.42	0.44	2.54	1.23	3.57	2.41	10.17	13.64
		median	3.35	54.00	5.50	0.50	1.00	1.00	18.50	3.00	84.00	12.00
		25%	3.23	48.75	4.00	0.28	1.00	1.00	16.25	2.00	80.75	8.50
		75%	3.40	58.50	7.50	0.80	1.75	2.00	20.00	3.75	88.25	12.00
	semideciduous forest	mean	4.44	50.10	10.60	1.99	32.50	20.40	3.40	39.80	14.70	13.60
		standard deviation	0.62	10.60	4.27	0.96	29.91	16.29	3.10	22.70	20.94	2.95
		median	4.35	53.00	10.00	1.80	22.00	17.50	3.50	39.00	8.00	12.00
		25%	4.03	41.00	8.25	1.50	9.75	8.75	2.00	24.50	2.50	12.00
		75%	4.60	57.00	12.75	2.50	48.50	26.00	4.00	54.25	16.75	15.50
5–25	campo cerrado	mean	3.85	20.00	7.40	0.27	1.50	1.10	8.30	6.00	74.90	8.40
		standard deviation	0.10	3.65	6.22	0.22	1.58	0.32	2.06	6.36	12.74	3.50
		median	3.90	20.50	6.00	0.20	1.00	1.00	8.00	4.00	78.00	7.00
		25%	3.80	17.00	3.00	0.20	1.00	1.00	7.25	4.00	76.50	6.00
		75%	3.90	23.50	9.00	0.20	1.00	1.00	8.75	4.75	79.50	10.00
	cerrado *sensu stricto*	mean	3.84	19.90	3.80	0.29	1.00	1.00	8.00	4.90	76.70	9.80
		standard deviation	0.16	4.93	1.55	0.14	0.00	0.00	2.11	0.88	5.27	2.39
		median	3.85	19.00	3.00	0.20	1.00	1.00	8.00	5.00	78.00	8.00
		25%	3.70	17.50	3.00	0.20	1.00	1.00	6.25	4.00	73.50	8.00
		75%	3.98	19.00	4.00	0.30	1.00	1.00	9.00	5.75	79.50	12.00

Table 2. Continued.

Depth cm	Vegetation		pH CaCl2	OM g/kg	P mg/kg	K mmolc/kg	Ca mmolc/kg	Mg mmolc/kg	Al mmolc/kg	V %	m %	clay %
	cerradão	mean	3.75	24.60	3.80	0.30	1.00	1.40	11.70	4.00	80.90	11.80
		standard deviation	0.08	5.10	1.75	0.17	0.00	0.70	3.23	1.15	4.89	4.26
		median	3.75	25.50	3.50	0.20	1.00	1.00	12.00	4.00	82.00	12.00
		25%	3.70	22.50	3.00	0.20	1.00	1.00	10.00	3.00	78.50	10.50
		75%	3.80	29.00	4.00	0.30	1.00	1.75	13.00	4.00	84.75	14.00
	semideciduous forest	mean	3.99	21.90	4.50	1.05	4.80	4.80	7.90	21.20	47.70	13.60
		standard deviation	0.24	4.12	0.71	0.48	3.55	3.39	2.56	15.12	22.23	3.86
		median	3.95	20.50	4.00	1.00	4.50	4.00	8.00	18.00	49.00	13.00
		25%	3.83	19.00	4.00	0.73	1.25	2.25	8.00	9.25	34.75	10.50
		75%	4.00	23.50	5.00	1.45	8.50	5.75	9.00	31.50	64.00	14.00
40–60	campo cerrado	mean	4.00	12.30	4.00	0.20	1.10	1.10	5.40	6.30	68.30	10.00
		standard deviation	0.09	2.36	3.94	0.00	0.32	0.32	1.78	1.49	7.20	5.08
		median	4.00	12.00	3.00	0.20	1.00	1.00	5.50	6.00	67.00	8.00
		25%	3.90	12.00	2.00	0.20	1.00	1.00	4.00	5.25	65.00	8.00
		75%	4.10	13.50	3.75	0.20	1.00	1.00	6.00	7.00	73.00	9.50
	cerrado *sensu stricto*	mean	3.96	11.90	2.60	0.22	1.00	1.20	5.40	6.50	67.80	11.00
		standard deviation	0.08	2.64	0.52	0.06	0.00	0.42	1.65	1.51	8.73	2.87
		median	4.00	13.00	3.00	0.20	1.00	1.00	5.50	6.00	71.00	10.00
		25%	3.90	9.75	2.00	0.20	1.00	1.00	4.25	6.00	60.75	8.50
		75%	4.00	14.00	3.00	0.20	1.00	1.00	6.00	7.75	73.00	13.50
	cerradão	mean	3.95	14.10	2.60	0.23	1.30	1.20	6.80	6.30	71.60	13.33
		standard deviation	0.10	2.85	0.97	0.09	0.67	0.42	1.23	2.58	4.90	4.47
		median	4.00	14.00	2.00	0.20	1.00	1.00	7.00	5.50	71.00	14.00
		25%	3.90	12.00	2.00	0.20	1.00	1.00	6.25	5.00	69.00	10.00
		75%	4.00	17.00	3.00	0.20	1.00	1.00	7.00	6.00	76.00	16.00
	semideciduous forest	mean	3.95	11.30	2.60	0.43	1.80	2.50	6.30	14.10	60.80	17.50
		standard deviation	0.10	2.26	0.52	0.31	1.75	1.65	1.06	12.86	15.55	6.92
		median	3.90	12.00	3.00	0.30	1.00	2.50	6.50	9.50	66.50	16.00
		25%	3.90	9.75	2.00	0.20	1.00	1.00	5.25	6.25	58.50	12.50
		75%	4.00	12.00	3.00	0.55	1.00	3.00	7.00	11.75	69.00	19.50
80–100	campo cerrado	mean	4.05	9.10	3.70	0.21	1.50	1.00	4.90	9.00	64.20	11.20
		standard deviation	0.08	3.21	2.87	0.03	1.58	0.00	1.73	6.58	11.34	5.18

