UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

VINÍCIUS DE LIMA DANTAS

DEFESAS CONTRA HERBIVORIA E DESCRITORES DA VEGETAÇÃO: RELAÇÕES COM VARIÁVEIS EDÁFICAS EM UMA ÁREA DE CERRADO

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de mestre em Ecologia e Recursos Naturais.

Orientador: Prof.Dr. Marco Antônio Batalha

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Vinícius de Lima Dantas

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Resumo

O solo, juntamente com o fogo e as variações climáticas, é considerado um dos principais determinantes do cerrado brasileiro, a savana mais rica do mundo. O solo pode influenciar as espécies de planta selecionando aquelas adaptadas a explorar e competir por recursos, mas também pode influenciar os padrões de alocações em defesas contra herbivoria. Embora muitos estudos tenham se voltado a entender as relações entre solo e vegetação no cerrado, poucos se focaram efeitos em escala local. De forma geral, nossa expectativa é de que descritores da comunidade, como composição florística, riqueza, equabilidade, diversidade e abundância total estejam relacionados com o solo, mesmo em escala local, dentro de uma determinada fisionomia, e que plantas em solos pobres em nutrientes invistam mais em defesas contra herbivoria devido ao alto custo em repor as folhas perdidas. Em uma área de cerrado, lançamos 100 parcelas contíguas de 25 m^2 cada, identificamos todos os indivíduos em nível de espécies, coletamos amostras de solo e medimos os seguintes traços foliares de defesa contra herbivoria: área foliar específica, razão C:N, quantidade de água, dureza, densidade de tricomas, quantidade de látex, e presença de alcaloides, terpenoides e taninos. Para testar a relação entre a composição florística e as variáveis do solo, usamos uma análise de redundância parcial, controlando a autocorrelação espacial. Para testar a relação entre as variáveis do solo e (1) a abundância das cinco espécies mais abundantes, (2) a abundância total, (3) a riqueza de espécies, (4) a equabilidade e (5) a diversidade de espécies; para prever a distribuição dos traços de defesa contra herbivoria por meio das variáveis do solo, utilizamos regressões múltiplas ou modelos autorregressivos, na presença de autocorrelação espacial. Encontramos uma baixa relação entre o solo e a composição florística, provavelmente devido à presença de espécies funcionalmente redundantes e espécies com dispersão limitada. O conteúdo de matéria orgânica esteve positivamente relacionado à abundância de *Myrsine umbellata*, a espécie mais abundante na área, e à abundância total, e negativamente relacionada à equabilidade, o que sugere que um mecanismo de retroalimentação positiva pode ser a causa da dominância de *Myrsine umbellata*. Também encontramos uma relação positiva entre soma de bases e a riqueza de espécies provavelmente refletindo um gradiente de fertilidade. Contrariamente às nossas expectativas, não encontramos relação entre o investimento total em defesas e a fertilidade do solo, provavelmente refletindo uma baixa variação nas variáveis do solo em escala local ou variações fenotípicas entre indivíduos da mesma espécie ou ambas. Entretanto, a presença de taninos esteve relacionada positivamente com o conteúdo de matéria orgânica, o que pode

refletir menor tolerância à herbivoria em solos mais pobres ou uma alta acumulação de matéria orgânica no solo devido à lenta taxa de decomposição de folhas com tanino. De forma geral, sugerimos que o solo é um importante fator estruturando a comunidade, mesmo em escala local, e que a dominância de espécies de cerrado pode estar relacionada a mecanismos de retroalimentação positiva.

Palavras-chave: autocorrelação espacial, matéria orgânica, modelos autorregressivos, *Myrsine umbellata*, riqueza, soma de bases, resistência contra herbivoria

Abstract

Together with fire and climate changes, soil is considered a major determinant in the Brazilian cerrado, the richest savanna in the world. Soil can influence plants by filtering species capable of acquiring resources and compete for them, but can also influence plant patterns of allocation in defense against herbivory. Although many studies focused on plant soil relationship in cerrado, few focused on the influence of soil at fine scale. We expected community descriptors, such as floristic composition, richness, evenness, diversity, and total abundance to be related to soil features at fine scale within a physiognomy. We also expected plants on nutrient-poor soils to present higher anti-herbivory defenses. In a cerrado site, we placed 100 contiguous 25 m^2 plots, in which we identified all woody individuals, measured soil variables and the following leaf traits: specific leaf area, C:N ratio, water content, toughness, trichomes, latex, and presence of tannins, alkaloids, and terpenoids. We did a partial redundancy analysis to test for relationship between soil features and floristic composition, controlled for spatial dependence. We also did multiple regression or spatial autoregressive models to test for relationships between soil features and: (1) the abundance of the five commonest species, (2) total abundance, (3) richness, (4) evenness, and (5) diversity and to predict defense traits based on soil features. We found no relationship between soil and floristic composition, probably due to functional redundancy or limited dispersal. Organic matter was positively related to *Myrsine umbellata*, the most abundant species, and total abundance, and negatively related to evenness, what suggests positive feedbacks to cause the dominance by *Myrsine umbellata*. We also found a positive relationship between sum of basis and species richness, probably reflecting a fertility gradient. Contrary to our expectations, we found no relationship between total defenses and total soil fertility or soil variables, what could result from low variability in soil fertility at fine scale or of high phenotypic variability. Presence of tannins was positively related to organic matter, possibly reflecting a strategy towards lower tolerance due to low reserve allocation or interactions with other resources. However, since tannins decrease leaf decomposition rates, organic matter could be accumulating in soil. Overall, we suggest that soil is an important factor structuring cerrado community even at fine scales and that the dominance of cerrado species could be related to positive plant-soil feedbacks.

Keywords: autoregressive models, anti-herbivory resistance, *Myrsine umbellata*, organic

matter, spatial autocorrelation, species richness, sum of basis.

Sumário

INTRODUÇÃO GERAL

Introdução Geral

O cerrado é um dos maiores domínios vegetacionais do país ocupando originalmente cerca de 23% do território brasileiro (Rizzini 1997), e foi avaliado como sendo a savana mais rica em espécies do mundo (Kier et al. 2005, Mendonça et al. 2008, Ratter et al. 2003). Por abrigar tantas espécies, estudos em escala local costumam encontrar uma alta variação na composição de espécies em áreas de cerrado (Carvalho and Martins 2009, Carvalho et al. 2008). No entanto, pouco se conhece sobre os fatores que determinam essa enorme variabilidade de formas e seu padrão de distribuição no espaço (Simon et al. 2009).

Um estudo recente usando abordagens filogenéticas, sugeriu que o fogo foi um fator chave para o surgimento do cerrado e sua separação das florestas há milhares de anos atrás (Simon et al. 2009). Também tem sido sugerido que variações climáticas têm um papel importante na distribuição do cerrado (Coutinho 1990, Oliveira-Filho & Ratter 2002) e existem evidências de que as matas de galeria vêm se expandido sobre áreas de cerrado em resposta a variações climáticas (Silva et al. 2008).

O solo também é um fator determinante na distribuição das espécies e na estruturação do cerrado, sendo um dos principais determinantes das variações fisionômicas encontradas no cerrado (Alvin & Araujo 1952, Coutinho 1990, Goodland & Pollard 1973, Haridasan 2000, Oliveira-Filho & Ratter 2002) e na diferenciação entre cerrado e outros tipos vegetacionais (Amorin & Batalha 2007, Ruggiero et al. 2002, Silva et al. 2008).

Outro fator que pode estar relacionado com os padrões de distribuição espacial das espécies de planta no cerrado é a herbivoria. No entanto, apesar de existir evidência para uma forte pressão dos herbívoros sobre as plantas do cerrado (Costa et al. 2008) a influência deste fator tem sido pouco estudada. A herbivoria exerce uma forte pressão seletiva sobre comunidade e populações de planta, aumentando a mortalidade de plantas, removendo biomassa que poderia ser alocada para crescimento e reprodução (Coley et al. 1985), e reduzindo a habilidade competitiva das plantas (Coley & Barone 1996). Desta forma a herbivoria aumenta a pressão sobre espécies mais palatáveis, favorecendo espécies que sejam mais resistentes ou tolerantes a herbivoria (Schädler et al. 2003, Mauricio 2000).

O padrão de alocação das planta para resistência ou tolerância à herbivoria depende amplamente do ambiente em que a planta está inserida (Nuñez-Farfán et al. 2007) e estudos empíricos mostraram que este padrão de alocação é influenciado pela disponibilidade

de recursos no solo (Fine et al. 2006). De forma geral, espécies em solos mais pobres tendem a investir mais recursos em resistência contra herbivoria, já que a baixa disponibilidade de recursos torna a tolerância mais custosa (Fine et al. 2006). Taxas maiores de herbivoria são encontradas em florestas estacionais do que em cerrado (Neves et al. 2010), o que foi atribuído à maior esclerofilia nas folhas de cerrado relacionada à menor disponibilidade de nutrientes. Assim, o solo parece exercer um papel ainda mais importante no cerrado, já que influencia o padrão de distribuição das defesas contra herbivoria, e assim, altera indiretamente o padrão de seleção de plantas pelos herbívoros.

Apesar de existirem muitos estudos pesquisando possíveis fatores que determinam a distribuição da vegetação do cerrado, a maioria deles tem se focado em variações em escala regional, principalmente em fatores relacionados com a separação entre as diferentes fisionomias do cerrado (Amorin & Batalha 2007, Carvalho & Martins 2009, Goodland & Pollard 1973, Marimon Junior & Haridasan 2005, Ruggiero et al. 2002) ou mesmo a separação entre o cerrado e outros tipos vegetacionais (Amorin & Batalha 2006, Ruggiero et al. 2002, , Silva et al. 2008, Simon et al. 2009). Devido à alta variação a curtas distâncias na composição de espécies, estudos em escala local poderiam ajudar a conhecer melhor os processos influenciando comunidades de cerrado. Variações no solo ocorrem a distâncias tão curtas quanto 1 m (Downes & Beckwith 1951, Souza & Martins 2004), assim, o solo é um forte candidato a influenciar a distribuição das espécies e de seus atributos funcionais em escala local. Este trabalho teve como objetivo estudar possíveis relações entre as variáveis do solo e as características da comunidade, como a distribuição espacial das espécies de plantas e de suas defesas contra herbivoria em escala local.

Referência bibliográficas

Alvin, P. T. & Araujo, W. (1952) El suelo como factor ecológico en el desarollo de vegetación en al centro-oeste del Brasil. Turrialba 2:153-160.

Amorim, P. K. & Batalha, M. A. (2006) Soil characteristics of a hyperseasonal cerrado compared to a seasonal cerrado and a floodplain grassland: implications for plant community structure. Brazilian Journal of Biology 66:661-667.

Amorim, P. K.& Batalha, M. A. (2007) Soil-vegetation relationships in hyperseasonal cerrado, seasonal cerrado, and wet grassland in Emas National Park (central Brazil). Acta oecologica 32:319-327.

Carvalho, D. A. & Martins, F. M. (2009) Shrub and tree species composition in the cerrado of southwest Minas Gerais. Cerne 2:142-154.

Carvalho, F.A.; Rodrigues, V. H. P.; Kilca, R. V.; Siqueira, A. S.; Araújo, G. M. & Schiavini, I. (2008) Composição florística, riqueza e diversidade de um cerrado sensu stricto no sudeste do estado de goiás. Bioscience Journal 4:64-72.

