UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS - RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
BIOLOGIA VEGETAL

Nutrição mineral e escleromorfismo foliar de grupos funcionais e comunidades vegetais savânicas

MARCELO CLARO DE SOUZA

Tese apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Biologia Vegetal).

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"*À minha família por tudo que representam em minha vida*"

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"*Toda ideia realmente nova é considerada maluca em um primeiro momento*"

Alfred North Whitehead (1861-1947)

Sumário

Nutrição mineral e escleromorfismo foliar de grupos funcionais e comunidades vegetais savânicas

1 - Resumo

As savanas (localizadas na Austrália, África do Sul e Brasil) abrigam a segunda maior biodiversidade do planeta. Tais savanas se desenvolveram sobre solos ácidos, pobres em nutrientes e com estações secas e chuvosas bem definidas. Dentre os filtros ecológicos limitantes à manutenção das savanas, fogo, fertilidade do solo, disponibilidade hídrica e herbivoria são considerados os mais importantes. Outros filtros muito importantes, mas considerados subfiltros da fertilidade do solo são: acidez do solo e disponibilidade de alumínio (Al). O Al é considerado um elemento tóxico para a maior parte das plantas, entretanto as espécies savânicas são consideradas insensíveis ao Al, sendo algumas espécies inclusive acumuladoras. Desta forma, foi estudado o perfil nutricional, acúmulo de Al e escleromorfismo foliar de espécies savânicas em três níveis: regional, nacional e intercontinental. Para os níveis nacional e intercontinental acrescentamos as variações de pluviosidade anual, fertilidade e acidez do solo. Em nível regional comparamos as variações no grau de escleromorfismo, concentração de nutrientes foliares, acúmulo de Al, fenologia e produção de metabólitos secundários em folhas jovens e maduras de espécies acumuladoras e não acumuladoras de Al em um fragmento de cerrado em Itirapina – SP. Em nível nacional comparamos as variações das concentrações de nutrientes foliares, acúmulo de Al e escleromorfismo foliar entre dois fragmentos de cerrado *sensu stricto* (*s. str.*): um na região central (Brasília – DF) e o outro na borda sudeste do cerrado (Itirapina – SP). Em escala global, estudamos as variações nutricionais, acúmulo de Al e escleromorfismo foliar entre as savanas Australiana, Brasileira e Sul Africana. Em escala regional observamos dois padrões distintos de desenvolvimento foliar entre os dois grupos de espécies. Em escala nacional, observamos menor ecleromorfismo e maior acúmulo de nutrientes foliares na comunidade de cerrado *s. str.* localizada na borda sudeste. Tais variações foram explicadas pela maior fertilidade do solo e estação seca mais

curta na borda sudeste. Em escala global observamos que a savana Brasileira (cerrado) possui solos mais ácidos que as demais savanas e possui maior disponibilidade hídrica. Em termos de fertilidade do solo, não houve variação significativa entre as savanas. Diante do exposto o cerrado foi considerado o bioma savânico menos escleromórfico e com o maior número de espécies acumuladoras de Al. A savana Sul Africana foi considerada a mais escleromórfica, mas apresentou maior concentração de N foliar. Provavelmente, o maior acúmulo de N foliar por parte das espécies africanas é reflexo da alta pressão por crescimento e desenvolvimento rápido impostos pelo fogo e altas taxas de herbivoria no continente Africano. A savana Australiana apresentou padrões ecofisiológicos e nutricionais intermediários entre as savanas. Tal disjunção entre as savanas pode ser explicada pela ação conjunta da acidez do solo, disponibilidade de Al trocável e precipitação anual.

Palavras chave: alumínio, área foliar específica, bioma, tropical

Mineral nutrition and leaf scleromorphism of functional groups and savanna's plant communities

2 - Abstract

Savannas (located in Australia, Brazil and South Africa) hold the second largest biodiversity on the planet. These savannas have developed their vegetation structure on acidic and nutrient-poor soils, under a well-defined dry and rainy seasons. Among the limiting ecological filters, fire, soil fertility, water availability and herbivory are considered the most important ones. Other filters, which may be considered subfilters of the soil fertility are acidity and aluminum (Al) availability in the soil. Aluminum is considered a toxic element for most plant species, however savanna plants are insensitive to Al, and some species are Al-accumulators. We studied leaf nutritional status, Al accumulation and leaf scleromorphism of savanna species at three levels: regional, national and intercontinental. For national and intercontinental analysis we evaluated variations in the annual

rainfall, soil fertility and soil acidity. At the regional level, we compared leaf scleromorphism, nutritional status, Al accumulation, leaf phenology and the concentration of secondary metabolites in young and mature leaves of Al-accumulator and non-accumulator species in a cerrado remnant in Itirapina-SP. At the national level we compared the nutritional status, Al accumulation and leaf scleromorphism variations between two cerrado *sensu stricto* (*s. str.*) fragments:, one in the core region (Brasília - DF) and another on the southeastern periphery of the cerrado (Itirapina - SP). On a global scale, we studied the dissimilarities on the nutritional status, Al accumulation and leaf scleromorphism between the Australian, Brazilian and South African savannas. At the regional level, we observed two distinct strategies of leaf development between Al-accumulator and non-accumulator species. At the national level, we concluded that the peripheral cerrado community was less scleromorphic than the community in the core. These variations were explained by the higher soil fertility and shorter dry season in the periphery as compared to the core region. The Brazilian savanna presented the highest annual rainfall and the soils were more acidic than the other tropical savannas in Australia ans South Africa. The Brazilian savanna is the least scleromorphic, and comprises many times more Al-accumulator species than the other Tropical savannas. Despite the lower leaf scleromorphism, South African species showed the highest leaf N concentration. This reflects the higher pressure for fast growth and development in S. Africa, due to great incidence of fire and herbivory. The Australian savanna presented an intermediate behavior amongst savannas. The disjunction between these savannas can be explained by the variations on soil acidity, Al availability and annual rainfall, which are distinct between the three sites.

Key words: aluminum, specific leaf area, biome, tropical

3 - Introdução geral

Aproximadamente 20% das terras emersas do planeta são compostas por solos ácidos (pH ~ 4)6-, ricos em alumínio (Al- e pobres em nutrientes minerais e matéria orgânica. Originalmente esses solos abrigavam milhares de km^2 de savanas tropicais. Entretanto, com a expansão das cidades e a necessidade de aumento na produção de alimentos, boa parte desta vegetação nativa foi substituída por culturas agrícolas altamente sensíveis aos efeitos fitotóxicos causados pelo Al edáfico.

Devido ao processo acelerado de substituição da vegetação nativa das savanas tropicais (principalmente do cerrado brasileiro- por culturas agrícolas, pouco sabemos a respeito da nutrição mineral dessas espécies. E praticamente desconhecemos os porquês do acúmulo e dependência de Al por certas espécies do cerrado, uma vez que o Al é considerado um elemento altamente tóxico para muitas espécies vegetais.

Baseado na hipótese de que o Al edáfico, em solos ácidos, reduz a absorção de nutrientes do solo, e que seu acúmulo é capaz de interferir no crescimento e desenvolvimento vegetal o objetivo do presente trabalho foi estudar as variações ecofisiológicas (escleromorfismo foliar-, nutricionais e acúmulo de Al em espécies vegetais savânicas, englobando análises em escala local a partir da utilização de grupos funcionais do cerrado (espécies acumuladoras e não acumuladoras de Al- localizados em um mesmo fragmento na região de Itirapina – SP; em escala regional comparando duas comunidades de cerrado *sensu stricto* localizadas na região central (Brasília)DF- e periférica (Itirapina- do cerrado; e em escala global, comparando comunidades savânicas localizadas na Austrália, África do Sul e Brasil.

4 - Revisão de literatura

4.1 - Savanas e o cerrado brasileiro

As savanas ocupam 20% da superfície terrestre e estão distribuídas, principalmente, pelos continentes africano, australiano e sul americano (Baudena e Rietkerk 2012-. Estas savanas se desenvolveram sobre solos ácidos (Hill et al 2010, Haridasan 2008-, com duas estações climáticas bem definidas (verão chuvoso e inverno seco- (Mott et al. 1985, Oliveira e Marquis 2002- e alta incidência de fogo (Lehmann et al 2011- e herbivoria (Sankaran et al 2005-. Durante milhões de anos, essa combinação de filtros ecológicos selecionou diferentes fisionomias savânicas compostas por gramíneas C_4, arbustos e espécies lenhosas (Lehmann et al 2011-. Apesar das similaridades entre as savanas, elas diferem significativamente em sua composição florística e características ecofisiológicas, devido as diferentes pressões impostas pelos filtros ecológicos em cada continente.

O Cerrado é composto pelas fisionomias: campo limpo, campo sujo, campo cerrado, cerrado *sensu stricto* e cerradão (Batalha 2011-. Inicialmente, o Cerrado ocupava 21% do território brasileiro (Souza e Habemann 2012- e abrigava a segunda maior diversidade de espécies do território brasileiro, perdendo em número absoluto de espécies apenas para a Floresta Amazônica (Guarim Neto e Morais, 2003-. Devido ao elevado número de espécies endêmicas e ameaçadas de extinção, o cerrado é considerado um dos 25 “hotspots” distribuídos ao redor do planeta, juntamente à Mata Atlântica (Myers et al 2000-. Entretanto, por ser considerado uma da últimas fronteiras agrícolas do planeta, o cerrado vem sendo severamente fragmentado desde o início dos anos 1960 e substituído por culturas agrícolas, principalmente por pastagens e soja no Brasil central (Phalan et al 2013- e cana)de)açúcar (Rodrigues e Ortiz 2006- e laranja no sudeste (Souza e Habermann 2012-.

4.2 - Grupos funcionais: espécies acumuladoras e não acumuladoras de Al

O termo “grupos funcionais” foi proposto por Cummins (1974- ao sugerir a possibilidade de agrupamento arbitrário de espécies distintas com padrões ou respostas ecofisiológicas semelhantes

em relação ao ecossistema (ex. acúmulo de nutrientes, deciduidade foliar, etc.-, promovendo a ligação entre diversidade de espécies e função no ecossistema (Blondel, 2003-.

De um modo geral, o número de estudos sobre grupos funcionais vegetais aumentou significativamente nas duas últimas décadas, entretanto a maior parte desses estudos foram conduzidos em florestas temperadas, seguido por número reduzido de estudos em florestas tropicais (Alvarez)Añorve et al 2008-. Apesar das savanas tropicais ocuparem aproximadamente 20% da superfície terrestre e abrigar um grande número de espécies vegetais (Grace et al 2006- pouco sabemos sobre seus grupos funcionais, principalmente em relação ao acúmulo de Al.

O Al é o terceiro elemento mais abundante na crosta terrestre, perdendo em número absoluto apenas para o O e Si, sendo por consequência o metal mais abundante na Terra (Zuckerman et al 2011-. Apesar de todas as espécies vegetais nativas de regiões com solos ácidos (pH~4- serem tolerantes aos efeitos fitotóxicos causados pelo Al edáfico, as espécies savânicas e florestais podem ser agrupadas em dois grupos funcionais distintos em relação ao acúmulo de Al: espécies acumuladoras e não acumuladoras de Al (Jansen et al 2002-. As espécies não acumuladoras de Al são capazes de acumular até 1000 mg $kg^{)1}$ de Al foliar, enquanto que as espécies acumuladoras, ou hyperacumuladoras, são capazes de acumular concentrações altíssimas de Al foliar (1000 e 10000 mg $kg^{)1}$- (Souza e Habermann 2012, Jansen et al 2002-, sendo que algumas espécies da família Vochysiaceae são capazes de acumular valores próximos a 20000 mg $kg^{)1}$ de Al (Haridasan 1982-, sendo consideradas hiper)acumuladoras de Al (Jansen et al 2002-.

4.3 – Escleromorfismo foliar, nutrição mineral de plantas e produção de metabólitos secundários

As vegetações savânicas são compostas por espécies esclermomórficas e o grau de esclermorfismo foliar, pode variar, entre diversos fatores, em função das concentrações de nitrogênio (N- nas folhas (Delgado et al 2013-. Assim, as espécies vegetais que possuem baixa área

foliar específica (AFE- e baixas concentrações de nutrientes foliares são mais escleromórficas que as espécies com alta AFE e maior concentração de nutrientes foliares. Tais variações, podem ser usadas para a distinção entre fisionomias (savana x floresta- (Franco et al 2005- e pares congenéricos (Habermann e Bressan 2011-.

Além das relações com o escleromorfismo foliar, as concentrações de nutrientes foliares estão relacionadas ao crescimento e maturação foliar, e a produção de metabólitos secundários de defesa. As espécies savânicas possuem basicamente duas estratégias de desenvolvimento foliar: 1 – alta absorção de nutrientes do solo e rápido desenvolvimento foliar (Kursar e Coley 2003-; e lenta absorção de nutrientes e lento desenvolvimento foliar. Nesse caso, estas espécies investem na produção de metabólitos secundários de defesa como compostos fenólicos, taninos, alcalóides e flavonóides, havendo significativa redução na produção desses compostos após a maturação foliar (Varanda et al. 2005-.

Devido ao sucesso em pesquisas agronômicas a nutrição mineral de plantas é uma das áreas mais estudadas, entretanto muito pouco se conhece sobre a nutrição mineral de plantas nativas das savanas. De acordo com os conhecimentos agronômicos o Al edáfico é um elemento altamente tóxico para as plantas (Menzies 2003-, capaz de comprometer o desenvolvimento do sistema radicular (Kopptike et al 2008- e interferir negativamente na absorção de nutrientes para o desenvolvimento vegetal (Marshner 1995-.

Entretanto, as espécies do cerrado, foram selecionadas sobre solos extremamente ácidos (pH~4- e com elevadas concentrações de Al trocável (Haridasan 2008-, de modo que estas espécies são insensíveis aos efeitos tóxicos do Al edáfico. Além da insensibilidade e habilidade para acumular elevadas concentrações de Al nas folhas, duas espécies do cerrado são alumino)dependentes: *Miconia albicans* (Melastomataceae- (Haridasan 1988- e *Vochysia elliptica* (Vochysiaceae- (Haridasan 2008-. Este autor observou severa redução no desenvolvimento dessas duas espécies ao cultivá)las em solos alcalinos e soluções nutritivas desprovidas de Al. Apesar de

tal insensibilidade ter sido sugerida por Haridasan (1982, 1987- ao observar que as concentrações de nutrientes foliares eram semelhantes entre as espécies acumuladoras e não acumuladoras de Al, existe a possibilidade de que o acúmulo de Al interfira nas reações metabólicas das espécies acumuladoras de Al, alterando a produção de metabólitos secundários e seus ciclos fenológicos.

Assim os objetivos desta tese foram: capítulo 1, testar a hipótese de as espécies acumuladoras e não acumuladoras de Al apresentarão similaridades fenológicas e nutricionais, além de apresentar níveis similares de escleromorfismo foliar; capítulo 2, testar a hipótese de que duas comunidades de cerrado *sensu stricto* localizadas nas regiões central e periférica do cerrado são igualmente escleromórficas e apresentam concentrações semelhantes de nutrientes e Al foliar; capítulo 3, testar a hipótese de que os fatores edafoclimáticos são responsáveis pelas variações no status nutricional, acúmulo de Al e escleromorfismo foliar antre as savanas australiana, brasileira e sul africana.

4.4 - Referências

ALVAREZ)AÑORVE, M.; QUESADA, M.; LA BARRERA, E. Remote sensing and plant functional groups physiology, ecology,and spectroscopy in Tropical Systems. In: Hyperspectral remote sensing of tropical and sub)tropical forests. p. 28)30, 2008.

BATALHA, M.A. O cerrado não é um bioma. Biota Neotropica, vol. 11, p. 21)24, 2011.

BLONDEL, J. Guilds or functional groups: does it matter? Oikos, vol. 100, p. 223–231, 2003.

CUMMINS, K.W. Structure and function of stream ecosystems. BioScience, vol. 24, p. 631)641, 1974.

GRACE, J.; SAN JOSÉ, J.; MEIRL, P.; MIRANDA, H.S.; MONTES, R.A. Productivity and carbon fluxes of tropical savannas. Journal of Biogeography, vol. 33, p. 387)400, 2006.

GUARIM NETO, G.; MORAIS, R.G. Recursos medicinais de espécies do cerrado de Mato Grosso: um estudo bibliográfico. Acta Botânica Brasílica, vol. 17, 561)584, 2003.

HARIDASAN, M. Aluminum accumulation by some cerrado native species of central Brazil. Plant and Soil, vol. 65, p. 265)273, 1982.

HARIDASAN, M. Distribution and mineral nutrition of aluminium accumulating species in different plant communities of the cerrado region of central Brazil. In: San Jos JJ, Montes R, editors. La Capacidad Bioproductiva de Sabanas. I.V.I.C., Caracas, Venezuela. pp. 309)348, 1987.

HARIDASAN, M. Nutritional adaptations of native plants of the cerrado biome in acid soils. Brazilian Journal of Plant Physiology, vol. 20, p.183)195, 2008.

HILL, M.J.; ROMÁN, M.O.; SCHAAF, C.B. Biogeography and dynamics of global tropical and subtropical savannas: a spatiotemporal view. In: Hill MJ, Hanan NP, editors. Ecosystem function in savannas: measurement and modeling at landscape to global scales, pp. 3)38, 2010.

JANSEN, S.; BROADLEY, M.R.; ROBBRECHT, E.; SMETS, E. Aluminum hyperaccumulation in Angiosperms: a review of its phylogenetic significance. Botanical Review, vol. 68, p. 235)269, 2002.

KOPITTKE, P.M.; BLAMEY, F.P.C.; MENZIES, N.W. Toxicities of soluble Al, Cu, and La include reputures to rhizodermal and root cortical cells of cowpea. Plant and Soil, vol. 303, p. 217)227, 2008.

KURSAR, T.A.; COLEY, P.D. Convergence in defense syndromes of young leaves in tropical rainforests. Biochemical Systematics and Ecology, vol. 31, p. 929–949, 2003

LEHMANN, C.E.R.; ARCHIBALD, S.A.; HOFFMANN, W.A.; BOND, W.J. Deciphering the distribution of the savanna biome. New Phytologist, vol. 191, p. 197)209, 2011.

MARSCHNER, H. Mineral nutrition of higher plants. London: Academic Press. 1995.

MENZIES, N.W. Toxic elements in acid soils: Chemistry and measurement. In: Rengel Z, editor. Handbook of soil Acidity, pp. 267)296, 2003.

MOTT, J.J.; WILLIAMS, J.; ANDREW, M.H.; GILLISON, A.N. Australian savanna ecosystems. In: Tothill JC, Mott JJ, editors. Ecology and Management of the World's Savanna Australian

Academy of Science, Canberra. pp. 56–82, 1985.

MYERS, N.; MITTERMEIER, R.A.; MITTERMEIER, C.G.; DA FONSECA, G.A.; KENT, J. Biodiversity hotspots for conservation priorities. Nature, vol. 403, p. 853)858, 2000.

OLIVEIRA, P.S.; MARQUIS, R. Introduction: development of research in the Cerrados. In: Oliveira PS, Marquis RJ, editors. The Cerrados of Brazil: ecology and natural history of a neotropical savanna,Columbia University Press, Columbia. pp. 1)10, 2002.

PHALAN, B.; BERTZKY, M.; BUTCHART, S.H.M.; DONALD, P.F.; SCHARLEMANN, J.P.W.; STATTERSFIELD, A.J.; BALMFORD, A. Crop expansion and conservation priorities in tropical countries. Plos One, vol. 8, p. e51759, 2013.

RIETKERK, M; BAUDENA, M. Complexity and coexistence in a simple spatial model for arid savanna ecosystems. Theoretical Ecology, 2012. DOI 10.1007/s12080)012)0165)1

RODRIGUES, D; ORTIZ, L. Em direção à sustentabilidade da produção de etanol de cana de açúcar no Brasil. Porto Alegre, Brazil: Amigos da Terra Brasil; São Paulo, Brazil: Vitae Civilis. 2006.

SOUZA, M.C.; HABERMANN, G. Towards a new ecophysiological approach to understand citrus crop yield abiotic stresses mirroring in the Brazilian savanna genetic resources. In: Ismail MD, Rahman M, Hasegawa H, editors. Water stress. 1ed. Rijeka: InTech, pp. 152)164, 2012.

VARANDA, E.M.; BAROSELA, J.R; OKI, Y.; PAIS, M.P.; CERRI, A. Defesas vegetais contra insetos folívoros. In: PIVELLO, R.; VARANDA, E.M. (eds- O Cerrado pé)de)gigante, ecologia & conservação, p 195)208, 2005.

