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Ecological strategies of Al-accumulating and non-accumulating functional groups from the cerrado *sensu stricto*

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ABSTRACT

The cerrado's flora comprises aluminum-(Al) accumulating and non-accumulating plants, which coexist on acidic and Al-rich soils with low fertility. Despite their existence, the ecological importance or biological strategies of these functional groups have been little explored. We evaluated the leaf flushing patterns of both groups throughout a year; leaf concentrations of N, P, K, Ca, Mg, S, Al, total flavonoids and polyphenols; as well as the specific leaf area (SLA) on young and mature leaves within and between the groups. In Al-accumulating plants, leaf flushed throughout the year, mainly in May and September; for non-accumulating plants, leaf flushing peaked at the dry-wet seasons transition. However, these behaviors could not be associated with strategies for building up concentrations of defense compounds in leaves of any functional groups. Al-accumulating plants showed low leaf nutrient concentrations, while non-accumulating plants accumulated more macronutrients and produced leaves with high SLA since the juvenile leaf phase. This demonstrates that the increase in SLA is slower in Al-accumulating plants that are likely to achieve SLA values comparable to the rest of the plant community only in the wet season, when sunlight capture is important for the growth of new branches.

Key words: aluminum, community, herbivory, mineral nutrition, phenology, specific leaf area.

INTRODUCTION

Aluminum (Al) is the most abundant metal and the third most common element within the Earth's crust (von Uexküll and Mutert 1995). In the soil, soluble

Al (Al³⁺) is toxic to most crops, causing physical damage to cell walls (Horst et al. 2010) and root tips (Kopittke et al. 2008). Chelation and/or exclusion of Al at the root tip seem to be critical strategies for avoiding Al in crop plants (Ryan et al. 2011) and native species (Brunner and Sperisen 2013).

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However, some species from the cerrado vegetation accumulate large amounts of Al, with no apparent damage to their metabolisms. These plants grow on the acidic and Al-rich soils from the cerrado and are known as Al-accumulating and non-accumulating species. They co-occur in the typical savanna-type vegetation, the cerrado *sensu stricto* (Haridasan 1982) and cerradão (dense cerrado) (Haridasan and Araújo 1988), and also in semi-deciduous forests (Araújo and Haridasan 1997, Haridasan and Araújo 2005) and gallery forests (Nascimento and Hay 1990).

Al-accumulating plants show 1000 to 15000 mg Al kg⁻¹ LDM (leaf dry mass), whereas non-accumulating plants store between 100 and 600 mg Al kg⁻¹ LDM (Haridasan 1982, Jansen et al. 2002a). Despite the large number of woody species in the cerrado (1000 - 2000) (Ratter et al. 2003), only some species from few families have been identified as Al-accumulating plants in the cerrado *sensu stricto*: *Miconia* sp., *Palicourea rigida*, *Qualea* sp. and *Vochysia* sp. (Haridasan 1982). Notwithstanding, Al-accumulating plants are widely distributed among the distinct vegetation types. Haridasan (1982) observed 35% of Al-accumulating species in a cerrado *sensu stricto*; Haridasan and Araújo (1988) found 18% of these plants in a cerradão growing on a dystrophic soil, but less than 8% when this forest physiognomy was growing on a mesotrophic soil, and only 7% of Al-accumulating species were observed in a semi-deciduous forest (Araújo and Haridasan 1997, Haridasan and Araújo 2005).

Similar to climates found in African and Australian savannas, the cerrado's 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, Camargo et al. 2011, Kissmann et al. 2012). Therefore, as in most tropical vegetation, leaves flush and develop during the spring-summer (Rossatto et al. 2009, Kushwaha et al. 2011, Camargo et al. 2013,

Alberton et al. 2014), as water availability and the warm weather enhance the photosynthetic rates and growth of new branches. However, we have found no comparative studies about leaf flushing in these two functional groups from the cerrado. Therefore, the first question we raise in this paper is whether these functional groups show distinct leaf phenology throughout a year.

