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Do litter manipulations affect leaf functional traits of savanna woody plants?

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Abstract Plant litter is the layer composed of dead plant material that covers soil surfaces in terrestrial ecosystems. It is an important pool of essential nutrients for soil and plants, serving also as a protective layer on the soil surface. In this study, we investigated the effects of litter addition and removal on leaf functional traits of woody Neotropical savanna trees. We measured maximum photosynthesis ($A_{\max}$), stomatal conductance (g_s), leaf transpiration (E), intrinsic water use efficiency (IWUE), specific leaf area (SLA), and chlorophyll content (CCI) in 15 species belonging to three different phenological groups (evergreen, briefly deciduous, and deciduous species) that were subjected to three distinct litter availability treatments (addition, removal, and control plots) in a Neotropical Savanna site in Brazil. Although SLA and CCI differed among phenology groups, they were not affected by the litter treatments. In contrast, when considered at the community level, we found that the availability of litter affected the leaf traits linked with the water status of the plants (E, g_s and IWUE). Plants in the litter removal plots exhibited lower g_s and E (25 % of reduction in comparison with control group) but higher IWUE, while plants in the litter addition plots had a 10 % decrease in IWUE but a 12 % increase in g_s and E compared with plants in control plots. Savanna woody plants responded promptly to litter manipulation by adjusting leaf water loss, which suggests that in the short term, changes in the amount of litter in Cerrado ecosystems can affect the soil water availability to the plant community.

Keywords Litter · Savanna · Leaf functional traits · Cerrado · Water use efficiency

Introduction

Litter is the organic matter that covers the soil surface in many terrestrial ecosystems and originates from the deposition of dead plant material, such as leaves, bark, needles, and twigs (Facelli and Pickett 1991; Berg 2000). The presence of the litter layer has important implications for the development and maintenance of soil properties and hence of the vegetation (Carson and Peterson 1990). It is an important reservoir of organic

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matter (Couteaux et al. 1995; Berg 2000) and plays a major role in decomposition and in other physical–chemical soil processes, acting as a regulator of carbon and nutrient fluxes between the vegetation and soil pools (Kellman 1979; Chambers et al. 2000; Reich et al. 2005). In addition to the water retention capacity, the litter layer also acts as a physical barrier, intercepting direct rainfall and solar radiation (Benkobi et al. 1993; Ponge et al. 1993), reducing evaporation from the soil surface; thus regulating soil microclimate (Sayer 2006) and soil water balance. It is a substantial source of nutrients for tropical ecosystems (Vitousek 1984), especially for savannas and forests growing in highly weathered dystrophic (nutrient-poor) oxysoils (Facelli and Pickett 1991).

Neotropical savannas are characterized by strong seasonality of climate, high evaporative demand, low nutrient availability in the soils, and frequent fires (Eiten 1972; Oliveira-Filho and Ratter 2002). The savanna of Central Brazil, known as Cerrado, covers more than 2 million km^2 and is the most floristically diverse savanna in the world (Solbrig 1996), and is a biodiversity hotspot (Myers et al. 2000). Although the Cerrado constitutes a complex mosaic of savanna vegetation types, soil nutrient availability usually limits tree growth and density, mainly because of the low availability of P and Ca (Lopes and Cox 1977a, b; Furley 1999; Silva et al. 2013). These factors combined with high soil acidity (pH around 5.5), high Al availability (Haridasan 2001), and fire disturbance, act in concert to maintain distinct tree densities in the Cerrado biome (Silva et al. 2013). The low nutrient concentration in the soils is reflected in the nutrient content of the leaves of many tree species (Haridasan and Araújo 1988; Haridasan 2001).

