

Defense syndromes against herbivory in a cerrado plant community

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Abstract Plants have traits against herbivory that may occur together and increase defense efficiency. We tested whether there are defense syndromes in a cerrado community and, if so, whether there is a phylogenetic signal in them. We measured nine defense traits from a woodland cerrado community in southeastern Brazil. We tested the correlation between all pairs of traits and grouped the species into defense syndromes according to their traits. Most pairwise correlations of traits were complementary. Plants with lower specific leaf area also presented tougher leaves, with low nitrogen, more trichomes, and tannins. We found five syndromes: two with low defenses and high nutritional quality, two with high defenses and low nutritional quality, and one with traits compensating each other. There were two predominant strategies against herbivory in cerrado: “tolerance” and “low nutritional quality” syndromes. Phylogeny did not determine the suite of traits species presented. We argue that herbivory exerts significant selection pressure on these plant defense traits.

Keywords Defense traits · Herbivores · Savanna · Trade-off

Introduction

Plants have two defense strategies against herbivory: tolerance, the ability to maintain fitness independently of herbivory damage; and resistance, the possession of traits that avoid or deter herbivory (Mauricio 2000). It is more difficult for plants growing in poor soils to replace biomass lost to herbivores, so resistance should be the predominant defense strategy in such situations (Fine et al. 2006). Defense traits can be structural (such as trichomes, spines, and leaf toughness), chemical, or nutritional (Agrawal and Fishbein 2006; Hanley et al. 2007). Structural defenses are morphological or anatomical traits that benefit the plant by preventing herbivory, such as protuberances or increased cell wall toughness (Craine et al. 2003; Hanley et al. 2007). Nutritional defenses are traits that reduce the absorption of nutrients by herbivores, especially nitrogen that tends to be diluted in materials of low nutritional value (While 1993; Agrawal and Fishbein 2006). Chemical defenses are toxic or repulsive compounds or enzyme inhibitors (Thaler et al. 1999; Craine et al. 2003). Structural and chemical traits have investment costs along with defense benefits and thus are under

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selection (Craine et al. 2003; Hanley et al. 2007; Núñez-Farfán et al. 2007). These traits may occur together and complement one another, increasing defense efficiency; for example, chemical and physical traits provide a greater level of defense when they occur together (Berenbaum et al. 1991). Thus, we expect some defense traits against herbivory to co-occur in a given species.

Whereas suites of traits against several kinds of herbivores tend to be favored because they decrease costs associated with defense, general responses should be present in the whole community (Núñez-Farfán et al. 2007). On the other hand, since defense against specific herbivores is more costly and can reduce resistance against other herbivores and pathogens, these unique defenses should be induced only in the presence of the specific herbivore (Thaler et al. 1999; Forgyce and Malcom 2000; Núñez-Farfán et al. 2007). Two or more traits may be positively correlated, resulting in suites of covarying traits that could define “defense syndromes” (Agrawal and Fishbein 2006). There are distinct co-occurring guilds of herbivores and their diffuse herbivory should favor selection for several defense strategies, but also for the ability to defend themselves against all guilds, and thus a level of general defenses is expected in most species too (Maddox and Root 1990). Cerrado (Brazilian savanna) plants grow in poor soils (Haridasan 2000), and their leaf replacement costs should be high (Fine et al. 2006). Herbivory damage should be minimized by cerrado plants. This can be achieved by both leaf phenology—that is, producing new leaves when herbivores are less abundant—and leaf traits, such as toughness, low levels of nitrogen and water, and high levels of phenolic compounds (Marquis et al. 2002). Herbivory has an important role in cerrado ecology, either directly by influencing plant growth and reproduction, or indirectly by the interaction with abiotic factors (Marquis et al. 2002). The cerrado has few and mostly rare mammalian herbivores, but an abundance of herbivorous insects (Marquis et al. 2002; Costa et al. 2008). Although the South American megafauna are extinct, some plant adaptations may be a legacy of past ecological interactions (Guimarães et al. 2008). Past herbivory interactions can also lead to anachronistic defenses (Bond and Silander 2007). Thus, defense traits in cerrado may be responses to both extinct large mammals (Bond and Silander 2007; Guimarães

et al. 2008) and current insect herbivores, particularly leaf-cutter ants (Costa et al. 2008). Herbivory restricts plant distribution, acting as an environmental filter (Harley 2003). Environmental filters tend to select species with similar traits that allow them to survive certain pressures (Fukami et al. 2005). Species with low investment in resistance are likely to be excluded by herbivory. Thus, we expect herbivory to be a strong environmental filter in cerrado, selecting for species with high investment in resistance traits.

Functional traits are generally phylogenetically conserved on plant lineages (Ackerly 2003). If so, phylogenetic proximity of two species and the traits inherited from common ancestry should reveal similar responses to environmental processes (Webb et al. 2002; Núñez-Farfán et al. 2007). However, strong selection pressure can lead to adaptive convergence in two distantly related species such that they respond similarly to the selection pressure (Webb et al. 2002; Núñez-Farfán et al. 2007). At lower phylogenetic levels, defense traits appear to be convergent, whereas, at higher levels, they appear to be more conserved (Agrawal and Fishbein 2006; Fine et al. 2006). For example, in the genus *Asclepias*, defense traits are not congruent with phylogeny, indicating phylogenetic overdispersion (Agrawal and Fishbein 2006). However, different genera tend to present different suites of defense traits, indicating phylogenetic clustering (Fine et al. 2006). Thus, at the community level, defense syndromes can be either conserved or convergent, depending on how traits are distributed on phylogeny.