ZUCKERMAN, B.; KOESTER, D.; DUFOUR, P.; MELIS, C.; KLEIN, B.; JURA, M. An aluminum/clacium)rich, iron)poor, white dwarf star: evidence for an extrasolar planetary lithosphere? The Astrophysical Journal, vol. 739, p. 101)110, 2011.

5 - Capítulo 1

Ecological strategies of al-accumulating and non-accumulating plants in the cerrado*

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Abstract

The flora of the Brazilian savanna (cerrado- comprises species which differ in aluminum (Al-accumulation in leaves: Al)accumulating and non)accumulating. Both groups grow on acidic soils with low fertility, high exchangeable Al, and are exposed to the same climate. Despite the existence of these groups, their ecological importance or biological strategies have not been suggested yet. We evaluated the leaf flushing pattern of both functional groups throughout the year, the leaf concentration of N, P, K, Ca, Mg, S, Al, total flavonoids, polyphenols, and the specific leaf area (SLA- in young and mature leaves within and between both groups. Non)accumulating species had constant leaf flushes throughout the year, whereas Al)accumulating had a peak of flushing at the end of the dry season (September-. Non)accumulating store more macronutrients in their leaves, regardless of the leaf phase, and show high SLA ever since the juvenile leaf phase. We propose the leaf flushing patterns in Al)accumulating and non)accumulating species is not related with the defense compounds in leaves of any group of plants. In addition, non)accumulating plants absorb more macronutrients and produce leaves with high SLA ever since the juvenile leaf phase, while leaves of Al)accumulating plants seem to face competition between Al and macronutrients. This may slow the increase of SLA in Al)accumulating plants, which achieve SLA values comparable to the rest of the plant community only in the wet season, when sunlight capture is important for growth of new branches.

Keywords: Aluminum, Community, Herbivory, Mineral nutrition, Phenology, Specific leaf area

Introduction

Aluminum (Al- is the most abundant metal and the third most common element in the Earth's crust (Guillard et al. 2012-. In the soil, soluble Al (Al^{3+}- is toxic to most crops, causing physical damage to cell walls (Horst et al. 2010- and root tips (Kopittke et al. 2008-, and Al chelation and/or exclusion at the root tip seem to be an important Al)avoiding strategy for crops (Ryan et al. 2011- and native plants (Brunner and Sperisen 2013-.

However, some plants are able to accumulate great amounts of Al, with no apparent damage to their metabolism. These plants frequently grow on Al)rich soils of tropical areas. In the Brazilian savanna, called 'Cerrado', Al)accumulating and non)accumulating plants co)occur (Haridasan 1982-. These are woody species growing in forest) and savanna)type physiognomies within the Cerrado vegetation. The soils of these areas are poor, acidic (pH < 4.0-, sandy and rich in Al (Haridasan 2008; Habermann and Bressan 2011-, and support the typical savanna)type physiognomy, called cerrado *sensu stricto* (*s. str.*-, with small trees and shrubs, where Al)accumulating and non)accumulating plants occur more frequently.

Al)accumulating plants show 1,000 to 15,000 mg Al per kg of leaf dry mass (LDM-, whereas non)accumulating plants store 100 to 600 mg Al per kg LDM (Haridasan 1982-. Despite the large number of woody species (1000 – 2000- in the Cerrado (Ratter et al. 2003-, only few species from few families have been identified as Al)accumulating plants: *Miconia* sp., *Palicourea rigida*, *Qualea* sp. and *Vochysia* sp. (Haridasan 1982-. Occurrences of Al)accumulating plants are extremely variable between vegetation. Haridasan (1982- observed 35% Al)accumulating plants in a cerrado *s. str*. Haridasan and Araújo (1988- found 18% in a 'Cerradão' (seasonal forest- growing on a dystrophic soil, but less than 8% when this forest physiognomy grows on mesotrophic soils, while Araújo (1992- found 7% Al)accumulating plants in a semidecidual forest.

Similar to climates found in African and Australian savannas, in the Cerrado, the dry season occurs in the fall)winter, from May to October, and the warm and rainy season between November

and April (Ferreira Júnior et al. 2003; Kissmann et al. 2012-. Therefore, for most tropical vegetation, leaves flush and develop during the spring)summer (Kushwaha et al. 2011-, as water availability and the warm weather enhance photosynthesis and growth of new branches. As far as we are concerned, there is no information about leaf flushing of these two important functional groups in the Cerrado. Therefore, the first question we raised in this paper is whether Al)accumulating and non)accumulating plants show distinct leaf phenology throughout a year.

Some Cerrado woody plants flush at the end of the dry season, probably because flushing early in the season avoids the exposure of tender tissues during the wet season, when herbivory is at its highest pressure, at least for coleoptera (Marquis et al. 2002; Pinheiro et al. 2002-, hemiptera and isoptera (Pinheiro et al. 2002-. Thus, the exposure of mature rather than young leaves in the wet season avoids injuries (Mantovani and Martins 1988-. But some species go further into herbivory protection and rapidly reach leaf maturity (Kursar and Coley 2003-, investing in secondary metabolites, including phenols, tannins, alkaloids and flavonoids (Varanda et al. 2005-. Therefore, the second question we raised is whether a possible distinct leaf phenology between Al functional groups is associated with patterns of secondary metabolites (flavonoids and polyphenols- in juvenile and mature leaves.

Finally, coriaceous leaves are characteristic of many cerrado plants. But Arens (1958- hypothesized that edaphic Al causes sclerophylly in cerrado plants and that it would help them survive seasonal droughts, not the herbivory pressure. However, coriaceous leaves are associated with low specific leaf area (SLA, $cm^2g^{)1}$- and reduced nutritional status (Gonçalves)Alvim et al. 2006-. Therefore, our third question is whether Al accumulation and nutritional status are associated with divergent SLA during leaf development in these groups. In this way, although both groups co)occur and grow on the same soils under the same climate, with apparent no phylogenetic correlations, Al has not yet been demonstrated to be essential to these plants. In this paper, we investigate possible ecological strategies for these groups that might be hidden behind leaf traits.

Material and Methods

Study site and species selection

This study was conducted in a cerrado *s. str.* fragment (22º13'S 47º53'W; 610 m of altitude; 260 ha- on the São José da Conquista farm, in central São Paulo state, Brazil. This vegetation was growing on an oxisol, which was sandy, acidic (pH < 4.0-, with low availability of macronutrients, as well as high exchangeable Al. The climate in the region is classified as CWA (Köppen 1948- with a wet summer and a dry winter. The mean monthly temperature varies between 32°C in February and 18°C in July, and the total annual rainfall is around 1520 mm (Camargo et al. 2011-.

The Al)accumulating group was comprised of four species from two families (Melastomataceae and Vochysiaceae-, and the non)accumulating group consisted of 18 species from 13 families (Table 1-. The small number of species in the Al)accumulating group is consistent with the few families of cerrado plants that have been identified as Al)accumulating plants (Haridasan 1982; Haridasan and Araújo 1988-. In the present study, Al)accumulating plants comprised 22% of the species. This percentage is very close to the average proportion of Al)accumulating species (20%- found in a Cerrado *s. str.* (Haridasan 1982- and in a Cerradão (Haridasan and Araújo 1988-. As also observed in a cerrado *s. str.* (Haridasan 1982- and in a Cerradão (Haridasan and Araújo 1988-, in the present study there are no congeneric species between Al)accumulating and non)accumulating plants (Table 1-.

Phenological observations

To evaluate the leaf flushing pattern of each functional group, 36 transects measuring 25 m x 2 m, 50 m distant from each other were established on the southern and eastern faces of the vegetation fragment. Phenological observations were performed monthly, from January to December 2011. The presence or the absence of leaf flush was registered according to Morellato et

al. (2000-. A total of 805 individuals, being 203 Al)accumulating and 602 non)accumulating plants were identified.

Leaf traits

Mature leaves were sampled in the second week of February (wet season- and young leaves in the first week of September (dry season- 2011. The canopy of each plant was divided into cardinal directions and leaves were collected from 4)6 plants per species, according to the availability of leaves in each season. Leaf subsamples from each cardinal direction on each plant (replications- were mixed, immediately taken to the laboratory, and washed under distilled water.

Five discs of known area (cm^2- were excised from each of the six leaves sampled per plant. The leaf discs were oven)dried to constant dry mass at 60°C, and SLA was calculated as the ratio between leaf area (cm^2- and leaf dry mass (g- (Habermann and Bressan 2011-. For the nutritional status, leaves were oven)dried at 60°C to constant dry mass, ground and digested in a nitric)percloric acids solution. Concentrations of Ca and Mg were determined by the atomic absorption spectrophotometer method, K was determined in a flame photometer, S was determined using a turbidimetric method, P and Al was quantified colorimetrically, and N was determined by the micro)Kjeldahl method of digestion and analysis (Sarruge and Haag 1974; Dantas and Batalha 2011-.

Secondary metabolites

Total polyphenol concentration was expressed as mg per LDM (g- (Cortés)Rojas et al. 2012-, which employed adaptations of the Folin)Denis colorimetric method. Leaves were dried at 50°C for 96 h, then ground to pass through a 20)mesh sieve, and 50 mg were extracted in 2.5 mL methanol:water (7:3- solution, after 1h in ultrasound bath. The crude extract was diluted 10 times, and using microtiter plates with 96 wells, we deposited 155 µL of distilled water, 20 µL of

Folin)Denis reagent, 20 µL of Na_2CO_3 saturated at 35%, and 5 µL of the crude extract in each well. Absorbance was measured at 760 nm using a microtiter plate reader after 30 min of incubation in the dark, at room temperature.

Total flavonoids, calculated as quercetin from a calibration curve and also expressed as mg per LDM (g-, was measured using adaptations (Woisky and Salatino 1998- of a method that employs microtiter plates with 96 wells. We poured 175 µL of methanol, 5 µL of $AlCl_3$ at 35% and 20 µL of the crude extract into each well, and absorbance was measured at 425 nm using a microtiter plate reader after 30 min of incubation in the dark, at room temperature.

Statistical analyses

The leaf flush pattern was described based on an activity index, which indicates the percentage individuals manifesting a certain phenophase on each observation date (Camargo et al. 2011-. Differences in leaf flushing between Al)accumulating and non)accumulating plants were tested using the Spearman's rank correlation (r*s*-.

A t)test at 5% of probability was used to compare leaf traits (concentrations of N, P, K, Ca, Mg, S, Al, flavonoids, total polyphenols and SLA- between young and mature leaves in Al)accumulating and non)accumulating plants, and also between these functional groups. To check normal distribution, data was transformed using a box)cox transformation (x**(1)(4/2--- (Box 1964-.

The relative percentage change (RPC=((C_y)C_m-/C_y-100%- in leaf nutrients (N, P, K, Ca, Mg, S, and Al- from young to mature leaves in Al)accumulating and non)accumulating plants was calculated according to Teklay (2004-, in which C_y is the concentration of a target leaf nutrient in young leaves, and C_m the concentration of a target leaf nutrient in mature leaves. Positive RPC values indicate *resorption* whereas negative values suggest *enrichment* of N, P, K, Ca, Mg, S, and Al from the juvenile to the mature leaf phase. We performed a t)test at 5% of probability to check

differences in RPC between the functional groups.

Results

According to the Spearman rank correlation, the leaf flushing differed (P = 0.02, r*s* = 0.65- between Al)accumulating and non)accumulating plants (Fig. 1-. Al)accumulating plants showed a leaf)flushing peak from August to November and in contrast, no flushing peak was observed for non)accumulating plants (Fig. 1-.

Leaves of Al non)accumulating plants showed higher macronutrients (except for S- concentrations in comparison to Al)accumulating plants, and while Al non)accumulators diminished nutrient concentrations (except for Ca and Mg- from the juvenile to the mature leaf phase, Al)accumulators maintained these concentrations (except for Mg- between leaf phases (Table 2-. In Al)accumulating plants, the Al concentration conspicuously increased from the juvenile to the mature leaf phase, whereas no change in the Al concentration was observed between leaf phases in Al non)accumulating plants (Table 2-.

Leaves of Al non)accumulating plants showed high and the same SLA between leaf phases, whereas Al)accumulating plants increased SLA from the juvenile to the mature leaf phase, when values became similar to those of Al non)accumulating plants (Table 2-.

In Al non)accumulating plants leaf flavonoids were higher than in Al)accumulating plants, and while Al non)accumulating plants decreased their leaf flavonoids from the juvenile to the mature phase, this compound had similar concentrations between leaf phases in Al)accumulating plants. Polyphenols, on the contrary, was higher in Al)accumulating in relation to Al non)accumulating plants, and for both plant groups this compound had similar concentrations between leaf phases (Table 2-.

Both Al non)accumulating and accumulating plants exhibited Ca leaf enrichment. As expected, Al)accumulating plants exhibited an Al enrichment of more than 200% from the juvenile

to the mature leaf phase, whereas Al non)accumulating plants showed an Al resorption of 27% between leaf phases (Table 3-.

Discussion

Our results demonstrate that the Al)accumulating group flush at the dry)wet seasons interface, while the non)accumulating group assume a consistent flush throughout the year. This answers our first question, but does this suggest an ecological strategy for these groups of plants in terms of exposing their leaves with different traits at different times?

For tropical plants, in general, it is described that young leaves suffer higher rates of herbivory, requiring greater diversity of secondary metabolites (Kursar et al. 1999- when compared to mature leaves (Coley and Barone 1996-. In the Cerrado, insects seem to prefer young leaves whereas pathogens attack more mature leaves (Marquis et al. 2001-. For instance, Varanda et al. (2008- demonstrated caterpillars' preference for young expanding leaves of *Xylopia aromatica*, an Al)non)accumulating plant from the Cerrado, as compared to their tannin)enriched mature leaves. Thus, secondary metabolites have always been associated with leaf protection against herbivores and/or pathogens.

The escape strategy (flushing at the dry)wet seasons interface- has been extensively debated (Silva and Batalha 2011- with no clear understanding for Cerrado plants. Except for some insect orders (Marquis et al. 2002; Pinheiro et al. 2002-, herbivory pressure in the Cerrado is apparently similar throughout the year (Marquis et al. 2002-. Insect leaf damage also seems to be independent of leaf age (Gonçalves)Alvin et al. 2011-, and the season of escape may also depend on herbivore species (Marquis et al. 2001-, although Silva and Batalha (2011- argue that herbivory is underestimated in the Cerrado.

For both groups of plants studied here the secondary metabolism seems to be under balance. Leaf polyphenols, which includes tannins, are higher in Al)accumulating in relation to

non)accumulating plants, whereas the opposite is observed for leaf flavonoids. Furthermore, no conspicuous differences in these metabolites appear between leaf phases in both groups, weakening any suggestion of escape strategy involving these compounds during leaf development. In addition, although high leaf Al concentration has been demonstrated to be associated with low leaf tannin concentration in *Qualea parviflora*, an Al)accumulating plant from the Cerrado, leaf tannin concentration does not influence the herbivory leaf damage in this species (Gonçalves)Alvin et al. 2011-. Therefore, Al accumulation does not seem to be associated with any pattern of defense compounds in leaves, weakening any suggestion of involvement of secondary metabolites in herbivory escape strategies for any functional group.

Non)accumulating plants store more macronutrients (except for S- than the other group of plants, and produce leaves with high SLA ever since the juvenile leaf phase. Therefore, in relation to Al)accumulating, non)accumulating plants emit new leaves that rapidly optimize light capture for photosynthesis. Species possessing high SLA, such as forest species (Hoffmann et al. 2005; Habermann and Bressan 2011; Rossato et al. 2013- and deciduous savanna species (Franco et al. 2005- show high leaf contents of nutrients, such as N and P that are closely related to photosynthetic activities (Reich et al. 2009-. This strategy, as also performed by non)accumulating plants, implies low leaf construction costs (Franco et al. 2005-.

Al)accumulating plants store less macronutrients than non)accumulating plants and gradually increase SLA from the juvenile to the mature leaf phase. In contrast to Al)non)accumulating plants, the astonishing enrichment of Al from the juvenile to the mature leaf phase in Al)accumulating plants might cause competition with macronutrients for allocation in the mesophyll of these plants. Competition among nutrients can only be detected by absorption dynamics studies, which is difficult to perform in the field. However, N, P, K, Ca and S concentrations remained unchanged between leaf phases in Al)accumulating plants, while N, P, K and S decreased from the juvenile to the mature leaf phase in non)accumulating plants.

Furthermore, many native species are described to face competition between Al and macronutrients for allocation in their leaves (Brunner and Sperisen 2013-.

Thus, the lack of metabolic resources (macronutrients, especially N and P- in Al)accumulating plants does not seem to support a great SLA ever since the juvenile leaf phase. This group of plants flushes at the end of the dry season and gradually increases SLA from the juvenile to the mature leaf phase and matches SLA values of the rest of the plant community only in the wet season, when possessing high SLA is important for light capture and photosynthesis. This strategy seems to be analogous to evergreen savanna species (Franco et al. 2005; Hoffmann et al. 2005; Habermann and Bressan 2011-, which have high leaf construction costs involving the development of non)photosynthetic tissues, such as fibers and cell walls rather than chloroplasts. In fact, sclerophylly in *Q. parviflora* is associated with low rates of macronutrient supply (Gonçalves)Alvin et al. 2006-.

One may still argue that there is no phylogenetic context between these groups of plants. However, when studying stem and leaf hydraulic traits between congeneric pairs from savanna and forest ecosystems, Hao et al. (2008- observed that phylogeny (genus-, rather than functional type (savanna *versus* forest species-, better explained variances observed in drought survival traits. On the other hand, when studying herbivory defense traits among 61 species from 29 families in a cerrado plant community, Silva and Batalha (2011- found that phylogeny did not determine the suit of anti)herbivory traits among the species. As mentioned above, Al accumulation is highly conserved in only 15)22% Cerrado woody species (Haridasan 1982; Haridasan and Araujo 1988-. Considering that both groups of plants grow on the same Al)rich soils and under the same climate, it is intriguing why the other 78)85% species have not conserved this trait. Therefore, Al)accumulating species might have survived some environmental filters that act in the Cerrado, while non)accumulating ancestors have not, since the Cerrado imposes many filters for species, guilds and functional groups (Silva and Batalha 2006-.

In conclusion, flushing at the dry)wet seasons interface for Al)accumulating plants, and throughout the year for non)accumulating plants is not related with patterns of defense compounds in leaves of any group of plants. In addition, non)accumulating plants absorb more macronutrients and produce leaves with high SLA ever since the juvenile leaf phase, while leaves of Al)accumulating plants seem to face competition between Al and macronutrients. This may slow the increase of SLA in Al)accumulating plants, which achieve SLA values comparable to the rest of the plant community only in the wet season, when sunlight capture is important for growth of new branches.

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References

Araújo GM (1992- Comparação da estrutura e do teor de nutrientes nos solos e nas folhas de espéci) es arbóreas de duas matas mesófilas semidecíduas no triângulo mineiro. PhD Thesis. Universidade de Brasília (UNB-, Brasil.

Arens K (1958- Considerações sobre as causas do xeromorfismo foliar. Boletim da FFCL)USP 15:23–56.

Box GEP, Cox DR (1964- An analysis of transformations. J Royal Stat Soc 26:211)252.

Brunner I, Sperisen C (2013- Aluminum exclusion and aluminum tolerance in woody plants. Front Plant Scien 4:1)12.

Camargo MGG, Souza RM, Reys P, Morellato LPC (2011-. Effects of environmental conditions associated to the cardinal orientation on the reproductive phenology of the cerrado savanna tree *Xylopia aromatica* (Annonaceae-. Ann Braz Acad Scien 83:1007)1019.

Coley P D, Barone JA (1996- Herbivory and plant defenses in tropical forests. Ann Rev Ecol Syst 27:305–335.

Cortés)Rojas DF, Chagas)Paula DA, Costa FB, Souza CRF, Oliveira WP (2012- Bioactive compounds in *Bidens pilosa* L. populations: a key step in standardization of phytopharmaceutical preparations. Braz J Pharmac 23: 28)35.

Dantas VL; Batalha MA (2011- Vegetation structure: fine scale relationships with soil in a cerrado site. Flora 206:341)346.

Franco AC, Bustamante M, Caldas LS, Goldstein G, Meinzer FC, Kozovits AR, Rundel P, Coradin VTR (2005- Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. Trees 19:326)335.

Ferreira Júnior LG, Yashioka H, Huete AR, Sano EE (2003- Seasonal landscape and spectral vegetation index dynamics in the Brazilian Cerrado: an analysis within the Large)Scale Biosphere)Atmosphere experiment in Amazônia (LBA-. Rem Sens Environ 87:534)550.

Gonçalves)Alvim SJ, Korndorf G, Fernandes GW (2006- Sclerophylly in *Qualea parviflora* (Vochysiaceae-: influence of herbivory, mineral nutrients, and water status. Plant Ecol 187:153–162.