Table 2. Continued.

| Depth cm	Vegetation		pH CaCl2	OM g/kg	P mg/kg	K mmolc/kg	Ca mmolc/kg	Mg mmolc/kg	Al mmolc/kg	V %	m %	clay %
		median	4.05	8.00	2.50	0.20	1.00	1.00	6.00	6.50	69.00	10.00
		25%	4.00	7.00	2.00	0.20	1.00	1.00	3.25	6.00	58.00	8.00
		75%	4.10	9.00	3.75	0.20	1.00	1.00	6.00	9.50	73.00	12.00
	cerrado sensu stricto	mean	4.02	9.80	2.20	0.20	1.10	1.10	4.30	7.40	59.80	12.00
		standard deviation	0.14	3.77	0.79	0.00	0.32	0.32	2.71	1.51	13.85	3.89
		median	4.00	9.00	2.00	0.20	1.00	1.00	4.00	7.50	59.50	10.00
		25%	3.93	7.00	2.00	0.20	1.00	1.00	3.00	6.25	56.50	10.00
		75%	4.15	11.25	2.00	0.20	1.00	1.00	5.00	8.00	68.00	15.00
	cerradão	mean	4.01	12.60	2.10	0.20	1.00	1.10	5.00	6.00	66.90	14.89
		standard deviation	0.07	3.13	0.57	0.00	0.00	0.32	1.56	1.15	8.48	5.58
		median	4.00	12.00	2.00	0.20	1.00	1.00	5.50	6.00	69.00	16.00
		25%	4.00	12.00	2.00	0.20	1.00	1.00	4.25	5.25	65.00	12.00
		75%	4.08	14.00	2.00	0.20	1.00	1.00	6.00	6.00	73.00	18.00
	semideciduous forest	mean	4.01	8.60	2.30	0.23	1.00	2.00	5.30	9.40	61.90	19.70
		standard deviation	0.07	0.84	0.67	0.05	0.00	0.94	1.49	2.41	9.88	6.90
		median	4.00	9.00	2.00	0.20	1.00	2.00	5.00	9.50	65.00	18.00
		25%	4.00	9.00	2.00	0.20	1.00	1.00	4.25	7.00	57.75	14.50
		75%	4.08	9.00	3.00	0.28	1.00	3.00	6.00	10.75	68.75	22.00
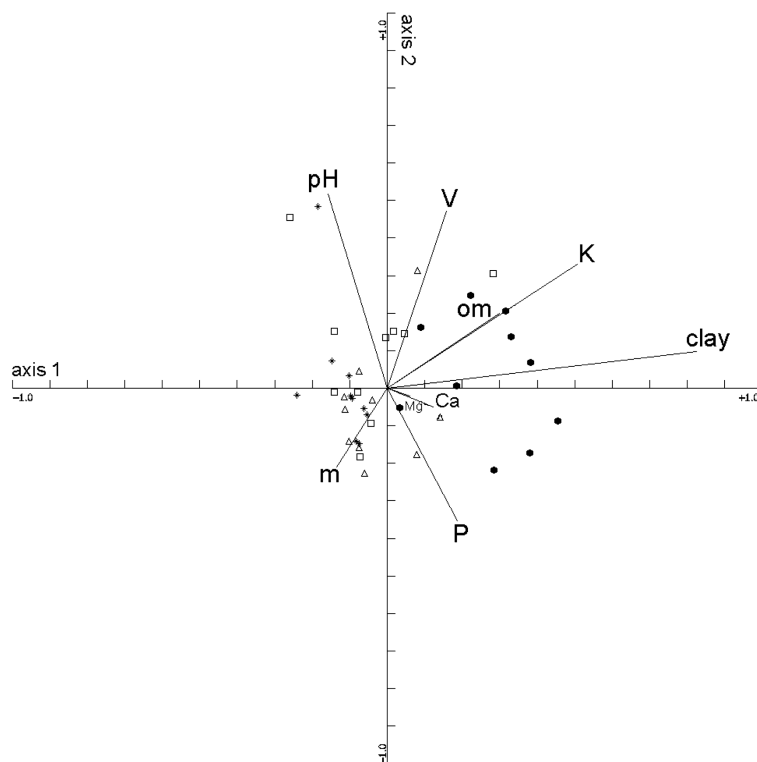
Figure 4. Biplot of the CCA ordination diagram, using the absolute density of woody species and surface soil (0–5cm) variables. Key: om = organic matter; Ca = calcium; Mg = magnesium; K = potassium; P = phosphorus; V = base saturation; m = aluminium saturation; clay = percentage of clay; and pH. Numbers indicate sample plots: 1 to 10 = "campo cerrado"; 11 to 20 = "cerrado *sensu stricto*"; 21 to 30 = "cerradão"; 31 to 40 = semideciduous forest.