The deposition of litter in Neotropical savannas is not a regular event throughout the year. Litter accumulation occurs mainly during the dry period, when most of the trees shed their leaves as a phenological response to the low rainfall and high evaporative demand (Meinzer et al. 1999; Kozovits et al. 2007; Villalobos-Vega et al. 2011; Rossatto 2013; Rossatto et al. 2013). The amount of litter fall in typical savanna vegetation (the Cerrado sensu stricto) is around 210–230 g m^2 year^{-1} (Nardoto et al. 2006; Peres et al. 1983), usually lower than in humid tropical forests where litter deposition ranges from 519 to 1,247 g m^2 year^{-1} (Chave et al. 2010). Plant species belonging to distinct phenological groups (evergreen, briefly deciduous, and deciduous species) have distinct contributions to litter biomass accumulation in Cerrado soils (Nardoto et al. 2006; Valenti et al. 2008).

Experiments manipulating the amount of litter in the soil offer a unique opportunity to study the effects of the litter layer on carbon and water cycles, decomposition processes, ecosystem productivity, and individual plants responses to these effects. By manipulating litter quantity, important ecosystem processes can be affected (Sayer 2006), especially those related to the accumulation and cycling of carbon, nutrients, and water resources, the rates of which mainly depend upon temperature and water availability in the soil superficial layers (Villalobos-Vega et al. 2011). As canopy cover is sparse in Neotropical savannas (Hoffmann et al. 2005), the soils tend to be more exposed to the climatic conditions, which results in higher temperatures and lower humidity during the dry season. In a litter addition/removal experiment over 4 years in central Brazil, Villalobos-Vega et al. (2011) showed that litter addition resulted in lower temperature fluctuations at the soil surface and higher soil water availability, but with the exception of an increase in Ca levels, litter addition did not affect soil nutrient availability in the superficial soil layers.

These findings suggest that variation in the amount of litter can alter the soil conditions for plants in savanna systems, which could affect not only leaf nutrient balance, but also leaf carbon gain and water loss (Ginter et al. 1979; Willms 1988; Xiong and Nilsson 1999; Sayer et al. 2006). Thus, the aim of this study was to investigate how well-known physiological leaf traits related to water status and carbon assimilation were affected by differential litter availability treatments. Specifically, we expected that plants growing in litter removal plots would show a more conservative strategy in terms of stomatal control of leaf carbon gain and water loss than plants in litter addition plots with higher soil water availability. As Villalobos-Vega et al. (2011) showed no differences in nutrient concentration for plots with litter addition, we expected that maximum carbon assimilation rates and chlorophyll content would not change among treatments. We tested these predictions among the three distinct phenological groups (deciduous, brevideciduous, and evergreens) that coexist within any Cerrado landscape (Franco et al. 2005).

Materials and methods

Study area

This study was conducted at the “Roncador” Ecological Reserve from the Brazilian Institute of Geography and Statistics (RECOR/IBGE), located 33 km south of Brasília, Brazil (15°56′S, 47°53′W, at an elevation of about 1,100 m above sea level). The average annual precipitation in this area is approximately 1,500 mm with a pronounced dry season from May through September and a mean annual temperature that ranges from 20 to 26 °C (Eiten 1972; Oliveira-Filho et al. 1989). The predominant soils are deep and well-drained Oxisols, but hydromorphic soils also occur associated with water courses (Oliveira 2011). The study area consisted of a typical savanna physiognomy (Cerrado sensu stricto) with 10–40 % tree crown cover and protected from fire for over 30 years.

Litter addition/removal treatments

The study site consisted of 15 plots each of 400 m^2 randomly assigned to one of the following treatments: (1) control plots—without any disturbance or changes in the natural litter material; (2) litter removal plots—litter layer was removed; and (3) litter addition plots—in which litter collected from the litter removal treatment was added (see Fig. 1 for experimental design). As described by Villalobos-Vega et al. (2011), the plots were located in a homogeneous savanna area with similar leaf area index and soil properties. Plant litter considered in this experimental study consisted of all dead organic material from the aboveground and belowground layer (twigs, branches, reproductive structures, and leaves). Litter removal and addition were manually made every 1–2 months between July 2004 and December 2008 (see Villalobos-Vega et al. 2011 for more details of the experimental design). The average difference in the amount of litter between addition and removal treatment plots was approximately 440 g m^{-2}, and differed among seasons (higher in the dry season), but litter fall was similar among treatments (Villalobos-Vega et al. 2011). Treatment plots differed at the end of the dry season in soil water content (%) at 5-cm depth (addition: 24 %; control: 25 % and removal: 15 %) but not at 60-cm depth (addition, control and removal—26 %); and in temperature fluctuation (maximum – minimum at 5-cm depth; addition: 1 °C; control: 2 °C and removal: 6 °C), and at 30-cm depth (addition: 0 °C; control: 0.5 °C and removal: 1.2 °C; data from Villalobos-Vega et al. 2011).