Some cerrado woody plants flush at the end of the dry season (September), most probably because flushing just before the beginning of the wet season (October) avoids exposure of tender tissues during the peak of the wet season (January) (Rossatto et al. 2009, Alberton et al. 2014), when some herbivores, such as coleoptera (Marquis et al. 2002, Pinheiro et al. 2002), hemiptera, and isoptera (Pinheiro et al. 2002) cause significant leaf damage. Thus, the exposure of mature rather than young leaves in the wet season could avoid injuries (Mantovani and Martins 1988). 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 raise is whether a possible distinct leaf phenology between both functional groups is associated with patterns of secondary metabolite production (flavonoids and polyphenols) in juvenile or mature leaves.

Finally, coriaceous leaves are characteristic of many cerrado plants. Arens (1958) hypothesized that edaphic Al causes sclerophyllous leaves in cerrado plants, which helps them survive seasonal droughts. However, coriaceous leaves are associated with low specific leaf area (SLA, cm² g⁻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 two functional groups. Although both groups co-occur and grow on the same soils under the same

climate, with restricted phylogenetic correlations [few Rubiaceae species are Al-accumulating or occur as non-accumulating species in the cerrado *sensu stricto* (Jansen et al. 2002a)], Al has not yet been demonstrated to be essential to these plants in this way. In this paper, we investigate possible ecological strategies for these groups that might be hidden behind leaf traits.

MATERIALS AND METHODS

STUDY SITE AND SPECIES SELECTION

This study was conducted in a cerrado *sensu stricto* fragment (22°13'S 47°53'W; 610 m of altitude; 260 ha) at São José da Conquista farm, in central state of São Paulo, Brazil. This vegetation grows on an oxisol, which is sandy, acidic (pH < 4.0), low in availability of macronutrients and high in exchangeable Al (Reys et al. 2013). The climate in this region is classified as Cwa (Köppen 1948) with wet summer and dry winter. The mean monthly temperature varies between 32°C in February and 18°C in July, and the total annual rainfall is of approximately 1520 mm (Camargo et al. 2011).

Using three plots of 15 x 15 m, we selected the most representative species among plots, considering only those with at least 4 individuals among plots. Searching for Al-accumulating species, as those described by Haridasan (1982, 2008), Medeiros and Haridasan (1985) and Haridasan and Araújo (1988, 2005), we grouped them into Al-accumulating and non-accumulating species. Only those species exhibiting more than 1000 mg kg⁻¹ (mg Al kg⁻¹ LDM) were considered Al-accumulating species, while those showing less than 1000 mg kg⁻¹ were regarded as non-accumulating species. 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 I).

The small number of species in the Al-accumulating group is consistent with the few

families from the cerrado to which Al-accumulating species belong, especially in the cerrado *sensu stricto* (Haridasan 1982, Medeiros and Haridasan 1985). In the present study, Al-accumulating plants comprised 22% of the species surveyed. This percentage is very close to the average proportion of Al-accumulating species (20%) previously reported as occurring in a cerrado *sensu stricto* (Haridasan 1982) and cerrado (Haridasan and Araújo 1988). Similar to what has been previously observed in a cerrado *sensu stricto* (Haridasan 1982) and in a cerrado (Haridasan and Araújo 1988), we did not observe any congeneric species between the Al-accumulating and non-accumulating groups in the present study (Table I).

PHENOLOGICAL OBSERVATIONS

The evaluation of leaf flushing pattern of the two functional groups was carried out monthly from 2005 to 2011 by the Phenology Laboratory at Unesp, Rio Claro, Brazil. These evaluations were performed on 36 transects, measuring 25 x 2 m and 50 m distant from each other, that were established on the southern and eastern faces of the experimental fragment (Camargo et al. 2013, Alberton et al. 2014). The presence or absence of leaf flushing was registered according to Morellato et al. (2000, 2010). A total of 804 individuals, being 227 Al-accumulating and 577 non-accumulating plants, were identified in the transects.

LEAF TRAITS

Mature leaves were sampled in the second week of February (wet season) and young leaves, in the first week of September 2011 (at the peak of the dry season). 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, taken to the laboratory, and washed under deionized water.

TABLE I
List of Al-accumulating and non-accumulating species
in a cerrado *sensu stricto*, southeastern Brazil.