Table 3. Canonical coeffcients and intraset correlation coefficients for axes 1 and 2, and weighted correlation matrix for the environmental variables supplied in the CCA using 0–5 cm depth soil data (canonical coefficients > 2.2 and intraset correlations > 0.5 in bold).

| | canonical coefficients | | intraset correlation coefficients | | | | | | | | | |
	axis 1	axis 2	axis 1	axis 2	pH	OM	P	K	Ca	Mg	V	m
PH	**−0.48**	**0.56**	−0.13	0.45	–							
OM	0.11	0.20	0.25	0.17	0.26	–						
P	−0.08	**−0.48**	0.16	−0.31	−0.10	−0.14	–					
K	**0.49**	**0.51**	0.43	0.29	0.11	−0.07	0.46	–				
Ca	0.05	**0.33**	0.10	−0.04	−0.49	−0.05	0.14	0.06	–			
Mg	−0.02	0.13	0.05	−0.02	0.45	0.01	0.08	0.06	**−0.59**	–		
V	−0.03	**0.66**	0.13	0.41	0.18	0.00	0.01	0.02	−0.23	0.08	–	
m	0.13	−0.38	−0.11	−0.18	0.31	−0.03	0.27	−0.03	−0.37	0.39	0.28	–
clay	**0.84**	**−0.42**	**0.70**	0.08	0.22	0.41	−0.02	0.15	−0.06	0.24	0.26	−0.09

axes the cumulative percentages of variance of 8.6%, 12.0%, 14.9%, and 17.2% for species data. For the species-environment correlation we have found 34.7%, 48.5%, 60.2%, and 69.5%. In this case, the sum of canonical eigenvalues was 1.54.