Gonçalves)Alvim SJ, Lana TC, Ranieri BD, Fernandes GW (2011- Test of hypotheses about herbivory and chemical defences of *Qualea parviflora* (Vochysiaceae- in Brazilian *Cerrado.* Braz J Bot 34:223)230.

Guillard O, Fauconneau B, Favreau F, Marrauld A, Pineau A (2012- An analytical procedure for the determination of aluminum used in antiperspirants on human skin in Franz™ diffusion cell. Toxic

Mech Meth 22:205–210.

Habermann G, Bressan ACG (2011- Root, shoot and leaf traits of the congeneric *Styrax* species may explain their distribution patterns in the cerrado sensu lato areas in Brazil. Funct Plant Biol 38:209)218.

Hao G)Y, Hoffmann WA, Scholz FG, Bucci SJ, Meinzer FC, Franco AC, Cao K)F, Goldstein G (2008- Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems. Oecologia 155:405)415.

Haridasan M (1982- Aluminium accumulation by some cerrado native species of central Brazil. Plant Soil 65:265)273.

Haridasan M (2008- Nutritional adaptations of native plants of the cerrado biome in acid soils. Braz J Plant Physiol 20:183)195.

Haridasan M, Araújo GM (1988-. Aluminium)accumulating species in two forest communities in the cerrado region of central Brazil. Forest Ecol Manag 24:15)26.

Hoffmann WA, Franco AC, Moreira MZ, Haridasan M (2005- Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. Funct Ecol 19:932–940.

Horst WJ, Wang Y, Eticha D (2010- The role of the root apoplast in aluminium)induced inhibition of root elongation and in aluminium resistance of plants: a review. Ann Bot 106:185)197.

Kissmann C, Tozzi HH, Martins S, Habermann G (2012- Germination performance of congeneric Styrax species from the Cerrado sensu lato areas and their distribution pattern in different physiognomies. Flora 207:673)681.

Kushwaha CP, Tripathi SK, Singh KP (2011- Tree specific traits affect flowering time in Indian drytropical forest. Plant Ecol 212:985)998.

Köppen W (1948- Climatología con un estudio de los climas de la Tierra. Mexico: Ed. Fondo de Cultura Económica)Pánuco.

Kopittke PM, Blamey FPC, Menzies NW (2008- Toxicities of soluble Al, Cu, and La include reputures to rhizodermal and root cortical cells of cowpea. Plant Soil 303:217)227.

Kursar TA, Coley PD (2003- Convergence in defense syndromes of young leaves in tropical rainforests. Bioch Syst Ecol 31:929)949.

Kursar TA, Coley PD, Corley DG, Gupta MB, Harrison LA, Ortega)Barría E, Windsor DM (1999- Ecologically guided bioprospecting in Panama. Pharmac Biol 37:114–126.

Mantovani W, Martins FR (1988- Variações fenológicas das espécies do cerrado da Reserva Biológica de Mogi Guaçu, Estado de São Paulo. Braz J Bot 11:101)112.

Marquis RJ, Diniz IR, Morais HC (2001- Patterns and correlates of interspecific variation in foliar insect herbivory and pathogen attack in Brazilian Cerrado. J Trop Ecol 17:127)148.

Marquis RJ, Morais HC, Diniz IR (2002- Interactions among cerrado plants and their herbivores: unique or typical? In: Oliveira PS, Marquis RJ (Eds-. The cerrados of Brazil, 306)328. Columbia University, New York,

Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Zipparro VB (2000- Phenology of Atlantic rain forest trees: a comparative study. Biotropica 32:811–823.

Pinheiro F, Diniz IR, Coelho D, Bandeira MPS (2002- Seasonal pattern of insect abundance in the Brazilian cerrado. Aust Ecol 27:132)136.

Ratter JA, Bridgewater S, Ribeiro JF (2003- Analysis of the floristic composition of the Brazilian cerrado vegetation III: comparison of the woody vegetation of 376 areas. Edinb J Bot 60: 57–109.

Reich PB, Oleksyn J, Wright IJ (2009- Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross)biome analysis of 314 species. Oecologia 160:207–212.

Rossatto DR, Hoffmann WA, Silva LCR, Haridasan M, Sternberg LSL, Franco AC (2013- Seasonal variation in leaf traits between congeneric savanna and forest trees in Central Brazil: implications for forest expansion into savanna. Trees 27:1139)1150.

Ryan PR, Tyerman SD, Sasaki T, Furuichi T, Yamamoto Y, Zhang WH, Delhaize E (2011- The

identification of aluminium)resistance genes provide opportunities for enhancing crop production on acid soils. J Exp Bot 62:9)20.

Sarruge JR, Haag HP (1974- Análises químicas em plantas. Piracicaba, ESALQ. 54 p.

Silva DM, Batalha MA (2011- Defense syndromes against herbivory in a cerrado plant community. Plant Ecol 212:181)193.

Silva IA, Batalha MA (2006- Taxonomic distinctness and diversity of a hyperseasonal savanna in central Brazil. Divers Distrib 12:725)730.

Teklay T (2004- Seasonal dynamics in the concentrations of mocronutrients and organic constitu) ents in green and senesced leaves of three agroforestry species in southern Ethiopia. Plant Soil 267:297)307.

Varanda EM, Barosela JR, Oki Y, Pais MP, Cerri A (2005- Defesas vegetais contra insetos folívoros. In: Pivello R, Varanda EM (Eds-. O Cerrado pé)de)gigante, ecologia & conservação, 195)208. São Paulo: Secretaria do Meio Ambiente.

Varanda EM, Costa AA, Barosela Jr (2008- Leaf development in *Xylopia aromatica* (Lam- Mart. (Annonaceae-: Implications for palatability to *Stenoma scitiorella* Walker 1864 (Lepidoptera: Elachistidae-. Braz J Biol 68:831)836.

Woisky RG, Salatino A (1998- Analysis of propolis: some parameters and procedures for chemical quality control. J Apic Res 37:99)105.

Tables, figures and captions

Table 1 List of Al)non)accumulating and Al)accumulating species in a cerrado *sensu stricto* fragment, southeastern Brazil.

Family	Species
Al-non-accumulating	
Annonaceae	*Annona coriacea*
Annonaceae	*Xylopia aromatica*
Apocynaceae	*Aspidosperma tomentosum*
Caryocaraceae	*Caryocar brasiliensis*
Erythroxylaceae	*Erythroxylum suberosum*
Erythroxylaceae	*Erythroxylum tortuosum*
Erythroxylaceae	*Erythroxylum pelleterianum*
Malpighiaceae	*Byrsonima basiloba*
Malpighiaceae	*Byrsonima intermedia*
Malpighiaceae	*Banisteriopsis variabilis*
Malvaceae	*Eriotheca gracilipes*
Myrsinaceae	*Rapanea umbelata*
Myrtaceae	*Myrcia bella*
Nyctaginaceae	*Guapira opposita*
Rubiaceae	*Tocoyena formosa*
Salicaceae	*Casearia sylvestris*
Sapotaceae	*Pouteria torta*
Styracaceae	*Styrax ferrugineus*
Al-accumulating	
Melastomataceae	*Miconia albicans*
Melastomataceae	*Miconia rubiginosa*
Melastomataceae	*Miconia fallax*
Vochysiaceae	*Qualea grandiflora*

Table 2 Mean values (± sd- of leaf concentrations of N, P, K, Ca, Mg, S, Al, flavonoids, total polyphenols and specific leaf area (SLA- in young (Y- and mature (M- leaves of Al)non)accumulating and Al)accumulating in a cerrado *sensu stricto* fragment, southeastern Brazil.

Traits	Phenophase	Al)non)accumulating		Al)accumulating	
N (g kg$^{)1}$-	Y	24.76 ± 11.07	aA	16.45 ± 4.52	aB
	M	19.03 ± 8.41	bA	13.33 ± 1.52	aB
P (g kg$^{)1}$-	Y	2.04 ± 1.43	aA	0.78 ± 0.30	aB
	M	1.12 ± 0.34	bA	0.73 ± 0.09	aB
K (g kg$^{)1}$-	Y	8.39 ± 5.85	aA	2.64 ± 1.22	aB
	M	4.19 ± 1.73	bA	2.19 ± 0.44	aB
Ca (g kg$^{)1}$-	Y	5.75 ± 3.29	aA	3.11 ± 0.88	aB
	M	5.62 ± 1.97	aA	3.58 ± 0.71	aB
Mg (g kg$^{)1}$-	Y	2.23 ± 0.77	aA	1.57 ± 0.42	aB
	M	2.09 ± 0.70	aA	1.22 ± 0.20	bB
S (g kg$^{)1}$-	Y	1.09 ± 0.56	aA	0.82 ± 0.18	aA
	M	0.83 ± 0.34	bA	0.92 ± 0.31	aA
Al (mg kg$^{)1}$-	Y	200.06 ± 138.49	aB	1546.60 ± 139.49	bA
	M	181.88 ± 140.77	aB	4867.36 ± 1782.85	aA
SLA (cm^2 g$^{)1}$-	Y	132.98 ± 50.23	aA	88.11 ± 13.85	bB
	M	122.23 ± 32.03	aA	145.54 ± 62.01	aA
Flavonoids (mg g$^{)1}$-	Y	5.11 ± 2.41	aA	2.10 ± 0.41	aB
	M	3.66 ± 2.81	bA	1.79 ± 0.23	aB
Polyphenols (mg g$^{)1}$-	Y	27.02 ± 12.26	aB	35.31 ± 2.71	aA
	M	26.28 ± 14.52	aB	37.19 ± 4.93	aA

Different lower case letters indicate significant differences ($P < 0.05$- between young (Y- and mature (M- leaves in each functional group. Different upper case letters indicate significant differences ($P < 0.05$- between Al)non)accumulating and Al)accumulating functional groups.

Table 3 Mean Relative Percentage Change (± sd- in the concentration of N, P, K, Ca, Mg, S and Al in Al)non)accumulating and Al)accumulating species in a cerrado *sensu stricto* fragment, southeastern Brazil. Positive values show resorption whereas negative values show enrichment of nutrients from the juvenile to the mature leaf phase.

Traits	Al-non-accumulating	Al-accumulating
N	6.29 ± 64.50 a	11.12 ± 34.52 a
P	15.27 ± 59.60 a	)9.00 ± 51.26 a
K	19.05 ± 70.02 a	)16.55 ± 91.19 a
Ca	)38.79 ± 108.06 a	)26.18 ± 50.05 a
Mg	1.91 ± 44.21 a	17.79 ± 25.67 a
S	4.01 ± 58.21 a	)14.26 ± 39.81 a
Al	27.07 ± 21.15 b	)207.40 ± 94.26 a

Different letters indicate significant differences ($P < 0.05$- between Al)non)accumulating and Al)accumulating functional groups.

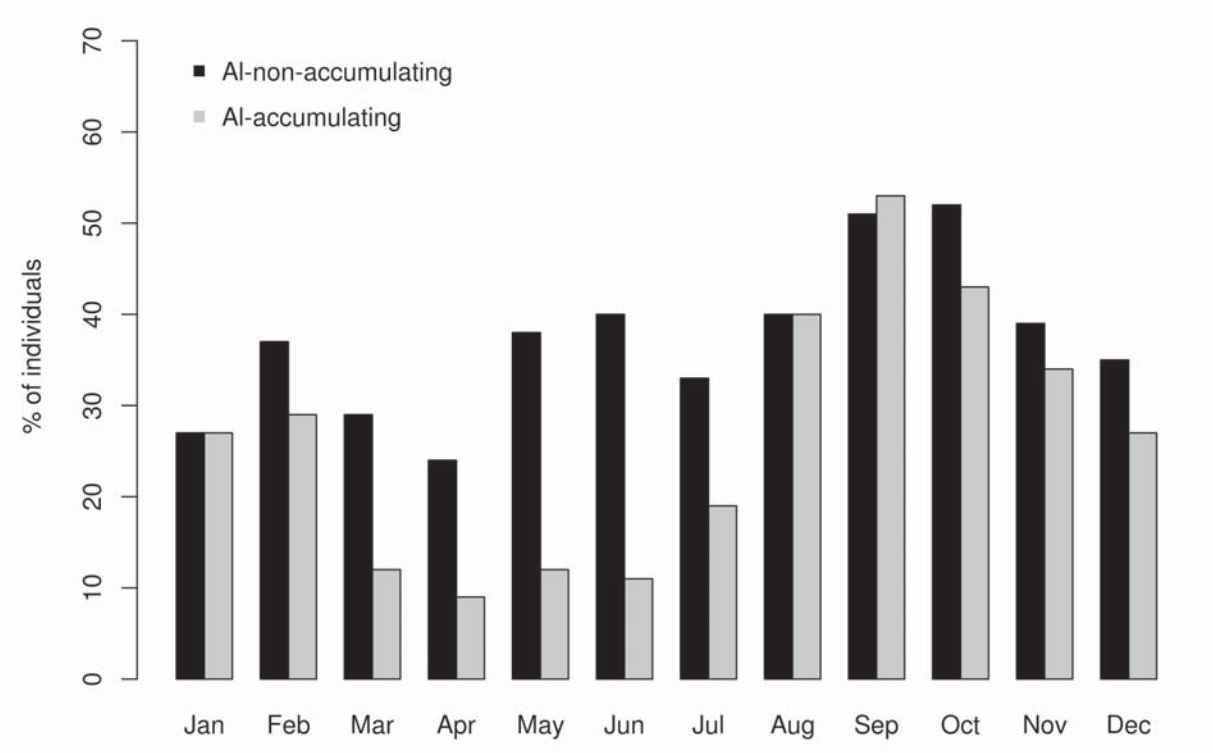

Fig. 1 Annual leaf flush distribution in Al)accumulating and Al)non)accumulating in 2011, in a cerrado *sensu stricto* fragment, southeastern Brazil.

6 - Capítulo 2

The duration of the dry season may be associated with leaf scleromorphism between similar physiognomies within Cerrado areas**

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** Este artigo será submetido para publicação no periódico **Trees**

Abstract – Water availability, soil fertility, fire and edaphic aluminum (AL- are considered limiting factors in the cerrado *sensu stricto* (Brazilian savanna-. Despite the low fertility and pH in the Al)rich soils of the cerrado, its flora is one of the richest among savannas. Cerrado woody species also have scleromorphic leaves, and the degree of scloermorphism is related to the water)nutrient availability in the soil. To better understand the function and structure of the cerrado vegetation within its own variations, we compared two cerrado communities, one in its core region in central Brazil (Brasília, DF- and the other on its southern periphery (Itirapina, SP-. We contrasted the length of the dry season, soil fertility, leaf concentrations of N, P, K, Ca, Mg and Al and scleromorphism (specific leaf area) SLA- between these communities. The dry season was shorter on the periphery, where the soil was more fertile although more acidic. Plants from the periphery had higher SLA and showed higher leaf concentration of N, P, Ca and Mg. We propose that the lower leaf scleromorphism on the periphery is due to shorter dry season.

Key words: Savanna, Mineral Nutrition, Aluminum toxicity

Introduction

Savannas occupy 20% of the emerged lands (Sankaran et al. 2005-, covering 21% of the Brazilian territory (Souza and Habermann 2012-, 25% of the Australian territory (Williams et al. 2005- and 40% of the land area in Africa (Okitsu 2005-. Savannas are composed of many physiognomies ranging from grasslands to seasonal forests, and the structure and functionality of the species are strongly influenced by ecological filters (Gottsberger and Silberbauer–Gottsberger 2006-. For instance, fire frequency, soil fertility, water availability and herbivory have been recognized as the main ecological filters for these landscapes (Sankaran et al. 2005-.

The use of leaf traits (e.g. leaf nutritional status and scleromorphism- has been successfully used to explain responses of savanna species to the variations in these ecological filters. However, in the savannas, species submitted to high frequency of fire and droughts and growing on poor soils possess decreased concentration of nutrients in their leaves, which tend to be more scleromorphic (low specific leaf area – SLA- (Sankaran et al. 2005; Wright et al. 2001-. In contrast, species submitted to low frequency of fire and drought events, and growing on soils that are less infertile and do not go through droughts so often are less scleropmorphic and have leaves that are rich in nutrients (Delgado et al. 2013; Sankaran et al. 2005; Prior et al. 2005; Wright et al. 2001-. Aluminum (Al- accumulation is an important leaf trait, especially in the Brazilian savanna (locally known as “cerrado”- because soils from the cerrado are acidic and rich in Al (Haridasan 2008-.Therefore, species in this environment have been selected into two groups of species in terms of Al use by their metabolism: Al)accumulators and Al)non)accumulators (Haridasan 1982-. Although Al function in their metabolism is still not understood, Al does not interfere in the uptake of other nutrients (Haridasan 1982-.

In the Cerrado, water restrictions are important during the dry season (Goodland and Ferri 1979; Gottsberger and Silberbauer–Gottsberger 2006-, and it has already been proposed that sclermorphic leaves of the Cerrado vegetation is due to the water restrictions imposed during most

part of the year. But the Cerrado domain is very big (≈1,776,000 km^2- in Brazil, and similar vegetation physiognomies occur in areas with distinct water availability (Gottsberger & Silberbauer–Gottsberger 2006- and on soils with different geological formations (Silva 2008-. Therefore, it is possible that the Cerrado domain, even between similar physiognomies, such as the typical cerrado *sensu stricto* (*s. str.*-, may vary in its structure with consequences for the adjacent vegetation. In this way, when we compared the soil fertility, the length of the dry season and leaf concentration of N, P, K, Ca, Mg and also Al, we expected to find important differences in scleromorphism (SLA- and nutritional status between cerrado areas in the core and on the southern periphery of this biome. Consequently, we tested the hypothesis that plants on the southern periphery are less scleromorphic and retain more nutrients in their leaves in comparison to the core region, where soils appear to be more weathered, acidic and poorer. Our findings may have ecological significance for understanding the structure of the Cerrado vegetation.

Material and methods

Site description and study description

The study was conducted in two cerrado *s. str.* fragments, one in the core region and the other on the southeastern periphery of the Cerrado domain. In the core of the Cerrado, the plant community was located at the Ecological Reserve of IBGE (15°57' S 47°52' W- in Brasília, the Brazilian Federal District. On the periphery, the plant community was growing on the São José da Conquista farm (22º13'S 47º53'W-, in Itirapina, São Paulo state. Both sites show a rainy summer and a dry winter.

A 30)year)dataset was used to estimate the mean annual rainfall, length of the dry and wet seasons and air temperature, from 1980 to 2010 (Walter 1986-. In the core of the cerrado, these data were provided by the National Institute of Meteorology (INMET 2013-. The total annual rainfall in the core of the Cerrado is around 1452 mm and the mean annual temperature around 21°C, while on

the periphery the total annual rainfall is around 1512 mm and mean annual temperature around 20°C (Figure 1-.

We studied 15 woody species in the core and 21 species on the southeastern periphery (Table 1-. In both communities three plots of 15 m x 15 m were established and the woody species that were common among plots were selected. The plants were sampled between February and March 2005 (in the core; Araújo 2006- and 2011 (on the periphery-. Soil sampling was also performed in the three plots.

SLA and nutritional status

Fully expanded mature leaves were randomly sampled from 4)6 plants per species, according to the availability. Leaves were washed with distilled water and oven)dried at 60°C until constant mass.

To determine the specific leaf area (SLA- six leaves per plant per species were used for obtaining 40 leaf discs of pre)determined area. The SLA was calculated as the ratio between leaf area (cm^2- and leaf dry mass (g- (Habermann and Bressan 2011-. Leaves from both communities were digested in an acid solution (nitric:percloric- and leaf N concentration was determined by the micro)Kjeldahl method. For the core's community the concentration of Ca, Mg, K and Al were determined by atomic absorption spectrophotometry and P was determined colorimetrically (Allen 1989-. For the periphery's community leaf concentrations of Ca and Mg were determined by atomic absorption spectrophotometry, K was determined using a flame photometer, and P and Al were quantified colorimetrically (Sarruge and Haag 1974-.

Soil characterization

Soil samples were randomly collected (0)30 cm in depth- from the three plots for analysis. Chemical parameters [pH, N, organic matter (OM-, P, K, Ca, Mg and Al] and physical properties

(percentage of clay, silt and total sand- were determined according to Raij et al. (1987-. Procedures are described in English in Dantas and Batalha (2011-.

Data analysis

The variations in pH, OM, P, K, Ca, Mg and Al between the soils from the core and periphery were analyzed using a t)test at 5% level. A t)test at 5% level was carried out to determine differences in the leaf concentration of N, P, K, Ca, Mg, Al and SLA between the core and peripheral communities. We used a standardized major axis (SMA- regression to test for significant differences in slopes and intercepts between leaf concentrations of N and P, Ca and Mg, SLA and N, and SLA and P (Warton et al. 2006- for both communities.