Family	Species	Leaf deciduousness
Al-non-accumulating		
Annonaceae	<i>Annona coriacea</i> Mart.	EG
Annonaceae	<i>Xylopia aromatica</i> (Lam.) Mart.	EG
Apocynaceae	<i>Aspidosperma tomentosum</i> Mart.	D
Caryocaraceae	<i>Caryocar brasiliensis</i> A.St.-Hil.	D
Erythroxylaceae	<i>Erythroxylum suberosum</i> A.St.-Hil.	BD
Erythroxylaceae	<i>Erythroxylum tortuosum</i> Mart.	BD
Erythroxylaceae	<i>Erythroxylum pelleterianum</i> A.St.-Hil.	D
Malpighiaceae	<i>Byrsonima basiloba</i> A.Juss.	EG
Malpighiaceae	<i>Byrsonima intermedia</i> A.Juss.	EG
Malpighiaceae	<i>Banisteriopsis variabilis</i> B.Gates	D
Malvaceae	<i>Eriotheca gracilipes</i> (K.Schum.) A.Robyns	D
Myrsinaceae	<i>Rapanea umbellata</i> Mart.	EG
Myrtaceae	<i>Myrcia bella</i> Cambess.	BD
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	BD
Rubiaceae	<i>Tocoyena formosa</i> (Cham. & Schltdl.) K.Schum.	D
Salicaceae	<i>Casearia sylvestris</i> Swartz	BD
Sapotaceae	<i>Pouteria torta</i> (Mart.) Radlk.	EG
Styracaceae	<i>Styrax ferrugineus</i> Nees & Mart.	BD
Al-accumulating		
Melastomataceae	<i>Miconia albicans</i> (Sw.) Triana	EG
Melastomataceae	<i>Miconia rubiginosa</i> (Bonpl.) A.DC.	EG
Melastomataceae	<i>Miconia fallax</i> DC.	EG
Vochysiaceae	<i>Qualea grandiflora</i> Mart.	BD

EG – evergreen, BD – brevideciduous, D - deciduous.

Five leaf discs of a known area (cm²) were excised from each of the six leaves that were 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 (cm²) and leaf dry mass (g) (Habermann and Bressan 2011).

For determining the nutritional status, leaves were oven-dried at 60°C (to avoid N volatilization) to constant dry mass, ground and digested in a nitric-perchloric acids solution. Leaf 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 measured by the micro-Kjeldahl method (Sarruge and Haag 1974, Dantas and Batalha 2011).

SECONDARY METABOLITES

The total polyphenol concentration was expressed as mg g⁻¹ LDM (Cortés-Rojas et al. 2012), which employed adaptations of the Folin-Denis colorimetric method. Leaves were dried at 50°C for 96h, ground to pass through a 20-mesh sieve (particles size ~ 840 µm), and 50 mg were extracted in a 2.5 mL methanol:water (7:3) solution, after 1h in ultrasound bath. The crude extract was diluted 10 times, and 155 µL of distilled water, 20 µL of Folin-Denis reagent, 20 µL of Na₂CO₃ saturated at 35%, and 5 µL of the crude extract were deposited into each well of a 96-well microtiter plate. Absorbance values were measured at 760 nm using a microtiter plate reader, after 30 min of incubation in the dark at room temperature.

The total flavonoid concentration, calculated as quercetin from a calibration curve and also expressed as mg LDM⁻¹ (g), was measured using adaptations (Woisky and Salatino 1998) of a protocol that also employed 96-well microtiter plates. We poured 175 µL of methanol, 5 µL of AlCl₃ at 35%, and 20 µL of the crude extract into each well, and absorbance values were measured at 425 nm using a microtiter plate reader, after 30 min of incubation in the dark, at room temperature.

STATISTICAL ANALYSES

We applied circular statistics to test for the occurrence of seasonality on leaf flushing of both functional groups (Morellato et al. 2000, 2010). The pattern of leaf flushing was described based on an activity index, which indicates the percentage of individuals manifesting a certain phenophase on each observation date (Camargo et al. 2013). To test data for the uniformity of average leaf flushing throughout the year or in a specific period of the year, we applied the Rayleigh test (Zar 1999).