Although defense syndromes have been examined at the genus level (Agrawal and Fishbein 2006; Becerra 2007) and between pairs of genera in forest tree communities (Fine et al. 2006), there are no studies at the community level. In the Brazilian cerrado, herbivory surveys have focused on one species (e.g., Varanda and Pais 2006) or one defense trait, such as the presence of extra-floral nectaries in ant associations (e.g., Oliveira 1997; Oliveira and Freitas 2004) or the presence of latex (e.g., Diniz et al. 1999). To add further insights to defense syndrome theory, it is necessary to examine defense traits from several species and relate this to the ecological and evolutionary constraints imposed by savanna environments.

If defense syndromes are phylogenetically overdispersed, then herbivory is likely the dominant

selective pressure; if, however, defense syndromes are phylogenetically conserved, a phylogenetic signal is likely and thus common ancestry may explain the association (Agrawal and Fishbein 2006). Because the cerrado is a nutrient-limited community, we expect cerrado plants to invest heavily in structural defenses, comprising mainly carbohydrates, and invest little in chemical defense, especially nitrogen compounds (Haridasan 2000; Craine et al. 2003).

In this study, we tested the complementarity of species defense traits and the influence of phylogeny on the distribution of these traits in woody plants. We address the following questions: (i) Do cerrado plant species present similar suites of traits that characterize defense syndromes? if so, (ii) What are these syndromes? and (iii) Is there a phylogenetic signal in herbivory defense syndromes?

Methods

Study area and sampling

We carried out this study in the campus of the Federal University of São Carlos, southeastern Brazil (21°58′05.3″S, 47°52′10.1″W, 815–890 m a.s.l.; Santos et al. 1999). Regional climate is seasonal, with dry winter and wet summer, defined as Cwa (Köppen 1931). The study site is located in the northeastern portion of the campus and is covered by woodland cerrado, on Oxisol (Santos et al. 1999).

We placed 100 contiguous plots of 5 × 5 m, in which we sampled all individuals belonging to the woody component with a stem diameter at soil level equal to or greater than 3 cm (Secretaria do Estado do Meio Ambiente 1997). We identified individuals to species level (Carvalho et al. 2010). For each species in the sample, we randomly selected 10 individuals to measure the traits (Cornelissen et al. 2003). If there were fewer than 10 individuals of a species in the sample, we searched for additional individuals nearby.

Defense traits

From each individual, we collected undamaged expanded leaves. We kept the leaves in a cooler to avoid water loss or deterioration, and measured the following traits as soon after collection as possible:

carbon:nitrogen ratio, specific leaf area, water content, latex content, trichome density, toughness, presence of alkaloid, terpenoid, and tannin (Agrawal and Fishbein 2006). Nutritional quality may be a defense, because low nutritional quality makes herbivory less likely (Mattson 1980). Nitrogen is a limiting nutrient to herbivores, and low levels of nitrogen increases feeding time and, consequently, the exposure to natural enemies and energy expenditure on consuming and processing food (Lavoie and Oberhauser 2004; Craine 2009). Plants with high nitrogen content, specific leaf area, and water content are more susceptible to herbivory (Weiher et al. 1999; Coley et al. 2006). In addition, plants with more structural defenses, such as cell wall toughness, have more mass per leaf area and consequently low specific leaf areas (Weiher et al. 1999; Cornelissen et al. 2003). Low specific leaf areas represent high investment in structural defenses, whereas high specific leaf areas indicate greater palatability (Weiher et al. 1999; Cornelissen et al. 2003). Since high water content increases the likelihood of herbivory, low water content may be a defense trait (Scriber and Slansky 1981; Coley et al. 2006). Latex reduces herbivory and preference: many herbivores die mired in latex, and experimental removal or addition of latex increases or decreases herbivory, respectively (Agrawal and Kono 2009). Trichome density has negative effects on herbivorous insect oviposition, preference, survivorship, and growth rate (Haddad and Hicks 2000; Agrawal and Fishbein 2006). High levels of leaf toughness reduce attack by herbivores, consumption of leaves, and herbivore growth rate (Pérez-Harguindeguy et al. 2003; Agrawal and Fishbein 2006). Alkaloids are chemicals containing nitrogen that have a range of toxic effects on herbivores (Craine 2009). Terpenoids and tannins are organic nitrogen-free chemical defenses that bind with protein, reducing nitrogen availability to herbivores (Bergvall and Leimar 2005; Craine 2009). Tannins also decrease preference by mammal herbivores (Bergvall and Leimar 2005; Craine 2009).

We measured carbon (C) and nitrogen (N) concentration in leaves and calculated the C:N ratio as an indicator of plant nutritional quality. We collected leaf samples from five individuals from each species. Analyzes were conducted using an elemental CHNS–O analyzer (CE Instruments/EA 1110) to determine carbon and nitrogen concentration. To measure

specific leaf area and water content, we collected two leaves from each individual, kept them in a cooler and weighed their fresh masses. We scanned the leaves and determined leaf area using the ImageJ 1.33 software (Rasband 2004). We oven-dried the leaves at 75°C over 72 h to obtain dry mass. Dividing leaf area by dry mass, we obtained specific leaf area (Cornelissen et al. 2003). Leaf water content was estimated as the difference between fresh and dry mass, divided by leaf area (Agrawal and Fishbein 2006). To measure latex content, we collected the latex on filter paper from the leaf base. Samples were oven-dried at 75°C for 24 h and then weighed. We counted the number of trichomes in a 6 mm diameter circle with a dissecting microscope, near the leaf tip, on both sides of the leaf (Agrawal and Fishbein 2006). We used a penetrometer (dynamometer DFE 010, Chatillon, with a cone tip) to measure leaf toughness in 10 leaves per species. We pushed the probe of the penetrometer through the leaf and recorded the maximum force required to penetrate it. We measured toughness either side of the mid-rib and meaned the data (Agrawal and Fishbein 2006).

