REGULAR ARTICLE

Leaf litter manipulations alter soil physicochemical properties and tree growth in a Neotropical savanna

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Abstract
Aim This study was aimed to assess the role that leaf litter play in nutrient cycling, nutrient soil availability and ecosystem processes in an oligotrophic tropical savanna.
Methods A four year experiment was performed in a Neotropical savanna from the Brazilian plateau (cerrado), in which litter levels were modified, and the resulting changes in biophysical and chemical soil properties were studied. Changes in organic matter decomposition, soil respiration and stem growth of the six most common tree species were also monitored.
Results Compared to litter removal plots, double litter plots had lower maximum soil temperature and higher soil water content, and litter decomposition rates in one

of three species studied, consistent with higher soil respiration rates observed in this treatment. With the exception of Ca, there were no significant differences in nutrients between the removal, natural and double litter plots, even though most nutrients tended to increase in the double litter plots by the end of the experimental period, while in the control plots nutrient levels remained relatively constant. Of the six tree species used for growth analysis, only one, *Sclerolobium paniculatum*, a fast growing species with shallow roots, had a significant increase in stem growth due to litter addition.
Conclusion Preliminary results over four years indicate that litter removal and addition resulted in some significant changes and tendencies that indicate that

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litter is effectively altering ecosystem processes. The information obtained also suggest that nutrient cycling in plots with natural litter levels (control plots) was in a closed loop; most nutrients released by litter decomposition and mineralization were absorbed and reutilized immediately by the plants, thus minimizing nutrient leakage outside the system.

Keywords Litter decomposition rates · Nutrient cycling · Soil fertility · Soil respiration · Tree growth · Tropical savannas

Introduction

Litter has two major roles in forest and savanna ecosystems: (i) it is an important component of nutrient and carbon cycling and (ii) it forms a protective layer on the mineral soil surface, helping to regulate soil microclimate (Sayer 2006). Litter manipulation can affect ecosystem carbon turnover, soil nutrients and several biophysical soil properties such as diurnal temperature fluctuations, water availability and bulk density of upper soil layers (e.g. Sayer et al. 2006). Litter manipulation may also affect both root activity and microbial communities, including those of decomposing organisms which may affect soil respiration rates (Sayer 2006; Ryan and Law 2005). If soil chemical composition is modified as a consequence of litter removal or addition, growth and carbon allocation patterns of plants may change as well. Because litter interacts with many variables simultaneously, predicting the consequences of changes to litter inputs at the ecosystem level is challenging. Experiments removing and adding litter can provide an empirical basis for assessing its role on ecosystems nutrient cycling, particularly in nutrient poor ecosystems such as Neotropical savannas. The decaying plant matter (e.g. leaves and small branches), in many tropical ecosystems, is critical for the maintenance of ecosystem production, and consequently its study may not only provide relevant information for understanding ecosystem processes but also for predicting changes due to land use.

Cerrado soils are nutrient deficient with low pH and cation exchange capacity (Furley and Ratter 1988; Furley 1999; Haridasan 2000, 2001). A long-term fertilization experiment in Brazilian savannas showed that (1) total leaf surface area and basal area

per tree increased with added nitrogen , and (2) despite being adapted to chronic nutrient limitations, woody cerrado species can exploit increases in nutrient availability by allocating resources to maximize carbon gain and enhance growth (Bucci et al. 2006). Increases in above-ground productivity of trees receiving nitrogen fertilization support the notion that cerrado trees are N limited, however, a highly efficient and complete resorption of P in leaves during senescence, supports the notion that cerrado trees are also P limited (Kozovits et al. 2007). Fertilization experiments can provide information on the nature of nutrient limitation for ecosystem function, but may produce artifacts on nutrient cycling due to the large amount of fertilizer added once or a few times. Furthermore, the chemical composition of the nutrients in fertilizers may differ from those released by litter decomposition, and there is a potential for interactions with other nutrients, as well as non-desirable effects on soil decomposing organisms. Litter manipulations, and particularly increases of litter inputs, may enhance nutrient availability without the potential artificial effects of fertilizers.

Savannas of central Brazil are highly seasonal environments characterized by a 5 months dry season, followed by a 7 months wet season. Despite the stressful conditions that persist through the dry season, most tree species maintain active leaves and produce new leaves during this period, even before the beginning of the wet season (Franco et al. 2005; Lenza and Klink 2006). Litter accumulates mainly during the dry season because most trees shed their leaves at this time and decomposition rates are low during this period (Kozovits et al. 2007) due to low water potentials in the upper layers (Bucci et al. 2008). The majority of litter decomposition occurs at the beginning of the wet season, when soil water content is high and litter is still abundant (Kozovits et al. 2007).