A multivariate ANOVA at 5% level 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 the Al-accumulating and non-accumulating plants, and between these functional groups. To obtain normality, data were Box-cox transformed ($x^{(1-(4/2))}$) (Box and Cox 1964). We used four replications (plants) per species which resulted in 16 Al-accumulating and 72 non-accumulating plants being assessed.

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 of both groups of plants was calculated according to Teklay (2004), in such a manner that C_y denoted the concentration of a target leaf nutrient in young leaves, and C_m denoted the concentration of a target leaf nutrient in mature leaves. Positive RPC values indicate *resorption*, whereas negative values suggest *enrichment* of nutrients from the juvenile to the mature leaf phase.

We performed a multivariate ANOVA at 5% level to test for differences in RPC between the functional groups. For N, P, K, Ca and Mg, RPC is expressed in g cm⁻²; for Al, this value is expressed in mg cm⁻².

RESULTS

Both Al-accumulating and non-accumulating species flushed throughout the year (Fig. 1A-B). Non-accumulating species exhibited seasonal leaf flushing ($p < 0.001$, $Z = 0.52$, $r = 0.50$) with a peak activity in September (mean angle = 246°), while Al-accumulating plants showed a bimodal flushing pattern, with high flushing intensity in May and September (Fig. 1A-B). According to Morellato et al. (2010), the Rayleigh test is not applicable (and its usage would be incorrect) when a bimodal phenological pattern is evident. Therefore, this test was not used for evaluating phenological results of the Al-accumulating plants.

Leaves of non-accumulating plants showed higher macronutrient (except for S) concentrations in relation to the Al-accumulating plants, and while non-accumulating plants diminished their nutrient concentrations from the juvenile to the mature leaf phase (except for Ca and Mg), Al-accumulating species maintained these concentrations (except for Mg) between leaf phases (Table II). Al concentration conspicuously increased from the juvenile to the mature leaf phase of Al-accumulating plants, whereas it remained unchanged between leaf phases in non-accumulating plants (Table II).

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

In non-accumulating plants, total leaf flavonoids concentration was higher than in Al-accumulating plants, and while non-accumulating plants decreased total leaf flavonoids concentration from the juvenile to the mature leaf phase, this compound had similar concentrations between leaf