Results

Climate and soil characterization

Both regions exhibited similar total annual rainfall and average temperature but the peripheral community showed a shorter and milder dry season (Jun) Aug-, while in the core a longer (May – Sep- and drier season occurred (Figure 1-.

The soil from the periphery was more acidic (pH < 4.0- but more fertile (richer in N, P, Ca and Mg- than the soil from the core region (pH > 4.0, and poorer in N, P, Ca and Mg-. In addition, the soil from the periphery showed higher percentages of clay and silt. The Al saturation in the soil matrix in relation to the other bases (m%- and the concentration of K did not differ between the sites (Table 2-.

Leaf traits

The plant community located on the periphery of the Cerrado showed higher leaf concentrations (g kg)1- of N (18.22 ± 8.05-, P (1.06 ± 0.34-, Ca (5.33 ± 1.97-, and Mg (1.96 ± 0.72- as compared to the plant community in the core region: N (14.36 ± 7.46-, P (0.64 ± 0.24-, Ca (3.71 ± 2.78-, and Mg (1.34 ± 0.66- (Figure 2-.

For Al)non)accumulator species, Al leaf concentration (mg kg)1- was similar between both communities (192.5 ± 124.8 in the core and 181.9 ± 140.1 in the periphery- (Figure 3a-. However, for Al)accumulator species, leaf concentration of this element was considerably higher in the core (7,401.0 ± 4,700.3- in comparison with the periphery (1,546.6 ± 139.5- (Figure 3b-.

The plant community in the periphery exhibited higher SLA values (125.56 ± 38.14- than those exhibited by plants in the core (69.01 ± 20.41- (Figure 4-. There were positive correlations between leaf concentration of N and P (Figure 5a-, and between Ca and Mg (Figure 5b- for both communities. Significant differences between plant communities were observed in the N x P relationship. However, such differences were not found between communities when analyzing the the Ca x Mg relationship (Table 3-. In addition, we found no correlation between SLA x N (Figure 6a- or between SLA x P (Figure 6b- (Table 3-.

Discussion

The total annual rainfall in the core (~1450 mm- was very akin to the periphery (~1500 mm- and these rainfall values are enough to support forest vegetation in the tropics (Gottsberger and Silberbauer–Gottsberger 2006; Silva et al. 2013-. In spite of similar annual rainfall, we observed a significant difference in the duration of the dry season between both communities (3 months on the periphery and 5 months in the core-. Water deficit can impair growth and development in plants in general (Chaves et al. 2002- and in Cerrado plants (Prado et al. 2004-. In addition, as N compounds are found mostly in the xylem sap (Pate 1973- it is natural that N uptake is diminished with the low

transpiration during the dry season (Prado et al. 2004-. Furthermore, in a cerrado species there is a strong negative relationship between leaf N concentration and leaf scleromorphysm (Delgado et al. 2013-. This supports the association between longer dry season and the higher scleromorphism observed in the core, as compared to the peripheral community.

In Australian savannas, wood species growing on poor soils and dry areas show decreased SLA and low nutrients in leaves as compared to species growing on soils that are more fertile and have higher water availability (Prior et al. 2005; Wright et al. (2001-. Leaf scleromorphism has also been used to discriminate between forest and savanna species in such a way that forest species are less scleromorphic (high SLA- than savanna species (Hoffmann et al. 2005-, since the limitation in forests is the capture of sunlight (Gvinish 1988; Habermann and Bressan 2011- while in savannas, surviving the dry season is the main challenge (Prado et al. 2004; Bucci et al. 2008-. After all, less scleromorphic leaves invest more in photosynthetic tissues, have higher ratios of mesophyll to epidermis, and mesophyll to leaf thicknesses (Delgado et al. 2013; Somavilla et al. 2013- and accumulate more N, P, Ca and Mg (Hoffmann et al. 2005- than scleromorphic leaves.

Soil acidity, edaphic Al and low soil fertility are common factors among Cerrado soils (Haridasan 2008-, but soils from different Cerrado areas may have different pH and fertility levels (Cianciaruso et al. 2013-. In the core, the soil is less fertile, more acidic although presenting similar m% in relation to the soil on the southern periphery. Calcium concentration was ten times greater in the soil from the periphery than the core, and the plant community from the periphery retained more nutrients in their leaves, including Ca. However, we do not believe that plants from the periphery accumulate more nutrients and Ca in their leaves due to richer soil on the southern periphery. Growth parameters of cerrado woody species are non)plastic to nutrient availability in the soil (Hoffmann and Franco 2003; Habermann and Bressan 2011-. In addition, in both communities the relationships between N and P and Ca and Mg were positive and significant. This not only indicates that these nutrients are important resources for cerrado *s. str.* communities but also demonstrates

that the soil)plant relationship is conserved for these nutrients, regardless of the plant community, region or soil fertility. As a consequence, differences in soil fertility between the core and the periphery cannot be responsible for higher leaf nutrient concentration on the periphery as compared to the core.

The leaf Al concentration was five times greater in the core in relation to the periphery. This can be ascribed to the presence of *Vochysia elliptica* and *V. thyrsoidea* in the core and the absence of this genus in the periphery. Species from the *Vochysia* genus are considered Al)hyper accumulators in the cerrado *s. str.* (Haridasan 1982; Haridasan and Araújo 1988- and in semi deciduous forests (Araújo 1992-. In addition, Al availability in Cerrado soils present no direct relationship with leaf Al concentration in hyper)accumulating plants (Andrade et al. 2011-. Therefore, and similar to our conclusions on the other nutrients, different leaf Al concentration between both communities cannot be ascribed to dissimilar soil Al concentrations between both regions.

We did not find significant relationship between SLA and N or SLA and P. In figure 6, one can clearly observe that N, P and SLA are grouped on the bottom for data coming from the core and spread at high values for data coming from the periphery. This suggests that both nutrients and SLA do not vary among species within the two communities, as these traits are consistently low in the core and high on the periphery. On the other hand, when these relationships are studied, for example, among species with different phenological behaviors (Franco et al. 2005- or between savanna and forest species (Hoffmann et al. 2005- and involving a single species (Delgado et al. 2013- these relationships are significant and positive. Thus, other factors are influencing these traits in these communities. As discussed above, distinct soil fertility between the studied regions does not seem to be the main factor.

Conclusions

In conclusion, we confirmed our hypothesis that plants on the southern periphery are less scleromorphic and retain more nutrients in their leaves in comparison to the core region, despite dissimilarities between their soil fertilities. This points out that similar vegetation physiognomies within the Cerrado biome can differ in functional traits. Based on 30)year data sets of climatic data, we propose that the length of the dry season may explain the distinct traits between both communities, despite their similar total annual rainfall.

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References

Allen SE (1989- Chemical analysis of ecological materials. Blackwell Scientific Publications, Ox) ford

Andrade LRM, Barros LMG, Echevarria GF Amaral LIV, Cotta MG, Rossatto DR, Haridasan M, Franco AC (2011- Al)hyperaccumulator Vochisiaceae from the Brazilian Cerrado store aluminum in their chloroplasts without apparent damage. Environmental and Experimental Botany 70:37)42.

doi: 10.1016/j.envexpbot.2010.05.013

Araújo GM (1992- Comparação do teor de nutrientes nos solos e nas folhas de espécies arbóreas de duas matas mesófilas semidecíduas no Triangulo Mineiro. PhD Thesis. Universidade Estadual de Campinas

Araújo JF (2006- Padrões nutricionais de espécies lenhosas do cerrado. Master dissertation, Universidade de Brasília.

Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, Franco AC, Zhang Y, Hao G (2008- Water relations and hydraulic architecture in Cerrado trees: adjustments to seasonal changes in water availability and evaporative demand. Braz J Plant Physiol 20:233)245. doi: 10.1590/S1677)04202008000300007

Chaves MM Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório Ml, Carvalho I, Faria T, Pinheiro C (2002- How plants cope with water stress in the field. Photosynthesis and growth. Ann Bot 89:907)916. doi: 10.1093/aob/mcf105

Cianciaruso MV, Silva IA, Manica LT, Souza JP (2013- Leaf habit does not predict leaf functional traits in cerrado woody species. Basic Appl Ecol 14:404)412. doi: 10.1016/j.baae.2013.05.002

Dantas VL, Batalha MA (2011- Vegetation structure: Fine scale relationships with soil in a cerrado site. Flora. 206:341)346. doi: 10.1016/j.flora.2010.11.003

Delgado MN, Gomes MRA, Báo SN, Rossatto DR (2013- Fertlisation residues alter leaf scleromorphy in an evergreen savannah shrub (*Maprounea brasiliensis*, Euphorbiaceae-. Aust J Bot 61:266)273. doi: 10.1071/BT12231

Franco AC, Bustamante M, Caldas LS, Goldstein G, Meinzer FC, Kozovits AR, Rundel P, Coradin VTER (2005- Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. Trees 19:326)335. doi: 10.1007/s00468)004)0394)z

Givnish TJ (1988- Adaptation to sun and shade: a whole plant perspective. Aust J Plant Physiol

15:63)92. doi:10.1071/PP9880063

Goodland R, Ferri MG (1979-. Ecologia do Cerrado. São Paulo – Itatiaia. v. 52, 193p.

Gottsberger G, Silberbauer–Gottsberger I (2006- Life in the Cerrado, a South American Tropical Seasonal Ecosystem. Vol. 1. Origin, Structure, Dynamics and Plant Use (Reta Verlag, Ulm, Ger) many-.

Habermann G, Bressan ACG (2011- Root, shoot and leaf traits of the congeneric Styrax species may explain their distribution patterns in the cerrado sensu lato areas in Brazil. Funct Plant Biol 38:209)218. doi: 10.1071/FP10182

Haridasan M, Araújo GM (1988- Aluminium accumulating species in two forest communities in the cerrado region of central Brazil. Forest Ecol Manag 24:15)26. doi: 10.1016/0378)1127(88-90021)7

Haridasan M (1982- Aluminium accumulation by some cerrado native species of central Brazil. Plant Soil. 65:265)273. doi: 10.1007/BF02374657

Haridasan M (2008- Nutritional adaptations of native plants of the cerrado biome in acid soils. Braz J Plant Physiol 20:183)195. doi: 10.1590/S1677)04202008000300003

Hoffmann W, Franco AC (2003- Comparative growth of tropical forest and savanna woddy plants using phylogenetically independent contrasts. J Ecol 91:475)484. doi:10.1046/j.1365)2745.2003.00777.x

Hoffmann WA, Franco AC, Moreira MZ, Haridasan M (2005- Specific leaf area explains differen) ces in leaf traits between congeneric savanna and forest trees. Funct Ecol 19:932)940. doi: 10.1111/j.1365)2435.2005.01045.x

INMET (2013- Available: http://www.inmet.gov.br/portal/. Accessed 10 October 2013.

Okitsu S (2005- Factors controlling geographical distribution in savanna vegetation in Namibia. African Study Monographs, Suppl. 30:135)151.

Pate JS (1973- Uptake, assimilation and transport of nitrogen compounds by plants. Soil Biol

Biochem 5:109)119. doi: 10.1016/0038)0717(73-90097)7

Prado CHBA, Wenhui Z, Rojas MHC, Souza GM (2004- Seasonal leaf das exchange and water potential in a woody cerrado species community. Braz J Plant Physiol 16:7)16. doi: 10.1590/S1677)04202004000100002

Prior LD, Bowman DMJS, Eamus D (2005- Intra)specific variation in leaf attributes of four savan) na tree species across a rainfall gradient in tropical Australia. Aust J Bot 53:323)335. doi: 10.1071/BT04080

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

Sankaran M, Hanan NP, Scholes RJ et al (2005- Determinants of woody cover in African savannas. Nature 438:846)849. doi:10.1038/nature04070

Sarruge JR, Haag HP (1974- Análises químicas em plantas. Piracicaba, ESALQ. 54 p.

Silva CR (2008- Geodiversidade do Brasil: conhecer o passado, para entender o presente e prever o futuro. Rio de Janeiro: CPRM. 264 p

Silva CR, Hoffmann WA, Rossato DR, Haridasan M, Franco AC, Horwarth WR (2013- Can savanna become forests? A coupled analysis of nutrient stock and fire thresholds in central Brazil. Plant Soil 373:829)842. doi:10.1007/s11104)013)1822)x

Souza MC, Habermann G (2012- Towards a new ecophysiological approach to understand citrus crop yield under abiotic stresses mirroring in the Brazilian savanna genetic resources. In: Rahman IMM, Hasegawa H (ed- Water Stress. Rijeka: InTech, 152)164. doi: 10.5772/31271

Walter H (1986- Vegetacão e zonas climaticas. EPU, Sao Paulo.

Warton DI, Wright IJ, Falster DS, Westboy M (2006- Bivariate line)fitting methods for allometry. Biol Rev 81:259)291. doi: 10.1017/S1464793106007007

Williams RJ, Carter J, Duff GA, Woinarski JCZ, Cook GD, Farrer SL (2005- Carbon accounting, land management, science and policy uncertainty in Australian savanna landscapes: introduction and overview. Aust J Bot 53:583–588. doi: 10.1071/BT05181

Wright IJ, Reich PB, Westoby M (2001- Strategy shifts in leaf physiology, structure and nutrient content between species of high)and)low)rainfall and high and low)nutrient habitats. Funct Ecol 15:423)434. doi: 10.1046/j.0269)8463.2001.00542.x

Figures, tables and captions:

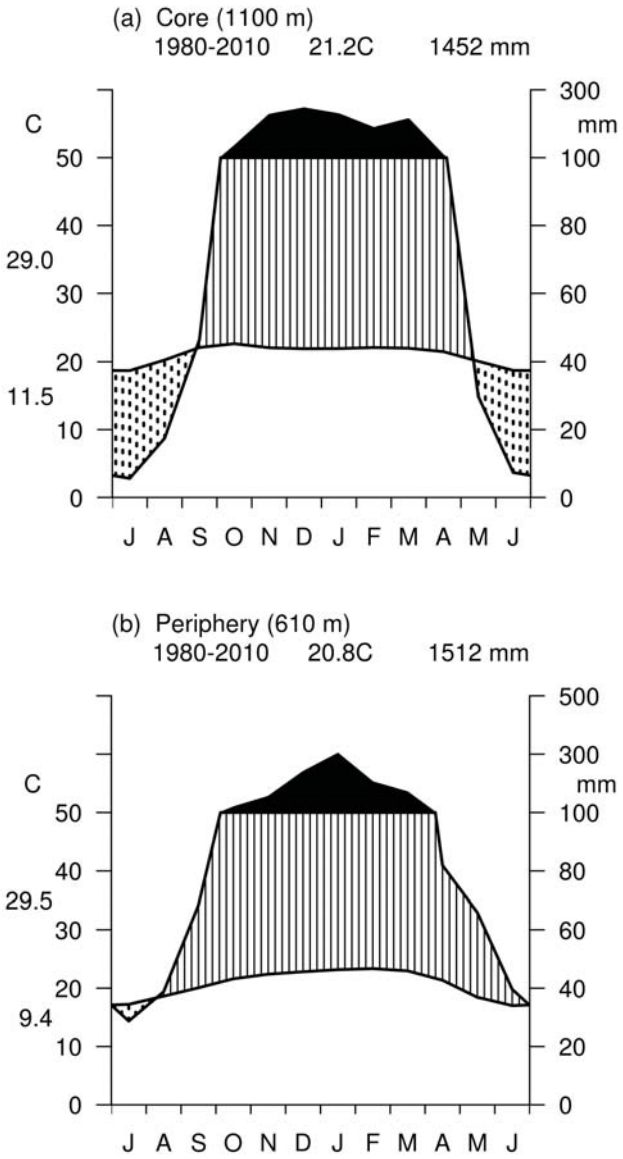

Figure 1. Climatic diagram displaying the length of the dry and wet seasons, elevation, annual rainfall and air temperature distribution for a period of 30 years (1980–2010- in the core (a- and southeastern periphery (b- of the cerrado.

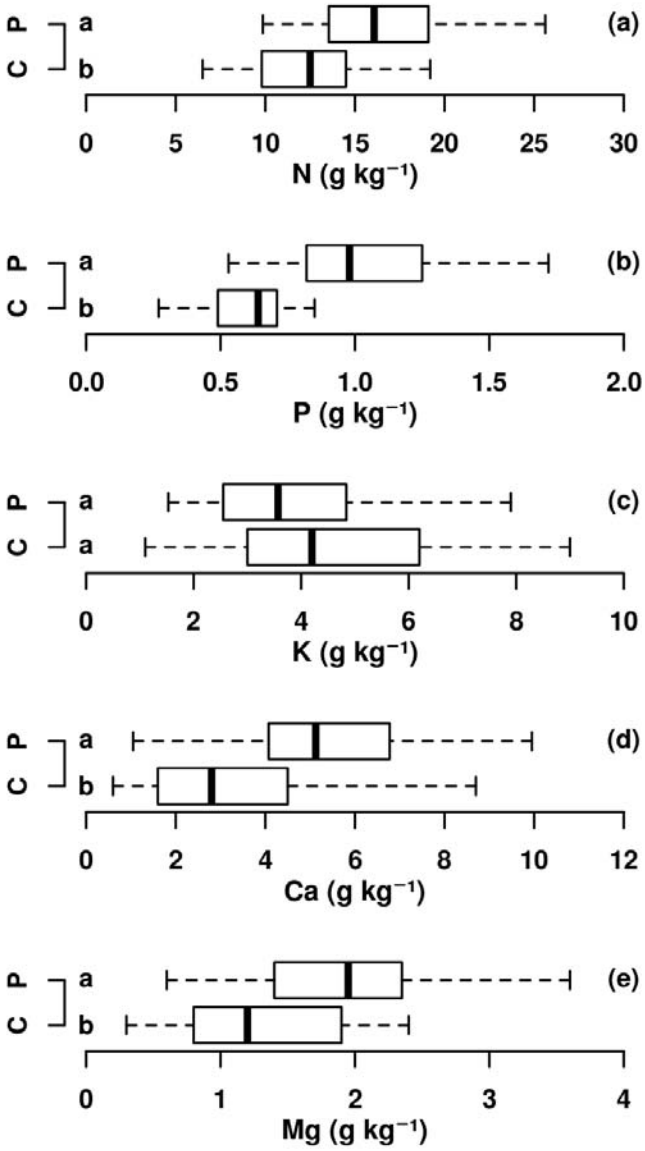

Figure 2. Box plots showing leaf nutrient concentration in two cerrado *sensu stricto* communities located in the core and southeastern periphery in Brazil. The line in the middle of each box indicates the 50th percentile of the observed distribution; the left and right parts of each box represent the 25th and 75th percentiles, respectively; the left and right error bars of each box are the 5th and the 95th percentiles of the observed distribution. Different letters indicate significant difference ($p < 0.05$- using a t)test at 5% level between the core (C- and the southeastern periphery (P- of the cerrado.

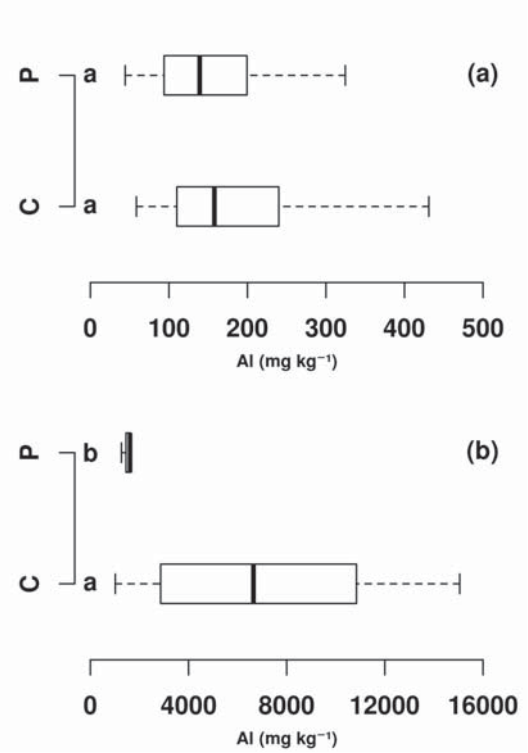

Figure 3. Box plots showing aluminum leaf concentration in Al)non)accumulator (a- and Al)accumulator (b- plants in the cerrado *sensu stricto* communities located in the core and southeastern periphery. Box plot characteristics are as described in Figure 2.