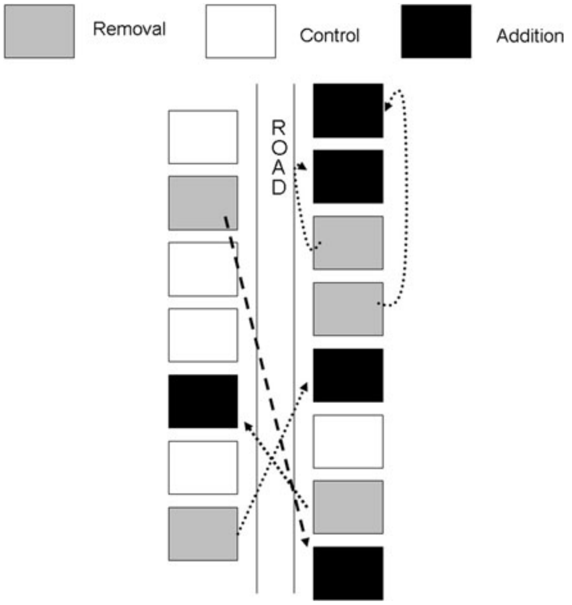

Fig. 1 The experimental design of litter removal and addition treatments. *Arrows* indicate the direction in which litter was transported from removal plots to addition plots. Redrawn from Villalobos-Vega et al. (2011)

Studied traits

To understand the responses of woody Cerrado species to litter addition and removal, we chose a set of leaf functional traits related to water loss, carbon gain and leaf structure. Our definition of leaf traits was based on that proposed by Violle et al. (2007), where a functional trait is “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level.” Leaf trait measurements were taken in species belonging to three different phenological groups, classified according to Franco et al. (2005): evergreen—having foliage that persists and remains green throughout the year; brevideciduous—which are species that remain leafless for short periods of <30 days in a year; and deciduous—remain leafless for a period longer than 30 days in a year. A floristic survey was made in the whole treatment area to identify the five most abundant species of each phenological group. For each

Table 1 List of the studied tree species by leaf phenology

Species	Family
Evergreens	
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	Araliaceae
Sclerolobium paniculatum Vogel	Fabaceae
Miconia pohliana Cogn.	Melastomataceae
Ouratea hexasperma (A.St.-Hil.) Baill.	Ochnaceae
Roupala montana Aubl.	Proteaceae
Brevideciduous	
Caryocar brasiliense A.St.-Hil.	Caryocaraceae
Hymenaea stigonocarpa Mart. ex Hayne	Fabaceae
Byrsonima pachyphylla A. Juss.	Maphigiaceae
Blepharocalyx salicifolius (Kunth) O. Berg	Myrtaceae
Styrax ferrugineus Nees & Mart.	Styracaceae
Deciduous	
Aspidosperma tomentosum Mart.	Apocynaceae
Kielmeyera coriacea Mart. & Zucc.	Clusiaceae
Acosmium dasycarpum (Vogel) Yakovlev	Fabaceae
Qualea grandiflora Mart.	Vochysiaceae
Erytroxylum suberosum A.St.-Hil.	Erytroxylaceae

treatment, we sampled three individuals per species, totaling 15 species (Table 1). To avoid pseudo replication, the mean individual response for each species in a plot for each treatment was used in the analyses. All species were found in all the studied treatments.