We estimated chemical defenses in leaves after the methods of Falkenberg et al. (2003). We measured alkaloid, terpenoid and tannin presence. We used three assays, Mayer, Dragendorff, and Wagner reactions, to determine the presence of alkaloids and those samples that reacted to at least two out of the three methods were accepted (Falkenberg et al. 2003). We used Liebermann–Burchard and Salkowisk reactions to test the presence of terpenoids and a ferric chloride reaction to determine the presence of tannins (Falkenberg et al. 2003).

We constructed a matrix with the mean of each trait for each species; when necessary, we log-transformed the variables to achieve normality; we standardized all defense traits to zero mean and unit variance. We also constructed a matrix with the phylogenetically independent contrasts (PICs) of traits, which corrects each variable for phylogenetic dependence by scaling the contrasts by their standard deviation related to phylogenetic distances, assuming a Brownian model of evolution (Felsenstein 1985). We applied a correlation test with Spearman's coefficient to all pairs of traits and to all pairs of PICs of traits.

We constructed a Euclidean distance matrix based on mean trait values for the species. We used K-means multivariate clustering (Legendre and Legendre 1998)

to separate the species into groups of defense traits, such that species within each group had more similar defense traits than to species in other groups. The number of groups varied from two to five, and we selected the best clustering number with the pseudo *F*-statistic (Calinski and Harabasz 1974). We ordinated the groups using principal component analysis and observed the relationship between groups in relation to the traits (Legendre and Legendre 1998). We carried out all analyzes in R (R Development Core Team 2009).

Phylogenetic analysis

We constructed a phylogenetic tree for the species in the sample using the Phylomatic software (Webb and Donoghue 2005). The lengths of the branches were estimated from maximum ages determined for genus, families, orders, and superior clades (Davies et al. 2004). We fixed the root and all dated nodes, and extrapolated branch lengths by placing the non-dated nodes evenly between dated nodes or between dated nodes and terminals (species), using the Bladj algorithm in the Phylomatic software (Webb and Donoghue 2005). We calculated phylogenetic distances among all pairs of species using the Phylocom 4.01b software (Webb et al. 2008). We did a Mantel correlogram with 999 randomisations, correlating the trait matrix to the phylogenetic distance matrix. We calculated the Mantel statistic for each distance class and we tested for significance by permutations, using Bonferroni's correction to test for global significance (Legendre and Fortim 1989). We also did a Mantel test (Manly 2000) with 999 randomisations for the entire matrix.

Results

We assessed 2,062 individuals, belonging to 61 species and 29 families, for their defense traits (Tables 1, 2). Spearman's coefficient between the pairs of traits and between PICs were low, with the highest values around 0.6 (Table 3), that is, the strength of complementarity among traits was low. We found significant negative correlations between C:N and specific leaf area, specific leaf area and water, specific leaf area and trichomes, specific leaf area and toughness, specific leaf area and tannins, and

Table 1 The woody species sampled in cerrado at Federal University of São Carlos (21°58′05.3″S, 47°52′10.1″W)

Family	Species	Individuals
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	10 (9)
Annonaceae	<i>Annona coriacea</i> Mart.	10 (8)
Annonaceae	<i>Annona crassiflora</i> Mart.	10 (9)
Annonaceae	<i>Xylopia frutescens</i> Aubl.	10 (8)
Araliaceae	<i>Schefflera macrocarpa</i> (Cham. & Schltdl.) Frodin	10 (6)
Araliaceae	<i>Schefflera vinosa</i> (Cham. & Schltdl.) Frodin & Fiaschi	10 (0)
Asteraceae	<i>Gochnatia pulchra</i> Cabrera	10 (0)
Asteraceae	<i>Piptocarpha rotundifolia</i> (Less.) Baker	10 (0)
Bignoniaceae	<i>Tabebuia ochracea</i> (Cham.) Standl.	10 (0)
Celastraceae	<i>Plenckia populnea</i> Reissek	10 (0)
Clusiaceae	<i>Kielmeyera coriacea</i> Mart. & Zucc.	10 (1)
Clusiaceae	<i>Kielmeyera grandiflora</i> (Wawra) Saddi	10 (0)
Connaraceae	<i>Connarus suberosus</i> Planch.	10 (9)
Dilleniaceae	<i>Davilla elliptica</i> A. St.-Hil.	10 (6)
Dilleniaceae	<i>Davilla rugosa</i> Poir.	10 (9)
Ebenaceae	<i>Diospyros hispida</i> A. DC.	10 (0)
Erythroxylaceae	<i>Erythroxylum cuneifolium</i> (Mart.) O.E. Schulz	10 (4)
Erythroxylaceae	<i>Erythroxylum suberosum</i> A. St.-Hil.	10 (0)
Erythroxylaceae	<i>Erythroxylum tortuosum</i> Mart.	10 (0)
Euphorbiaceae	<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	10 (1)
Fabaceae	<i>Acosmium dasycarpum</i> (Vogel) Yakovlev	10 (0)
Fabaceae	<i>Acosmium subelegans</i> (Mohlenbr.) Yakovlev	10 (6)
Fabaceae	<i>Bauhinia rufa</i> (Bong.) Steud.	10 (0)
Fabaceae	<i>Dalbergia miscolobium</i> Benth.	10 (0)
Fabaceae	<i>Dimorphandra mollis</i> Benth.	10 (3)
Fabaceae	<i>Machaerium acutifolium</i> Vogel	10 (6)
Fabaceae	<i>Stryphnodendron adstringens</i> (Mart.) Coville	10 (0)
Fabaceae	<i>Stryphnodendron obovatum</i> Benth.	10 (1)
Lacistemataceae	<i>Lacistema</i> sp. Sw.	10 (9)
Lauraceae	<i>Ocotea pulchella</i> (Nees) Mez	10 (0)
Malpighiaceae	<i>Banisteriopsis megaphylla</i> (A. Juss.) B. Gates	10 (9)
Malpighiaceae	<i>Byrsonima coccolobifolia</i> Kunth	10 (0)
Malpighiaceae	<i>Byrsonima verbascifolia</i> (L.) DC.	2 (0)
Malpighiaceae	<i>Heteropterys umbellata</i> A. Juss.	10 (6)
Melastomataceae	<i>Leandra lacunosa</i> Cogn.	10 (7)
Melastomataceae	<i>Miconia albicans</i> (Sw.) Triana	10 (0)
Melastomataceae	<i>Miconia ligustroides</i> (DC.) Naudin	10 (0)
Melastomataceae	<i>Miconia rubiginosa</i> (Bonpl.) DC.	10 (9)
Myrsinaceae	<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roem. & Schult.	10 (4)
Myrsinaceae	<i>Myrsine umbellata</i> Mart.	10 (0)
Myrtaceae	<i>Campomanesia adamantium</i> (Cambess.) O.Berg	10 (0)
Myrtaceae	<i>Myrcia bella</i> Cambess.	10 (0)
Myrtaceae	<i>Myrcia guianensis</i> (Aubl.) DC.	10 (0)
Myrtaceae	<i>Myrcia</i> sp. DC. ex Guill	10 (6)
Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.	10 (3)