Coley, P. D.; Bryant, J. P. & Chapin III, F. S. (1985) Resource availability and plant antiherbivore defense. Science 230:895-899.

Coley, P. D. & Barone, J. A. (1996) Herbivory and plant defenses in tropical forests. Annual Review Ecology, Evolution and Systematics 27:305-335.

Costa, A. N.; Vasconcelos, H. L.; Vieira-Neto, E. H. M. & Bruna, E. M. (2008) Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants. Journal of Vegetation Science 19:849-854.

Coutinho, L. M. (1990) Fire in the ecology of the Brazilian Cerrado. Ecol Stud 84:82-105

Downes, R. G. & Beckwith, R. S. (1951) Studies in the variation of soil reaction. I. Field variation at Barooga, N.S.W. Australian Journal of Agricultural Research 2:60-72.

Fine, P. V. A.; Miller, Z. J.; Mesones, I.; Irazuzta, S.; Appel, H. M.; Stevens, M. H. H.; Sããksjãrvi, I.; Shultz, J. C. & Coley, P. D. (2006) The growth-defense trade-off and habitat specialization by plants in amazonian forests. Ecology 87:150-162

Goodland, R. & Pollard, R. (1973) The Brazilian cerrado vegetation: a fertility gradient. Journal of Ecology 61:219-224.

Haridasan, M. (2000) Nutrição mineral de plantas nativas do cerrado. Revista Brasileira de Fisiologia Vegetal 12:54-64.

Kier, G.; Dinerstein, E.; Ricketts, T. H.; Wolfgang, K.; Kreft, H. & Barthlott, W. (2005) Global patterns of plant diversity and floristic knowledge. Journal of Biogeography 32:1107-1116.

Marimon Junior, B. H. & Haridasan, M. (2005) Comparação da vegetação arbórea e características edáficas de um cerradão e um cerrado *sensu stricto* em áreas adjacentes sobre solos distróficos no leste do Mato Grosso, Brasil. Acta Botanica Brasilica 19:913-926.

Mauricio, R. (2000) Natural selection and the joint evolution of tolerance and resistance as plant defenses. Evolutionary Ecology 14:491-507.

Mendonça, R. C. et al. (2008) Vascular flora of the Cerrado biome: Checklist with 12,356 species. In: Sano, S. M.; Almeida, S. P., Ribeiro, J. F. (eds) Cerrado: Ecology and Flora. Embrapa Cerrados/Embrapa Informação Tecnológica, Brasília, pp 421–1279.

Neves, F. S.; Araújo, L. S.; Espírito-Santo, M. M.; Fagundes, M.; Fernandes, G. W.; Sanchez-Azofeifa, G. A. & Quesada, M. (2010) Canopy herbivory and insect herbivore diversity in a dry forest–savanna transition in Brazil. Biotropica 42:112-118

Núñez-Farfán, J.; Fornoni, J. & Valverde, P. L. (2007) The evolution of resistance and tolerance to herbivores. Annual Review of Ecology, Evolution and Systematics 38:541-566.

Oliveira-filho, A. T. & Ratter, J. A. (2002) Vegetation phisiognomies and woody flora of the cerrado of the cerrado biome. In: Oliveira PS, Marquis RJ (eds) The cerrados of Brazil: ecology and natural history of neotropical savannas, Columbia University Press, New York, pp 13-32

Ratter, J. A.; Bridgewater, S. & Ribeiro, J. F. (2003) Analysis of the floristic composition of the Brazilian cerrado vegetation III: comparison of the woody vegetation of 376 areas. Edinburgh Journal of Botany 60:57–109.

Rizzini, C. T. (1997) Tratado de Fitogeografia do Brasil. Âmbito Cultural, Rio de Janeiro.

Ruggiero, P. G. C.; Batalha, M. A.; Pivello, V. R. & Meirelles, S. T. (2002) Soil-vegetation relationships in cerrado (Brazilian savana) and semideciduous Forest, Southeastern Brazil. Plant Ecology 160:1-16

Schädler, M.; Jung, G.; Auge, H. & Brandl R (2003) Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. Oikos 103:121-132

Silva, L. C. R.; Sternberg, L.; Haridasan, M.; Hoffmann, W. A.; Miralles-Wilhelm, F. & Franco, A.C. (2008) Expansion of gallery forest into central Brazilian savannas. Global Change Biology 14:2108–2118

Simon, M. F.; Gretherc, R.; Queiroz, L. P.; Skemae, C.; Penningtone, R. T. & Hughes, C. E. (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proceedings of the National Academy of Sciences 48: 20359–20364.

Souza, A.F. & Martins, F. R. (2004) Microsite espaecialization and spatial distribution of *Geonoma brevispata*, a clonal palm in south-eastern Brazil. Ecological Research 19:521-532

CAPITULO 1: ESTRUTURA DA VEGETAÇÃO: RELAÇÕES EM ESCALA LOCAL COM VARIÁVEIS EDÁFICAS NUMA ÁREA DE CERRADO[1]

[1]Trabalho submetido à revista *Biotropica* com o título "Vegetation structure: fine scale relationships with soil in a cerrado site". Aqui o artigo se encontra dividido em sessões para facilitar a leitura, mas a versão original foi submetida sem as sessões seguindo as normas para artigos submetidos para a categoria "Insights".

Vegetation Structure: Fine Scale Relationships with Soil in a *Cerrado* Site

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ABSTRACT – Soil is a major determinant in the Brazilian *cerrado*, considered at larger

scales a fertility gradient. We provide evidence that soil may be filtering the occurrence of

cerrado species even at fine scale and that positive plant-soil feedbacks can be responsible for

the abundance of the dominant species.

Keywords: autoregressive models, organic matter, savanna, soil-vegetation relationships,

spatial autocorrelation, species richness, sum of basis.

INTRODUCTION

THE BRAZILIAN *CERRADO* IS THE RICHEST SAVANNA IN THE WORLD, with about 7000 plant species, of which about 1500 are shrubs or trees (Castro *et al.* 1999). Due to its high richness, high degree of endemism, and present conservation status, the *cerrado* is one of the biodiversity hotspots in the world. (Myers *et al.* 2000). Together with fire and seasonality, soil is a main determinant of changes in plant species and vegetation structure in the Brazilian *cerrado*, whose physiognomic variation is considered by some authors to be a fertility gradient (for example, Goodland & Pollard 1973).

The *cerrado* tends to occur on well-drained, acid, and nutrient-poor soils, with high levels of exchangeable aluminum, and, at increased water availability or soil fertility, it tends to be replaced by forest (Goodland & Ferri 1979, Oliveira-Filho & Ratter 2002). The *cerrado* productivity gradient is related to higher availability of bases in the soil (Goodland & Ferri 1979), whereas the sclerophyllous features of the *cerrado* vegetation are attributed to direct and indirect effects of high aluminum contents and low nutrient availability (Arens 1958, 1963; Goodland & Ferri 1979, Sarmiento 1984).

Although many studies about the *cerrado* focused on soil-vegetation relationship, few of them were carried out at fine scale (Ferreira *et al.* 2009). Since the *cerrado* flora is extremely rich, being possible to find high species turnover even at small distances, studying the processes that influence this turnover could help us to understand what drives *cerrado* responses to the environment. As long as changes in soil features can be found at distances as small as 1 m (Souza & Martins 2004), soil is an important candidate to exert fine scale effects upon the *cerrado* vegetation, because at fine scale, other factors, such as climate and fire frequency, are more homogeneous.

We looked for relationships between soil and vegetation at fine scale in a *cerrado* site,

trying to answer the following questions:(1) is floristic composition related to soil features?;(2) are total abundance, richness, evenness, and diversity related to soil features? We assumed soil to be an important environmental filter at fine scale in *cerrado* plant communities. Thus, we expected floristic composition to change with fertility reflecting, to some extent, success in exploring resources and competing with other species (Magurran 2004). Moreover, species not only respond to soil, but also influence it as well. Additionally, we expected that, on nutrient-rich soils, where resources are available and competition may be lower (MacArthur 1972, Bertness & Callaway 1994) total abundance, richness, evenness and diversity would be higher.

METHODS

We studied a *cerrado* woodland site at Federal University of São Carlos, southeastern Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W). The area is on dystrophic Oxisols, 850 m asl, under mesothermic, subtropical climate, with wet summers and dry winters (Cwa; Köppen 1931). Mean annual temperature and precipitation lies around 21.3°C and 1315.18 mm, respectively.

We placed a grid of 100 25-m^2 contiguous plots and sampled all individuals of the woody component (stem diameter at soil level ≥ 3 cm; SMA 1997). We identified them to species level using identification keys based on vegetative characters (Mantovani *et al.* 1985, Batalha & Mantovani 1999). We used Plantminer (Carvalho *et al.* 2010) to correct species names, to find author names of all species, and to include them into families according to the latest phylogenetic classification.

We collected soil samples from soil surface (0-5 cm deep), the most correlated with *cerrado* vegetation structure (Ruggiero *et al.* 2002, Amorim & Batalha 2006). In each plot,

we collected a composite sample, mixing five sub-samples, four in the corners of each plot and one in the center, analysed at the University of São Paulo, according to Embrapa (1997), Silva (1999) and Raij *et al.* (2001). We determined pH, organic matter, available phosphorus, total nitrogen, exchangeable K^+, Ca^{2+}, Mg^{2+}, and Al^{3+}. We calculated sum of bases, cation exchange capacity, base saturation, and aluminum saturation. We also determined sand, silt, and clay proportions (for a complete description see Silva & Batalha 2008).

When necessary, we transformed variables to achieve normality. We calculated correlograms using Moran index (Moran 1950) as spatial autocorrelation index. Subsequently, we used only those soil variables that had the range of autocorrelation at distances smaller than 25 m, since, in this case, soil features would have enough variability to influence plant species distribution. Although the greatest distance between pairs of plots was higher than 50 m, beyond 25 m the results for spatial dependence were not reliable due to the small number of pairs of plots to compare.

To avoid collinearity, we tested for correlations among soil variables and, when the coefficient of correlation was higher than 0.7, we excluded one of the soil features in the subsequent analysis. We also preferred more synthetic variables. We standardised soil variables to zero mean and unit variance. To answer the first question, we did a partial redundancy analysis (Jongman *et al.* 1995), using the vegetation and soil matrices, and using the spatial coordinates to control for spatial autocorrelation. We also selected the five commonest species and did stepwise multiple regressions with soil features as explanatory variables. When we found significant relationships in the multiple regressions, we tested the residuals for spatial autocorrelation with Moran's index, since spatial dependence could cause type I error (Dormann *et al.* 2007). Since residuals were normally distributed, we used autoregressive model to account for spatial autocorrelation (Dormann *et al.* 2007). To answer the second question, we counted the numbers of individuals (abundance) and species

(richness) per plot and calculated evenness (Pielou 1975) and Shannon's diversity (Shannon and Weaver 1949), using them as response variables. We selected the best stepwise model using the Akaike Information Criteria (AIC). We did all analyses in R (R Development Core Team 2009), using the vegan (Oksanen *et al.* 2009) and spdep (Bivand *et al.* 2009) packages.