In the detrended correspondence analysis (DCA) for the most abundant species, the first and second axes contributed with 21.50 and 8.00% of the vari-ance, respectively. The ordination diagram of this analysis showed three different groups (Figure 5). The first and biggest one was mainly formed by typical cerrado species, as *Miconia albicans* Triana (micoalbi), *Erythroxylum suberosum* A. St-Hil. (erytsube), *Dalbergia miscolobium* Benth. (dalbmisc), *Pouteria torta* (Mart.) Radlk. (pouttort), *Anadenanthera falcata* (Benth.) Speg. (anadfalc), and *Caryocar brasil-*
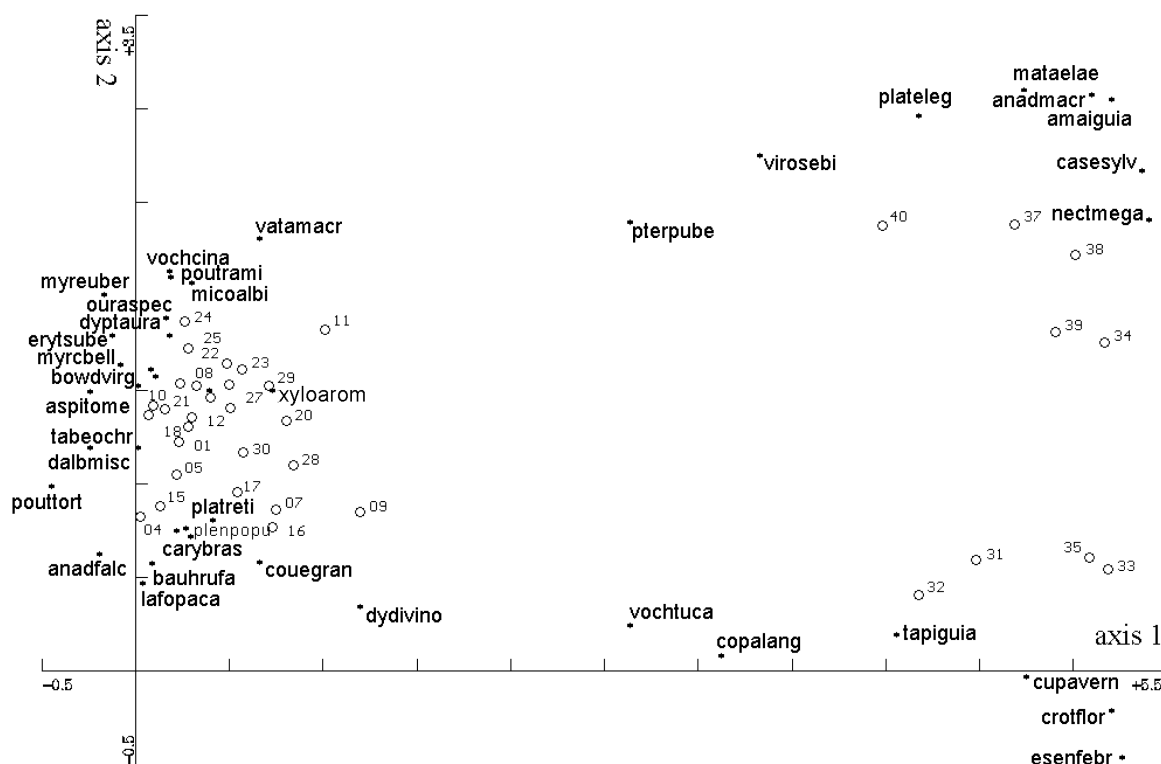
Figure 5. Biplot of the DCA ordination diagram, using the absolute density of the most abundant woody species in the Pé-de-Gigante Reserve (São Paulo, Brazil). Numbers indicate sample plots: 1 to 10 = "campo cerrado"; 11 to 20 = "cerrado *sensu stricto*"; 21 to 30 = "cerradão"; 31 to 40 = semideciduous forest Species names are shortened (see Table 1).

iense Cambess. (carybras), associated with cerrado plots. The other two groups, distinguished by the second axis, were composed of semideciduous forest quadrats but related to different forest species: one group was characterised by *Nectandra megapotamica* (Spr.) Mez (nectmega), *Casearia sylvestris* Sw. (casesylv), *Platypodium elegans* Vogel (plateleg), *Anadenanthera macrocarpa* (Benth.) Brenan (anadmacr), *Amaioua guianensis* Aubl. (amaiguia), *Matayba elaegnoides* Radlk. (mataelae), *Virola sebifera* Aubl. (virosebi), and *Pterodon pubescens* Benth. (pterpube), while the other group was characterised by *Tapirira guianensis* Aubl. (tapiguia), *Copaifera langsdorffii* Desf. (copalang), *Cupania vernalis* Cambess. (cupavern), *Vochysia tucanorum* Mart. (vochtuca), *Croton floribundus* Spr. (crotflor), and *Esenbeckia febrifuga* (A. St-Hil.) A. Juss. ex Mart. (esenfebr). We could not make any distinction among the three cerrado physiognomies based on this analysis.