Table 1 continued

Family	Species	Individuals
Myrtaceae	<i>Myrcia tomentosa</i> (Aubl.) DC.	10 (6)
Myrtaceae	<i>Psidium laurotitanum</i> Cambess. in A.St.-Hil.	9 (7)
Nyctaginaceae	<i>Guapira noxia</i> (Netto) Lundell	10 (7)
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	10 (7)
Ochnaceae	<i>Ouratea spectabilis</i> (Mart. ex Engl.) Engl.	10 (7)
Phyllanthaceae	<i>Phyllanthus acuminatus</i> Vahl	10 (8)
Rubiaceae	<i>Palicourea coriacea</i> (Cham.) K.Schum.	10 (8)
Rubiaceae	<i>Rudgea viburnoides</i> (Cham.) Benth.	10 (0)
Rubiaceae	<i>Tocoyena formosa</i> (Cham. & Schltld.) K.Schum.	10 (0)
Rutaceae	<i>Fagara rhoifolia</i> (Lam.) Engl.	10 (7)
Salicaceae	<i>Casearia sylvestris</i> Sw.	10 (4)
Styracaceae	<i>Styrax ferrugineus</i> Nees & Mart.	10 (1)
Thymelaeaceae	<i>Daphnopsis</i> sp. Mart.	10 (6)
Verbenaceae	<i>Aegiphila lhotskiana</i> Cham.	10 (0)
Verbenaceae	<i>Lippia velutina</i> Schauer	10 (9)
Vochysiaceae	<i>Vochysia tucanorum</i> Mart.	10 (0)

In parentheses is the number of individuals sampled outside of the plots (see “Methods” section)

latex and trichomes (Table 3). We found significant positive correlations between C:N and toughness, water and latex, and water and toughness (Table 3). We found the same pattern for PICs, except that all correlations for latex were not significant, tannins were correlated with alkaloids and not to specific leaf area, and C:N and trichomes were positively correlated (Table 3).

We found five groups of defense traits (Table 2; Fig. 1). The first group was defined primarily by the latex content; the second group by high values of specific leaf area and low C:N; the third group by low trichome densities and C:N; the fourth group by low values of specific leaf area, high values of C:N and the presence of chemical defenses; and the fifth group by high values of trichomes and alkaloids (Fig. 1). The number of species varied among the groups (2, 28, 4, 26, and 1, respectively). We found no relationships between trait distances and phylogenetic distances using either the Mantel correlogram (Fig. 2) or the entire matrix (Mantel's $r = 0.06$, $P = 0.16$).

Discussion

The “defense syndrome triangle” predicts three defense syndromes (Agrawal and Fishbein 2006):

the “low nutritional quality” syndrome comprises plants with low nutritional quality and many (mechanical and chemical) defenses traits, making herbivory unlikely; the “nutrition and defense” syndrome comprises plants with high nutritional quality complemented by several defenses; and the “tolerance or escape” syndrome comprises plants with few defense traits but high nutritional quality—plants in this syndrome are predicted to be tolerant of or to escape (for example, by changing phenological patterns) from herbivory. In cerrado, plants are known to have low nitrogen and water content, with high toughness, trichomes, and phenolic compounds (Marquis et al. 2002), and are from the “low nutritional quality” syndrome. Because the soils of the cerrado are infertile the “tolerance or escape” syndrome is not expected (Fine et al. 2006).