The following leaf traits were studied: stomatal conductance (g_s), leaf transpiration (E), maximum CO_2 assimilation on a leaf area basis (A_{max}), specific leaf area (SLA, the ratio of fresh leaf area and dry mass), and the chlorophyll content index (CCI). Given the major role of chlorophyll in photosynthesis and that major parts of leaf N and Mg are incorporated into chlorophyll, CCI can also be considered an indirect and nondestructive measurement of leaf nutritional status (Filella and Penuelas 1994; Moran et al. 2000). We also calculated IWUE, the leaf-level ratio of A_{max} to g_s, based on the assumption that plants control stomata to optimally satisfy the trade-off between the amount of carbon assimilated and the amount of water transpired (Cowan and Farquhar 1977; Larcher 2003; Gilbert et al. 2011).

Maximum CO_2 assimilation, stomatal conductance, and transpiration were determined under ambient conditions using a portable open photosynthesis system (LCA-4, Analytical Development Co., Hoddesdon, UK) coupled with a halogen light source providing a light intensity between 1,200 and 1,300 µmol m^{-2} s^{-1}, sufficient to saturate the leaf photosynthetic apparatus of the most savanna plants (Prado and Moraes 1997; Franco et al. 2005). Gas exchange measurements were conducted toward the peak of the wet season in January and February 2009. We measured three sunlit leaves of each premarked individual between 0800 and 1200 h. Measurements of a chlorophyll content index (CCI) were obtained using a chlorophyll meter (CCM-200 Chlorophyll Content Meter, Opti-Sciences) on the same leaves used in the gas exchange measurements. Three measurements were taken on each leaf. This nondestructive optical method provides reliable estimates of relative chlorophyll content (Markwell et al. 1995; Gamon and Surfus 1999). After CCI measurements, leaves were collected, run through a scanner, and its area determined using the software AREA (Caldas et al. 1992). Leaves were then oven dried at 70 °C until obtainment of constant mass, for calculation of SLA (SLA—the ratio of leaf area to leaf dry mass).

Statistical analysis

We used a factorial ANOVA to test for effects of phenology ($n = 3$ groups; deciduous, brevideciduous, and evergreen; 5 species per group), and litter treatments ($n = 3$—control, removal, and addition) on the studied traits. Species average values of each trait corresponded to a replicate. We compared the means with a Fisher LSD test ($\alpha = 0.05$), when significant effects were detected. All data were normally distributed ($P > 0.45$ Kolmogorov–Smirnov test) and displayed homogeneity of variances, (Cochran $C > 0.18$; df = 8, $P > 0.10$). A linear regression was used to test the relationships between g_s and E and g_s and A_{max} on the different litter treatments. Significance of the relationships and pairwise comparisons for differences in slope, elevation, and shift among litter treatments were tested using the SMATR software version 2.0 (Warton et al. 2006) on log-transformed data for g_s and A_{max}.

Results

The effect of litter treatments and type of leaf phenology

Litter manipulations significantly affected leaf traits linked with regulation of water loss (Table 2).

Table 2 Results of the factorial ANOVA on the influence of litter treatment (LT; control, addition, and removal) and leaf phenology (LP; deciduous, brevideciduous, and evergreen) on the studied traits

Trait	Source of variation	df	*F*	*P*
SLA	LT	2	0.207	0.813
	LP	2	6.793	0.003
	LT*LP	4	0.306	0.871
	Error	36		
$A_{\max}$	LT	2	0.168	0.846
	LP	2	2.353	0.109
	LT*LP	4	0.338	0.850
	Error	36		
CCI	LT	2	0.840	0.508
	LP	2	5.794	0.015
	LT*LP	4	0.864	0.495
	Error	36		
g_s	LT	2	5.675	0.007
	LP	2	3.117	0.056
	LT*LP	4	0.840	0.508
	Error	36		
E	LT	2	6.146	0.005
	LP	2	0.909	0.412
	LT*LP	4	0.733	0.575
	Error	36		
IWUE	LT	2	4.979	0.012
	LP	2	0.558	0.577
	LT*LP	4	0.864	0.494
	Error	36		