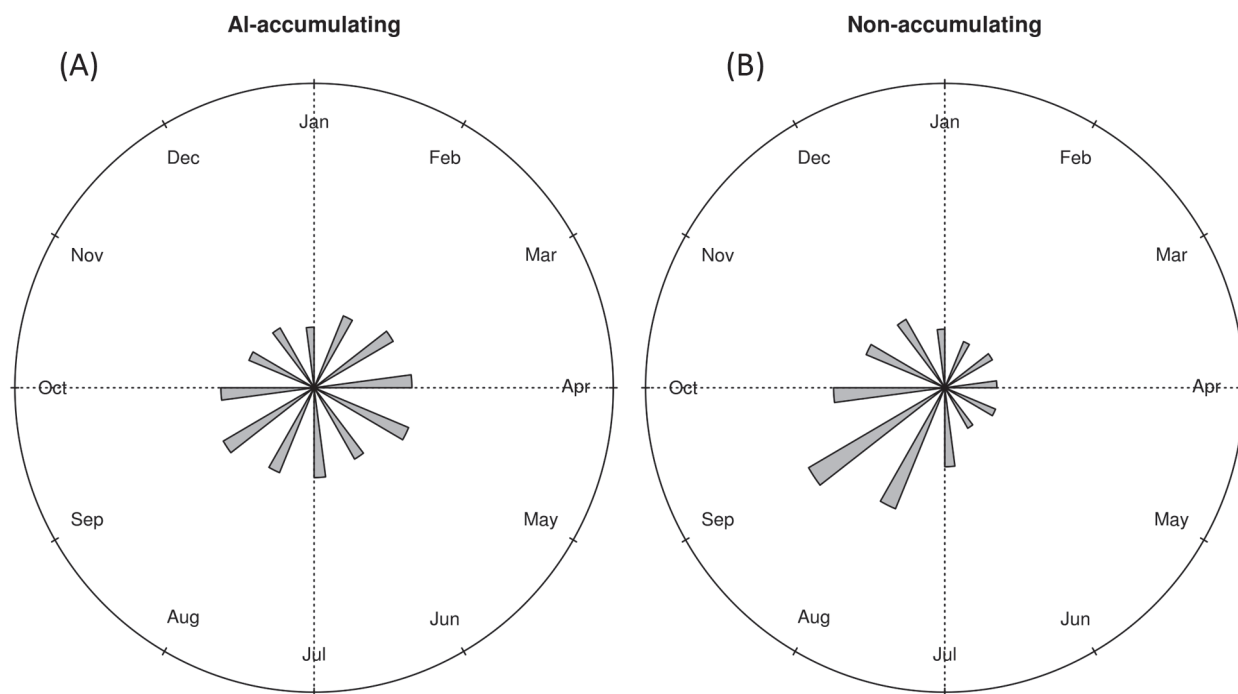


Fig. 1 - Average annual leaf-flushing distribution in **(A)** Al-accumulating and **(B)** non-accumulating plants between 2005 and 2011, in a cerrado *sensu stricto*, southeastern Brazil.

phases in Al-accumulating plants. Total polyphenols concentration, on the contrary, was higher in Al-accumulating in relation to non-accumulating plants, and for both groups this compound showed similar concentrations between leaf phases (Table II).

As expected, Al-accumulating plants exhibited Al enrichment of more than 100% from the juvenile to the mature leaf phase, whereas non-accumulating plants showed Al resorption of 14% between leaf phases. In addition, Al-accumulating plants showed a seven-fold higher N resorption when compared to the non-accumulating plants (Table III).

DISCUSSION

For cerrado species, leaf flushing generally occurs at the transition from the dry to the wet season (Rossatto et al. 2009, Alberton et al. 2014). However, non-accumulating plants flushed at the end of the dry season (September), while Al-accumulating plants flushed throughout the year, but more intensely at

the end of both the dry (September) and the wet (April/May) season. In addition, in the present study, Al-accumulating plants were composed of evergreen and semi-deciduous species, and non-accumulating plants consisted of evergreen, deciduous and semi-deciduous species. This shows that despite the diverse phenological behavior of cerrado species, Al-accumulating and non-accumulating species flush differently (Fig. 1A-B), and future studies should address specific issues regarding the leaf ecological strategies for both functional groups.

For tropical plants, young leaves generally suffer higher rates of herbivory, requiring greater diversity of secondary metabolites (Kursar et al. 1999) in comparison to mature leaves (Coley and Barone 1996). In the cerrado, insects seem to prefer young leaves whereas pathogens more often attack mature leaves (Marquis et al. 2001). For instance, Varanda et al. (2008) demonstrated caterpillars' preference for young expanding leaves of *Xylopia*

TABLE II
Mean values (\pm 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-accumulating and non-accumulating plants in a cerrado *sensu stricto*, southeastern Brazil.

Traits	Phenophase	Al-non-accumulating		Al-accumulating	
N (g kg ⁻¹)	Y	24.76 \pm 11.07	aA	16.45 \pm 4.52	aB
	M	19.03 \pm 8.41	bA	13.33 \pm 1.52	aB
P (g kg ⁻¹)	Y	2.04 \pm 1.43	aA	0.78 \pm 0.30	aB
	M	1.12 \pm 0.34	bA	0.73 \pm 0.09	aB
K (g kg ⁻¹)	Y	8.39 \pm 5.85	aA	2.64 \pm 1.22	aB
	M	4.19 \pm 1.73	bA	2.19 \pm 0.44	aB
Ca (g kg ⁻¹)	Y	5.75 \pm 3.29	aA	3.11 \pm 0.88	aB
	M	5.62 \pm 1.97	aA	3.58 \pm 0.71	aB
Mg (g kg ⁻¹)	Y	2.23 \pm 0.77	aA	1.57 \pm 0.42	aB
	M	2.09 \pm 0.70	aA	1.22 \pm 0.20	bB
S (g kg ⁻¹)	Y	1.09 \pm 0.56	aA	0.82 \pm 0.18	aA
	M	0.83 \pm 0.34	bA	0.92 \pm 0.31	aA
Al (mg kg ⁻¹)	Y	200.06 \pm 138.49	aB	1546.60 \pm 139.49	bA
	M	181.88 \pm 140.77	aB	4867.36 \pm 1782.85	aA
SLA (cm ² g ⁻¹)	Y	132.98 \pm 50.23	aA	88.11 \pm 13.85	bB
	M	122.23 \pm 32.03	aA	145.54 \pm 62.01	aA
Flavonoids (mg g ⁻¹)	Y	5.11 \pm 2.41	aA	2.10 \pm 0.41	aB
	M	3.66 \pm 2.81	bA	1.79 \pm 0.23	aB
Polyphenols (mg g ⁻¹)	Y	6.48 \pm 1.88	aB	7.53 \pm 0.08	aA
	M	6.02 \pm 1.95	aB	7.81 \pm 0.53	aA