We found all three plant defense syndromes proposed by Agrawal and Fishbein (2006) (Supplementary material). Two plant functional groups in this study (groups 2 and 3) defined by their defense traits corresponded to the “tolerance” syndrome. Species in this syndrome had low trichome, latex, chemical, and toughness levels, but had high nutritional quality with high leaf nitrogen levels and specific leaf areas. Leaves with low levels of defense are more prone to herbivory both in the field and

Table 2 Defense traits (mean \pm SD, presence or absence of chemical defenses) of species sampled in cerrado at Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W)

Group	Species	C:N	SLA	Water	Latex	Trichomes	Toughness	Alkaloids	Terpenoids	Tannins
1	<i>Kielmeyera coriacea</i> Mart. & Zucc.	28 \pm 5	77 \pm 13	31 \pm 3	5 \pm 5	1 \pm 1	1.1 \pm 0.2	0	1	1
1	<i>Kielmeyera grandiflora</i> (Wawra) Saddi	34 \pm 9	77 \pm 13	41 \pm 9	9 \pm 3	0 \pm 0	1.9 \pm 0.4	0	0	1
2	<i>Acosmium subelegans</i> (Mohlenbr.) Yakovlev	17 \pm 3	82 \pm 14	17 \pm 5	0 \pm 0	56 \pm 123	1.0 \pm 0.2	0	1	1
2	<i>Aegiphila lhotskiana</i> Cham.	15 \pm 2	104 \pm 15	27 \pm 5	0 \pm 0	841 \pm 193	0.7 \pm 0.2	0	1	1
2	<i>Banisteriopsis</i> <i>megaphylla</i> (A. Juss.) B. Gates	15 \pm 3	127 \pm 28	18 \pm 6	0 \pm 0	617 \pm 331	0.4 \pm 0.2	0	0	1
2	<i>Byrsonima</i> <i>coccolobifolia</i> Kunth	22 \pm 3	97 \pm 16	20 \pm 0	0 \pm 0	14 \pm 12	0.8 \pm 0.1	0	0	1
2	<i>Casearia sylvestris</i> Sw.	16 \pm 3	124 \pm 20	10 \pm 0	0 \pm 0	143 \pm 114	0.7 \pm 0.2	0	0	1
2	<i>Dalbergia miscolobium</i> Benth.	18 \pm 3	76 \pm 10	20 \pm 0	0 \pm 0	11 \pm 10	0.8 \pm 0.3	0	0	1
2	<i>Daphnopsis</i> sp. Mart.	24 \pm 6	132 \pm 44	17 \pm 5	0 \pm 0	1 \pm 1	1.2 \pm 0.2	0	0	1
2	<i>Davilla elliptica</i> A. St.-Hil.	29 \pm 3	129 \pm 43	16 \pm 5	0 \pm 0	216 \pm 158	0.9 \pm 0.3	0	0	1
2	<i>Davilla rugosa</i> Poir.	28 \pm 3	188 \pm 40	11 \pm 3	0 \pm 0	228 \pm 134	0.8 \pm 0.3	0	0	1
2	<i>Dimorphandra mollis</i> Benth.	13 \pm 1	102 \pm 15	12 \pm 4	0 \pm 0	623 \pm 173	0.3 \pm 0.1	0	0	1
2	<i>Erythroxylum</i> <i>cuneifolium</i> (Mart.) O.E. Schulz	18 \pm 2	160 \pm 42	11 \pm 3	0 \pm 0	1 \pm 2	0.4 \pm 0.2	0	1	1
2	<i>Erythroxylum suberosum</i> A. St.-Hil.	18 \pm 3	90 \pm 13	19 \pm 3	0 \pm 0	0 \pm 1	1.3 \pm 0.4	0	1	1
2	<i>Erythroxylum</i> <i>tortuosum</i> Mart.	20 \pm 1	91 \pm 14	20 \pm 0	0 \pm 0	2 \pm 1	0.9 \pm 0.4	0	0	1
2	<i>Fagara rhoifolia</i> (Lam.) Engl.	17 \pm 3	106 \pm 15	13 \pm 5	0 \pm 0	247 \pm 101	0.5 \pm 0.2	0	1	1
2	<i>Gochnatia pulchra</i> Cabrera	21 \pm 6	103 \pm 23	10 \pm 0	0 \pm 0	2700 \pm 803	0.8 \pm 0.1	0	1	1
2	<i>Guapira noxia</i> (Netto) Lundell	10 \pm 1	104 \pm 24	31 \pm 7	0 \pm 0	17 \pm 25	0.9 \pm 0.2	0	1	1
2	<i>Guapira opposita</i> (Vell.) Reitz	11 \pm 1	120 \pm 28	19 \pm 7	0 \pm 0	38 \pm 55	0.8 \pm 0.2	0	1	1
2	<i>Heteropterys umbellata</i> A. Juss.	17 \pm 4	118 \pm 22	11 \pm 3	0 \pm 0	27 \pm 45	0.4 \pm 0.1	0	0	1
2	<i>Lacistema</i> sp. Sw.	28 \pm 8	157 \pm 43	10 \pm 0	0 \pm 0	519 \pm 86	0.6 \pm 0.2	0	0	1
2	<i>Leandra lacunosa</i> Cogn.	29 \pm 3	126 \pm 26	22 \pm 4	0 \pm 0	257 \pm 35	0.8 \pm 0.3	0	0	1
2	<i>Machaerium acutifolium</i> Vogel	11 \pm 2	92 \pm 11	14 \pm 5	0 \pm 0	214 \pm 123	0.9 \pm 0.2	0	0	1
2	<i>Miconia ligustroides</i> (DC.) Naudin	27 \pm 3	97 \pm 22	19 \pm 3	0 \pm 0	5 \pm 7	0.6 \pm 0.1	0	0	1