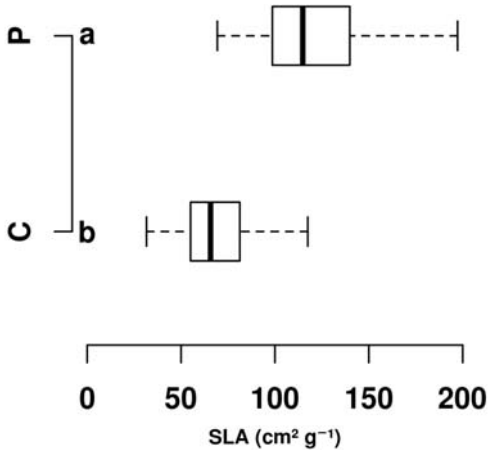

Figure 4. Box plots of specific leaf area (SLA- in the cerrado *sensu stricto* communities located in the core and periphery. Box plot characteristics are as described in Figure 2.

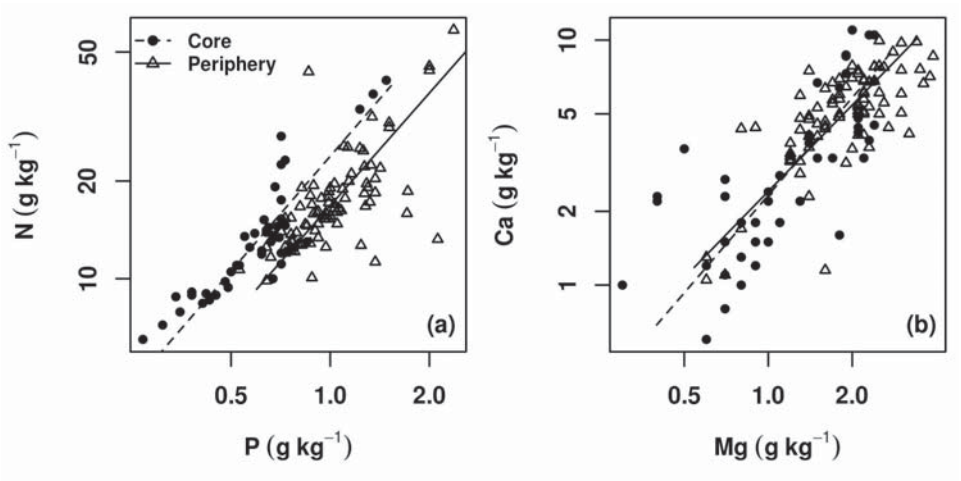

Figure 5. Standardized major axis (SMA- relationships between leaf concentrations of N *versus* P and Ca *versus* Mg for two cerrado *sensu stricto* communities in core and periphery. Axes are log10 scaled.

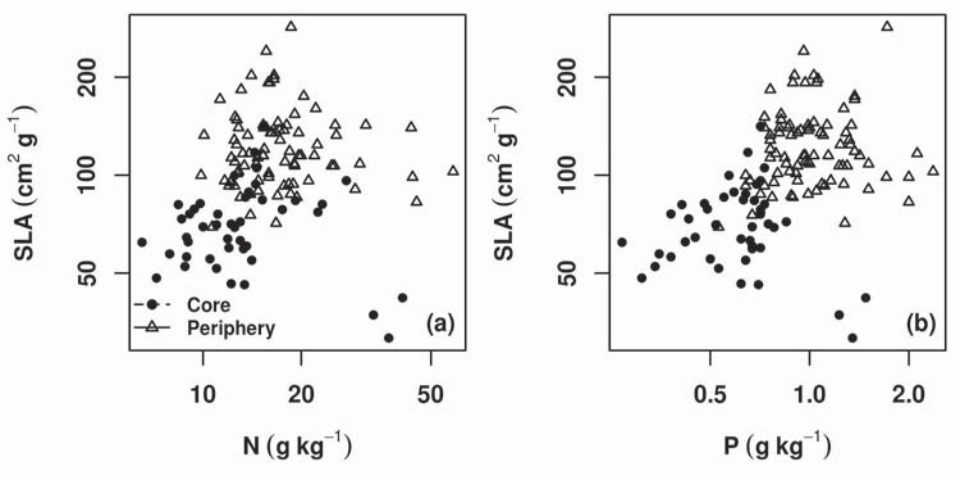

Figure 6. Standardized major axis (SMA- relationships between leaf concentrations of N *versus* SLA and P *versus* SLA for two cerrado *sensu stricto* communities in core and periphery. Axes are log10 scaled.

Table 1. List of species selected from two cerrado *sensu stricto* communities located in the core and in the southeastern periphery. *Al)accumulator species.

Family	Specie	Site
Annonaceae	*Annona coriacea*	Periphery
Annonaceae	*Xylopia aromatica*	Periphery
Apocynaceae	*Aspidosperma tomentosum*	Periphery
Araliaceae	*Schefflera paniculata*	Core
Calophyllaceae	*Kielmeyera coriacea*	Core
Caryocaraceae	*Caryocar brasiliensis*	Core/Periphery
Erythroxylaceae	*Erythroxylum suberosum*	Periphery
Erythroxylaceae	*Erythroxylum tortuosum*	Periphery
Erythroxylaceae	*Erythroxylum pelleterianum*	Periphery
Fabaceae	*Sclerobium paniculatum*	Core
Fabaceae	*Dalbergia miscolobium*	Core
Fabaceae	*Stryphnodendron adstringens*	Core
Malpighiaceae	*Byrsonima crassa*	Core
Malpighiaceae	*Byrsonima basiloba*	Periphery
Malpighiaceae	*Byrsonima intermedia*	Periphery
Malpighiaceae	*Banisteriopsis variabilis*	Periphery
Malvaceae	*Eriotheca gracilipes*	Periphery
Melastomataceae	*Miconia pohliana**	Core
Melastomataceae	*Miconia rubiginosa**	Periphery
Melastomataceae	*Miconia fallax**	Periphery
Myrsinaceae	*Rapanea umbelata*	Periphery
Myrtaceae	*Blepharocalyx salicifolius*	Core
Myrtaceae	*Myrcia bella*	Periphery
Nyctaginaceae	*Guapira noxia*	Core
Nyctaginaceae	*Guapira opposita*	Periphery
Ochnaceae	*Ouratea hexasperma*	Core
Rubiaceae	*Tocoyena formosa*	Periphery
Salicaceae	*Casearia sylvestris*	Periphery
Sapotaceae	*Pouteria torta*	Periphery
Styracaceae	*Styrax ferrugineus*	Periphery
Vochysiaceae	*Vochysia elliptica**	Core
Vochysiaceae	*Vochysia thyrsoidea**	Core
Vochysiaceae	*Qualea grandiflora**	Core/Periphery
Vochysiaceae	*Qualea parviflora**	Core

Table 2. Soil properties of two cerrado *sensu stricto* communities in the core and on the southeastern periphery.

Soil parameter	Site		P value
	Core	Periphery	
pH ($CaCl_2$-	4.6 ± 0.2	3.9 ± 0.1	**<0.001**
Organic matter (g $dm^{)3}$-	28.3 ± 0.4	20.7 ± 2.4	0.138
N (%-	0.14 ± 0.2	0.17 ± 0.3	**<0.001**
P (mg $dm^{)3}$-	1.6 ± 0.4	2.2 ± 0.3	**0.031**
K ($mmol_c$ $dm^{)3}$-	1.0 ± 0.5	1.3 ± 0.2	0.298
Ca ($mmol_c$ $dm^{)3}$-	0.2 ± 0.2	1.9 ± 0.5	**0.001**
Mg ($mmol_c$ $dm^{)3}$-	0.3 ± 0.4	1.1 ± 0.2	**0.011**
Al ($mmol_c$ $dm^{)3}$-	8.5 ± 2.4	13.4 ± 1.5	**0.013**
m %	85.4 ± 8.1	75.9 ± 3.3	0.07
Clay %	65.4 ± 6.9	13.2 ± 0.8	**<0.001**
Sand %	19.7 ± 4.3	84.5 ± 1,2	**<0.001**
Silt %	14.2 ± 2.8	2.3 ± 0.6	**0.001**

Significant results (P<0.05- are shown in bold

Table 3. Results of standardized major axis regression (SMA- analysis of pairwise combinations of foliar N *versus* P, Ca *versus* Mg, N *versus* SLA and P *versus* SLA in two cerrado *sensu stricto* communities in the core and on the southeastern periphery.

Y and X	Site	R^2	P	Intercept	Slope
N and P	core	0.772	**<0.001**	**1.378**	1.176
	periphery	0.451	**<0.001**	**1.225**	1.153
Ca and Mg	core	0.549	**<0.001**	0.367	1.324
	periphery	0.535	**<0.001**	0.383	1.170
SLA and N	core	0.015	0.416	3.664	)1.388
	periphery	0.001	0.772	3.763	)1.216
SLA and P	core	0.018	0.375	1.944	)1.180
	periphery	0.006	0.472	)2.189	1.054

Significant results (P<0.05- are shown in bold

7 - Capítulo 3

Leaf scleromorphism and nutritional status in woody plants: A comparison across Australian, Brazilian and South African savannas[***]

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Abstract

Background: Fire incidence, water availability, soil fertility and herbivory are the most important ecological filters in savannas (Australian, Brazilian and South African savannas-, affecting the leaf scleromorphism and limiting nutrient uptake. Soils from savannas are considered acidic and rich in aluminum (Al-. However, some species from these environments can be considered Al)accumulators.

Methods/Principal Findings: We investigated how much soil fertility and annual rainfall affects the leaf nutritional status and Al accumulation, and leaf scleromorfism (specific leaf area – SLA- among the three savannas. The Brazilian savanna presented the most acidic soil (pH < 5.0- and highest annual rainfall. Their species were the least scleromorphic (higher SLA-, accumulate 3)8 times more Al in their leaves, exhibiting a plant community that is richer in Al)accumulator species in relation to the other two savannas. The South African savanna grows on less acidic soils (pH > 5.5-, face severe droughts and exhibit the smallest number of Al)accumulator species, although storing more nutrients in their leaves that are highly scleromorphic (low SLA-. Species from Australian savanna have an intermediate behavior between the Brazilian and South African savannas.

Conclusions: Savannas demonstrate distinct strategies to retain nutrients in their leaves. The higher occurrence of Al)accumulating species in the Brazilian savanna can be ascribed to the Al availability and acidity developed in these soils after continents have drifted apart and become influenced by different climatic conditions. While higher rainfall may have increased acidity and Al in the soils in Brazil, severe droughts, fire and the megafauna pressures may have selected S. African savannas to accumulate more nutrients and N to allow plants grow tall quickly. The variation on leaf scleromorphism among the three savannas can be attributed to the higher incidence in Brazil and lower incidence in South Africa. Therefore the Brazilian savanna plants were the less scleromorphic while the South African's were the most scleromorphic.

Keywords: specific leaf area, aluminum, mineral nutrition, cerrado, bush, climate

Introduction

In the past (~200 million year ago- the landmasses that currently comprise the Australian, Brazilian and South African savannas (hereafter referred to as savannas-, were all connected to each other in a single great landmass, the ancient continent of Gondwana (Storey 1995-. Then, as Gondwana broke up, these landmasses gradually drifted apart for about 150 million years forming the earth's continents as we know now. Today, the world's tropical savannas grow at approximately similar latitudes, under broadly comparable rainfall regimes) wet summer and dry winter (Mott et al. 1985, Oliveira and Marquis 2002- and largely on acidic soils (Hill et al. 2010, Haridasan 2008-. Savannas occur on all the southern continents, cover approximately 20% of earth's land surface and are a biologically unique and economically important tropical biome. (Sankaran et al. 2005, Grace et al. 2006-.

Across the globe, these savannas are structurally similar in that they consist of woody trees and shrubs scattered in a grassy matrix (Sankaran et al. 2005, Lehmann et al. 2011-. However, the phylogenetic histories of the plant communities on the three continents are different, and the tree and grass species that dominate in each of the continents are often unique and characteristic of that region. For example, African savannas are often dominated by Acacias and Combretums, while Australian systems tend to be dominated by Eucalypts. However, it remains unknown whether these savannas, which are structurally similar and which occur in comparable climates, but which are characterized by different species, function differently or similarly across the different continents (Lehmann et al. 2009-.

In the present study, we address this question by comparing the functional traits and trait phylogenies of woody savanna species from across the three southern continents.

The functional traits that we use for these comparisons are specific leaf areas (SLA- and leaf nutrient concentrations (mainly N and P-, because of their relationships to CO_2 assimilation and leaf life span (Franco et al. 2005-. Also, both traits are frequently used to explain ecophysiological differences between vegetation's physiognomies (*e.g.*, forest *versus* savanna- and among congeneric species from different environments (Hoffmann et al. 2005, Habermann

and Bressan 2011-. Here, we use these traits to explore functional and phylogenetic differences across the world's tropical savannas. Further, we consider leaf Al concentrations, which is an important indicator of plant strategies in dealing with acidic soils, and are common to most of the world's savannas. Aluminum (Al-, the most abundant metal in Earth's crust, is a major contributor to soil acidity (Robson 1989-. Acidic soils (pH < 5.0-, together with high availability of exchangeable Al and low concentrations of bases (P, N, K, Ca and Mg- in the soil are widely known to limit growth and survival of crop plants (Yang et al. 2013-, since Al causes damage to the root tip, reducing major nutrient uptake (Kopttike et al. 2008-.

Currently, most of our understanding of Al uptake in native savanna species comes from Brazilian savannas, where the high leaf Al concentrations are widely reported. Broadly, these are classified as Al)tolerant (or Al)non)accumulators-, concentrating up to 600 mg of Al per kg of leaf dry mass (LDM- or as Al)accumulators, which may accumulate more than 1000 and up to 15,000 mg Al $kg^{)1}$ LDM (Haridasan 1982-. When analyzing the Al)accumulator species, the high Al concentration is not associated with low leaf uptake/concentration of the other nutrients in the leaves of Brazilian savanna woody plants (Haridasan 1982-. However, when the Al)accumulator species are examined all together, as a functional group, Al seems to compete with the other nutrients in the mesophyll (Souza et al., unpublished data-. Most importantly, Al accumulation is not an exclusive trait to Brazilian savanna species, but it is also reported for many species from savannas and tropical forests around the world (Jansen et al. 2002-. Therefore, there might be a strong phylogenetic bases for Al accumulation.

Biological leaf traits may have distinct evolutionary histories, and therefore, traits may have converged or be conserved through evolution, exhibiting phylogenetic signals (Harvey and Pagel 1991-. Plants from the Fabaceae family, which consistently occur in all savannas and have common ancestors, have helped establish broad phylogenetic relationships between plant species and communities of different savannas (Batalha et al. 2011; Simon et al. 2009-. However, little is known about the phylogenetic signals of leaf traits, such as SLA, concentration of macronutrients (N, P, K, Ca and Mg- and Al accumulation across these

savannas. The phylogeny of leaf traits may be ecologically important and provides novel insights into the underlying forces structuring communities (Pipenbaher et al. 2013-.

We compiled a dataset of leaf traits (SLA, leaf concentration of nutrients and Al- in savanna species from Brazil and South Africa, and supplemented this with new samples from Australian and Brazilian savannas. We then used this dataset to address the following questions: 1) How variable are leaf nutritional status, Al accumulation and leaf scleromorphysm (SLA- among earth's major savannas and what are the environmental correlates of this variation? 2) Are there any phylogenetic signals in these leaf traits? 3) How is trait diversity structured across the phylogenetic tree and what can we infer about the roles of phylogeny and ecology in driving leaf traits in these ecosystems?

Material and methods

Data for this study were obtained from bibliographical survey, and supplementary new data collected from Australian and Brazilian savannas. Samplings performed by other authors (bibliographical- and by us in the field (supplementary- were conducted in the wet season. The bibliographical dataset provided leaf concentrations of N, P, K, Ca, Mg, Al and SLA sampled in mature leaves of adult shrubs or woody plants from the South African and Brazilian savannas. When species were duplicated between papers/sites, the mean value across all studies was computed and used in the analysis (Appendix 1-. Out of the 110 species, 43 occurred in the Australian savanna, 40 in the Brazilian and 27 in the South African. No common species occurred between the three continents.

Australian plants were sampled between February and March 2013. We sampled the most representative plant species (4)6 plants per specie- in different savanna)type physiognomies, located on Tiwi island (11°36'S 130°42'E-, Darwin (site 1: 12°24'S 130°55'E; site 2: 12°36'S 131°00'E-, Pinne Creek (13°56'S 131°53'E-, Daily Waters (16°05'S 133°25'E-, Tennant Creek (19°24'S 134°12'E-, and Alice Springs (23°59'S 133°56'E-. These sites comprise all the Australian savanna)type physiognomies.

Brazilian plants data extracted from Araújo (2006- were sampled at the Reserva do IBGE (15°57' S 47°52'W- and plants data extracted from Medeiros and Haridasan (1985- and Haridasan (1982- were sampled at the Fazenda Água Limpa farm (15°57'S 47°55'W-. The same number (4)6 plants per species- was used when sampling supplementary data in the field from the most representative species on a remnant of the Brazilian savanna, located at Itirapina, on the São José da Conquista farm (22°10'S 47°52'W-, São Paulo state, during February 2010.

In South Africa, plants data extracted from Ratnam et al (2008- and Higgings et al. (2012- were sampled in March 2003 and 2004 from approximately 100 sites across Kruger National Park (24°29'S 31°30'W-, comprising different savanna)type physiognomies. In addition, leaf Al concentration was obtained from the same experimental sites in South Africa and added to the dataset.

Climatological data

We used a 30)year climatic dataset for each country. In Brazil, the National Institute of Meteorology provided us the data of annual rainfall (INMET 2013-. In Australia, annual rainfall was provided by the Bureau of Meteorology (BOM 2013-, and for South Africa these data were extracted from Zambatis (2006-.

SLA, leaf macronutrient and Al concentrations and soil parameters

Leaf samples were washed in distilled water, oven)dried for 72h at 60°C and ground. The Australian samples were analyzed in accordance with the same procedures used to analyze the South African samples (Ratnam et al. 2008-. Nitrogen content was determined by combustion, with a LECO CHN analyzer (LECO Corp, St Joseph, MI-, and total P was assessed by inductively coupled plasma (ICP- spectrometry (Leman Labs, Hudson, MA-, after acid digestion of samples with HNO_3)$HClO_4$ (Olsen and Sommers 1992-. To determine leaf concentrations of K, Ca, Mg and Al, dried leaves were digested into a nitric)percloric acid solution, following determination by ICP.

Brazilian samples were analyzed using similar methods as performed by Araújo (2006-, Haridasan (1982- and Medeiros and Haridasan (1985-. Leaves were acidic digested, the concentrations of Ca and Mg were determined by the atomic absorption spectrophotometer method, K was determined in a flame photometer, S was determined using a turbidimetric method, P and Al were quantified colorimetrically, and N was determined by the micro)Kjeldahl method (Sarruge and Haag 1974, Allen 1989-.

The SLA obtained from bibliographical data (Higgins et al. 2012 and Araújo, 2006-, as well as those obtained from supplementary samples from the fields was calculated as the ratio between leaf area (cm^2- and leaf dry mass (g- (Habermann and Bressan 2011- (Appendix 1-.

Soil samples were collected in all previously described sites from the three continents at 0)30 cm in depth. Soil parameters (pH, organic matter, N, P, K, Ca, Mg and Al- from Australia and South Africa were determined according to the international standard for soil analysis (Robertson et al. 1999-. Brazilian soils were analyzed in accordance with Dantas and Batalha (2011- (Appendix 1-.

Phylogenetic and statistical procedures

The phylogenetic tree for the studied species was built according to Webb and Donoghue (2005- using the Phylomatic software (Figure 1-. Phylogenetic distances among species from different families were estimated from the current Phylomatic tree (R20120829-. The resolution of the phylogenies was improved using the TreeTime software (Hedges et al. 2006-. The undated nodes in the phylogenetic tree were replaced with dated nodes using the Branch Length Adjustment Algorithm (*bladj* function- in Phylocom (Webb et al. 2008-. The existing polytomies of the base backbone tree were randomly resolved using the *multi2di* command from the *ape* R package (Paradis et al. 2004-.

The phylogenetic signal (Blomberg's *k*- (Blomberg et al. 2003- of the leaf traits (leaf concentrations of N, P, K, Ca, Mg, Al, as well as N:P, Ca:Mg, and SLA- was estimated using the

picante R package (Kembel et al. 2010-. In this way, when $k \sim 1$ there is no phylogenetic signal, when $k > 1$ there is a positive phylogentic signal (convergence- and when $k < 1$ there is a negative phylogenetic signal (divergence- (Ackerly 2009-.