RESULTS

We sampled 2062 individuals, belonging to 61 species and 27 families. The five commonest species were *Myrsine umbellata* Mart. (567 individuals), *Vochysia tucanorum* Mart. (168 individuals), *Myrcia guianensis* (Aubl.) DC. (131 individuals), *Miconia albicans* (Sw.) Triana (125 individuals), and *Piptocarpha rotundifolia* (Less.) Baker (103 individuals). The richest families were Fabaceae (with eight species), Myrtaceae (with six species), Malpighiaceae and Melastomataceae (with four species each), and Annonaceae, Erythroxylaceae e Rubiaceae (with three species each), summing 50 percent of all species sampled.

Soil was dystrophic ($P < 0.5$ $cmol_c/kg$, $K^+< 0.1$ $cmol_c/kg$, $Mg^{2+}< 0.2$ $cmol_c/kg$, $Ca^{2+}< 0.4$ $cmol_c/kg$), acidic ($pH < 4$), and with high concentration of Al^{3+} (> 1.7 $cmol_c/kg$). The only soil features that showed a complete range of variation at the scale of our study were organic matter, calcium, aluminum, sum of basis, aluminum saturation, cation exchange capacity, and H+Al. Many of these variables were correlated with each other (Table 1) and, thus, for statistical analyses, we used only organic matter, sum of basis, and aluminum saturation, which were related to many others, but not correlated with each other.

The first axis of the redundancy analysis explained 12.86% ($p= 0.005$) of the variation in floristic composition and was more related to organic matter and exchangeable aluminum. The commonest species, *Myrsine umbellata*, showed a significant relationship with soil, but

only with organic matter (z=4.36; p<0.001; table 2). The other four commonest species showed no relationship with soil features. Total abundance was positively related with organic matter (t= 4.43; p<0.001), species richness was positively related with sum of basis ($t = 3.19$; $p = 0.002$), and evenness was negatively related with organic matter (z=-3.3192, p<0.001). We found no relationship between diversity and soil features (Table 2).

DISCUSSION

Albeit significant, we found low explanatory power for floristic composition in relation to soil features at fine scale, as found by other studies that could not distinguish floristic composition among different *cerrado* physiognomies based on soil (Ruggiero *et al.* 2002, Marimon Junior & Haridasan 2005, Amorin & Batalha 2007). Floristic composition seems to be more related to soil features between different neighbor vegetation types, such as wet grassland, seasonal forest and *cerrado* (Amorin & Batalha 2007, Ruggiero *et al.* 2002, Silva *et al.* 2008). Within *cerrado* physiognomies, there seems to be functionally redundant species, corroborating the traditional idea that savannas are more stable in functional than floristic terms (Sarmiento 1996). Another possibility that remains to be tested is whether neutral processes prevail at fine scale, which is likely to occur in species-rich communities (Hubbel 2005), such as the *cerrado*. Nevertheless, since we found relationships between soil features and the abundance of the commonest species, total abundance, richness, and evenness in the regression analyses, there seems to be a deterministic relationship, at least to some extent, between resource availability and vegetation structure within *cerrado* physiognomies.

The soil features related to vegetation structure were organic matter and sum of basis. Organic matter is related to high soil fertility, since the negatively charged surfaces of organic matter retain nutrients and some organic molecules chelate micronutrient, making them

available for plant roots (Salisbury & Ross 1991). In *cerrado* organic matter is the main source of nitrogen and sulfur, both at critic low levels in *cerrado* (Goodland & Ferri 1979). Moreover, organic matter provides clay aggregation stability, which allows water and air to move through the soil and permits roots to penetrate with little resistance (Motta *et al.* 2002). Organic matter may be even more important than clay in providing nutrients for plants in *cerrado* communities (Goodland &Ferri 1979). Sum of basis is calculated as the sum of total calcium, potassium, and magnesium, which are related to hydration regulation and, thus, to water availability. Calcium and potassium are related to enzymatic activation; calcium, to plant growth; and magnesium, to basal metabolism (Larcher 2000).

All the relationships we found with organic matter may be associated with the abundance of *Myrsine umbellata.* Since *Myrsine umbellata* is by far the commonest species in the community, the negative relationship between organic matter and evenness and its positive relationship with total abundance, probably reflects the abundance of this species. We expected higher evenness to be related to higher nutrient availability because of the lack of competition exclusion of inferior competitors, but we did not corroborate this idea. Given that changes in organic matter in surface soil are likely to be caused by the vegetation itself (Sparovek & Camargo 1997, Ruggiero *et al.* 2002, Silva *et al.* 2008), a possible explanation for the positive relationship between organic matter and the dominance of *Myrsine umbellata* could be that this species increases soil organic matter, which could, in turn, favor this species, in a mechanism of positive feedback (Kulmatisky *et al.*2008).

Richness showed a positive relationship with sum of basis, which could be related to environmental filtering in nutrient-poor soils and more resources in nutrient-rich soils allowing coexistence of more species. We did not find any relationship between richness and exchangeable aluminum, contrary to Carvalho and Martins (2009), who compared different *cerrado* physiognomies. Maybe, at fine scale, variations in aluminum could not be wide

enough to influence plants, especially because *cerrado* species are adapted to deal with it (Sarmiento 1984). Richness and evenness were related with different non-correlated soil features, and these two community descriptors are the components of diversity. Thus, the lack of relationship between diversity and soil features could reflect different spatial patterns of distribution of sum of basis (positively related with richness) and organic matter (positively related with evenness) that would cancel out each other.

In conclusion, although it was not possible to infer cause-and-effect relationships, our study indicated that soil is an important factor structuring *cerrado* community, even at fine scales. Soil was not related to floristic composition, suggesting functional redundancy among plants, but some soil features were related to community descriptors, such as abundance, richness, and evenness. There can be a positive feedback between *Myrsine umbellata*, by far the most abundant species, and organic matter, which remains to be tested. Moreover, fine scale studies should be carried out among different *cerrado* physiognomies to partition soil-vegetation relationships within and among habitats.

LITERATURE CITED

AMORIM, P. K., AND M. A. BATALHA. 2006. Soil characteristics of a hyperseasonal *cerrado* compared to a seasonal *cerrado* and a floodplain grassland: implications for plant community structure. Braz. J. Biol. 66: 661-667.

AMORIM, P. K., AND M. A. BATALHA. 2007. Soil-vegetation relationships in hyperseasonal *cerrado*, seasonal *cerrado*, and wet grassland in Emas National Park (central Brazil). Acta Oecol. 32: 319-327.

ARENS, K. 1958. O *cerrado* como vegetação oligotrófica, pp 59-57. Bol Fac Fil Ciênc Ltr Universidade de São Paulo, São Paulo, BR.

ARENS, K. 1963. As plantas lenhosas dos campos *cerrado*s como vegetação adaptada às deficiências minerais do solo. In: Ferri MG (ed) III Simpósio sobre o *cerrado*, pp 13-115. Edgard Blucher /Edusp, São Paulo, BR.

BATALHA, M. A., AND W. MANTOVANI. 1999. Chaves de identificação das espécies vegetais vasculares baseadas em caracteres vegetativos para a ARIE *Cerrado* Pé-de-Gigante (Santa Rita do Passa Quatro, SP). Rev. Inst. Florest.11: 137-158.

BERTNESS, M. D., AND R. CALLAWAY.1994. Positive interactions in communities. Trends Ecol. Evol. 5: 191-193.

BIVAND, R., L. ANSELIN, R. ASSUNÇÃO, O. BERKE, A. BERNAT, M. CARVALHO, Y. CHUN, C. DORMANN, S. DRAY, R. HALBERSMA, E. KRAINSKI, N. LEWIN-KOH, H. LI, J. MA, G. MILLO, W. MUELLER, H. ONO, P. PERES-NETO, M. REDER, M. TIEFELSDORF, ANDD. YU. 2009. spdep: Spatial dependence: weighting schemes, statistics and models. R package version 0.4-34. http://CRAN.R-project.org/package=spdep.

CARVALHO, D. A., AND F. M. MARTINS. 2009. Shrub and tree species composition in the *cerrado* of southwest Minas Gerais. Cerne 15: 142-154.

CARVALHO, G. H., M. V. CIANCIARUSO, AND M. A. BATALHA. 2010. Plantminer: a web tool for checking and gathering plant species taxonomic information. Environmental Modelling and Software: in press.

CASTRO, A. A. J. F., F. R. MARTINS, J. Y. TAMASHIRO, AND G. J. SHEPHERD. 1999. How rich is the flora of Brazilian *cerrado*s. Ann. Missouri Bot. Gard. 86: 192-224.

DORMANN, C. F., J. M. MCPHERSON, M. B. ARAÚJO, R. BIVAND, J. BOLLIGER, G. CARL, R.G. DAVIES, A. HIRZEL, W. JETZ, W. D. KISSLING, I. KÜHN, R. OHLEMÜLLER, P. R. PERES-NETO, B. REINEKING, B. SCHRÖDER, F. K. SCHURR, AND R. WILSON. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30: 609-628.

Embrapa. 1997. Manual de métodos de análise do solo. Embrapa, Rio de Janeiro, BR.

FERREIRA, J. N., M. M. DA C. BUSTAMANTE, AND E. A. DAVIDSON. 2009. Linking woody species diversity with plant available water at a landscape scale at a Brazilian savanna. J. Veg. Sci. 20: 826-835.

GOODLAND, R., AND M. G. FERRI.1979. Ecologia do *Cerrado*. Universidade de São Paulo, São Paulo, BR.

GOODLAND, R.,AND R. POLLARD. 1973. The Brazilian *cerrado* vegetation: a fertility gradient. J. Ecol. 61:219-224.

HUBBEL, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Funct. Ecol. 19: 166-172.

JONGMAN, R..H..G., C. J. F. TER BRAAK, AND O. F. R. VAN TONGEREN. 1995. Data analysis in community and landscape ecology. Cambridge University, Cambridge, UK.

KÖPPEN, W. 1931. Grundriss der Klimakunde. Berlin, Gruyter.

KULMATISKY, A., K. H. BEARD, J. R. STEVENS, AND S. M. COBBOLD. 2008. Plant-soil feedbacks: a meta-analytical review. Ecol. Letters11: 1-13.

LARCHER, W. 2000. Ecofisiologia Vegetal. Rima, São Carlos, BR.

LOPES, A. S. 1984. Solos sob "*cerrado*". Características, propriedades e manejo. Associação Brasileira para Pesquisa da Potassa e do Fosfato, Piracicaba, BR.

MACARTHUR, R. H. 1972. Geographical Ecology. Harper & Row, New York, U.S.A.

MAGURRAN, A. E. 2004. Measuring biological diversity. Blackwell Science, Oxford, UK.

MANTOVANI, W., H. F. LEITÃO FILHO, AND F. R. MARTINS. 1985. Chave baseada em caracteres vegetativos para identificação de espécies lenhosas da Reserva Biológica de Moji Guaçu, SP. Hoehnea 12: 35–66.

MARIMON JUNIOR, B. H., AND M. HARIDASAN. 2005. Comparação da vegetação arbórea e características edáficas de um cerradão e um *cerrado sensu stricto* em áreas adjacentes

sobre solos distróficos no leste do Mato Grosso, Brasil. Acta Bot. Bras. 19: 913-926.