Table 2 continued

Group	Species	C:N	SLA	Water	Latex	Trichomes	Toughness	Alkaloids	Terpenoids	Tannins
2	<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roem. & Schult.	20 ± 1	126 ± 21	12 ± 4	0 ± 0	308 ± 93	0.5 ± 0.1	0	1	1
2	<i>Phyllanthus acuminatus</i> Vahl	28 ± 1	207 ± 41	10 ± 0	0 ± 0	0 ± 0	0.3 ± 0.1	0	0	1
2	<i>Plenckia populnea</i> Reissek	21 ± 5	106 ± 12	12 ± 4	0 ± 0	0 ± 0	0.7 ± 0.2	0	1	1
2	<i>Stryphnodendron</i> <i>adstringens</i> (Mart.) Coville	18 ± 1	81 ± 15	22 ± 4	0 ± 0	24 ± 48	0.7 ± 0.1	0	0	1
2	<i>Stryphnodendron</i> <i>obovatum</i> Benth.	18 ± 3	121 ± 30	17 ± 7	0 ± 0	5 ± 2	0.4 ± 0.1	0	0	1
2	<i>Xylopia frutescens</i> Aubl.	21 ± 2	197 ± 34	10 ± 0	0 ± 0	140 ± 131	0.4 ± 0.1	0	1	1
3	<i>Annona crassiflora</i> Mart.	25 ± 5	117 ± 25	20 ± 0	0 ± 0	380 ± 82	0.7 ± 0.1	0	0	0
3	<i>Lippia velutina</i> Schauer	17 ± 3	164 ± 60	14 ± 5	0 ± 0	926 ± 130	0.5 ± 0.1	0	0	0
3	<i>Palicourea coriacea</i> (Cham.) K.Schum.	18 ± 5	112 ± 21	29 ± 5	0 ± 0	2 ± 4	0.9 ± 0.4	0	1	0
3	<i>Vochysia tucanorum</i> Mart.	21 ± 3	107 ± 16	24 ± 5	0 ± 0	9 ± 14	1.2 ± 0.2	0	1	0
4	<i>Acosmium dasycarpum</i> (Vogel) Yakovlev	17 ± 3	79 ± 9	20 ± 5	0 ± 0	1040 ± 334	1.2 ± 0.2	0	0	1
4	<i>Annona coriacea</i> Mart.	28 ± 4	86 ± 17	27 ± 7	0 ± 0	204 ± 72	2.1 ± 0.5	0	0	1
4	<i>Bauhinia rufa</i> (Bong.) Steud.	19 ± 2	67 ± 5	16 ± 5	0 ± 0	954 ± 227	1.1 ± 0.2	0	1	1
4	<i>Byrsonima verbascifolia</i> (L.) DC.	40 ± 7	74 ± 7	25 ± 7	0 ± 0	2056 ± 793	0.7 ± 0.1	0	0	1
4	<i>Campomanesia</i> <i>adamantium</i> (Cambess.) O.Berg	28 ± 3	81 ± 14	13 ± 5	0 ± 0	604 ± 401	1.1 ± 0.2	0	1	1
4	<i>Conarus suberosus</i> Planch.	30 ± 6	65 ± 6	20 ± 0	0 ± 0	1403 ± 561	1.4 ± 0.2	0	1	1
4	<i>Diospyros hispida</i> A. DC.	33 ± 5	62 ± 7	23 ± 5	0 ± 0	708 ± 278	1.0 ± 0.3	0	1	1
4	<i>Miconia albicans</i> (Sw.) Triana	31 ± 7	91 ± 17	17 ± 5	0 ± 0	65100 ^a	0.7 ± 0.2	0	0	1
4	<i>Miconia rubiginosa</i> (Bonpl.) DC.	38 ± 4	64 ± 7	20 ± 0	0 ± 0	281 ± 52	0.7 ± 0.1	0	0	1
4	<i>Myrcia bella</i> Cambess.	33 ± 6	89 ± 12	17 ± 5	0 ± 0	1020 ± 308	1.2 ± 0.2	0	1	1
4	<i>Myrcia guianensis</i> (Aubl.) DC.	29 ± 4	64 ± 8	20 ± 0	0 ± 0	661 ± 370	1.3 ± 0.3	0	0	1
4	<i>Myrcia</i> sp. DC. ex Guill	28 ± 2	78 ± 8	12 ± 5	0 ± 0	1095 ± 504	0.9 ± 0.2	0	0	1
4	<i>Myrcia splendens</i> (Sw.) DC.	39 ± 5	104 ± 24	10 ± 0	0 ± 0	1067 ± 385	0.8 ± 0.1	0	0	1
4	<i>Myrcia tomentosa</i> (Aubl.) DC.	25 ± 3	87 ± 13	16 ± 5	0 ± 0	419 ± 138	1.1 ± 0.3	0	1	1
4	<i>Myrsine umbellata</i> Mart.	31 ± 3	84 ± 20	20 ± 0	0 ± 0	0 ± 0	1.1 ± 0.3	0	0	1