CCA using only the semideciduous forest data was not significant according to Monte Carlo permutation test (F = 1.44, p = 0.12), probably as a consequence of the small number of quadrats (10) in this analysis.

Nevertheless, these results were considered here, with caution. For the first axis, eigenvalue was 0.32, and cumulative percentage of variance was 20.00% for species data and 47.80% for species-environment correlation (Figure 6). The best correlated environmental variable for the first axis was the sum of bases (intraset correlation = 0.75 and canonical coefficient = 0.89 with significant t value). Intraset correlation and canonical coefficient values for the amount of aluminium in the first axis were −0.72 and −0.31, respectively, showing that it was negatively correlated to that axis. Percentage of clay was mainly correlated with the third axis (intraset correlation = 0.77; canonical coefficient = 1.16, with significant t value). The ordination diagram with the first and third axes showed that *Pterodon pubescens* and *Virola sebifera* were associated with high sum of bases values while *Myrcia guianensis* O. Berg, *Didymopanax vinosum* (Cham. & Schlchtndl.) Seem, and *Xylopia aromatica* A. St-Hil. were related to high contents of exchangeable aluminium in the soil (Figure 6).

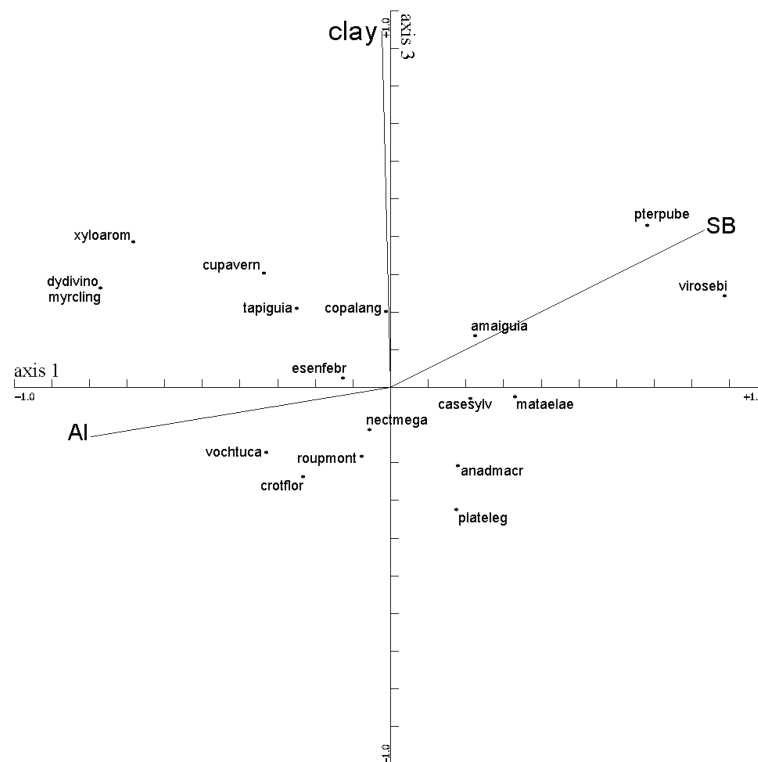The intraset correlation and the canonical coefficient values for exchangeable aluminium saturation

Figure 6. Biplot of the CCA ordination diagram of semideciduous forest species and quadrats, using the absolute density of the most abundant woody species and the following soil surface variables: sum of bases (SB), exchangeable aluminium (Al) and percentage of clay (clay). Species names are shortened (see Table 1).

were not significant (Table 3). However, the CCA ordination diagram (Figure 4) showed numerous quadrats related to the aluminium saturation vector.