*LT*LP* interaction between litter treatment and leaf phenology; *df* degrees of freedom; *SLA* specific leaf area; A_{max} maximum CO_2 assimilation rate; *CCI* chlorophyll content index; g_s stomata conductance; *E* transpiration rate; *IWUE* intrinsic water use efficiency

Compared with trees in the control plots, trees growing in the litter addition treatment showed an increase of around 12 % in g_s (Fig. 2a), which in turn was coupled with a similar increase in *E* (Fig. 2b). Plants in litter removal plots showed the opposite pattern. Relative to plants in control plots, g_s and *E* of plants in litter removal plots decreased by around 25 % (Fig. 2a, b). These changes in g_s affected IWUE (Fig. 2c), while $A_{\max}$ was not influenced by litter manipulations (Fig. 2d). Relative to plants in control plots, IWUE of plants in litter removal plots increased by about 15 %, while it decreased by 10 % in litter addition plots (Fig. 2c). SLA and CCI were not affected by changes in the amount of litter in the soil (Fig. 2e, f).

Stomatal conductance (Fig. 3a), leaf transpiration (Fig. 3b), IWUE (Fig. 3c), and CO_2 assimilation (Fig. 3d) did not differ between phenological groups (Table 2). However, phenology had a significant effect on SLA and CCI (Table 2). Deciduous and brevideciduous species had similar SLA and CCI values; while evergreen species had lower values of SLA (Fig. 3e), but higher values of CCI (Fig. 3f). The interaction between litter treatment and leaf phenology was not significant ($F_{4,36} < 1.40$; $P > 0.25$) for any of the studied traits (Table 2).

Relationships between leaf traits

The relationships between stomatal conductance and leaf transpiration for the three litter treatments are depicted in Fig. 4a. Irrespective of the litter treatment that plants were subjected to, they shared statistically similar slopes and intercepts (common slope = 0.99; Test statistic = 5.58; $P = 0.061$). However, we found a significant shift along the common axis (Fig. 4a; Wald-Statistic = 14.92; $P < 0.01$) where the relationship for litter addition treatment was right-shifted in relation to the control ($P = 0.02$), while the relationship in litter removal treatment was left-shifted in relation to the control group ($P = 0.032$). g_s and $A_{\max}$ were related to each other only in litter removal ($r^2 = 0.60$; $P = 0.01$) and litter addition ($r^2 = 0.24$; $P = 0.04$) treatments (Fig. 4b). These relationships did not differ in their slope (common slope = 1.06; Test statistic = 0.71; $P = 0.691$); however, the relationship differed in the intercept (Wald-Statistic = 16.10; $P < 0.01$) so that the $A_{\max}$ vs g_s relationship in the litter removal treatment was elevated (Fig. 4b) in relation to the same relationship in the litter addition treatment ($P < 0.01$).

Discussion

At the community level, litter addition or removal affected leaf functional traits that were related to leaf water loss (Fig. 2). Such effects were independent of the species phenology and were possibly a response to distinct levels of soil water availability and of soil temperature fluctuations following changes in soil cover by the litter layer. In the same study site, Villalobos-Vega et al. (2011) found that litter addition significantly decreased maximum soil temperature in