Using the leaf traits described above, we decomposed the trait diversity between nodes of the phylogenetic tree using a quadratic entropy index, with the *decdiv* function for R (Pavoine et al. 2010-. When traits are conserved trait diversity is skewed to the root of a phylogenetic tree (low diversity-, and when traits converge trait diversity can be found at the tips of the tree (high diversity- (Pavoine et al. 2010-. Therefore, a skewness test was performed to check if the leaf traits were clustered in a single)node, few nodes or near the root of a phylogenetic tree (Pavoine et al. 2010-. The decomposition of the trait diversity was performed using all leaf traits among the 110 species.

We used ANCOVA model to test the hypothesis that the savannas present different degrees of leaf scleromorphysm. In this model, SLA was a dependent variable, N was covariate and site was grouping factor with three levels. We used a one)way)ANOVA between the Tropical savanna communities to check variances of the studied parameters (leaf concentrations of N, P, K, Ca, Mg, Al, N:P, Ca:Mg and SLA- and soil properties (pH, N, P, K, Ca, Mg, Al and organic matter (OM--. Mean results were compared by the Tukey's test at 5% of probability.

We also used a phylogenetic ANOVA with 999 randomizations (Garland et al. 1993- using the R package *geiger* (Harmon et al. 2008-. This is because standard statistical analysis assumes independence between samples. Therefore, a phylogenetic ANOVA was used to avoid species' independence from each other, as there are mandatory phylogenetic relationships among them (Busserolles et al. 2013-.

Bivariate relationships between N and P in the three savannas were analyzed using a standard major axis regression (SMA-. Test for common slopes and elevation were conducted only when a significant relationship ($p<0.05$- occurred between variables in each community (Warton et al. 2006-. Variations between lines were calculated using a multiple comparison

matrix between the communities. Data were log)transformed and the analyses were performed using the R package *smatr* (Warton et al. 2012-.

To understand the role of environmental factors on the distribution of traits amongst the three communities, we tested the influence of pH and Al in the soil and the total annual rainfall on the distribution of species between the three communities from the three continents using a Redundancy analysis (RDA- (R package *vegan*; Oksanen et al. 2012-. Phylogenetic and statistical analyses were carried out using the R package (R Development Core Team 2012-.

Results

Soils from the savannas did not differ in the concentrations of OM, N, P, K, Ca, Mg and Al, but differed significantly in the soil pH ($p<0.05$-. In Brazil, savanna's soils were very acidic (pH = 4.15 ± 0.66- whereas in Australia and South Africa the savanna's soils were less acidic, and soil pH were 5.64 ± 0.66 in Australia and 6.04 ± 0.18 in South Africa.

The average annual rainfall is much higher in the Brazilian's savanna (mean = 1482 mm- than in Australia (mean = 1081 mm- and South Africa (mean = 555 mm- (Appendix 1-. Thus, the tropical savannas lie at different points along a rainfall gradient: wet (Brazilian-, intermediate (Australian- and dry (South African-.

K values were smaller than 1 for all leaf traits (Table 1-, meaning that leaf traits had a negative phylogenetic signal. For some traits (N, K, Al and SLA- the phylogenetic signal was significant, while for others (P, Ca, Mg, N:P and Ca:Mg- was not significant (Table 1-. When the trait diversity was decomposed across the nodes of the tree (Figure 2- the results from the skewness test for single) and few)node tests were not different from random ($p=0.82$ and $p=0.54$ respectively-. On the other hand, a significant variation occurred between the tips skewness ($p=0.001$- and the random test.

In the ANCOVA, the interaction between SLA and site ($F=18.29$-, and SLA and covariate (leaf N concentration- ($F=25.87$- were both significant ($p<0.001$-. The standard

ANOVA demonstrated different nutritional status, Al accumulation pattern and SLA among the savannas of the three continents ($p<0.05$-. This resulted in different levels of leaf scleromorphism (Table 1- among the three savannas in such a manner that the Brazilian savanna can be considered the least scleromorphic and the South African the most scleromorphic. The phylogenetic ANOVA indicated a significant variation among savannas for leaf concentrations of N, P, Ca, Mg, N:P and Ca:Mg. The leaf concentration of K and Al and also SLA were not statistically different among the three savannas (Table 1-.

The bivariate analysis (SMA- pointed out a significant correlation between N and P for the three savannas (Figure 3-, and there was, indeed, a common slope (0.99- but a significant variation on intercepts occurred among them.

The RDA analysis showed a conspicuous disjunction between the three plant communities. For this analysis, leaf concentrations of N, P, K, Ca, Mg, Al, the N:P and Ca:Mg relationships, as well as SLA were used as leaf traits; pH and Al content in the soil and annual rainfall were used as environmental variables. The RDA1 and RDA2 explained, simultaneously, 18% of the disjunction between the three savannas (Figure 4-.

Discussion

Leaf nutritional status, SLA and leaf scleromorphism are part of vegetation traits that are influenced by ecological filters (Batalha et al. 2011-. On the other hand, the most important ecological filters acting over savannas are the incidence of fire, soil fertility, water availability and herbivory (Sankaram et al. 2005, Silva et al. 2013, Delgado et al. 2013-. For million years, savannas have been subjected to different intensities of these filters, resulting in convergence or overdispersion of the leaf traits. In this paper, we demonstrate that trait diversity decomposition was not skewed either in a single)node or in few nodes, but it was toward the root and tips, suggesting that the leaf traits, herein, nutritional status and scleromorphism are phylogenetically overdispersed. For instance, we observed that the rate of evolution of Myrtales was concentrated in the root, about 100)50 Myr (million years ago-, which coincides with the major

diversification of angiosperms in mid)Cretaceous (Crane et al. 1995-. For Fabales, however, the high rate of evolution was concentrated in the tips of the phylogenetic tree for Acacia genus about 10)5 Myr, which matches the time for the origin of the modern savanna during the late Miocene (Cerling et al. 1997-.

Ancova, standard and phylogenetic Anovas show that there was many significant differences in SLA, leaf nutritional status and Al accumulation among the three savannas, resulting in different degrees of leaf scleromorphysm. We observed an association between the increased annual rainfall in the Brazilian savanna and elevated SLA, while the opposite was observed in South Africa (low SLA and rainfall-. This is a counterintuitive and unexpected result because SLA usually increases with the decreasing of sunlight (Gvinish 1988; Hoffmann et al. 2005, Franco et al. 2005; Habermann and Bressan 2011-, and no study has reported the influence of rainfall. On the other hand, it is believed that between Cretaceous (~150 Myr- and Quaternary (~2 Myr- the global climate has suffered many changes, most of then related with rainfall distribution (Maley 1996, Bush et al. 2011-. Thus, taking our results as important traits that have long been influenced by environmental filters found in the savannas (Sankaram et al. 2005; Batalha et al. 2011; Lehmann et al. 2014-, we suggest that the distinct rainfall regimes occurring in savannas of these three continents modulate SLA of local plant communities.

Although growing on soils with the same fertility in the three continents, considerably high rainfall and SLA found in Brazil made us expect high leaf N concentration in Brazil as a result of the lowest leaf scleromorphysm (Delgado et al. 2013-. Once more, different than expected, the highest N concentration was observed in leaves of plants from the S. African savanna. As an explanation, we noticed that 37% of S. African species are composed by Fabaceae species, and 30% of total species is comprised exclusively by *Acacia* species, which are N_2)fixing plants (Wright and Westoby 2003-. On the other hand, the Brazilian savanna plant community used in this research shows only 7.5% Fabaceae species. Then, what would be the reason for the increased occurrence of leguminous species in South African savannas, as already reported by many researchers (Staver et al. 2012; Higgins et al. 2012-? In the Brazilian savanna

the mega fauna has been extinct 50,000 to 10,000 years ago (Hansen and Galetti 2009-, whereas South African savannas has suffered the most continuous pressure from the megafauna (elephants, giraffes, antelopes, rhinos, etc- among the savannas (Staver et al. 2012 for references-. In addition, fire has also been considered a strong vegetation modulator in this continent (Sankaran et al. 2005, Lehmann et al. 2014-. Thus, to scape fire and the megafauna herbivory, S. African species require huge amounts of N in order to grow tall quickly (Staver et al. 2012 for references-. Therefore, as N uptake is physiologically difficult in N)deficient areas, and mainly under severe drought conditions (Marschner 1995-, such as in S. African savannas, leguminous species that accumulate N are more important in South African savannas, which influenced our comparisons.

The similar response patterns in the N x P relationship between the Brazilian and South African plant communities reinforce the same contribution of these nutrients to the development of the savannas between these two continents (South America and Africa-, possibly before they have drifted apart. However, our data indicated a disjunction between this Afro)American flora and the Australian plant community (Fig. 3-. Since N and P are considered the most limiting nutrients for many terrestrial plants (Chapin III et al. 2012-, this may suggest that in the past the east (Australia- and the west (South America and South Africa- Gondwanas were exposed to different environmental pressures, leading to a functional disjunction in the flora from the east and the west sides.

It is widely known that rainfall lixiviates important bases (K, Ca and Mg- in the soil, acidifying it and, consequently, increasing the Al^{3+} availability (Robson 1989-. Soils from the Brazilian savanna are predominantly acidic (pH < 4.0- oxisoils, rich in Al^{3+} and poor in nutrients (Haridasan 2008-, whereas soils from the Australian and South African savannas are less acidic (pH > 5.0- alfisoils, poor in Al^{3+} and with higher availability of Ca and Mg in relation to Oxisoils (Hill et al. 2010-. In this way, we found many Al)accumulators in the Brazilian savanna (*Miconia albicans*, *M. fallax*, *M. ferruginata*, *M. pohliana* and *M. rubiginosa* (Melastomataceae-, *Palicourea rigida* (Rubiaceae- and *Qualea grandiflora*, *Q. multiflora*, *Q.*

parviflora, *Vochysia elliptica* and *V. thyrsoidea* (Vochysiaceae--, only two Al)accumulators in Australia (*Pogonolobus reticulatus* (Rubiaceae- and *Xanthostemon paradoxus* (Myrtaceae-- and a single Al)accumulating species in South Africa (*Combretum zeyherei* (Combretaceae--. This strengthens the hypothesis that Al availability in the soil could be a selective pressure for Al accumulating plants throughout the evolution.

However, in the Brazilian savanna there is no direct relationship between Al availability in the soil and Al accumulation among Vochysiaceae species (Andrade et al. 2011-, indicating that there is a minimum Al tolerance required for plant survival in the Brazilian savanna, as Al)accumulators represented between 18 (Haridasan and Araújo 1988- and 35% (Haridasan 1982- plant communities in the Brazilian savanna. Therefore, it raises the hypothesis that environmental stresses might have exerted selective pressures on the flora of these three savannas after landmasses have drifted apart and formed the continents. From this standpoint, higher rainfall caused soil acidification and made Al more available in the Brazilian savanna, while fire and severe drought may have modulated the South African savannas. This is corroborated by our results obtained from the redundancy analysis, showing that the combination of annual rainfall, pH and Al concentration in the soil explained the disjunction among the savannas and the highest number of Al)accumulators in Brazil.

Therefore, the Al accumulation is a primitive trait, strongly influenced by phylogeny, worldwide distributed and most commonly observed in tropical forests growing on acidic soils (pH 3)5- subjected to high rainfall (Jansen et al. 2002-. As Al transport from roots to shoots occurs via xylem sap (Watanabe and Osaki 2001- in Al)accumulating species and reaches leaves through the transpiration stream (Shen and Ma 2001-, it raises the hypothesis that savannas that are influenced by elevated rainfall, such as the Brazilian savanna, would facilitate nutrient uptake, including Al, whereas severe droughts in the South African savanna would not make Al uptake easy by plants. In fact, there are many other savanna and savanna)forest species described as Al)accumulators in Brazil: *Miconia burchellii* (Melastomataceae-, *Symplocos platyphylla* (Symplocaceae-, *Palicourea squarrosa*, *Coussarea* spp., *Faramea cyanea*, *Rudgea*

viburnoides (Rubiaceae-, *Vochysia rufa*, *V. haenkeana*, *V. tucanorum, V. divergens*, *Qualea dichotoma*, *Callisthene major*, *Salvertia convallariodora* (Vochysiaceae- (Haridasan 1982, 1987, Haridasan and Araújo 1988-, and some forest species in Australia: *Ceratopetalum apetalum*, *Schizomeria ovata* (Cunoniaceae-, *Cardiwellia sublimis*, *Helicia glabriflora, Orites excelsa* (Proteaceae-, *Hedyotis auricularia*, *Lasianthus strigosus* (Rubiaceae-, *Quintinia verdonii* (Escalloniaceae- and *Tetrasynandra pubescens* (Monimiaceae- (Webb 1954-.

Conclusions

In summary, despite the similarities on the soil fertility in the three sites, the savannas demonstrate distinct strategies to keep nutrients in their leaves. The Brazilian savanna can be considered the wettest savanna and the least scleromorphic, whereas the South African savannas are the driest and the most scleromorphic among the three savannas. The higher occurrences of Al)accumulating species in the Brazilian savanna can be ascribed to the Al availability and acidity developed in these soils very probably after continents have drifted apart and become influenced by different rainfall conditions.

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References

Ackerly D (2009- Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. Proc Natl Acad Sci USA 106: 19699–19706.

Allen SE (1989- Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford.

Andrade LRM, Barros LMG, Echevarria GF, Amaral LIV, Cotta MG, Rossatto DR, Haridasan M, Franco AC (2011- Al)hyperaccumulators: Vochysiaceae from the Brazilian Cerrado store aluminum in their chloroplasts without apparent damage. Env Exp Bot 70: 37)42.

Araújo JF (2006- Padrões de absorção de nutrientes por espécies lenhosas comuns do cerrado sensu stricto. Universidade de Brasília, master dissertation.

Batalha MA, Silva IA, Cianciaruso MV, França H, Carvalho GH (2011- Phylogeny, traits, environment, and space in cerrado plant communities at Emas National Park. Flora 206: 9494)956.

Blomberg SP, Garland T Jr, Ives A (2003- Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57: 717–745.

BOM (2013- Available : http://www.bom.gov.au. Acessed 8 October 2013.

Bush MB, Gosling WD, Colinvaux PA (2011- Climate and vegetation chance in the lowlands of the Amazon basin. In (Bush M, Flenley J, Gosling W- Tropical rainforest responses to climatic change. pp 61)84. Springer, Berlin, Heidelberg, Germany.

Busserolles F, Fitspatrick JL, Paxton JR, Marshall NJ, Collin SP (2013- Eye)Size Variability in Deep)Sea Lanternfishes (Myctophidae-: An Ecological and Phylogenetic Study. PlosOne 8: e58519.

Cerling TE, Harris JM, MacFadden BJ, Leakey MG, et al. (1997- Global vegetation change through the Miocene/Pliocene boundary. Nature 389: 153)158.

Chapin III FS, Matson PA, Vitousek PM (2012- Plant nutrient use. In:__ Principles of terrestrial ecosystem ecology. Springer New York. pp. 229)258.

Crane P R, Friis EM, Pedersen KR (1995- The origin and early diversification of angiosperms. Nature 374: 27)33.

Dantas VL, Batalha MA (2011- Vegetation structure: Fine scale relationships with soil in a cerrado site. Flora 206: 341)346.

Delgado Mn, Gomes MRA, Báo SN, Rossatto DR (2013- Fertlisation residues alter leaf sclero) morphy in an evergreen savannah shrub (*Maprounea brasiliensis*, Euphorbiaceae-. Aust J Bot 61: 266)273.

Franco AC, Bustamante M, Caldas LS, Goldstein G, Meinzer FC, Kozovitz AR, Rundel P, Coradin VTR (2005- Leaf functional traits of neotropical savanna trees in relation to seasonal water deficit. Tree 19: 326–335.

Garland T, et al. (1993- Phylogenetic analysis of covariance by computer simulation. Syst Biol 42: 265)292.

Givnish TJ (1988- Adaptation to sun and shade: a whole plant perspective. Aust J Plant Physiol 15: 63–92.

Grace J, San José J, Meirl P, Miranda HS, Montes RA (2006-. Productivity and carbon fluxes of tropical savannas. J Biog 33: 387)400.

Habermann G, Bressan ACG (2011- Root, shoot and leaf traits of the congeneric *Styrax* species may explain their distribution patterns in the cerrado sensu lato areas in Brazil. Funct Plant Biol 38: 209)218.

Hansen DM, Galetti M (2009- The forgotten megafauna. Science 324: 42)43.

Haridasan M (1982- Aluminum accumulation by some cerrado native species of central Brazil. Plant Soil 65: 265)273.

Haridasan M (1987- Distribution and mineral nutrition of aluminium accumulating species in different plant communities of the cerrado region of central Brazil. In: San Jos JJ, Montes R, editors. La Capacidad Bioproductiva de Sabanas. I.V.I.C., Caracas, Venezuela. pp. 309)348.

Haridasan M (2008- Nutritional adaptations of native plants of the cerrado biome in acid soils. Braz J Plant Physiol 20: 183)195.

Haridasan M, Araújo GM (1988- Aluminium)accumulating species in two forest communities in the cerrado region of central Brazil. For Ecol Manage 24: 15)26.

Harmon L, Weir JT, Brock CD, Glor RE, Challenger W (2008- GEIGER: investigating evolutionary radiations. Bioinformatics 24: 129)131.

Harvey PH, Pagel MD (1991- The comparative method in evolutionary biology. Oxford: Oxford University Press.

Hedges SB, Dudley J, Kumar S (2006- TimeTree: a public knowledge)base of divergence times among organisms. Bioinformatics 22: 2971)2972.

Higgins SI, Bond WJ, Combrink H, Craine JM, February EC, Govender N, Lannas K, Moncreiff G, Trollope WSW (2012- Which traits determine shifts in the abundance of tree species in a fire)prone savanna? J Ecol 100: 1400)1410.

Hill MJ, Román MO, Schaaf CB (2010- Biogeography and dynamics of global tropical and subtropical savannas: a spatiotemporal view. In: Hill MJ, Hanan NP, editors. Ecosystem function in savannas: measurement and modeling at landscape to global scales, pp. 3)38.

Hoffmann WA, Franco AC, Moreira MZ, Haridasan M (2005- Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. Funct Ecol 19: 932)940.

INMET (2013- Available: http://www.inmet.gov.br/portal/. Accessed 10 October 2013.

Jansen S, Broadley MR, Robbrecht E, Smets E (2002- Aluminum hyperaccumulation in Angiosperms: a review of its phylogenetic significance. Bot Rev 68: 235)269.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010- Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26: 1463)1464.

Kopittke PM, Blamey FPC, Menzies NW (2008- Toxicities of soluble Al, Cu, and La include reputures to rhizodermal and root cortical cells of cowpea. Plant Soil 303: 217)227.

Lehmann CER, Anderson M, Sankaran M, et al (2014- Savanna vegetation)fire)climate relationships differ among continents. Science 343: 548)552.

Lehmann CER, Archibald SA, Hoffmann WA, Bond WJ (2011- Deciphering the distribution of the savanna biome. New Phytol 191: 197)209.

Lehmann CER, Prior LD, Bowman DMLS (2009- Fire controls population structure in four dominant tree species in a tropical savanna. Oecologia 161:505)515.

Maley J (1996- The African rain forest – main characteristics of changes in vegetation and

climate from the upper cretaceous to the quaternary. Proc Royal Soc Edinb. 104: 31)73.

Marschner H (1995- Mineral nutrition of higher plants. London: Academic Press.

Medeiros RA, Haridasan M (1985- Seasonal variations in the foliar concentrations of nutrients in some aluminium accumulating plants of the cerrado region of central Brazil. Plant Soil 88: 433)436.

Mott JJ, Williams J, Andrew MH, Gillison AN (1985- Australia savanna ecosystems. In: Tothill JC, Mott JJ, editors. Ecology and Management of the World's Savanna Australian Academy of Science, Canberra. pp. 56–82.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013- Vegan: community ecology package. http://CRAN.R)project.org/package=vegan. Accessed 4 Oct 2013

Oliveira PS, Marquis R (2002- Introduction: development of research in the Cerrados. In: Oliveira PS, Marquis RJ, editors. The Cerrados of Brazil: ecology and natural history of a neotropical savanna,Columbia University Press, Columbia. pp. 1)10.

Olsen SR, Sommers LE (1992- Phosphorus. In: Page AL, Miller RH, Keeney DR, editors. Methods of soil analysis. Part 2. American Society of Agronomy Madison, pp. 403–430.

Paradis E, Claude J, Strimmer K (2004- APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289)290.

Pavoine S, Baguette M, Bonsall MB (2010- Decomposition of trait diversity among the nodes of a phylogenetic tree. Ecol Monogr 80: 485)507.

Pipenbaher N, Skornik S, Carvalho GH, Batalha MA (2013- Phylogenetic and functional relationships in pastures and meadows from the North Adriatic Karst. Plant Ecol 214: 501)519.

R Development Core Team (2012- R: a language and environment for statistical computing. R foundation for statistical computing, Vienna. URL: http://www.r)project.org.