Comparing exchangeable aluminium and pH variation along soil depth in the four studied physiognomies (Figure 7), we found decreasing values of exchangeable aluminium from the surface soil to higher depths. Considering the exchangeable aluminium, we could notice higher values at surface soil in the more closed cerrado physiognomy ("cerradão") which decreased towards the more open physiognomy ("campo cerrado"); semideciduous forest showed the lowest levels of exchangeable aluminium at the surface soil. However, the values in the four vegetation physiognomies became very similar down to higher depths. Figure 7 also showed that the amounts of aluminium in the soil varied inversely according to pH.

Spearman tests showed strong negative correlations (significant at 0.01 level) between exchangeable aluminium and pH values, at 0–5 and 5–25 cm soil depths in the semideciduous forest (−0.934, at 0–5 cm), cerrado *sensu stricto* (−0.779 at 5–25 cm) and

campo cerrado (−0.807 at 0–5 cm), but not in cerradão.

Discussion

Canonical correspondence analysis showed that the edaphic variables considered here explained only part of the physiognomical gradient variation, as indicated by the low eigenvalues and cumulative percentages of variance, and by the difference between the sum of unconstrained eigenvalues and the canonical eigenvalues. This considerable difference between the sum of the unconstrained eigenvalues and the canonical eigenvalues pointed out that important environmental variables have not been taken into account. We suggest that one of such variables is the water dynamics in the soil. However, this fact did not invalidate the relationships showed, since they were statistically significant.

The most superficial was soil, the best were its properties related to the vegetation physiognomic variation. The correspondence between soil and veg-
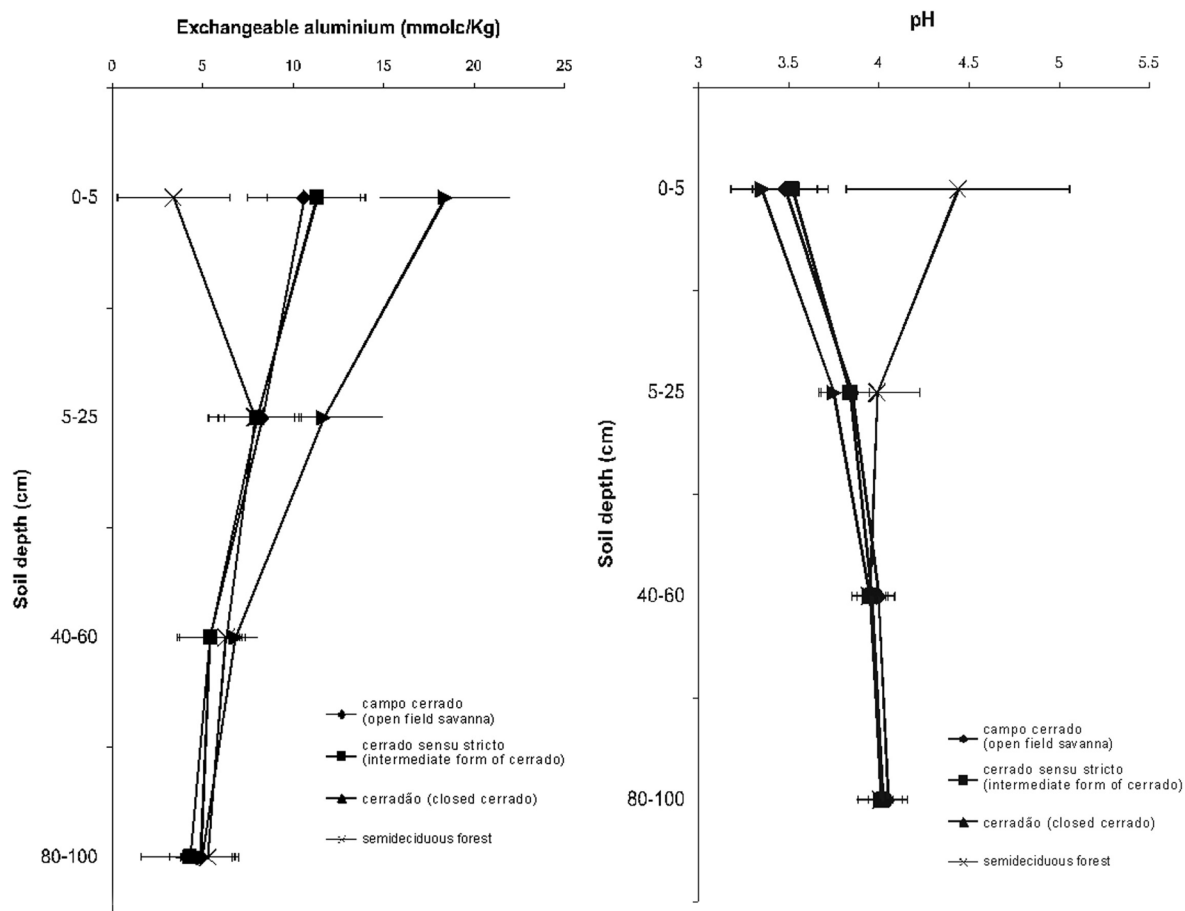
Figure 7. Variation of exchangeable aluminium and pH (mean and standard deviation) down to soil profile in "campo cerrado", "cerrado *sensu stricto*", "cerradão", and semideciduous forest at Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, São Paulo, Brazil).