Because of the very low soil nutrients and soil organic matter in the central Brazilian savannas, we hypothesized that the major nutrient sources for growth are nutrients released by decomposing litter. Altering the amount of litter on the savanna floor by removal or addition should result in relatively rapid changes in nutrient availability and tree growth, and consequently should alter biophysical conditions such as soil temperature, water content and organic matter

decomposition. We expected that the results from the present experiment would provide useful information on regulatory processes of savanna ecosystems.

Materials and methods

Study system and experimental design

The study was carried out at the Instituto Brasileiro de Geografia e Estatistica (IBGE) Ecological Reserve, a field experimental station located 33 km south of Brasilia, Brazil (lat. 15° 56′, long 47° 53′ W, alt. 1100 m). The IBGE includes areas of all major physiognomies of cerrado vegetation from open to closed savannas, and evergreen gallery forests restricted to flood plains of small rivers and streams IBGE (1995). Annual precipitation averages 1500 mm (www.recor.org.br). There is a pronounced dry season from May through September with the months of June, July, and August being nearly rainless. Mean annual temperature is 22°C. Maximum and diurnal air temperature differences can be as large as 20°C during a typical dry season day. The study site was located in an area protected from fire for at least 30 years. Two 320 m × 50 m areas (parallel to a narrow abandoned dirt road) were divided into 40 m segments. In each segment the corner of a 20×20 m plot was randomly located with two conditions: (1) plots had to be at least ten meters away from the abandoned dirt road and (2) plot edges had to be at least five meters from the border of each segment. Fifteen permanent plots were established.

An inventory of all woody stems with diameter >5 cm (30 cm above the soil surface) was conducted in all plots. A total of 748 individuals representing 53 species, 42 genera and 25 plant families were inventoried in a Cerrado sensu stricto physiognomy. Six most abundant species which represented 46% of all individuals in the study site were selected for intensive studies: *Qualea grandiflora* Mart. (Vochysiaceae), *Caryocar brasiliense* Camb. (Caryocaraceae), *Ouratea hexasperma* (A.St.-Hil.) Bailll. (Ochnaceae), *Sclerolobium paniculatum* Vogel. (Fabaceae), *Scheflera macrocarpa* (Cham. & Schltdl) Frodin. (Araliaceae) *and Miconia pohliana* Cogn. (Melastomataceae). The 15 permanent plots were grouped in five blocks of similar tree basal area and species composition. Three treatments were randomly assigned within each block: removal of litter (from here on referred as 'litter removal'), addition of litter ('double

litter') and no litter manipulation ('natural litter') (Fig. 1). Litter removal was carried out roughly once a month during the dry season from July 2004 to August 2007. The litter collected from each removal plot was placed in plastic bags, weighed and transported to the litter addition plots in the same block, and spread on the forest floor (Fig. 1). The transport of the litter material from the removal to the double litter plots was done in the same day. Litter removal was done less frequently during the rainy season because the amount of litter fall during the wet season is relatively low compared to the dry season Valenti et al. 2008.

Soil water content and temperature

Five soil samples were collected at random locations within each of the 15 experimental plots during the dry season (September, 17 of 2007). Samples were collected at 5, 30 and 60 cm depth and immediately placed in tin canisters. A total of 45 samples were collected for each collecting period: 5 plots*3 treatments* 3 depths. Samples were weighed and then oven dried at 105°C until they approached constant weight to obtain gravimetric water content.

Soil temperatures at 1, 5, 15 and 30 cm were measured with copper-constantan thermocouples in three 1 m×1 m subplots in one randomly selected plot
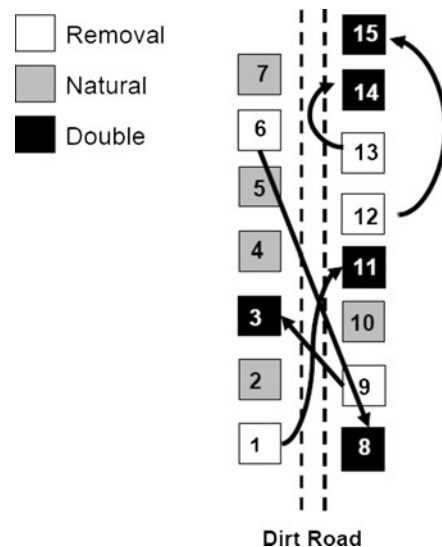

Fig. 1 A Scheme of the experimental designed. The fifteen permanent plots were grouped in five blocks with similar characteristics. The arrows indicate the direction in which the litter obtained from the removal plots was added to the double litter plots

of each of the three treatments during a four days period from October 18 to October 21 of 2005. Temperatures were measured every minute, and 30 min averages were recorded using a data logger (CR10X, Campbell Scientific, Logan, UT). Since all the experimental plots were located in a homogenous savanna stand with similar leaf area index and soil type, we expected our measurements to reflect the overall treatment effects.