MORRAN, P. A. P. 1950. Notes on continuous stochastic phenomena. Biometrika 37: 17-23

MOTTA, P. E. F., N. CURI, AND D. P. FRANZMEIER. 2002. Relation of soil and geomorphic surfaces in the Brazilian *cerrado*. In: Oliveira PS, Marquis RJ (eds) The *cerrado*s of Brazil: ecology and natural history of neotropical savannas, pp 13-32. Columbia University Press, New York, U.S.A.

MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

OKSANEN, J., R. KINDT, P. LEGENDRE, B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. HENRY, H. STEVENS,ANDH. WAGNER. 2009. vegan: Community Ecology Package. R package version 1.15-2. http://CRAN.R-project.org/package=vegan

OLIVEIRA-FILHO, A.T., AND J. A. RATTER.2002. Vegetation phisiognomies and woody flora of the *cerrado* biome. In: Oliveira PS, Marquis RJ (eds) The *cerrado*s of Brazil: ecology and natural history of neotropical savannas, pp 13-32. Columbia University, New York, U.S.A.

Pielou, E.C. 1975. Ecological diversity. Wiley, New York, U.S.A.

R DEVELOPMENT CORE TEAM. 2009. R: A language and environment for statistical computing. Wien, R Foundation for Statistical Computing. Avalable via DIALOG. http://www.r-project.org. Accessed 21 Oct 2009.

RAIJ, B. VAN, J. A. QUAGGIO, H. CANTARELLA, M. E. FERREIRA, A. S. LOPES, AND O. C. BATAGLIA. 1987. Análise química do solo para fins de fertilidade. Fundação Cargill, Campinas, BR.

RUGGIERO, P. G. C., M. A. BATALHA, V. P. PIVELLO, AND S. T. MEIRELLES. 2002. Soil-vegetation relationships in *cerrado* (Brazilian savana) and semideciduous Forest, Southeastern Brazil. Plant Ecol. 160:1-16.

SALISBURY, F. B., AND C. W. ROSS.1991. Plant physiology. Belmont: Wadsworth Publishing

Company, California, U.S.A.

SARMIENTO G. 1984. The ecology of neotropical savannas. Harvard University Press, Massachusetts, U.S.A.

SARMIENTO G.1996. Biodiversity and water relations in tropical savannas. In: Solbrig O. T., E. Medina, and J. F. Silva (Eds) Biodiversity and Savanna Ecosystem Processes, pp 61-75, Springer, Berlin, DE.

SHANNON, C. E.,AND W. WEAVER. 1949. The mathematical theory of communication. The University of Illinois Press, Urbana, U.S.A.

SILVA, F. C. 1999. Manual de análises químicas de solos, plantas e fertilizantes. Embrapa, Brasília, BR.

SILVA, D. M., AND M. A. BATALHA. 2008. Soil–vegetation relationships in *cerrado*s under different fire frequencies. Plant Soil 311: 87-96

SILVA, L. C. R., L. STERNBERG, M. HARIDASAN, W. A. HOFFMANN, F. MIRALLES-WILHELM, AND A. C. FRANCO. 2008. Expansion of gallery forest into central Brazilian savannas. Glob. Change Biol. 14: 2108–2118.

SMA SECRETARIA DE ESTADO DO MEIO AMBIENTE. 1997.*Cerrado*: bases para conservação e uso sustentável das áreas de *cerrado* do estado de São Paulo. SMA, São Paulo, BR.

SOUZA, A. F., AND F. R. MARTINS. 2004. Microsite specialization and spatial distribution of *Geonoma brevispata*, a clonal palm in south-eastern Brazil. Ecol. Res. 19: 521-532.

SPAROVEK, G., AND O. A. CAMARGO. 1997. Sampling strategies for tropical forest nutrient cycling studies: a case study in São Paulo, Brazil. Ver. Bras. Ci. Solo 21: 635-642.

Table 1. Pearson's correlation for soil variables varying within the scale of our study. OM (organic matter; g/kg); Ca^{+2} (mg/kg), Al^{+3}(mmolc/kg); SB (sum of basis; mmolc/kg); m (aluminum saturation; %); CEC (cation exchange capacity; mmolc/kg); H+Al (mg/kg). Data were collected at a *cerrado* site at São Carlos, Brazil (approximately, 21º58'05.3"S, 47º52'10.1"W)

	OM	Ca^{2+}	Al^{3+}	SB	m	CEC	H+Al
OM	1.00	-	-	-	-	-	-
Ca^{+2}	0.30	1.00	-	-	-	-	-
Al^{+3}	0.66	-0.16	1.00	-	-	-	-
SB	0.42	0.94	-0.09	1.00	-	-	-
m	0.03	-0.82	0.61	-0.83	1.00	-	-
CEC	0.82	0.12	0.74	0.23	0.23	1.00	-
H+Al	0.78	0.01	0.77	0.12	0.34	0.99	1.00

Table 2. Regression analyses using the abundance of the five commonest species, total abundance, richness, evenness, and diversity as response variables and soil features as explanatory variables. Best model selected according to the Akaike Information Criterion. Soil features were: OM (Organic matter; g/kg); Al^{3+} (mmolc/kg); SB (Sum of basis; mmolc/kg). Data collected at a *cerrado* site at São Carlos, Brazil (approximately, 21º58'05.3"S, 47º52'10.1"W).

	Stepwise model	R^{2a}	Moran's ssd[b]	Rho[c]	Moran's ssd[d]	OM[e]	Al^{3+e}	SB[e]
Myrsine umbellata	OM, SB	0.22***	5.54***	0.63***	-0.16[ns]	4.4***	-	-1.18[ns]
Vochysia tucanorum	OM, Al^{+3},SB	0.01[ns]	-	-	-	0.23[ns]	-0.23[ns]	0.46[ns]
Myrcia guianensis	OM, Al^{+3},SB	0.03[ns]	-	-	-	0.81[ns]	0.07[ns]	-1.19
Miconia albicans	OM, Al^{+3},SB	0.01[ns]	-	-	-	0.19[ns]	-0.26[ns]	0.28[ns]
Piptocarpha rotundifolia	SB	0.01[ns]	-	-	-	-	0.23[ns]	-
Total abundance	OM	0.16***	1.57[ns]	-	-	4.4***	-	-
Richness	Al^{+3}, SB	0.11**	-0.17[ns]	-	-	-	1.71[ns]	3.16**
Pielou's evenness	OM, SB	0.13***	5.12***	0.59***	0.19[ns]	-3.22***	-	0.50[ns]
Diversity	OM, SB	0.06*	3.26***	0.42*	-0.11[ns]	0.22[ns]	-	0.14[ns]

[a]: coefficient of multiple regression (linear regression when there is one variable in the model); [b]: Moran's statistic standard deviate before correcting for spatial dependence; [c]: *Rho* statistic for autoregressive models; [d]: Moran's statistic standard deviate after correcting for spatial

dependence; ^{e}: *t* statistic for each variable include in the model; ^{ns}: not significant; *: p<0.05; **: p<0.01; ***: p<0.00.

CAPITULO 2: DEFESAS CONTRA HERBIVORIAS E VARIÁVEIS EDÁFICAS EM ESCALA LOCAL NUMA SAVANA BRASILEIRA[1]

[1] Trabalho submetido à revista *Plant and Soil* com o título "Fine scale relationship between anti-herbivory defense traits and soil features in a Brazilian savanna".

Fine scale relationship between anti-herbivory defense traits and soil features in a Brazilian savanna

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Abstract – Herbivory selective pressure causes evolution of chemical, mechanical, and phenological leaf defenses. Plant allocation to defense depends on environmental resources. Soil is a major environmental filter in the Brazilian savanna known as "cerrado", and so we expected plants on nutrient-poor soils to present higher anti-herbivory defenses. In a cerrado site, we measured soil variables and the following leaf traits: specific leaf area, C:N ratio, water content, toughness, trichomes, latex, and presence of tannins, alkaloids, and terpenoids. We did multiple regressions or spatial autoregressive models, to predict defense traits based on soil features. Contrary to our expectations, we found no relationship between total defenses and total soil fertility or soil variables, what could result from low variability in soil fertility at fine scale or of not taking phenotypic plasticity into account. Presence of tannins was positively related to organic matter, possibly reflecting a strategy towards lower tolerance due to low reserve allocation or interactions with other resources. Since tannins decrease leaf decomposition rates, organic matter could be accumulating in soil. We did not find other relationships between defense traits and soil features, but we found variability in soil features at local scale, which could be affecting plant community processes.

Keywords: anti-herbivory strategy, resistance, defense traits, organic matter, soil fertility, spatial autocorrelation.

Introduction

Herbivory is an ecological and evolutionary agent, exerting a strong selective influence at population and community levels, by increasing plant mortality, removing biomass that might be allocated to growth or reproduction (Coley et al. 1985), and reducing plant competitive ability (Coley and Barone 1996). Thus, herbivory restricts plants potential distribution to regions that they might tolerate (Fine et al. 2006). This pressure results in the evolution of chemical, mechanical, phenological, and physiological defenses in plants (Coley and Barone 1996; Strauss and Agrawal 1999), such as differences in leaf water, leaf nitrogen, leaf toughness (Coley 1983), timing of leaf flush (Aide 1992), production of secondary compounds (Howe and Jander 2008), and increased capacity to tolerate herbivory (Strauss and Agrawal 1999).

The evolution and maintenance of each defensive strategy is affected by the relative fitness costs and benefits that each strategy involves (Núñez-Farfán et al. 2007). Thus, a mixed pattern of defense allocation on tolerance to herbivory (recovery after herbivory) and resistance to herbivory (traits that decrease the amount of attack by herbivores) may be evolutionarily unstable when they are limited by factors other than herbivory, such as the environment (Núñez-Farfán et al. 2007). Low resource environments favor the establishment of species with low growth rate and highly defended long-lived leaves, since plant costs of recovering leaf loss would be high (Coley et al. 1985). In other words, higher investments in resistance would be favored when tolerance is too expensive. Fine et al. (2006) corroborated this idea, suggesting the existence of a universal growth vs. defense trade-off on high vs. low resource environments.

Different vegetation types are limited by different resources; hence, it could be expected that the type of resource should also influence plant tolerance to herbivory. It was suggested

that the effect of resources on plant tolerance to herbivory may depend not only on low vs. high fertility gradients, but also on: (1) what resource is primarily limiting the plant; (2) whether there is an alternative resource affecting plant growth; and (3) whether the acquisition of one of these resources by the plant is affected by herbivory (Wise and Abrahamson 2005). So, this "Limiting Resource Model" can result in higher, lower, or equal tolerance to herbivory, depending on the combination of these factors (Wise and Abrahamson 2005).

Soil chemical and physical features are main limiting resources in tropical regions and, thus, strongly influence plant community (Sollings 1998). Chemical and physical soil features that affect most plant distribution are phosphorous, aluminum toxicity, depth of water table, amount and arrangement of pores of different sizes, availability of base-metal cations, micronutrients, and nitrogen (Sollings 1998). Soil, together with fire and climate, is the main determinant of vegetation in the cerrado, a Brazilian savanna (Coutinho 1990; Haridasan 2000). Cerrado soils are usually poor, acidic, well-drained, and with high levels of exchangeable aluminum (Lopes 1984; Queiroz-Neto 1982; Reatto et al. 1998). The pseudo-xeromorphic features of the cerrado vegetation may be related to aluminum toxicity (Arens 1958) or oligotrophism (Arens 1963).