etation was much higher for surface soil data and lowest for soil at 80–100 cm. Furley (1976) studied catenary slopes in Central America and showed strong correlation between vegetation patterns and surface soils properties. He also found that soil below surface horizons (10–15 cm) were extremely uniform. He stated that "Clearly, there is an intimate relationship between the properties of the surface soil horizons and the nature and abundance of plant species which affects nutrient, as well as water absorption and retention in the biomass and upper rhizosphere". Such a considerable correspondence between plant variation and surface soil features could be explained by the fact that vegetation itself influences soil characteristics at the upper layers, for instance by transferring organic matter through nutrient cycling (Challinor 1968; Sparovek and Camargo 1997). Kellman (1979) showed soil enrichment under some savanna trees in the Mountain Pine Ridge (Belize, Central

America), which, in some cases, approached levels found in the nearby rain-forest soils. Furthermore, some studies pointed out positive correlation between cerrado soils and vegetation types and forms, which were mainly restricted to the upper soil layers (Alvim and Araújo 1952; Goodland and Pollard 1973).

Several authors examined the influence of fertility, as the availability of nutrients on plant density and other vegetation characteristics. Some studies showed a positive correlation between soil fertility and the cerrado physiognomic gradient (Alvim and Araújo 1952; Goodland and Pollard 1973) but others did not show any correlation (Askew et al. 1971; Gibbs et al. 1983; Ribeiro 1983; Haridasan 1992). Furthermore, other authors showed correlation only for a few plant species (Silva Júnior et al. 1987; Furley and Ratter 1988; Ratter et al. 1977). In our study, we found a positive relationship between the semideciduous forest and higher quantities of nutrients; this relationship

was strong for the soil top layers and considerably less evident in deeper layers. Contrarily, cerrado physiognomies showed no correlation with soil fertility.

We could verify that the content of clay, especially in the surface but also down to 60 cm depth, was one of the most important variables to distinguish vegetation physiognomies (Figure 4, Table 3). Clay, as a colloidal component of the soil, is related to base adsorption, which depends on the pH (Ellis and Mellor 1995). In consequence, percentage of clay showed to be the most important variable to distinguish semideciduous forest from the cerrado physiognomies, as the forest quadrats were associated with higher values of clay and bases. Nevertheless, increasing proportions of clay in the soil adds to water retention (Ellis and Mellor 1995) and such higher soil water availability has been suggested as a very important factor to determine the occurrence of whether savanna or forest in the bordering regions (Furley 1992).

We also verified that potassium was another important soil variable, mainly associated with forest plots; its importance decreased gradually from surface to lower soil depths. This element is easily washed out from plant leaves by rain and deposited in the soil surface, what could explain the results obtained.

This lack of relationship that we found between cerrado forms and soil fertility was also showed in other vegetation types. For example, Sollins (1998) suggested that the failure in detecting correlation between plant distribution and soil chemical properties in the tropical lowland rain forests could be due to: lack of range in soil fertility across the sites studied, or soil testing methods were not able to measure the nutrients available to plants, or even due to temporal and spatial variability of soil properties.