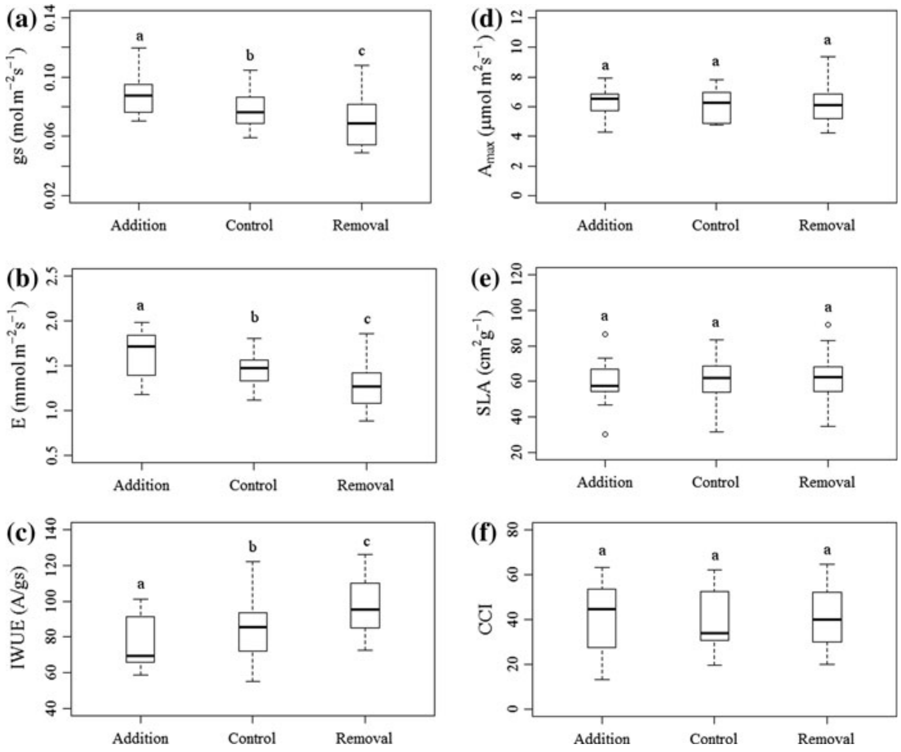

Fig. 2 Effects of litter addition, and removal on leaf functional traits of savanna trees. **a** stomatal conductance (g_s); **b** leaf transpiration (E); **c** leaf intrinsic water use efficiency (IWUE); **d** maximum CO_2 assimilation (A_{max}); **e** specific leaf area (SLA), and **f** chlorophyll content index (CCI). The *continuous line within the box* shows the median, and *error bars* show 10 and 90 percentiles ($n = 3$ phenological groups per treatment). *Different letters* indicate differences according Fisher LSD test ($P < 0.05$)

all sampled soil layers and increased soil water content in the uppermost (0–5 cm) soil layer, while litter removal resulted in higher maximum soil temperature in all sampled soil layers and lower soil water content in the uppermost soil layer. A thicker litter layer increases soil insulation buffering soil temperature variations. In addition, it increases light interception and creates a barrier to water vapor diffusion reducing water loss by evaporation from the soil (Fowler 1988; West 1979).

Our results suggest that the Cerrado tree community has responded to changes in litter quantity deposited on the soil surface, by stomatal regulation of transpiration with no significant changes in A_{max}. In the case of a higher exposure of the soil surface by litter removal, E and g_s decreased, while plants maintained a similar A_{max}, resulting in higher water use efficiency (Fig. 2c). Plants of the litter addition plots showed the opposite pattern (Figs. 2, 4b). We associate this increase in E and g_s in plants of the litter addition plots to the higher water availability in the uppermost soil layers. However, the lack of a concomitant increase in A_{max} meant a less efficient use of water (lower IWUE) in comparison to plants in the other two litter treatments. The lack of response in A_{max} and CCI to litter addition or removal (Fig. 3) suggests that the photosynthetic metabolism and leaf structure (SLA) of Cerrado trees is optimally adjusted to these nutrient deficient soils. In fact, long-term N and P fertilization experiments have shown that Cerrado trees apparently have the capacity to exploit increases in nutrient availability by allocating resources to maximize shoot growth, specially number of leaves, while leaf nutrient concentrations (Bucci et al. 2006) or SLA (Kozovits et al. 2007) remain unaffected.