Although the cerrado flora is extremely rich, being possible to find high species turnover even at small scale, few studies have focused on environmental factors influencing vegetation characteristics of cerrado at local scales, within cerrado physiognomies. Given the importance of soil on limiting the cerrado vegetation and since changes in soil features can be found at distances as small as 1 m (Downes and Beckwith 1951, Souza and Martins 2004), soil is likely to influence changes at such a scale. Thus, it is possible that the influence of soil on plant the trade-off between growth and resistance (hereafter called "defense") found by Fine at al. (2006) could remain even at fine scale, and tolerance to herbivory in relation to soil could be responding to soil and, thus, be a determinant of vegetation features at more

homogeneous conditions, such as those found at local scale. So, we asked the following questions:

(1) Is soil fertility related to total resistance against herbivory in a cerrado site? Overall, we expected the investment in defense traits against herbivory to increase from nutrient-rich to nutrient-poor soils (Fine et al. 2006);

(2) If not, is total resistance related to different soil features when considered separated? We expected investments in defense to increase with the decrease of mineral nutrients or soil features related to nutrient availability and with the increase of soil features related to toxicity or oligotrophism, such as aluminum and aluminum saturation.

(3) Are different defense traits related to different soil features? We expected the increase in a given defense trait to be related to lower levels of mineral nutrients or soil features related to fertility, and with higher level of features related with aluminum. We also expect structural defenses to respond better, since it has been demonstrated to tropical forests that mature leaves invest more in physical than in chemical defenses (Coley and Barone 1996).

Materials and Methods

Vegetation sampling

We studied a cerrado woodland site at Federal University of São Carlos, southeastern Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W). The area is on dystrophic Oxisol, 850 m above sea level, under mesothermic, subtropical climate, with wet summers and dry winters (Cwa; Köppen 1931). Mean annual temperature and precipitation lies around 21.3°C and 1315.18 mm, respectively. In this site, we placed 100 5 m x 5 m contiguous plots, in which we sampled all individuals of the woody component, that is, individuals with stem diameter at

soil level equal to or higher than 3 cm (SMA 1997). We identified them to species level using identification keys based on vegetative characters (Batalha and Mantovani 1999; Mantovani et al. 1985) and comparing the collected material to vouchers lodged at the Federal University of São Carlos and State University of Campinas herbaria. We used Plantminer (Carvalho et al. 2010) to check species names, to include all species into families according to the latest phylogenetic classification, and to find author names of all species.

For each species in the sample, we picked 10 individuals at random. When, for a given species, there were less than 10 individuals in the sample, we made an additional effort to look for more individuals nearby the plots. Thus, sample size was 10 individuals per species (Cornelissen et al. 2003). From September 2008 to April 2009, for each individual in the sample, we collected fully expanded and hardened leaves, without obvious symptoms of pathogen or herbivore attack, and measured the following leaf defense traits: nutritional quality, specific leaf area, water content, latex content, number of trichomes, toughness, and presence of alkaloids, terpenoids, and tannins (Agrawal and Fishbein 2006).

We measured total carbon (C) and nitrogen (N) concentration to calculate the C:N ratio, as an indicator of leaf nutritional quality. For each species, carbon and nitrogen concentration were determined in five replicates at University of São Paulo. Nutritional quality is an important constitutive plant defense, since high C:N ratios difficult nitrogen acquisition by herbivores (Agrawal and Fishbein 2006).

Low values of specific leaf area tend to correspond to relatively high investments in leaf defenses, particularly structural ones (Cornelisen et al. 2003). Specific leaf area also indicates rapid growth and high leaf palatability (Agrawal and Fishbein 2006). Similarly, water leaf content is related to increased leaf palatability and, so, low levels of leaf water should help avoiding herbivory (Agrawal and Fishbein 2006), since it is related to low palatability (Schädler et al. 2003). To measure specific leaf area and leaf water content, we collected two

leaves from each individual, kept them in a cooler, and weighted them still fresh. We scanned the leaves to determine leaf area with the Image J 1.33 software (Rasband 2004) and oven-dried them at 80°C for 72 h to obtain leaf dry mass. We obtained specific leaf area by dividing leaf area by leaf dry mass (Cornelisen et al. 2003). We calculated water content by the difference between fresh mass and dry mass, divided by leaf area (Agrawal and Fishbein 2006).

Trichomes are also important physical defenses against herbivores. Using five replicates for each species, we counted the number of trichomes, on both leaf surfaces, in 28 mm² discs, with a dissecting microscope. We also measured leaf toughness, which is related to nutritional and defense constituents, probably influencing herbivore activity (Agrawal and Fishbein 2006). We used a force gauge penetrometer (Chatillon DFE 010) with a cone tip, drilling the leaf at both sides of the mid-rib.

Latex is an important chemical strategy against herbivory (Agrawal and Fishbein 2006). We measured latex by cutting the tip of an intact leaf in the field and collecting the exuding latex onto a filter paper disc. When latex ceased to flow, this disc were placed on another dry filter paper disc, oven-dried at 60°C for 72 h, and weighted (Agrawal and Fishbein 2006). We analysed compounds frequently present in Brazilian plants that could act as chemical defenses against herbivores (Lima 2000): alkaloids, terpenoids, and tannins. We carried out the tests following Falkenberg et al. (2003): a series of three assays, Mayer, Dragendorff, and Wagner reactions, to determine alkaloid presence; Liebermann-Burchard and Salkowisk reactions to test terpenoid presence; and ferric chloride reaction to determine tannin presence.

Soil sampling

We collected soil samples from soil surface (0-5 cm deep), the one most correlated with

cerrado vegetation structure (Amorim and Batalha 2006; Ruggiero et al. 2002). In each plot, we collected a composite sample, mixing five sub-samples, four in the corners of each plot and one in the center. They were analysed at the University of São Paulo, according to Embrapa (1997), Silva (1999), and Raij et al. (2001). We determined pH, organic matter, available phosphorus, total nitrogen, exchangeable K+, Ca+2, Mg+2, and Al+3. We calculated sum of bases, cation exchange capacity, base saturation, and aluminum saturation. We also determined sand, silt, and clay proportions.

Soil pH was determined in $CaCl_2$ solution, using 10 ml of soil in 25 ml of solution. $CaCl_2$ was used to avoid salt and oxides influences. Organic matter was determined by organic carbon oxidation with potassium dichromate and subsequent potassium dichromate titration with ammonic ferrous sulfate, using 0.5 g of soil and 10 ml of potassium dichromate solution. A correction factor (1.33) was used to compensate partial carbon oxidation. Available phosphorus was determined by spectrophotometry after anion exchange resin extraction, using 2.5 cm^3 of soil. Total nitrogen was determined by digestion with H_2SO_4, followed by distillation with NaOH, using from 0.5 to 1 g of soil, 1 g of H_2SO_4, and 15 ml of NaOH.

Cations K+, Ca+2, Mg+2, and Al+3 were extracted with 1 M KCl, using 10 cm^3 of soil and 100 ml of solution. Then, potassium, calcium, and magnesium were determined by an EDTA complexometry. Aluminum was determined by NaOH titration. Sum of bases was calculated as the sum of potassium, calcium, and magnesium. Cation exchange capacity was calculated as sum of bases plus H+ and Al+3 concentrations. Base saturation was calculated as a percentage of total cation exchange capacity. Aluminum saturation was calculated as a percentage of sum of bases and Al+3.

We quantified soil sand, silt, and clay proportions using the Boyoucus method: first, soil particles were settled using a dispersant, suspension was separated from the sediment, and clay content was calculated by suspension density using a densimeter; then, the sediment was

sieved to separate the sand, which was weighted. Silt proportion was calculated by the difference.

Statistical analyses

We plotted all soil variables in a correlograms to test which soil variables had full range of variability at the scale of our study. We did not consider for statistical analysis spatially autocorrelated variables that had a range between positive and negative values of autocorrelation smaller than 25 m, since their scale of variability were greater than the sampling scale.

We also calculated Pearson's correlation between all pairs of variable selected above, to choose variables not highly correlated with each other, thus, avoiding multicolinearity effects in the analysis (Zar 1999). Since many of the variables were correlated, we decide to pick only the less correlated and redundant ones ($r < 0.70$).

To answer the first question, we did a linear regression between defense and fertility indices per plot. To obtain defense index per plot, we followed Fine et al. (2006), but we weighted total defense by species abundance per plot; thus, we followed these steps: (1) for each species and each quantitative defense trait, we calculated trait mean value; (2) we standardised all defense traits, both quantitative and qualitative, to zero mean and unit variance; (3) we summed all values of defense traits, obtaining a single value of total defense per species; (4) we weighted the matrix of species abundance per plot with these values; and (5) we summed all weighted values obtaining total defense per plot. For, specific leaf area and water content, we used their inverse, since higher values of these traits represent low defense.

To calculate fertility index, we used a similar procedure: (1) we first log- or square root-transformed soil variables to achieve normality; (2) we standardised them; and (3) we

summed the values per plot of soil variables related to soil fertility and the inverse of soil variables related with low fertility (for example, exchangeable aluminum). This approach has the problem of considering traits (and here also soil features) to have equal weights, but it is preferable than to assign subjectively different weights (Fine et al. 2006). To answer the second question, we did stepwise multiple linear regressions with soil features as explanatory variables and the defense index as response variable.

To answer the third question, we did stepwise multiple regressions with each defense trait as response variable and the soil features selected above as explanatory variables. We obtained trait value per plot by weighting the species abundance matrix by species mean trait value, and then summing all values of each plot. Soil and trait values per plot were log- or square root-transformed to achieve normality, and soil variables were standardised to zero mean and unit variance. When regression residuals were spatially autocorrelated, we used tests that accounted for spatial autocorrelation, instead of multiple regressions, to avoid type I error. Since all residuals that were autocorrelated were normally distributed, we used simultaneous autoregressive models to correct spatial dependence (Dormann et al. 2007).

We selected the best stepwise regression models with the Akaike Information Criterion. We tested the residuals of the multiple regressions for spatial autocorrelation among plots using Moran's I index (Moran 1950), assuming data to be stationary and anisotropic. We did all analyses with the *vegan* (Oksanen et al. 2009) and *spdep* (Bivand et al. 2009) packages for R (R Development Core Team 2009).

Results

We sampled 2,062 individuals, belonging to 61 species and 27 families, for which we measured defense traits (Table 1). The richest families were Fabaceae (eight species),

Myrtaceae (seven species), Malpighiaceae and Melastomataceae (four species each), and Annonaceae, Erythroxylaceae, and Rubiaceae (three species each), accounting for half of the species sampled. Only two species presented latex *Kielmeyera grandiflora* and *Kielmeyera coriacea*. *Tocoyena formosa* was the only species to present alkaloids, whereas 26 species presented terpenoids and 57 species presented tannins (Table 1). Soil was dystrophic (P < 0.5 $cmol_c$ kg^{-1}, K+ < 0.1 $cmol_c$ kg^{-1}, Mg+2 < 0.2 $cmol_c$ kg^{-1}, Ca+2 < 0.4 $cmol_c$ kg^{-1}), acidic (pH < 4), and with high concentration of Al+3 (> 1.7 $cmol_c$ kg^{-1}). All soil variables presented spatial autocorrelation, but the only soil variables that showed a complete range of variation (from positive to negative autocorrelation) at the scale of our study were organic matter, calcium, aluminum, sum of basis, aluminum saturation, cation exchange capacity, and hydrogen ions, showing that the others have greater scales of variation. Organic matter, Al+3, cation exchange capacity and H+ showed a range of variability of 15 m, whereas Ca+2, sum of basis and aluminum saturation showed a range of variability of 25 m (Figure 1). After selecting less correlated soil variables, only organic matter, sum of basis, and Al+3 remained for statistical analysis.