Although canonical coefficients were not significant, the plots in cerrado physiognomies showed a tendency of being associated with higher values of aluminium saturation in the soil surface. High ratios between exchangeable aluminium and bases are one of the main agricultural limitations of cerrado soils (Lopes 1984). Based on that, Arens (1963) launched the "aluminium-toxic oligotrophism hypothesis" to explain the xeromorphic appearance of some cerrado plants. This hypothesis says that high quantities of soluble aluminium in the soil cause toxicity to plants, as aluminium competes with other elements, such as essential nutrients, for the same chemical sites, promoting soil impoverishment.

In our study, the amounts of exchangeable aluminium varied substantially among physiognomies only at the soil surface (Figure 7). This may indicate that: a) the mineral substrate is similar in terms of aluminium content in the four vegetation physiognomies; b) if the "aluminium-toxic oligotrophism hypothesis" were true, then we should observe significant differences in the contents of aluminium among cerrado physiognomies, and c) quantities of aluminium would increase or at least remain constant along the soil profile. Therefore, items b and c were not corroborated by our results.

Nevertheless, aluminium values were higher in the surface soil covered by cerrado forms than by semideciduous forest, but similar in the deeper soil layers of all physiognomies. These results are in agreement with Haridasan (1992) who suggested that high amounts of aluminium in the soil do not seem to limit forest development in the cerrado region.

We could also verify (Figure 7 + Spearman indices) a clear negative correlation between the amount of aluminium and the pH. To a very large extent, aluminium solubility and concentration in the exchangeable form are controlled by soil acidity. The decrease of exchangeable aluminium with pH has been shown by many studies (Goedert 1987; Ellis and Mellor 1995).

Haridasan (1982) also showed that some typical cerrado species (especially Rubiaceae and Vochysiaceae species) accumulate aluminium in their leaves, therefore we suggest that high amounts of aluminium found at the surface soil in cerrado physiognomies were associated with the transfer of this element from such plant species to the first soil layers through litter deposition and decomposition. If this is correct then the aluminium accumulation process is part of a plant physiological mechanism to improve nutrient uptake, instead of being a response to toxicity caused by high levels of aluminium in the soil.

There is also evidence that some plant species can modify the rizosphere environment by exuding a large variety of organic compounds which, for instance, combine with aluminium ions in the soil solution and reduce aluminium effects (Tyler and Falkengren-Grerup 1998). This fact could explain the low levels of aluminium detected in the semideciduous forest plots.

The three cerrado physiognomies analysed here could not be floristically distinguished by the DCA, indicating that cerrado physiognomies in the Pé-de-Gigante Reserve are similar regarding species com-

position and plant density. However, the DCA showed a clear distinction between semideciduous forest and cerrado physiognomies. Therefore, we identified two groups according to species composition and plant density: one of cerrado species, that we will call "cerrado *sensu lato* group", and another group of semideciduous forest species.

The DCA also distinguished two groups of semideciduous forest. Although these groups are physiognomically similar, they could be separated by the abundance of different species. Considering the species surveyed in these quadrats, the CCA analyses showed that some of them were related to high contents of exchangeable aluminium while others tended to be related to higher values of sum of bases in the soil surface. This distinction indicates an internal gradient in the forest.

The genera *Vochysia* and *Xylopia*, which were sampled in our survey, have been pointed out as transitional in Central America savanna-forest boundaries (Rommey 1959 *apud* Kellman and Miyanishi (1982)). In Central Brazil, Ratter et al. (1977) described *Vochysia haenkeana* Mart. as typical of dystrophic "cerradão" physiognomies. In the present study, *Vochysia tucanorum* was related to low values of soil bases, showing a similar relationship. *Platypodium elegans*, in our research, occupies an intermediate position in relation to the sum of bases (Figure 5) Ratter et al. (1977) also pointed out this species as tending to be associated with higher values of sum of bases and to be characteristic of both "cerradão" and forest.

In conclusion, the present study shows a clear distinction between semideciduous forest and cerrado physiognomies concerning their soil properties. The semideciduous forest was related to higher percentages of clay along the soil profile, higher values of base saturation, and lower values of aluminium saturation in the soil surface. The whole set of cerrado plots, or "cerrado *sensu lato*", was associated with higher values of aluminium saturation and exchangeable aluminium.

As cerrado physiognomies could not be distinguished floristically, nor by the analysed soil properties, other factors instead of compositional variation and these soil properties must be influencing the structural differences among vegetation physiognomies.

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