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

TABLE III
Mean Relative Percentage Change (\pm sd) in the concentration of N, P, K, Ca, Mg, S and Al in Al-accumulating and non-accumulating species in a cerrado *sensu stricto*, southeastern Brazil. Positive values show resorption whereas negative values show enrichment of nutrients from the juvenile to the mature leaf phase. N, P, K, Ca, Mg and S are expressed in g cm⁻² and Al is expressed in mg cm⁻².

Traits	Al-non-accumulating	Al-accumulating	p
N	6.86 \pm 51.91	43.45 \pm 16.78	<0.02
P	20.78 \pm 43.28	33.39 \pm 19.14	ns
K	23.30 \pm 53.58	32.40 \pm 33.95	ns
Ca	-87.44 \pm 245.57	7.39 \pm 56.62	ns
Mg	-19.45 \pm 101.05	42.93 \pm 28.35	<0.04
S	7.49 \pm 43.25	20.80 \pm 31.14	ns
Al	14.24 \pm 54.18	-101.18 \pm 72.27	<0.001

aromatica, a non-accumulating species from the cerrado, as compared to their tannin-enriched mature leaves. Thus, secondary metabolites have

frequently been associated with leaf protection against herbivores and 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-Alvim 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. The total leaf polyphenols, which include 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 any of the plant groups, weakening any suggestion of escape strategy involving these compounds during leaf development. Indeed, although high leaf Al concentration has been demonstrated to be associated with low leaf tannin concentration in *Qualea parviflora*, an Al-accumulating species from the cerrado, leaf tannin concentration does not influence the herbivory leaf damage in this species (Gonçalves-Alvim et al. 2011). In addition, colonies of *Atta sexdens* (Hymenoptera: Formicidae) significantly declined when the ants were fed with mature leaves of *Q. parviflora* due to the Al accumulation in the ants' body (Rébula et al. 2008). Nascimento et al. (1990) and Nascimento (1987) also observed lower herbivory rates in two Al-accumulating species (*Vochysia rufa* and *V. divergens*) in relation to *Curatella americana*, a non-accumulating species from the cerrado. These authors ascribed ant's death and the low herbivory rate to Al toxicity, contrasting with the theory proposed by Arens (1958), who suggested that Al accumulation in leaves of cerrado plants help them survive seasonal droughts. Therefore, our results also show that Al accumulation is not associated with strategies for building up concentrations of defense compounds in leaves, thus weakening any suggestion of involvement of secondary metabolites in herbivory escape strategies for any of these functional groups.

Non-accumulating plants store more macronutrients (except for S) than Al-accumulating plants, and produce leaves with high SLA since the juvenile leaf phase. Therefore, in relation to the Al-accumulating plants, the non-accumulating plants emit new leaves at the end of the dry season which rapidly optimize light capture for photosynthesis. Species possessing high SLA, such as forest species (Hoffmann et al. 2005, Habermann and Bressan 2011, Rossatto et al. 2013) and deciduous savanna

species (Franco et al. 2005) show high leaf nutrient contents, such as N and P that are closely related to photosynthetic activities (Reich et al. 2009). This strategy, which is performed by the non-accumulating plants, implies low leaf construction costs (Franco et al. 2005).