Concerning total defense index, we found no relationship with soil variables, either when we used total fertility index or when we used soil features separately (Table 2). We found positive relationship between the presence of tannins and organic matter (t = 4.37, p < 0.001), but no other defense trait distribution was related to any of the soil features (Table 2).

Discussion

Contrary to our expectation, total investment in defense traits against herbivory did not increase from nutrient-rich to nutrient-poor soils. Fine et al. (2006) found a relationship between total defenses and total soil fertility at large scale, comparing different vegetation

types, but, at fine scale, within a plant community, this relationship does not seem to hold, maybe because the variation in soil features is much larger in regional scale. Moreover, our study focused in the effects of soil variables in the establishment of well versus poorly defended species in space, but did not account for phenotypic plasticity in plant traits in response to nutrient availability, which could be assessed by measuring trait values for every individual at the community.

When taking into account each defense trait separately, we found positive significant relationships between the presence of tannins and organic matter. This could be resulting from higher investments in this chemical defense in response to high soil nutrient availability, since negatively charged surfaces of organic matter retains nutrients and some organic molecules chelate micronutrient, making them available for plant roots (Salisbury and Ross 1991). Organic matter also provides clay aggregation stability, which allows water and air to move through the soil readily and permits roots to penetrate with little resistance (Motta et al. 2002). It was also suggested that organic compounds could favor plant growth, although there is not much support to this idea (Salisbury and Ross 1991). Thus, our result goes in the opposite direction of what was expected by the trade-off suggested by Fine et al. (2006), since we found a greater abundance of well chemically defended species in richer soils, where species should be less defended since they are more tolerant, and they had found high defenses in poor soils due to low tolerance.

The discussion of whether a species have higher or lower investments in tolerance in high nutrient availability is still a poorly resolved matter (Wise and Abrahamson 2007). Whereas some studies have suggested higher tolerance to herbivory in poor soils, others have suggested the opposite (Hawkes and Sullivan 2001). Although the second idea seems more counterintuitive, some authors have suggested mechanisms to explain lower tolerance in richer soils. Tolerance to herbivory could be negatively correlated to nutrient availability,

when nutrient levels are high and root reserve allocation is reduced (Strauss and Agrawal 1999). Since root reserves are known to be important to tolerance, species growing on rich soils could have low tolerance to herbivory (Strauss and Agrawal 1999) and, hence, high investment in defenses.

Another explanation is possible according to the Limiting Resource Model (Wise and Abrahamson 2005), which intents to explain why many studies have found strong support to both greater and lower tolerance to herbivory in low resources environments (Hawkes and Sullivan 2001). The model provides a series of predictions depending on which are the first and the second plant limiting resources and whether herbivory is affecting or not resource acquisition by plant. Thus, depending on the combination of these factors, it is possible to find higher, lower, or equal tolerance to herbivory, as empirical data has demonstrated (Wise and Abrahamson 2007; Wise and Abrahamson 2008). According to the predictions of the model, low tolerance on rich soils should happen when there is an alternate resource whose acquisition are being affected by herbivory, as, for example, carbon from the atmosphere. Since a species that grows on rich soils is growing at the maximum it could grow without limitation by soil resources, when herbivory affects carbon acquisition, this species would have a much higher decrease in fitness than when herbivory occurs on plants growing on poor soils.

However, the fact that organic matter is related to increasing mineral availability (Salisbury and Ross 1991) should lead us to find the abundance of individuals with tannins to be also related to nutrient content, for example, sum of basis, what we did not find. This may be related to the fact that, at small scale, what matters is not total nutrient in soil, but whether it is availability to the plant, which is increased when organic matter level is high. Conversely, the lack of relation with sum of basis could be an indication that higher abundance of species with tannins is not a consequence of higher organic matter in soil, but

high organic matter in soil is a consequence of higher abundance of species with tannins. Studies in other vegetation types have shown that plant defensive strategies against herbivory are affected by belowground biota and decomposition rates, since lower leaf nutritional quality or higher leaf toxicity could affect not only herbivores, but also the decomposition system (Bardgett et al. 1998, Loranger et al. 2002). As long as leaf decomposition rate is negatively correlated with leaf tannins (Loranger et al. 2002), it could lead to the accumulation of organic matter.

Tannins were the only defense trait related to soil features. Since we sampled only mature leaves, the fact that many species presented tannins (57 from 61 species) is an indication that mature leaves uses chemical as well as structural defenses. The results found for tropical forests – that mature leaves invest in mechanical defensive traits and young leaves in chemical traits – may not stand for cerrado. Nevertheless, we found high variability in many soil features at local scale, suggesting that although many of them do not seem to influence the establishment of well or poorly defended species, community processes at fine scale must be related to soil distribution and this may influence plant community at some level.

References

Agrawal AA, Fishbein M (2006) Plant defense syndromes. Ecology 87: 132-149

Aide TM (1992) Dry season leaf production and escape from herbivory. Biotropica 24:532-537

Amorim PK, Batalha MA (2007) Soil-vegetation relationships in hyperseasonal, seasonal cerrado, and wet grassland in Emas National Park (central Brazil). Acta Oecol 32:319-327

Arens K (1958) O cerrado como vegetação oligotrófica. Bol Fac Fil Ciênc Ltr, Universidade de São Paulo, pp 59-57

Arens K (1963) As plantas lenhosas dos campos cerrados como vegetação adaptada às deficiências minerais do solo. In: Ferri MG (ed.) III Simpósio sobre o cerrado, Edgard Blucher /EDUSP, São Paulo, pp 13-115

Bardgett RD, Wardle DA, Yates GW (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influences soil organisms. Soil Biol. Biochem. 14:1867-1878

Batalha MA, Mantovani W (1999) Chaves de identificação das espécies vegetais vasculares baseadas em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). Rev Inst Florest 11:137-158

Bivand R, Anselin L, Assunção R, Berke O, Bernat A, Carvalho M, Chun Y, Dormann C, Dray S, Halbersma R, Krainski E, Lewin-Koh N, Li H, Ma J, Millo G, Mueller W, Ono H, Peres-Neto P, Reder M, Tiefelsdorf M, Yu D (2009) spdep: Spatial dependence: weighting schemes, statistics and models. R package version 0.4-34. http://CRAN.R-project.org/package=spdep

Carvalho GH, Cianciaruso MV, Batalha MA (2010) Plantminer: a web tool for checking and gathering plant species taxonomic information. Environmental Modelling and Software: in

press.

Coley PD (1983) Herbivory and defensive characteristics of tree species in lowland tropical forest. Ecol Monogr 53:209-233

Coley PD, Bryant JP, Chapin III FS (1985) Resource availability and plant antiherbivore defense. Science 230:895-899

Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. Annu Rev Ecol Syst 27:305-335

Coutinho LM (1990) Fire in the ecology of the Brazilian Cerrado. Ecol Stud 84:82-105

Cornelissen JHC, Lavorel S, Garniel E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Steege H ter, Morgan HD, Heijden MGA van der, Pausas JG and Poorter H (2003) A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. Aust J Bot 51:335-380

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, WD Kissling, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FK, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609-628

Downes RG, Beckwith RS (1951) Studies in the variation of soil reaction. I. Field variation at Barooga, N.S.W. Aust J Agr Res 2:60-72

Embrapa (1997) Manual de métodos de análise do solo. Embrapa, Rio de Janeiro

Falkenberg MB, Santos RI, Simões CMO (2003) Introdução à análise fitoquímica. In Simões CMO, Schenkel G, Gomann G, Mello JCP, Mentz L, Petrovick P (ed) Farmacognosia: da planta ao medicamento. Universidade Federal do Rio Grande do Sul, Porto Alegre

Fine PVA, Miller ZJ, Mesones I, Irazuzta S, Appel HM, Stevens MHH, Sããksjãrvi I, Shultz JC, Coley PD (2006) The growth-defense trade-off and habitat specialization by plants in amazonian forests. Ecology 87:150-162

Goodland R, Ferri MG (1979) Ecologia do Cerrado. Universidade de São Paulo, São Paulo

Goodland R, Pollard R (1973) The Brazilian cerrado vegetation: a fertility gradient. J Ecol 61:219-224

Haridasan M (2000) Nutrição mineral de plantas nativas do cerrado. Rev Bras Fisiol Veg 12:54-64

Hawkes CV, Sullivan JJ (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis. Ecology 82:2045–2058

Howe GA, Jander G (2008) Plant Immunity to insect herbivores. Annu Rev Plant Biol 59:41-66

Köppen W (1931) Grundriss der Klimakunde. Berlin, Gruyter.

Lima MIS (2000) Substâncias do metabolismo secundário de algumas espécies nativas e introduzidas no Brasil. In: Larcher W (ed) Ecofisiologia Vegetal, Rima, São Carlos, pp 33-68

Lopes AS (1984) Solos sob "cerrado". Características, propriedades e manejo. Associação Brasileira para Pesquisa da Potassa e do Fosfato, Piracicaba

Loranger G, Ponge j-F, Imbert D, Lavelle P (2002) Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. Biol Fertil Soils 35:247-252.

Mantovani W, Leitão Filho HF, Martins FR (1985) Chave baseada em caracteres vegetativos para identificação de espécies lenhosas da Reserva Biológica de Moji Guaçu, SP. Hoehnea 12:35–66

Morran PAP (1950) Notes on continuous stochastic phenomena. Biometrika 37:17-23

Motta PEF, Curi N, Franzmeier DP (2002) Relation of soil and geomorphic surfaces in the Brazilian cerrado. In: Oliveira PS, Marquis RJ (eds) The cerrados of Brazil: ecology and natural history of neotropical savannas, Columbia University Press, New York, pp 13-32

Núñez-Farfán J, Fornoni J, Valverde PL (2007) The evolution of resistance and tolerance to

herbivores. Annu Rev Ecol Evol Syst 38:541-566

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2009) vegan: Community Ecology Package. R package version 1.15-2. http://CRAN.R-project.org/package=vegan

Queiroz-Neto JP (1982) Solos da região do cerrado e suas interpretações (revisão de literatura). Rev Bras Cien Solo 6:1-12

R Development Core Team. 2009. R: A language and environment for statistical computing. Wien, R Foundation for Statistical Computing. Avalable via DIALOG. http://www.r-project.org. Accessed 21 Oct 2009

Raij B van, Quaggio JA, Cantarella H, Ferreira ME, Lopes AS, Bataglia OC (1987) Análise química do solo para fins de fertilidade. Fundação Cargill, Campinas

Rasband W (2004) ImageJ: Image process and analysis in Java. National Institutes of Health, Bethesda

Reatto A, Correia JR, Spera ST (1998) Solos do bioma cerrado: aspectos pedológicos. In: Sano SM, Almeida SP. Cerrado: ambiente e flora. Embrapa, Planaltina, pp 47-86

Ruggiero PGC, Batalha MA, Pivello VR, Meirelles ST (2002) Soil-vegetation relationships in cerrado (Brazilian savana) and semideciduous Forest, Southeastern Brazil. Plant Ecol 160:1-16