Table 2 continued

Group	Species	C:N	SLA	Water	Latex	Trichomes	Toughness	Alkaloids	Terpenoids	Tannins
4	<i>Ocotea pulchella</i> (Nees) Mez	30 ± 6	70 ± 12	14 ± 5	0 ± 0	1445 ± 710	1.4 ± 0.2	0	1	1
4	<i>Ouratea spectabilis</i> (Mart. ex Engl.) Engl.	32 ± 7	63 ± 12	22 ± 5	0 ± 0	0 ± 0	2.3 ± 0.5	0	1	1
4	<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	31 ± 2	74 ± 9	20 ± 0	0 ± 0	0 ± 0	0.9 ± 0.2	0	0	1
4	<i>Piptocarpha rotundifolia</i> (Less.) Baker	28 ± 8	96 ± 22	20 ± 0	0 ± 0	1304 ± 419	1.1 ± 0.3	0	1	1
4	<i>Psidium laurotteanum</i> Cambess. in A.St.-Hil.	38 ± 6	74 ± 14	18 ± 4	0 ± 0	1583 ± 133	1.3 ± 0.1	0	1	1
4	<i>Rudgea viburnoides</i> (Cham.) Benth.	25 ± 4	81 ± 14	33 ± 5	0 ± 0	687 ± 258	1.2 ± 0.2	0	0	1
4	<i>Schefflera macrocarpa</i> (Cham. & Schltldl.) Frodin	31 ± 5	52 ± 17	36 ± 11	0 ± 0	2392 ± 450	1.0 ± 0.3	0	0	1
4	<i>Schefflera vinosa</i> (Cham. & Schltldl.) Frodin & Fiaschi	27 ± 5	62 ± 5	28 ± 6	0 ± 0	1572 ± 1038	0.9 ± 0.2	0	1	1
4	<i>Styrax ferrugineus</i> Nees & Mart.	36 ± 4	70 ± 19	20 ± 5	0 ± 0	437 ± 12	1.5 ± 0.3	0	1	1
4	<i>Tabebuia ochracea</i> (Cham.) Standl.	20 ± 3	77 ± 13	21 ± 3	0 ± 0	620 ± 148	1.3 ± 0.4	0	0	1
4	<i>Tapirira guianensis</i> Aubl.	34 ± 4	75 ± 11	20 ± 0	0 ± 0	18 ± 31	0.7 ± 0.1	0	0	1
5	<i>Tocoyena formosa</i> (Cham. & Schltldl.) K.Schum.	27 ± 6	86 ± 11	20 ± 5	0 ± 0	1627 ± 959	0.8 ± 0.3	1	1	1

Group = group from K-means partitioning, Water = water content (mg cm^{-2}), SLA = specific leaf area ($\text{cm}^2 \text{g}^{-1}$), Toughness (N), Trichomes = trichome density (trichomes cm^{-2}), Latex (mg), C:N = carbon:nitrogen ratio

^a Measure without standard deviation, because it was based on a single leaf due to elevated number of trichomes

under laboratory conditions (Pérez-Harguindeguy et al. 2003). Thus, although we did not measure herbivory damage, these species are expected to tolerate herbivory more than the other groups. Two other species groups (groups 4 and 5) corresponded to the “low nutritional quality” syndrome. They had traits that deter herbivory—trichomes, toughness, and chemicals—and their leaves had high C:N ratios and low specific leaf areas; in other words, less palatable, but resistant leaves. Species with these characteristics are predicted to experience little herbivory (Pérez-Harguindeguy et al. 2003). Lastly, a species group (group 1) corresponded to the “nutrition and defense” syndrome, with tougher leaves and latex complementing high water content and absence of trichomes. Leaves in this syndrome have a

combination of strong and weak defenses (e.g., high toughness and low trichomes density), increased water content and nutritional quality. Species in this syndrome are used by the few herbivores that can overcome specific (latex) barriers and are avoided by generalist herbivores (Pérez-Harguindeguy et al. 2003). Three of the groups (1, 3, and 5) had one or a few species and differed by one trait only (presence of alkaloids, absence of tannins, or presence of latex). Thus, there were two major strategies of defense against herbivory in the cerrado woody species we sampled: “tolerance” and “low nutritional quality”.

Most pairwise correlations of traits were complementary. For instance, plants with lower specific leaf area also presented tougher leaves, low nitrogen content, more trichomes, and tannins. These traits act

Table 3 Pairwise correlations of defense traits among cerrado species at Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W)

	C:N	SLA	Water	Latex	Trichomes	Toughness	Alkaloids	Terpenoids	Tanins
C:N		-0.41**	0.21	0.15	0.26*	0.38**	0.01	-0.19	0.14
SLA	-0.47***		-0.54***	-0.01	-0.09	-0.60***	-0.11	-0.05	-0.15
Water	0.20	-0.53***		0.23	-0.16	0.57***	0.11	-0.13	-0.19
Latex	0.16	-0.15	0.30*		-0.12	0.13	0.00	-0.06	0.19
Trichomes	0.22	-0.28*	-0.05	-0.26*		-0.15	0.10	-0.09	-0.05
Toughness	0.39**	-0.61***	0.49***	0.22	0.08		-0.06	0.05	0.07
Alkaloids	0.02	-0.04	0.06	-0.02	0.19	-0.04		0.07	-0.28*
Terpenoids	-0.09	-0.12	0.01	0.02	0.10	0.23	0.14		0.03
Tanins	0.17	-0.26*	-0.15	0.05	0.06	0.07	0.03	-0.03	

Lower diagonal values are based on raw data, upper diagonal values are phylogenetically independent contrasts (PICs)