Ratnam J, Sankaran M, Hanan NP, Grant RC, Zambatis N (2008- Nutrient resorption patterns of plant functional groups in a tropical savanna: variation and functional significance. Oecologia 157: 141)151.

Robertson GP, Bledsoe CS, Coleman DC, Sollins P (1999- Standard soil methods for long)term ecological research, Oxford Univ., Press New York.

Robson AD (1989- Soil acidity and plant growth. Academic Press, Sydney.

Sankaran M, Hanan NP, Scholes RJ, et al (2005- Determinants of woody cover in African sa) vannas. Nature 438: 846)849.

Sarruge JR, Haag HP (1974- Análises químicas em plantas. Piracicaba – ESALQ, 54.

Shen R, Ma JF (2001- Distribution and mobility of aluminum in an Al)accumulating plant, *Fagopyrum esculentum* Moench. J Exp Bot 52: 1683)1687.

Silva CR, Hoffmann WA, Rossato DR, Haridasan M, Franco AC, Horwarth WR (2013- Can savanna become forests? A coupled analysis of nutrient stock and fire thresholds in central Brazil. Plant Soil 373: 829)842.

Simon MF, et al. (2009- recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proc Natl Acad Sci. 106: 20359)20364.

Staver AC, Bond WJ, Cramer MD, Wakeling JL (2012-. Top)down determinants of nich structure and adaptation among African Acacias. Ecology Letters. 15: 673–679

Storey BC (1995- The role of mantle plumes in continental breakup: case histories from Gondwanaland. Nature 377: 301)308.

Warton DI, Duursma RA, Falster DS, Taskinen S (2012- SMATR 3) an R package for estimation and inference about allometric lines. Methods Ecol Evol 3: 257)259.

Warton DI, Wright IJ, Falster DS, Westoby D (2006- Bivariate linefitting methods for allometry. Biol Rev 81: 269)291.

Watanabe T, Osaki M (2001- Influence of aluminum and phosphorus on growth and xylem sap composition in *Melastoma malabathricum* L. Plant Soil 237: 63)70.

Webb CO, Donoghue M J (2005- Phylomatic: tree assembly for applied phylogenetics. Mol Ecol Notes 5: 181)183.

Webb CO, et al. (2008- Phylocom: software for the analysis of phylogenetic community

structure and trait evolution. Bioinformatics 24: 2098)2100.

Webb LJ (1954- Aluminium accumulation in the Australian)New Guinea flora. Aust J Bot 2: 176)197.

Wright IJ, Westoby M (2003- Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. Functional Ecology, 17: 10)19.

Yang ZB, Rao IM, Horst WJ (2013- Interaction of aluminium and drought stress on root growth and crop yield on acid soils. Plant Soil 372: 3)25.

Zambatis N (2006- Scientific Services, Kruger National Park. Available on <http://www.tydonsafaris.com/climate.htm>. Accessed 22 august, 2013.

Tables, figures and captions

Table 1 - Average leaf concentrations of nutrients, aluminum, and specific leaf area (SLA-, in savanna plant communities in Australia, Brazil and South Africa and association between species leaf traits and phylogeny. Distinct letters between the three plant communities (in rows- represent significant differences ($p < 0.05$- by the Tukey test. Significant effects are indicated in bold type.

Leaf traits	Site			Standard ANOVA	Phylogenetic ANOVA	Phylogeny	
	Australia (*n*=43-	Brazil (*n*=40-	South Africa (*n*=27-	*p*) value		*k*	*p*)value
N (g kg)^{1}-	13.37±4.79 ^{b}	16.44±6.95 ^{b}	22.76±5.25 ^{a}	**<0.0001**	**0.003**	0.267	**0.039**
P (g kg)^{1}-	0.54±0.22 ^{c}	0.93±0.34 ^{b}	1.39±0.43 ^{a}	**<0.0001**	**0.001**	0.206	0.511
K (g kg)^{1}-	8.08±5.13 ^{a}	4.89±3.24 ^{b}	6.98±2.17 ^{a}	**0.001**	0.114	0.322	**0.026**
Ca (g kg)^{1}-	7.51±4.96 ^{b}	4.81±2.29 ^{c}	14.72±5.36 ^{a}	**<0.0001**	**0.001**	0.268	0.162
Mg (g kg)^{1}-	2.43±1.00 ^{b}	1.77±0.66 ^{c}	3.50±0.82 ^{a}	**<0.0001**	**0.001**	0.221	0.305
Al (mg kg)^{1}-	275.52±1091.98 ^{b}	2285.25±4078.58 ^{a}	658.21±2405.38 ^{b}	**0.006**	0.197	0.493	**0.003**
N:P	26.48±10.04 ^{a}	18.17±5.27 ^{b}	17.25±4.76 ^{b}	**<0.0001**	**0.009**	0.178	0.869
Ca:Mg	3.41±2.25 ^{ab}	2.73±0.98 ^{b}	4.28±1.36 ^{a}	**<0.0001**	**0.004**	0.268	0.156
SLA (g cm)^{2}-	66.06±21.25 ^{b}	99.88±37.44 ^{a}	79.13±12.15 ^{b}	**0.001**	0.127	0.430	**0.001**

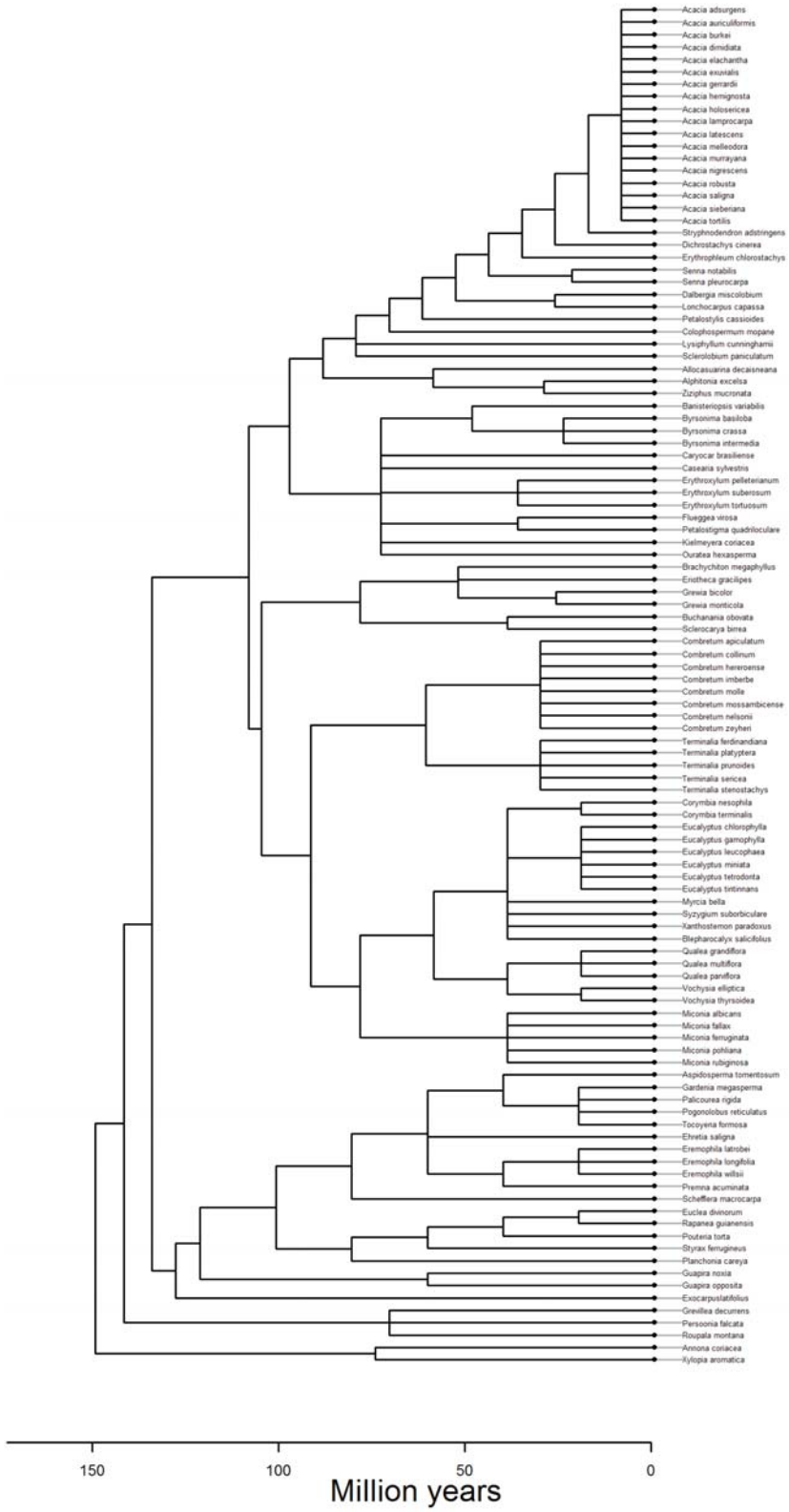

Figure 1 – Phylogenetic tree assembled for the savanna species from Australia, Brazil and South Africa.

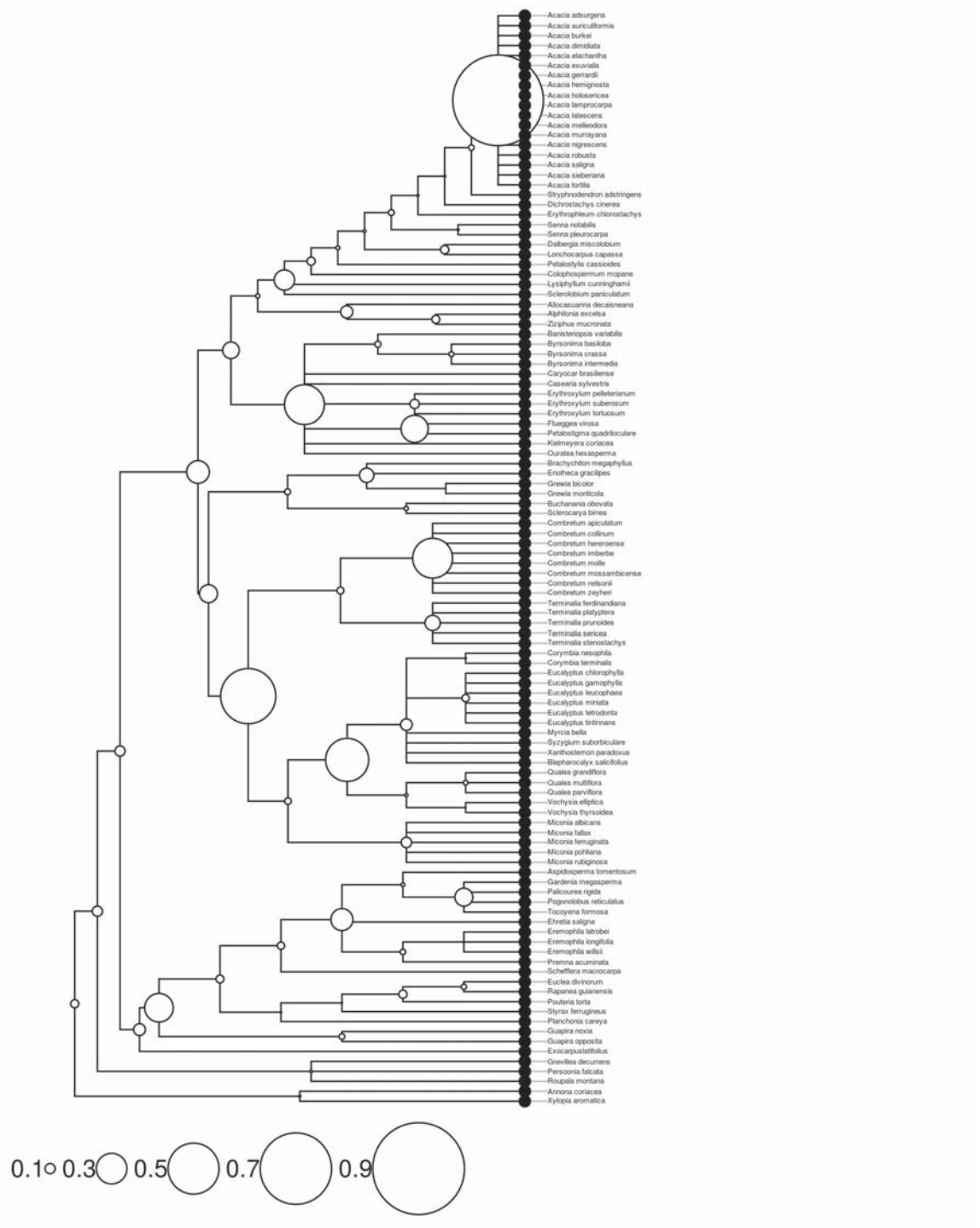

Figure 2: Decomposition of trait diversity among the nodes of the phylogenetic tree assembled for the woody species sampled from Australian, Brazilian and South African savannas.

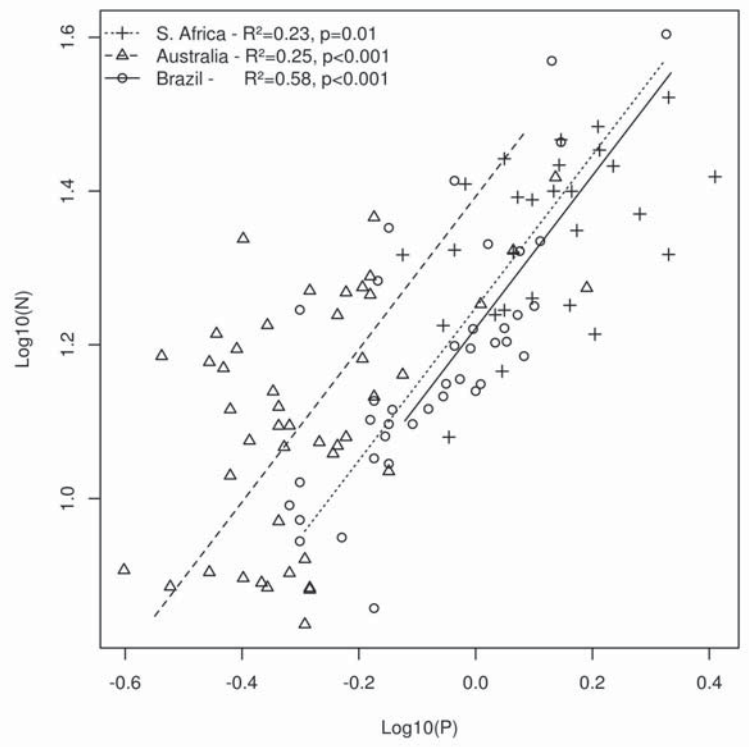

Figure 3: Standardized major axis (SMA- relationships between leaf concentrations of N and P for Australian (Intercept=1.39-, Brazilian (Intercept=1.25- and South African (Intercept=1.22- savanna's woody plant species. Australian, Brazilian and South African slopes = 0.99.

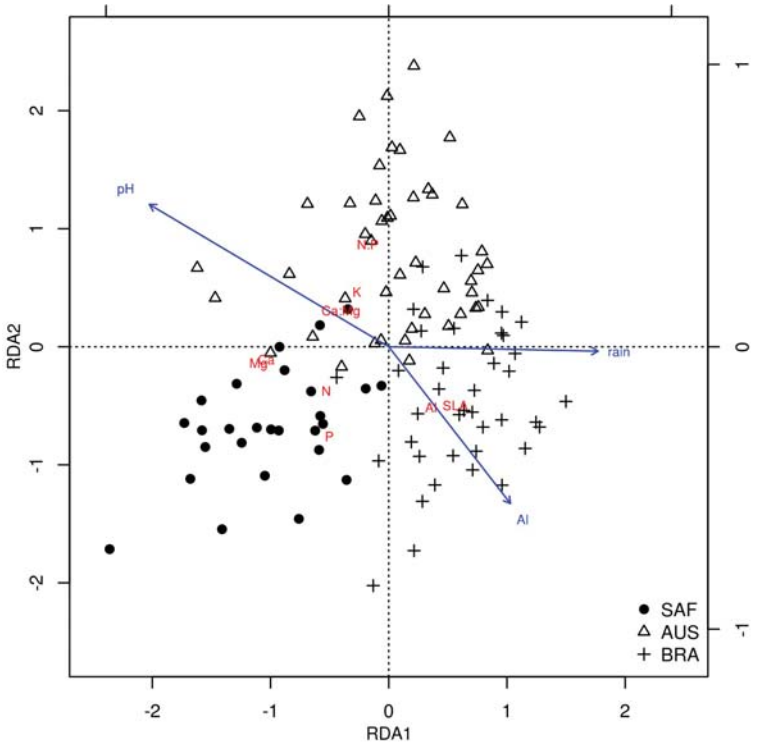

Figure 4) Redundancy analysis (RDA- of the environmental variables (soil pH, total Al concentration in the soil and total annual rainfall (rain-- related to the variations on leaf nutritional status, Al accumulation and specific leaf area SLA among the Australian, Brazilian and South African savanna plant communities.

5 - Considerações Finais

Haridasan (1982- propôs que a absorção e acúmulo de Al não interfere na absorção e concentração foliar dos demais nutrientes às espécies nativas do cerrado, não havendo diferença entre as espécies acumuladoras e não acumuladoras de Al. Entretanto, ao agrupar as espécies em grupos funcionais, nós observamos dois padrões ecofisiológicos, fenológicos e nutricionais distintos entre esses grupos. Assim, nossos resultados divergiram dos resultados apresentados por Haridasan (1982- fazendo)se necessário experimentos complementares para o melhor entendimento sobre as funções metabólicas do Al nas espécies do cerrado.

Finalmente, surpreendeu)nos a presença de algumas espécies acumuladoras de Al nas savanas Australiana e Sul Africana em solos com baixa disponibilidade de Al trocável. Estas observações são tão intrigantes quanto o acúmulo de Al por *Callisthene fasciculata*. Isso porque esta espécie se desenvolve exclusivamente em florestas semidecíduas do Brasil com solos alcalinos. Dessa forma, fica claro a necessidade de darmos continuidade aos estudos sobre nutrição mineral de espécies savânicas, principalmente em relação ao acúmulo e função do Al nessas plantas.

Appendix 1

Table 1: Mean values of the leaf traits, soil properties and annual rainfall from Australian, Brazilian and South African savannas. Leaf traits unitites: N, P, K, Ca and Mg (g kg^{-1}); Al (mg kg^{-1}) and SLA (cm^2 g^{-1}). Soil properties unities: N (%); OM (g dm^{-3}); P (mg dm^{-3}); Al, Ca, K, Mg (mmolc dm^{-3}). Annual rainfall (mm). These values are average values available on: 1 – Souza et al (unpublished data), 2 – Araújo (2006), 3 – Haridasan (1982), 4 – Medeiros and Haridasan (1985), 5 – Higgins et al (2012), 6 – Ratnam et al (2008). We used Plantminer (Carvalho et al 2010) to search for families and synonyms concerning our species list.