Salisbury FB, Ross CW (1991) Plant physiology. Belmont: Wadsworth Publishing Company, California

Schädler M, Jung G, Auge H, Brandl R (2003) Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. Oikos 103:121-132

Silva FC (1999) Manual de análises químicas de solos, plantas e fertilizantes. Embrapa, Brasília

SMA Secretaria de Estado do Meio Ambiente (1997) Cerrado: bases para conservação e uso

sustentável das áreas de cerrado do estado de São Paulo. SMA, São Paulo

Sollings P (1998) Factors influencing species composition in tropical lowland rain Forest: does soil matter? Ecology 79:23-30

Souza AF and Martins FR (2004) Microsite espaecialization and spatial distribution of *Geonoma brevispata*, a clonal palm in south-eastern Brazil. Ecol Res 19:521-532

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Tree 5:179-185

Wise MJ, Abrahamson WG (2005) Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. Oikos 109:417-428

Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. Am Naturalist 169:443-454

Wise MJ, Abrahamson WG (2008) Applying the limiting resource model to plant tolerance of apical meristem damage. Am Naturalist 172:635–647

Zar JH (1999) Biostatistical analysis. Prentice-Hall, New Jersey

Table 1: Leaf defense traits (mean ± standard deviations) from woody species collected in a cerrado site at Federal University of São Carlos, Brazil (approximately, 21º58'05.3"S, 47º52'10.1"W), in the rainy season of 2008. Water leaf content (mg.cm^{-2}); specific leaf area (cm^2 g^{-1}); leaf toughness (N); leaf trichomes density per area (cm^{-2}); latex content (mg); C:N ratio; presence (1) or absence (0) of chemical defenses: alkaloids (A), terpenoids (Te), and tannins (Ta).

Species	Family	Water	Specific leaf area	Toughness	Latex	Trichomes	Nutritional quality	A	Te	Ta
Acosmium dasycarpum (Vogel) Yakovlev	Fabaceae	0.02±0.005	78.626±8.710	1.227±0.240	0.000±0.000	1040.200±334.030	16.784±2.733	0	0	1
Acosmium subelegans (Mohlenbr.) Yakovlev	Fabaceae	0.017±0.005	82.041±14.153	1.018±0.216	0.000±0.000	55.600±123.210	16.630±3.164	0	1	1
Aegiphila lhotskiana Cham.	Lamiaceae	0.027±0.005	103.966±15.022	0.712±0.228	0.000±0.000	841.200±192.836	14.721±2.374	0	1	1
Annona coriacea Mart.	Annonaceae	0.027±0.007	86.254±17.198	2.084±0.498	0.000±0.000	203.800±71.852	28.189±4.422	0	0	1
Annona crassiflora Mart.	Annonaceae	0.020±0.000	117.139±25.048	0.701±0.080	0.000±0.000	379.600±81.929	24.607±4.933	0	0	0
Banisteriopsis megaphylla (A.Juss.) B.Gates	Malpighiaceae	0.018±0.006	127.473±28.145	0.422±0.198	0.000±0.000	617.400±330.540	14.820±3.313	0	0	1
Bauhinia rufa Steud.	Fabaceae	0.016±0.005	67.283±5.410	1.132±0.239	0.000±0.000	954.400±227.058	19.447±1.707	0	1	1
Byrsonima coccolobifolia Kunth	Malpighiaceae	0.020±0.000	97.4±16.128	0.776±0.097	0.000±0.000	13.800±12.357	22.468±2.805	0	0	1
Byrsonima verbascifolia Rich. ex	Malpighiaceae	0.025±0.007	74.42±6.576	0.680±0.113	0.000±0.000	2056.500±792.667	40.168±6.681	0	0	1

Juss.

Campomanesia adamantium (Cambess.) O.Berg	Myrtaceae	0.013±0.005	81.004±14.263	1.073±0.203	0.000±0.000	603.800±401.108	27.663±2.903	0	1	1
Casearia sylvestris Sw.	Salicaceae	0.010±0.000	123.956±19.570	0.667±0.223	0.000±0.000	143.200±114.154	15.955±2.912	0	0	1
Connarus suberosus Planch.	Connaraceae	0.02±0.000	65.119±5.599	1.444±0.232	0.000±0.000	1403.000±561.190	29.951±5.808	0	1	1
Dalbergia miscolobium Benth.	Fabaceae	0.02±0.000	76.002±10.460	0.760±0.256	0.000±0.000	11.400±9.762	17.965±2.736	0	0	1
Daphnopsis sp Mart.	Thymelaeaceae	0.017±0.005	132.102±43.950	1.231±0.222	0.000±0.000	0.600±0.894	23.764±5.592	0	0	1
Davilla elliptica A.St.-Hil.	Dilleniaceae	0.016±0.005	129.334±42.730	0.852±0.257	0.000±0.000	215.600±158.371	28.791±2.862	0	0	1
Davilla rugosa Poir.	Dilleniaceae	0.011±0.003	188.293±39.525	0.824±0.252	0.000±0.000	227.800±133.607	28.312±3.456	0	0	1
Dimorphandra mollis Benth.	Fabaceae	0.012±0.004	102.249±14.677	0.285±0.115	0.000±0.000	623.400±173.259	12.824±1.495	0	0	1
Diospyros hispida A.DC.	Ebenaceae	0.023±0.005	62.249±6.733	1.040±0.320	0.000±0.000	708.000±278.318	33.142±5.446	0	1	1
Erythroxylum cuneifolium O.E.Schulz	Erythroxylaceae	0.011±0.003	160.394±42.361	0.399±0.154	0.000±0.000	1.000±2.236	18.156±1.648	0	1	1
Erythroxylum suberosum A.St.-Hil.	Erythroxylaceae	0.019±0.003	90.410±12.658	1.338±0.409	0.000±0.000	0.400±0.894	18.381±3.089	0	1	1
Erythroxylum tortuosum Mart.	Erythroxylaceae	0.02±0.000	90.593±13.504	0.942±0.362	0.000±0.000	1.600±1.342	20.375±1.497	0	0	1
*Fagara rhoifoli*a Engl. in Engl. & Prantl	Rutaceae	0.013±0.005	105.943±14.723	0.452±0.155	0.000±0.000	247.000±100.814	16.721±3.276	0	1	1
Gochnatia pulchra Cabrera	Asteraceae	0.010±0.000	103.086±803.475	0.76±0.589	0.000±0.000	2699.6±803.475	21.030±5.893	0	1	1
Guapira noxia (Netto) Lundell	Nyctaginaceae	0.031±0.007	104.277±23.772	0.878±0.240	0.000±0.000	17.200±24.773	10.427±0.679	0	1	1
Guapira opposita (Vell.) Reitz	Nyctaginaceae	0.019±0.007	120.074±27.549	0.795±0.185	0.000±0.000	37.600±55.162	11.283±0.918	0	1	1

Species	Family									
Heteropterys umbellata A.Juss.	Malpighiaceae	0.011±0.003	117.969±21.672	0.379±0.144	0.000±0.000	27.000±44.688	17.185±4.415	0	0	1
Ilex cerasifolia Loes.	Aquifoliaceae	0.01±0.000	156.835±42.937	0.630±0.169	0.000±0.000	519.000±85.758	27.948±7.895	0	0	1
Kielmeyera coriacea Mart. & Zucc.	Clusiaceae	0.031±0.003	77.096±13.265	1.103±0.213	0.005±0.005	0.800±1.304	27.690±5.027	0	1	1
Kielmeyera grandiflora A.St.-Hil.	Clusiaceae	0.041±0.009	76.627±12.924	1.880±0.396	0.009±0.003	0.000±0.000	33.816±9.240	0	0	1
Leandra lacunosa Cogn.	Melastomataceae	0.022±0.004	126.108±25.624	0.846±0.321	0.000±0.000	256.800±35.231	28.718±3.329	0	0	1
Lippia velutina Schauer	Verbenaceae	0.014±0.005	164.427±59.599	0.452±0.109	0.000±0.000	925.800±130.239	17.302±2.669	0	0	0
Machaerium acutifolium Mart. ex Benth.	Fabaceae	0.014±0.005	91.939±10.788	0.881±0.211	0.000±0.000	214.200±123.401	10.702±2.371	0	0	1
Miconia albicans Steud.	Melastomataceae	0.017±0.005	90.741±17.495	0.727±0.249	0.000±0.000	65100.000[a]	30.919±6.920	0	0	1
Miconia ligustroides Naudin	Melastomataceae	0.019±0.003	96.689±21.997	0.568±0.100	0.000±0.000	5.400±6.504	26.619±2.556	0	0	1
Miconia rubiginosa DC.	Melastomataceae	0.02±0.000	64.441±7.438	0.712±0.100	0.000±0.000	281.000±52.192	38.415±4.261	0	0	1
Myrcia bella Cambess.	Myrtaceae	0.017±0.005	88.552±11.776	1.164±0.218	0.000±0.000	1020.000±307.864	32.868±5.892	0	1	1
Myrcia guianensis (Aubl.) DC.	Myrtaceae	0.02±0.000	64.426±8.164	1.269±0.312	0.000±0.000	660.800±369.921	28.653±3.666	0	0	1
Myrcia sp DC. ex Guill.	Myrtaceae	0.0125±0.005	77.878±7.813	0.860±0.153	0.000±0.000	1094.750±503.692	28.172±1.701	0	0	1
Myrcia splendens (Sw.) DC.	Myrtaceae	0.010±0.000	104.432±23.877	0.848±0.098	0.000±0.000	1067.000±384.667	38.978±4.806	0	0	1
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	0.016±0.005	87.259±13.447	1.083±0.253	0.000±0.000	418.600±137.671	25.046±2.835	0	1	1
Myrsine coriacea Nadeaud	Myrsinaceae	0.012±0.004	125.938±21.262	0.517±0.075	0.000±0.000	307.800±93.106	19.588±0.689	0	1	1
Myrsine umbellata G.Don	Myrsinaceae	0.020±0.000	84.201±19.922	1.091±0.321	0.000±0.000	0.200±0.447	30.977±3.458	0	0	1
Ocotea pulchella Mart.	Lauraceae	0.014±0.005	69.967±12.467	1.356±0.208	0.000±0.000	1445.200±710.185	30.018±6.148	0	1	1