Al-accumulating plants store less macronutrient than non-accumulating plants and gradually increase SLA from the juvenile to the mature leaf phase. In contrast to non-accumulating plants, the astonishing Al enrichment from the juvenile to the mature leaf phase in Al-accumulating plants could be associated with competition against macronutrients for allocation in the mesophyll of these plants, as described for many native species (Brunner and Sperisen 2013). Competition among nutrients can be detected only by studies of nutrient absorption dynamics, which are difficult to perform in the field. However, although N, P, K, Ca and S concentrations were lower in the leaves of Al-accumulating plants, these values remained unchanged between leaf phases, indicating absence of competition between Al and macronutrients in these plants.

Thus, the lack of metabolic resources (macronutrients, especially N and P) in Al-accumulating plants does not seem to support a high SLA since the juvenile leaf phase. This group of plants flushes throughout the year and gradually increases SLA from the juvenile to the mature leaf phase, and are likely to match 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 that exhibited by evergreen savanna species (Franco et al. 2005, Hoffmann et al. 2005, Habermann and Bressan 2011), which have high leaf construction costs involved in the development of non-photosynthetic tissues, such as fibers and cell walls rather than chloroplasts. In fact, the sclerophyllous leaf morphology in *Q. parviflora* is associated with low supply rates of macronutrient to their mesophyll (Gonçalves-Alvim et al. 2006).

One may still argue that there is no phylogenetic context between the two groups of plants studied here, since the Al accumulation trait is restricted to three families occurring in the cerrado *sensu stricto*: Melastomataceae (*Myconia* sp.), Rubiaceae (*Palicourea rigida*) and Vochysiaceae (*Qualea* sp., *Vochysia* sp., *Salvertia convallariodora*) (Haridasan 1982, 1987, 2008, Jansen et al. 2002a, b, 2003, 2004). However, when studying herbivory defense traits among 61 species from 29 families in a cerrado plant community, Silva and Batalha (2011) found that phylogeny does 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 Araújo 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. Al-accumulating species might have survived some environmental filters that act over cerrado species, while non-accumulating ancestors have not, since the cerrado imposes many filters on species, guilds and functional groups (Silva and Batalha 2006).

In conclusion, flushing at the dry-wet season transition for non-accumulating plants, and throughout the year for Al-accumulating plants can not be associated with strategies for building up concentrations of defense compounds in leaves of either of the groups. In addition, non-accumulating plants accumulate more macronutrients and produce leaves with high SLA as of the juvenile leaf phase, while leaves of Al-accumulating plants show a low level of nutrient status. This demonstrates that the increase in SLA is slower in Al-accumulating plants that are likely to achieve SLA values comparable to the rest of the plant community only in the wet season, when sunlight capture is important for the growth of new branches.

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RESUMO

A flora do cerrado é composta por espécies acumuladoras e não acumuladoras de alumínio (Al), coexistentes em solos ácidos, ricos em Al e com baixa fertilidade. Apesar da coexistência desses grupos funcionais, sua importância ecológica e suas estratégias biológicas são pouco conhecidas. Nós estudamos os padrões fenológicos de brotação foliar de ambos os grupos ao longo do ano, as concentrações foliares de N, P, K, Ca, Mg, S, Al, flavonoides totais e polifenóis e a área foliar específica (AFE) em folhas jovens e maduras, dentro e entre os grupos. Para as espécies acumuladoras de Al as brotações foliares foram distribuídas ao longo do ano, com maior intensidade entre maio e setembro; para as espécies não acumuladoras de Al observamos um pico de brotação durante a transição das estações seca e chuvosa. No entanto, estes comportamentos não podem ser associados às estratégias ligadas ao acúmulo foliar de metabólitos secundários por estes grupos funcionais. As espécies acumuladoras de Al apresentaram menores concentrações de nutrientes foliares, enquanto que as não acumuladoras concentraram mais macronutrientes e produziram folhas com alta AFE desde a fase juvenil.

Isso demonstra que o aumento de AFE é mais lento nas espécies acumuladoras de Al, que devem atingir valores de AFE comparáveis ao resto da comunidade apenas na estação úmida, quando a captação de luz é importante para o crescimento de novos ramos.

Palavras-chave: alumínio, comunidade, herbivoria, nutrição mineral, fenologia, área foliar específica.

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