Reference	Country	Family	Species	Leaf Traits							Soil Properties								Annual rainfall
				N	P	K	Ca	Mg	Al	SLA	pH	N	OM	P	Al	Ca	K	Mg	
1	Australia	Fabaceae	Acacia adsurgens	13,16	0,46	10,60	4,55	1,44	29,94	39,90	5,27	0,08	1,79	0,67	0,72	6,23	4,04	6,35	471,4
1	Australia	Fabaceae	Acacia auriculiformis	23,22	0,67	5,55	6,95	2,53	39,83	94,20	5,41	0,16	58,98	12,06	8,16	6,00	2,41	9,00	1726,4
1	Australia	Fabaceae	Acacia dimidiata	15,05	0,35	4,33	4,82	2,85	60,68	74,23	5,34	0,12	30,38	6,37	4,44	6,12	3,23	7,68	1485,4
1	Australia	Fabaceae	Acacia elachantha	13,06	0,38	6,54	8,30	1,26	38,82	35,65	5,95	0,09	18,78	6,32	0,88	25,06	9,96	13,12	567,6
1	Australia	Fabaceae	Acacia hemignosta	15,65	0,39	7,59	4,79	5,42	18,34	49,16	5,09	0,08	17,03	4,39	7,36	0,96	2,12	4,09	1244,3
1	Australia	Fabaceae	Acacia holosericea	15,32	0,29	9,30	4,95	1,45	40,40	45,42	5,27	0,08	1,79	0,67	0,72	6,23	4,04	6,35	471,4
1	Australia	Fabaceae	Acacia lamprocarpa	11,89	0,41	2,62	2,66	1,63	56,10	72,36	5,27	0,08	43,93	9,29	6,07	0,60	0,67	1,75	1884,4
1	Australia	Fabaceae	Acacia latescens	6,86	0,51	2,07	1,57	2,55	83,59	66,65	5,28	0,11	63,11	10,53	9,00	0,02	0,04	1,75	2042,3
1	Australia	Fabaceae	Acacia melleodora	16,81	0,44	10,51	5,51	1,62	64,52	40,71	5,95	0,09	18,78	6,32	0,88	25,06	9,96	13,12	567,6
1	Australia	Fabaceae	Acacia murrayana	21,77	0,40	10,54	4,61	1,92	96,51	52,27	6,54	0,03	3,44	0,38	0,72	7,64	2,61	2,49	284,2
1	Australia	Casuarinaceae	Allocasuarina decaisneana	8,07	0,25	7,29	12,32	1,55	209,00	25,39	6,54	0,03	3,44	0,38	0,72	7,64	2,61	2,49	284,2
1	Australia	Rhamnaceae	Alphitonia excelsa	18,41	0,66	3,71	4,59	3,65	35,37	118,18	5,41	0,16	58,98	12,06	8,16	6,00	2,41	9,00	1726,4
1	Australia	Malvaceae	Brachychiton megaphyllus	13,57	0,67	6,97	10,14	3,07	71,48	102,02	5,33	0,11	41,86	10,05	5,65	3,59	1,85	5,38	1726,4
1	Australia	Anacardiaceae	Buchanania obovata	7,65	0,52	2,75	10,23	3,74	53,27	68,91	5,33	0,11	41,86	10,05	5,65	3,59	1,85	5,38	1726,4
1	Australia	Myrtaceae	Corymbia nesophila	14,78	0,37	4,53	1,56	2,02	46,11	60,51	5,28	0,11	63,11	10,53	9,00	0,02	0,04	1,75	2042,3
1	Australia	Myrtaceae	Corymbia terminalis	7,77	0,43	7,81	7,03	2,45	43,29	50,01	6,64	0,11	35,78	11,98	1,04	43,90	15,87	19,89	663,7
1	Australia	Boraginaceae	Ehretia saligna	18,79	1,55	20,87	10,61	1,67	32,87	116,73	6,64	0,11	35,78	11,98	1,04	43,90	15,87	19,89	663,7
1	Australia	Scrophulariaceae	Eremophila latrobei	18,54	0,60	12,14	6,52	1,92	85,06	60,82	5,27	0,08	1,79	0,67	0,72	6,23	4,04	6,35	471,4
1	Australia	Scrophulariaceae	Eremophila longifolia	15,20	0,64	12,78	10,35	1,61	106,36	40,14	6,54	0,03	3,44	0,38	0,72	7,64	2,61	2,49	284,2
1	Australia	Scrophulariaceae	Eremophila willsii	13,78	0,45	10,31	9,69	1,26	111,10	58,34	6,54	0,03	3,44	0,38	0,72	7,64	2,61	2,49	284,2
1	Australia	Fabaceae	Erythrophleum chlorostachys	18,08	0,61	5,46	5,35	1,40	30,04	71,35	5,93	0,09	35,37	9,82	3,77	22,31	8,51	11,21	1174,28
1	Australia	Myrtaceae	Eucalyptus chlorophylla	8,00	0,48	9,71	11,66	2,14	38,07	46,59	6,64	0,11	35,78	11,98	1,04	43,90	15,87	19,89	663,7
1	Australia	Myrtaceae	Eucalyptus gamophylla	10,71	0,38	5,43	10,34	2,11	86,05	35,32	6,54	0,03	3,44	0,38	0,72	7,64	2,61	2,49	284,2
1	Australia	Myrtaceae	Eucalyptus leucophaea	7,88	0,40	9,30	9,21	2,04	132,34	33,00	5,27	0,08	1,79	0,67	0,72	6,23	4,04	6,35	471,4
1	Australia	Myrtaceae	Eucalyptus miniata	12,43	0,46	2,35	2,77	1,96	80,11	64,69	5,32	0,11	48,95	10,21	6,77	2,40	1,25	4,17	1884,4
1	Australia	Myrtaceae	Eucalyptus tetrodonta	8,02	0,35	3,16	3,36	2,00	39,22	60,56	5,33	0,11	41,86	10,05	5,65	3,59	1,85	5,38	1726,4
1	Australia	Myrtaceae	Eucalyptus tintinnans	11,44	0,57	9,46	4,09	2,24	21,59	74,68	5,09	0,08	17,03	4,39	7,36	0,96	2,12	4,09	1244,3
1	Australia	Santalaceae	Exocarpus latifolius	14,49	0,75	19,74	8,71	4,73	84,16	67,41	5,41	0,16	58,98	12,06	8,16	6,00	2,41	9,00	1726,4
1	Australia	Euphorbiaceae	Flueggea virosa	17,90	1,02	29,33	14,29	5,24	24,31	74,81	6,64	0,11	35,78	11,98	1,04	43,90	15,87	19,89	663,7
1	Australia	Rubiaceae	Gardenia megasperma	8,34	0,51	12,28	6,64	3,00	43,15	64,66	6,02	0,13	47,38	12,02	4,60	24,95	9,14	14,44	1485,4
1	Australia	Proteaceae	Grevillea decurrens	12,44	0,48	3,24	3,92	2,57	98,89	97,48	5,21	0,08	34,96	7,66	6,50	0,72	1,16	2,53	1684,9
1	Australia	Fabaceae	Lysiphyllum cunninghamii	10,85	0,71	8,10	28,60	3,02	32,64	76,26	6,64	0,11	35,78	11,98	1,04	43,90	15,87	19,89	663,7
1	Australia	Proteaceae	Persoonia falcata	7,61	0,52	6,06	1,53	2,15	94,72	49,16	5,25	0,10	33,59	8,17	6,22	2,72	1,94	4,95	1485,4
1	Australia	Euphorbiaceae	Petalostigma quadriloculare	7,68	0,30	3,27	3,31	1,93	114,66	61,40	5,25	0,10	33,59	8,17	6,22	2,72	1,94	4,95	1485,4
1	Australia	Fabaceae	Petalostylis cassioides	17,51	0,44	11,26	3,46	1,37	80,32	71,11	5,90	0,05	2,61	0,52	0,72	6,94	3,33	4,42	377,80
1	Australia	Lecythidaceae	Planchonia careya	11,71	0,58	6,10	5,64	3,32	41,88	86,47	5,33	0,11	41,86	10,05	5,65	3,59	1,85	5,38	1726,4
1	Australia	Rubiaceae	Pogonolobus reticulatus	11,84	0,54	6,69	11,17	2,47	7004,76	72,32	5,26	0,06	24,75	8,05	3,14	1,19	1,30	1,75	1726,4
1	Australia	Lamiaceae	Premna acuminata	21,01	1,16	15,08	14,66	1,98	22,10	112,08	6,64	0,11	35,78	11,98	1,04	43,90	15,87	19,89	663,7
1	Australia	Fabaceae	Senna notabilis	19,45	0,66	13,03	10,23	1,75	73,53	90,58	5,27	0,08	1,79	0,67	0,72	6,23	4,04	6,35	471,4
1	Australia	Fabaceae	Senna pleurocarpa	26,17	1,37	11,71	14,90	2,08	120,46	71,92	6,54	0,03	3,44	0,38	0,72	7,64	2,61	2,49	284,2
1	Australia	Myrtaceae	Syzygium suborbiculare	11,67	0,47	3,65	11,27	3,92	163,85	70,13	5,41	0,16	58,98	12,06	8,16	6,00	2,41	9,00	1726,4
1	Australia	Combretaceae	Terminalia ferdinandiana	12,02	0,60	7,10	4,71	2,43	58,86	95,49	5,25	0,10	33,59	8,17	6,22	2,72	1,94	4,95	1485,4

1	Australia	Combretaceae	Terminalia platyptera	9,34	0,46	3,39	3,05	2,21	15,02	72,39	5,09	0,08	17,03	4,39	7,36	0,96	2,12	4,09	1244,3
1	Australia	Myrtaceae	Xanthostemon paradoxus	7,66	0,44	4,55	8,97	2,45	2299,65	66,02	5,09	0,08	17,03	4,39	7,36	0,96	2,12	4,09	1244,3
1	Brazil	Annonaceae	Annona coriacea	16,66	1,12	5,61	7,25	2,03	131,00	107,27	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
1	Brazil	Apocynaceae	Aspidosperma tomentosum	17,80	1,26	4,84	7,90	3,23	378,60	111,40	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
1	Brazil	Malpighiaceae	Banisteriopsis variabilis	15,95	1,08	4,34	6,88	3,15	223,73	165,83	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2	Brazil	Myrtaceae	Blepharocalyx salicifolius	11,10	0,71	6,80	8,60	1,90	668,00	84,05	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Malpighiaceae	Byrsonima basiloba	12,05	0,70	2,93	6,54	2,30	370,33	94,43	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2,3	Brazil	Malpighiaceae	Byrsonima crassa	10,50	0,50	5,70	7,30	1,90	209,25	55,69	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Malpighiaceae	Byrsonima intermedia	25,91	0,92	3,25	6,01	2,28	98,38	100,58	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2,3,4	Brazil	Caryocaraceae	Caryocar brasiliense	14,10	0,89	3,55	5,02	1,88	309,11	139,51	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Salicaceae	Casearia sylvestris	20,98	1,19	5,48	3,80	2,10	129,68	138,07	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2	Brazil	Fabaceae	Dalbergia miscolobium	22,50	0,71	3,70	1,50	1,00	103,00	116,01	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Malvaceae	Eriotheca gracilipes	13,80	1,00	4,08	5,48	1,80	114,15	112,04	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
1	Brazil	Erythroxylaceae	Erythroxylum pelleterianum	29,08	1,40	4,72	8,51	2,73	96,68	219,24	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
1,3	Brazil	Erythroxylaceae	Erythroxylum suberosum	21,62	1,29	6,44	7,06	1,93	75,10	126,89	4,15	0,10	21,75	1,20	7,85	0,65	0,70	0,70	1482,0
1	Brazil	Erythroxylaceae	Erythroxylum tortuosum	16,62	0,99	3,76	4,39	1,53	70,48	119,25	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2	Brazil	Nyctaginaceae	Guapira noxia	37,10	1,35	11,30	3,90	2,30	209,00	69,49	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Nyctaginaceae	Guapira opposita	40,19	2,12	5,29	4,76	1,85	91,28	151,08	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2,3	Brazil	Clusiaceae	Kielmeyera coriacea	12,50	0,78	6,20	3,30	1,70	261,00	54,00	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
4	Brazil	Melastomataceae	Miconia albicans	17,60	0,50	4,80	4,20	1,20	11000,00	82,73	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Melastomataceae	Miconia fallax	13,05	0,72	2,24	4,19	1,08	1648,25	94,02	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
3	Brazil	Melastomataceae	Miconia ferruginata	15,32	1,21	2,75	4,05	1,63	4310,00	88,38	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
2,3	Brazil	Melastomataceae	Miconia pohliana	8,90	0,59	2,66	2,88	1,13	3482,25	62,68	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Melastomataceae	Miconia rubiginosa	12,66	0,66	1,98	3,60	1,28	1373,85	107,79	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
1	Brazil	Myrtaceae	Myrcia bella	13,58	0,88	3,38	5,98	1,93	153,05	123,37	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2,4	Brazil	Ochnaceae	Ouratea hexasperma	13,40	0,67	5,55	7,45	2,05	204,00	68,77	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
3,4	Brazil	Rubiaceae	Palicourea rigida	16,00	1,13	10,85	7,91	3,00	11655,00	102,20	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Sapotaceae	Pouteria torta	15,68	0,98	2,68	1,29	0,68	179,68	128,50	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
1,2,3	Brazil	Vochysiaceae	Qualea grandiflora	14,09	1,02	3,98	2,09	1,11	4002,41	71,33	4,15	0,10	21,75	1,20	7,85	0,65	0,70	0,70	1482,0
3	Brazil	Vochysiaceae	Qualea multiflora	14,30	0,94	4,48	3,07	1,99	11460,00	75,64	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
3	Brazil	Vochysiaceae	Qualea parviflora	12,50	0,71	3,94	3,47	1,59	11201,80	83,76	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Primulaceae	Rapanea guianensis	15,80	0,92	4,72	4,74	2,25	95,65	95,61	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
3,4	Brazil	Proteaceae	Roupala montana	8,80	0,50	3,70	2,50	1,60	495,00	49,30	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
2	Brazil	Araliaceae	Schefflera macrocarpa	9,80	0,48	4,70	3,80	1,40	197,00	34,50	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
2,4	Brazil	Fabaceae	Sclerolobium paniculatum	11,28	0,67	4,20	0,95	0,70	141,00	60,38	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
2	Brazil	Fabaceae	Stryphnodendron adstringens	19,20	0,68	3,10	1,30	0,80	135,00	83,87	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Styracaceae	Styrax ferrugineus	13,08	0,83	1,98	5,00	1,60	140,25	103,23	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
1	Brazil	Rubiaceae	Tocoyena formosa	17,33	1,18	3,82	5,18	2,85	377,15	112,27	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
2,3,4	Brazil	Vochysiaceae	Vochysia elliptica	9,38	0,50	2,85	2,57	0,67	11766,40	77,49	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
2,3	Brazil	Vochysiaceae	Vochysia thyrsoidea	7,20	0,67	3,49	3,09	1,02	11429,75	41,05	4,30	0,10	31,30	1,40	6,70	0,30	1,10	0,40	1452,0
1	Brazil	Annonaceae	Xylopia aromatica	21,43	1,05	4,85	4,46	1,78	138,70	166,78	4,00	0,09	12,20	1,00	9,00	1,00	0,30	1,00	1512,0
6	S. Africa	Fabaceae	Acacia burkei	30,47	1,62	10,50	13,51	3,61	189,50	83,20	6,23	0,13	31,84	6,53	7,16	7,72	0,28	5,08	614,5
5,6	S. Africa	Fabaceae	Acacia exuvialis	25,11	1,36	5,75	11,26	2,51	47,10	81,92	6,04	0,11	25,21	3,84	5,15	6,74	0,23	4,89	583,2
5,6	S. Africa	Fabaceae	Acacia gerrardii	27,15	1,39	7,46	12,31	3,54	90,15	87,54	5,85	0,09	19,75	1,01	3,15	1,81	0,15	1,57	561,9
5,6	S. Africa	Fabaceae	Acacia nigrescens	28,40	1,63	5,82	18,11	4,66	276,90	78,67	6,04	0,11	25,21	3,84	5,15	6,74	0,23	4,89	583,2
6	S. Africa	Fabaceae	Acacia robusta	25,65	0,96	8,99	9,79	1,76	31,38	82,56	5,89	0,08	18,61	1,71	3,62	3,48	0,17	2,64	579,7
6	S. Africa	Fabaceae	Acacia saligna	20,75	0,75	6,49	10,94	3,72	57,85	84,73	5,89	0,08	18,61	1,71	3,62	3,48	0,17	2,64	579,7
6	S. Africa	Fabaceae	Acacia siberiana	21,05	0,92	2,31	20,39	4,17	362,00	80,62	5,92	0,08	17,47	2,40	4,08	5,14	0,19	3,71	559,0
6	S. Africa	Fabaceae	Acacia tortillis	33,25	2,14	3,56	16,96	2,82	239,39	83,11	6,10	0,11	27,03	4,79	5,81	8,38	0,26	6,00	578,5
6	S. Africa	Fabaceae	Colophospermum mopane	20,77	2,14	7,68	12,46	2,76	92,79	97,80	6,08	0,10	24,65	4,47	5,62	6,43	0,23	4,40	597,5
5,6	S. Africa	Combretaceae	Combretum apiculatum	18,22	1,25	7,91	10,37	4,03	98,03	93,54	6,04	0,11	25,21	3,84	5,15	6,74	0,23	4,89	583,2
5,6	S. Africa	Combretaceae	Combretum collinum	22,32	1,49	5,53	10,51	3,06	84,30	81,36	5,97	0,10	23,01	2,95	4,48	6,41	0,22	4,83	572,8
5,6	S. Africa	Combretaceae	Combretum hereroense	20,87	1,16	6,46	11,30	3,31	82,52	70,98	6,04	0,11	25,21	3,84	5,15	6,74	0,23	4,89	583,2
5,6	S. Africa	Combretaceae	Combretum imberbe	17,84	1,45	6,97	22,15	3,31	499,88	81,67	6,08	0,12	27,80	4,32	5,50	7,27	0,25	5,29	583,2
6	S. Africa	Combretaceae	Combretum molle	17,34	1,08	4,69	10,48	4,17	80,14	90,90	5,89	0,08	18,61	1,71	3,62	3,48	0,17	2,64	560,5
6	S. Africa	Combretaceae	Combretum mozambicum	26,22	2,57	10,01	27,82	3,79	621,20	87,45	5,89	0,08	18,61	1,71	3,62	3,48	0,17	2,64	578,3
6	S. Africa	Combretaceae	Combretum nelsonii	24,66	1,18	4,68	7,38	1,71	44,04	82,65	5,85	0,09	19,75	1,01	3,15	1,81	0,15	1,57	561,9
5,6	S. Africa	Combretaceae	Combretum zeyheri	16,79	0,88	5,29	15,95	3,64	12663,67	82,68	5,89	0,08	18,61	1,71	3,62	3,48	0,17	2,64	560,5
5,6	S. Africa	Fabaceae	Dichrostachys cinerea	27,67	1,12	5,11	11,90	3,21	126,82	60,73	6,04	0,11	25,21	3,84	5,15	6,74	0,23	4,89	583,2

5,6	S. Africa	Ebenaceae	Euclea divinorum	12,02	0,90	10,59	12,06	4,71	189,65	50,68	5,92	0,08	17,47	2,40	4,08	5,14	0,19	3,71	559,0
5,6	S. Africa	Malvaceae	Grewia bicolor	25,10	1,46	10,00	16,91	4,69	245,02	74,77	5,95	0,09	20,43	2,65	4,28	5,12	0,20	3,75	572,8
5,6	S. Africa	Malvaceae	Grewia monticula	27,07	1,72	9,40	17,49	3,76	243,00	66,70	6,04	0,11	25,79	3,77	5,16	4,77	0,21	3,33	588,2
5,6	S. Africa	Fabaceae	Lonchocarpus capassa	29,30	1,40	6,67	10,22	4,21	58,44	64,91	5,97	0,09	21,23	2,94	4,51	5,01	0,20	3,60	606,0
5,6	S. Africa	Anacardiaceae	Sclerocarya birrea	14,64	1,11	5,64	23,36	4,56	353,49	62,58	6,00	0,11	25,78	3,22	4,67	7,05	0,23	5,39	561,9
6	S. Africa	Combretaceae	Terminalia prunoides	16,36	1,60	7,01	17,58	2,71	323,57	70,02	5,97	0,10	23,01	2,95	4,48	6,41	0,22	4,83	591,3
5,6	S. Africa	Combretaceae	Terminalia sericea	17,58	1,12	5,85	8,42	2,66	40,07	71,18	5,89	0,08	18,61	1,71	3,62	3,48	0,17	2,64	560,5
6	S. Africa	Combretaceae	Terminalia stenostachys	23,45	1,91	9,41	12,54	3,37	28,06	75,07	5,97	0,10	23,01	2,95	4,48	6,41	0,22	4,83	614,5
5,6	S. Africa	Rhamnaceae	Ziziphus mucronata	24,47	1,25	8,59	25,23	4,18	602,80	108,36	6,23	0,13	31,84	6,53	7,16	7,72	0,28	5,08	614,5

References:

1 – Souza et al – unpublished data (original from Australian and Brazilian savanna)

2 – Araújo JF (2006) Padrões de absorção de nutrientes por espécies lenhosas comuns do cerrado sensu stricto. Universidade de Brasília, master dissertation.

3 – Haridasa M (1982) Aluminum accumulation by some cerrado native species of central Brazil. Plant Soil 65:265-273.

4 – Medeiros RA, Haridasan M (1985) Seasonal variations in the foliar concentrations of nutrients in some aluminium accumulating plants of the cerrado region of central Brazil. Plant Soil 88:433-436.

5 – Higgins SI, Bond WJ, Combrink H, Craine JM, February EC, Govender N, Lannas K, Moncreiff G, Trollope WSW (2012) Which traits determine shifts in the abundance of tree species in a fire-prone savanna? J Ecol 100:1400-1410.

6 – Ratnam J, Sankaran M, Hanan NP, Grant RC, Zambatis N (2008) Nutrient resorption patterns of plant functional groups in a tropical savanna: variation and functional significance. Oecologia 157:141-151.

Carvalho GH, Cianciaruso MV, Batalha MA (2010) Plantminer: a web tool for checking and gathering plant species taxonomic information. Environ Model Softw 25:815-816.