Species	Family									
Ouratea spectabilis Engl.	Ochnaceae	0.0225±0.005	62.808±11.806	2.325±0.474	0.000±0.000	0.000±0.000	32.138±6.722	0	1	1
Palicourea coriacea (Cham.) K.Schum.	Rubiaceae	0.029±0.005	111.645±20.856	0.883±0.380	0.000±0.000	2.400±4.336	17.939±5.496	0	1	0
Pera glabrata (Schott) Poepp. ex Baill.	Peraceae	0.020±0.000	73.580±9.122	0.931±0.197	0.000±0.000	0.000±0.000	31.028±1.942	0	0	1
Phyllanthus acuminatus Vahl	Phyllanthaceae	0.010±0.000	207.404±40.957	0.290±0.060	0.000±0.000	0.000±0.000	27.659±1.464	0	0	1
Piptocarpha rotundifolia Baker	Asteraceae	0.020±0.000	95.997±21.772	1.123±0.344	0.000±0.000	1304.400±418.845	28.332±7.607	0	1	1
Plenckia populnea Reissek	Celastraceae	0.012±0.004	106.168±12.255	0.654±0.204	0.000±0.000	0.000±0.000	21.158±5.185	0	1	1
Psidium laurotteanum Cambess. in A.St.-Hil.	Myrtaceae	0.018±0.004	73.770±14.123	1.259±0.139	0.000±0.000	1583.200±133.412	38.277±5.824	0	1	1
Rudgea viburnoides (Cham.) Benth.	Rubiaceae	0.033±0.005	80.721±14.276	1.226±0.248	0.000±0.000	687.000±257.630	25.226±3.647	0	0	1
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	Araliaceae	0.036±0.011	52.195±16.763	1.044±0.330	0.000±0.000	2392.200±450.335	31.360±5.455	0	0	1
Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	Araliaceae	0.028±0.006	61.864±5.268	0.910±0.231	0.000±0.000	1571.600±1038.238	27.194±4.838	0	1	1
Stryphnodendron adstringens (Mart.) Coville	Fabaceae	0.022±0.004	81.427±14.873	0.727±0.125	0.000±0.000	23.600±48.387	18.030±1.465	0	0	1
Stryphnodendron obovatum Benth.	Fabaceae	0.017±0.007	121.016±30.463	0.434±0.143	0.000±0.000	4.600±2.302	18.448±2.972	0	0	1
Styrax ferrugineus Nees & Mart.	Styracaceae	0.020±0.005	69.605±19.303	1.462±0.335	0.000±0.000	437.400±12.341	36.008±3.902	0	1	1

Species	Family									
Tabebuia ochracea Standl.	Bignoniaceae	0.021±0.003	77.181±13.026	1.284±0.358	0.000±0.000	620.200±148.288	19.923±2.948	0	0	1
Tapirira guianensis Aubl.	Anacardiaceae	0.020±0.000	74.561±10.860	0.730±0.141	0.000±0.000	18.000±31.369	33.766±3.630	0	0	1
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	Rubiaceae	0.020±0.005	86.199±10.765	0.790±0.300	0.000±0.000	1626.600±959.065	27.202±5.748	1	1	1
Vochysia tucanorum Mart.	Vochysiaceae	0.024±0.005	106.929±16.193	1.192±0.182	0.000±0.000	9.000±14.213	21.216±2.549	0	1	0
Xylopia frutescens Aubl.	Annonaceae	0.010±0.000	197.119±33.671	0.412±0.122	0.000±0.000	140.400±130.856	21.432±1.796	0	1	1

[a] counted on one leaf, with a eletronic microscope, due to an extremely high number of trichomes

Table 2: Results and models of the regression analysis of defense traits against herbivory as a function of soil variables. Defense traits used were: Total defenses index; SLA: specific leaf area ($cm^2\ g^{-1}$); C:N ratio; Water leaf content ($mg.cm^{-2}$); leaf toughness (N); Leaf latex content (mg); leaf trichomes density per area (cm^{-2}); presence of chemical defenses: alkaloids, terpenoids and tannins. The stepwise model is the model that best explained variation in defense traits according to the Akaike Information Criterion. Soil features were: OM (Organic matter; gkg-1); Al3+ (Exchangeable aluminum; mmolc kg-1); SB (Sum of basis; mmolc kg-1). Data were collected at a cerrado site at Federal University of São Carlos, Brazil (approximately, 21º58'05.3"S, 47º52'10.1"W).

	Stepwise model	$R2^{a}$	Moran's ssd[b]	Rho[c]	Moran's ssd[d]
Total defenses index	Total fertility index	0.002^{ns}	-	-	-
Total defenses index	SB	0.002^{ns}	-	-	-
SLA	OM	0.15^{***}	2.0^{*}	0.24^{ns}	0.18^{ns}
C:N ratio	OM	0.19^{***}	1.68^{*}	0.19^{ns}	0.35^{ns}
Water leaf content	OM	0.17^{***}	1.75^{*}	0.20^{ns}	0.13^{ns}
Leaf toughness	OM	0.16^{***}	2.24^{*}	0.25^{ns}	0.11^{ns}
Leaf latex content	OM, SB, Al+3	0.01^{ns}	-	-	-
Leaf trichomes density	OM, SB, Al+3	0.02^{ns}	-	-	-
Alkaloids	OM, SB, Al+3	0.04^{ns}	-	-	-
Terpenoids	OM, SB, Al+3	0.02^{ns}	-	-	-
Tannins	OM	0.16^{***}	0.58^{ns}	-	-

[a]: coefficient of multiple regression (linear regression when there is one variable in the model)
[b]: Moran's statistic standard deviate before correcting for spatial dependence
[c]: Rho statistic for autoregressive models
[d]: Moran's statistic standard deviate after correcting for spatial dependence
[ns]: not significant; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$
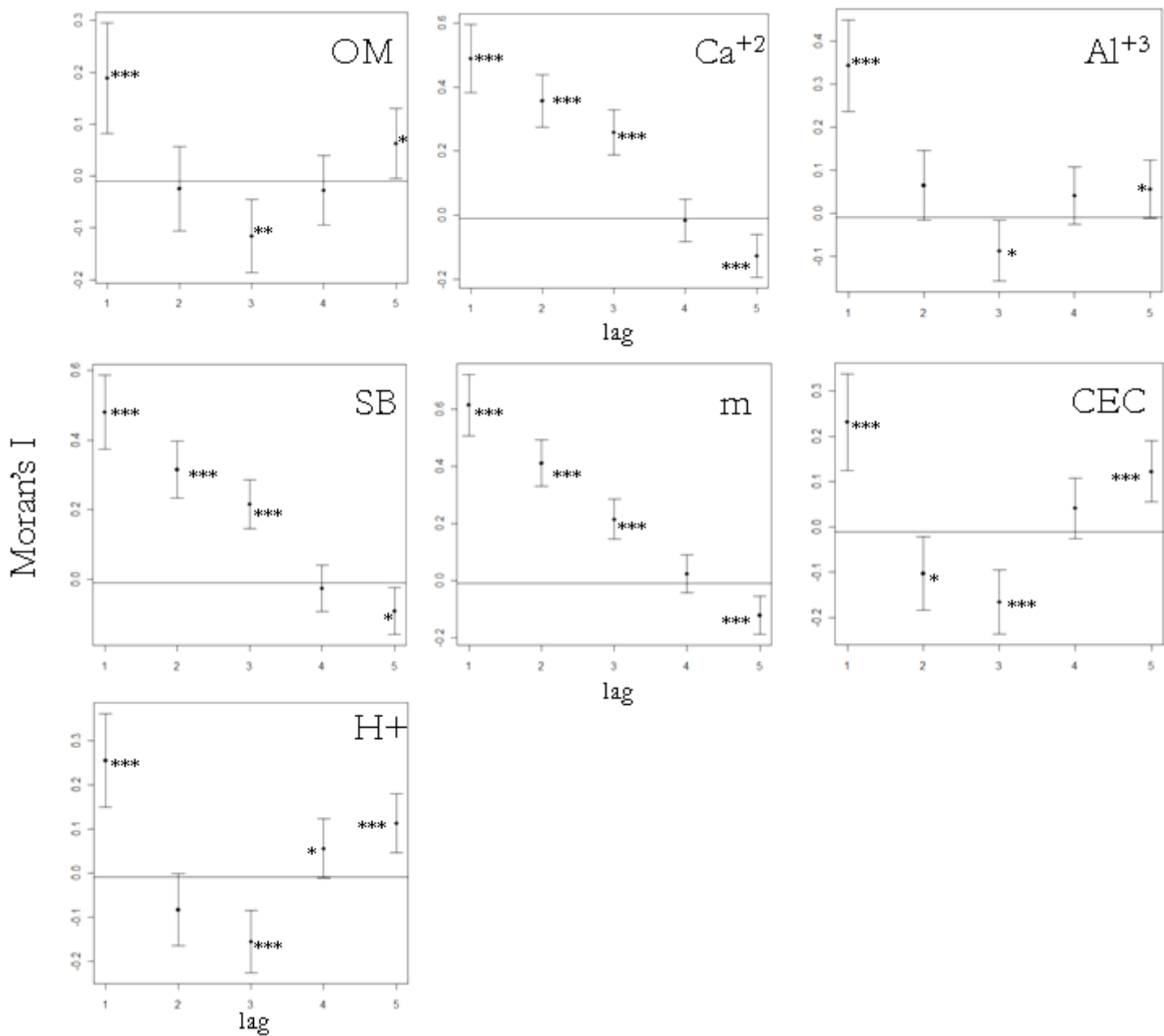
Figure 1: Correlograms of soil variables using Moran's index as response variable and lag distances as explanatory variables. Each lag unit represents a distance of 5 m. "*" represents significant autocorrelation. Significant points over the line represents positive autocorrelation and above the line negative autocorrelation. Soil features are: OM (Organic matter; gkg-1); Ca2+ (exchangeable calcium; mmolc kg-1); Al3+ (exchangeable aluminum; mmolc kg-1); SB (sum of basis; mmolc kg-1); m (aluminum saturation; %); CEC (cation exchange capacity; mmolc kg-1); H (exchangeable hydrogen; mmolc kg-1). *: p<0.05; **: p<0.01; ***: p<0.001. Data were collected at a cerrado site at Federal University of São Carlos, Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W).

CONCLUSÃO GERAL

Conclusões gerais

Este trabalho nos permitiu chegar às seguintes conclusões:

- Embora não seja possível inferir relações de causa e efeito, nossos resultados indicaram que o solo é um fator importante estruturando comunidades de cerrado mesmo em escala local;

- O solo não se relacionou com a composição florística, o que parece indicar redundância funcional de algumas espécies;

- O solo se relacionou com descritores da comunidade como abundância, riqueza e equabilidade, o que sugere um papel determinístico para o solo, contrariando previsões da teoria neutra;

- A alta dominância de *Myrsine umbelata* parece estar relacionada com mecanismos de retroalimentação positiva, que favorecem uma maior distribuição dessa espécie no cerrado em questão;

- Os investimentos totais em defesas contra herbivoria não foram influenciados pela fertilidade total do solo em escala local, o que provavelmente resulta da baixa variação da fertilidade nessa escala. Assim, essa relação parece ser verdadeira apenas quando comparamos diferentes tipos vegetacionais;

- Dos nove traços de defesa contra herbivoria medidos, o único que se relacionou com os nutrientes do solo foi a presença de taninos. Tendo em vista que esse traço se relacionou positivamente com o conteúdo de matéria orgânica do solo, o que significa maior investimento em defesas em solos mais férteis, sugerimos três possibilidades: (1) um maior investimento em defesas em solos mais ricos, para compensar a baixa alocação em reservas, importantes para tolerar a herbivoria; (2) a limitação por um recurso alternativo, o que de acordo com o modelo dos recursos limitantes levaria a uma diminuição da tolerância à herbivoria em solos mais ricos, e consequentemente, a necessidade de compensar com investimentos em defesa; ou (3) defesas contra herbivoria alteram as condições do solo, pois folhas com taninos se decompõem mais lentamente levando à acumulação de matéria orgânica no solo próximo às plantas com taninos;

- Mais trabalhos deveriam estudar o cerrado em escala fina para particionar a relação entre solo e vegetação entre associação dentro de hábitat e entre diferentes hábitats;