SLA specific leaf area

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

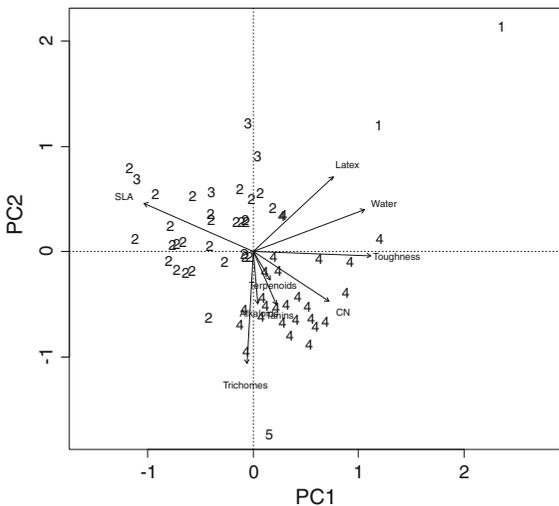


Fig. 1 Biplot of principal component analysis with defense traits of species in cerrado at the Federal University of São Carlos (21°58'05.3"S, 47°52'10.1"W). Each species is represented by the number of its group from K-means partitioning. Water = water content (mg cm^{-2}), SLA = specific leaf area ($\text{cm}^2 \text{g}^{-1}$), Toughness (N), Trichomes = trichome density (trichomes cm^{-2}), Latex (mg), C:N = carbon:nitrogen ratio

together to defend the plant against herbivory, as predicted by plant defense theory (Agrawal and Fishbein 2006). Nevertheless, there were also trade-offs between antagonist traits. Leaves with more water content were tougher and had lower specific leaf area. Although two correlations with latex and one with alkaloids also indicated trade-offs, there were only two species with latex and one with

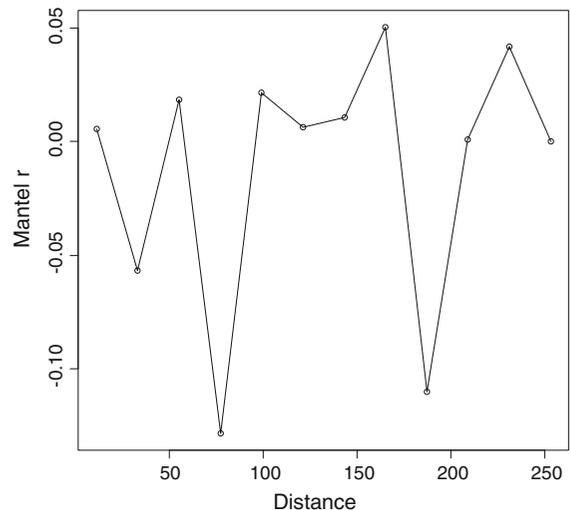


Fig. 2 Mantel correlogram between the trait and the phylogenetic distances matrices for cerrado species. No correlation was significant at $\alpha' = 0.004$ (Bonferroni correction)

alkaloids. Relationships among traits are usually synergistic or present no trade-off (Steward and Keeler 1988; Agrawal and Fishbein 2006). Leaf trait relationships may suffer morphometric constraints, that is, the range a given trait can assume depends on the variation of other traits. However, herbivory might also favor selection for traits with multiple functions (Steward and Keeler 1988). In addition, other factors such as nutrient-poor soils or fire, rather than herbivory, may influence the suites of traits. For example, low soil nitrogen levels result in an

imbalance between nitrogen uptake and carbohydrate production, and the surplus carbohydrates are transformed into scleromorphic structures, resulting in tougher leaves with low specific leaf area and low nitrogen content (Gottsberger and Silberbauer-Gottsberger 2006). Even if a trait evolved in response to other functions, it might contribute to anti-herbivore resistance of a given syndrome; for example, trichomes may have evolved as a protection from water loss, but they also deter herbivores (Agrawal and Fishbein 2006).

We did not find a phylogenetic signal, and phylogeny did not determine the suite of traits among the species. Thus, herbivory is likely the biotic factor selecting for the observed trait clustering (Agrawal and Fishbein 2006). Furthermore, the two predominant strategies are expected to provide defenses against a wide spectrum of herbivores (Núñez-Farfán et al. 2007). Diverse suites of herbivores from different phylogenetic groups and guilds attack the same phenotypic hosts (Maddox and Root 1990). Since the selective pressure is caused by diffuse herbivory, the plant defenses that have evolved are broad spectrum defenses against many herbivores (Maddox and Root 1990). The herbivore community is thus expected to be dominated by generalists rather than specialists (Agrawal and Fishbein 2006).

Caution is advised in extrapolating these results to other savannas because the dominant herbivores in cerrado are leaf-cutter ants, whereas they are large mammals in other savannas (Costa et al. 2008). Although some studies indicated that herbivory in cerrado is low (Marquis et al. 2002), it may have been underestimated and a recent study concluded that herbivory in cerrado is greater than or comparable to other terrestrial communities (Costa et al. 2008). Herbivory can decrease reproductive fitness or even cause mortality of plants (Mundim 2009). With the potential effect of herbivory and the nutrient-poor soils, the tolerance defense syndrome is unexpected among cerrado species (Fine et al. 2006). The tolerance syndrome may have evolved in response to fire, which removes leaves less selectively than herbivores (Bond and Keeley 2005). Furthermore, cerrado plants may adjust their leaf phenology to escape in time from insect attack (Marquis et al. 2001). Cerrado presents several environmental filters (Gottsberger and Silberbauer-Gottsberger 2006), and the interactions of filters are known to reduce species

pool, that is, species that survive a given filter are still subjected to other filters (Silva and Batalha 2006). As stated above, traits may be combined in defense against herbivory (Agrawal and Fishbein 2006). If so, herbivory will act on traits already selected by other filters. Thus, the relatively few defense syndromes we found may arise from synergistic interaction of several environmental filters, which have reduced the species pool to those species with the phenotypic traits required to survive all environmental effects, including drought, fire, infertile soils, and herbivory.

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