Litter quantity and quality affect soil microbial processes, which in turn control annual to millennial variations in vegetation structure by affecting tree growth, nutrient uptake, and water use efficiency (Silva and Anand 2011). The role of the litter in the maintenance of these processes and in affecting vegetation properties is well known for temperate ecosystems (Vitousek and Sanford 1986; Silva and Anand 2011), and the nutrients released from dead plant material are rapidly reabsorbed by trees roots and decomposers. After 4 years of experimental manipulation of the litter layer, only Ca levels increased in the

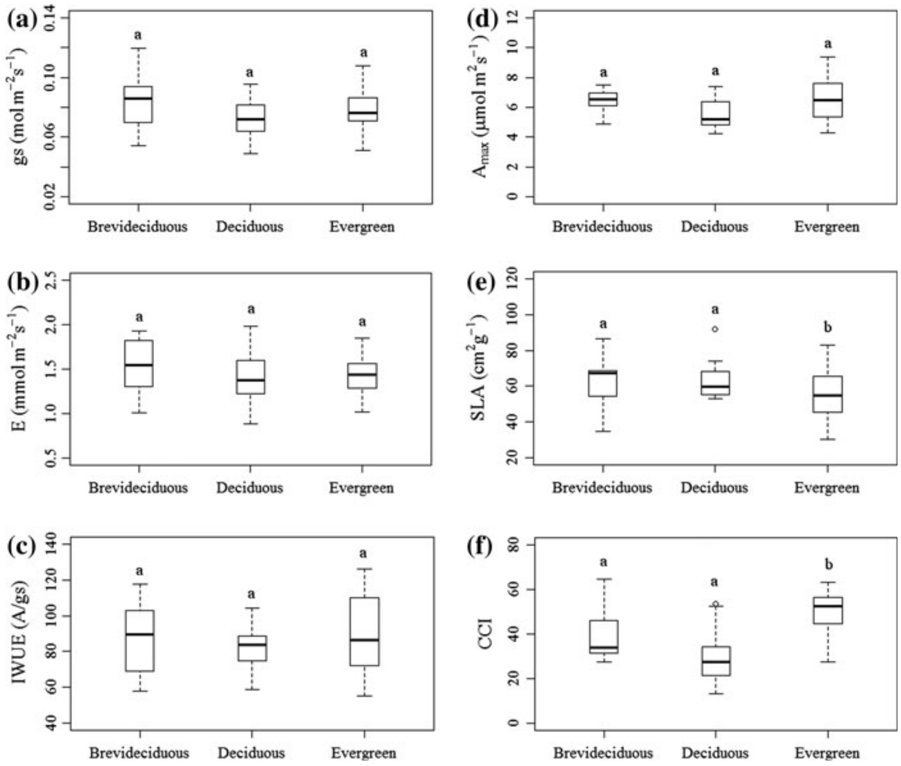

Fig. 3 Effects of phenology on leaf functional traits of savanna woody species. **a** stomatal conductance (g_s); **b** leaf transpiration (E); **c** leaf intrinsic water use efficiency (IWUE); **d** maximum CO_2 assimilation (A_{max}); **e** specific leaf area (SLA), and **f** chlorophyll content index (CCI). The *continuous line within the box* shows the median and *error bars* show 10 and 90 percentiles ($n = 5$ species per phenological group). *Different letters* indicate differences according to Fisher LSD test ($P < 0.05$)

topsoil of litter addition plots (Villalobos-Vega et al. 2011). Ca is a relatively immobile nutrient once it reaches the leaves, and therefore, is not subjected to retranslocation in comparison with other mobile nutrients such as N, P, and K, which can readily move from old to new leaves (Hill 1980). These factors coupled with the high nutrient resorption efficiency of Cerrado trees (44–55 % of leaf N and 30–80 % of leaf P are reabsorbed before leaf fall; Kozovits et al. 2007) and the slow litter layer decomposition (Nardoto et al. 2006) in Cerrado support the idea that most of the nutrients remain in the vegetation itself (Kozovits et al. 2007) and may explain why the leaf chlorophyll content and maximum carbon assimilation rates did not change in response to litter manipulation.

Given the lack of observed changes in soil nutrient pools with litter addition or removal (Villalobos-Vega et al. 2011), any changes in essential nutrient availability by experimental manipulation of the litter layer was either rapidly absorbed by the ground layer vegetation or impacted the amount of resources allocated to the leaf canopy of the trees. Our results partially support the idea that the Cerrado ecosystem may be a very well-buffered system, where the changes in some important aspects of plant physiology might take a number of years to appear given the slow rates of litter decomposition.

SLA and CCI were the only leaf traits that were affected by leaf phenology, while traits related to leaf water loss and A_{max} did not differ among the phenological groups. Deciduous and brevideciduous species had similar SLA and CCI values, while evergreen species had lower values of SLA, but higher values of CCI. Data for a very restricted number of species suggest that evergreen Cerrado trees have more N and P immobilized in the leaf canopy than deciduous and brevideciduous trees (Bucci et al. 2006), but similar N and P leaf resorption efficiencies (Kozovits et al. 2007). Differences in the dominance of leaf phenological groups within a Cerrado landscape may affect the litter chemistry, and if this effect is meaningful enough to influence leaf trait syndromes of the woody vegetation is currently unknown. However, the lack of a significant interaction between litter treatment and leaf phenology for any of the studied leaf traits suggests the observed patterns would remain irrespective of any changes in nutrient availability of the topsoil caused

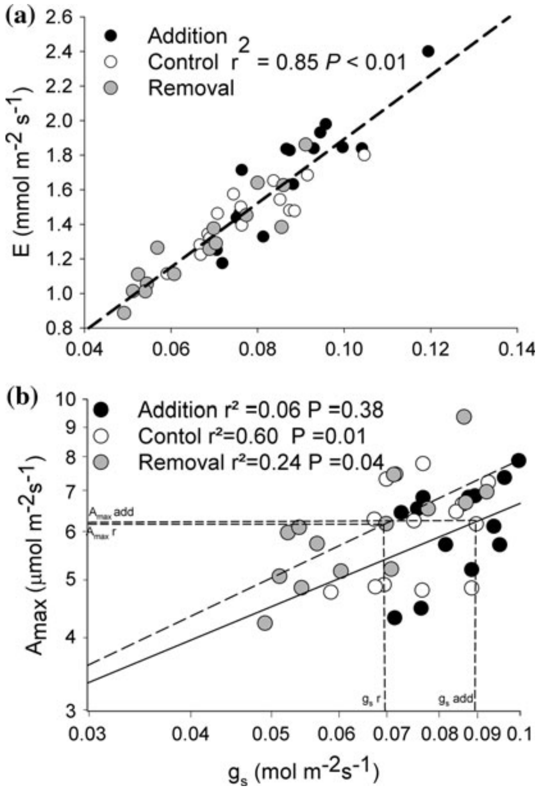

Fig. 4 Relationships between traits in the different treatments: **a** linear relationship between stomatal conductance (g_s) and leaf transpiration (E); and **b** log–log relationship between stomatal conductance (g_s) and leaf maximum CO_2 assimilation (A_{max}). In **a** there is a common slope. In **b** the *solid line* represents the correlation for the addition treatment, and the *dashed line* the removal treatment. *Each point* represents the average of the studied leaf trait for each species. g_s r—average values of stomatal conductance for removal treatment; g_s add—average values of stomatal conductance for addition treatment; A_{max} r—average values of maximum photosynthesis for removal treatment; A_{max} add—average values of maximum photosynthesis for addition treatment

by differences in leaf phenology patterns across different savanna vegetation types.

We have to take into consideration that changes in some physiological traits may be dependent on a time–response to treatment (Güsewell et al. 2003) so 4 years might not be sufficient time to allow us to observe a significant response. Our results might not represent the entire year because all measurements were taken only during the wet season. However, because of the higher water vapor deficit (Rossatto et al. 2013) and higher litter production in the dry season, the observed differences in leaf water status between litter addition and removal plots would be expected to increase. Previous studies have observed that the main effect of litter was determined by its physical structure, even more important than any chemical role in the organic matter (Dyksterhuis and Schmutz 1947; Xiong and Nilsson 1999; Hovstad and Ohlson 2008). We can conclude that the role of litter in the Cerrado ecosystem in the short term is as a buffer of soil microclimate, influencing ecosystem water balance, more than its effects on soil nutrient pools, being perhaps more critical for immobile nutrients, such as Ca, which are not readily retranslocated from senescing leaves.

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