Rate of litter decomposition

A decomposition experiment was performed to assess the rates of litter decomposition in the three litter treatments. The leaf mass per unit area (LMA) of the six most abundant species was measured to choose three abundant species with similar leaf phenology but representing a large range of LMA: *S. macrocarpa*, *S. paniculatum* and *O. hexasperma*. Senescent leaves of these focal species were collected by gently shaking the trees at the end of the dry season of 2006 from August to September. The litter samples were sun-dried and stored at room temperature until the onset of the rainy season in November of 2006 when there was sufficient soil moisture and an active community of decomposers to initiate decomposition in the field. Litter bags (20 cm×20 cm, 1 mm mesh size) were filled with 10 g of air-dry leaves from one of the three focal species, sealed with rustles staples and individually marked. Water content of air-dry samples was determined by oven drying subsamples of the air-dry senesced leaves.

Litter bags were placed in the field on November 20, 2006, in 2 m×2 m subplots that were randomly located within each experimental plot. Each subplot had a total of 18 litter bags divided in 6 sets with 3 litter bags per set (one per species). Each set of bags was connected by a cord to make easier the collection of individual sets. The bags were placed in contact with the ground, underneath the most recently fallen leaves. Five collections were carried out 20, 60, 90, 150 and 420 days after placing the litter bags in the field. Once the litter bags were collected, the litter was oven-dried at 55°C until it approached constant weight. Roots or other plant parts were removed prior to the collection of the litter bags. We collected a total of 36 litter bags each time, sampling only four plots per treatment and one litter bag per plot (4 plots*3 treatments*3 species=36 bags). We could not use all

the 15 plots because we did not have enough leaf material to place bags in every plot.

Soil respiration

Soil respiration was measured to assess the intensity of biological activity. To measure soil respiration, thin-walled PVC collars were inserted in four randomly placed locations within each plot. The collars were installed at least one day before measurements to avoid recording artificial amounts of CO_2 fluxes caused by the disruption of the soil due to collar insertion. The collars were 10 cm in diameter and approximately 7 cm in height. The insertion depth of the collars was 3 cm, to minimize cutting of fine roots. This insertion depth was chosen because it has been shown that soil respiration rates decrease with increasing depth of collar insertion (Wang et al. 2005). Soil temperatures were measured simultaneously with soil respiration using a Li-Cor soil temperature probe Type E.

Soil respiration was measured using a Li-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) with an attached soil respiration chamber (Li-6400-09). The method includes scrubbing a small amount of CO_2 inside the chamber and then measuring the rate of CO_2 increase. The ambient air CO_2 concentration (the target) next to the soil surface was determined by placing the soil chamber with the opening near the ground. Measurements begin after scrubbing the CO_2 concentration below ambient (ΔCO_2) and finished when CO_2 levels reaches the same ΔCO_2 above the target. Target values were set before every measurement cycle. The ΔCO_2 was set at 5 μmol mol^{-1} or at 10 μmol mol^{-1} depending on the CO_2 fluxes recorded prior to the measurements (Wang et al. 2005).

The structure of data collection was hierarchical (nested design). In the first three collections (August 2006, November 2006 and August 2007) we had two consecutive days of measurements with three measurements per subplot and four subplots per treatment. For the last collection (October 2007), we had only one day of measurements because of weather conditions.

Soil nutrients

To evaluate nutrient availability and pH, composite soil samples of 250 g were collected from four depths

(5, 10, 25 and 50 cm) from each plot, once a year from 2004 to 2008. For chemical analysis a total of 60 samples (5plots per treatment, 3 treatments, 4 depths) were obtained during each collecting period. Samples were collected using an auger, and placed in plastic bags and transported to the laboratory for analysis. Soil pH was measured in 1:2.5 soil-water suspension and in 1 M KCl, exchangeable Ca, Mg and Al were determined in soil extracts of 1 M KCl and exchangeable K and available P, Fe, Mn, Zn and Cu in Mehlich's extract of a diacid mixture of 0.05 M HCl and 0.0125 M H_2SO_4. The cations in soil extracts were determined by atomic absorption spectrophotometry and P by colorimetry (Allen 1989). Total N in soil was determined by Kjeldahl digestion and distillation. Soil organic carbon was determined by the method of Walkley and Black (Allen 1989).

Stem growth

Fifteen trees of each of the six focal species were selected to measure stem growth. When possible, three individuals per species per plot were included. Dendrometer bands were installed on all trees. Dendrometers were made manually and consisted of a stainless steel tape encircling a tree stem, with one end passing through a collar (which is attached to the other end) and connected back to itself with a stainless steel spring, as described by Cattelino et al. (1986). Three months after dendrometer installation (allowing for stem-dendrometer adjustment) a permanent mark was made on the metal band next to the collar. As stem diameter increases, the mark moves away from the collar and the spring is stretched, keeping the dendrometer tight. A flexible ruler was used to measure stem diameter changes with an accuracy of 0.5 mm. Stem growth was recorded monthly form July 2005 to February 2006 and every 2 months from April 2006 to June 2008. Stem growth was expressed as percentages in relation to initial stem circumference.

Litter production and leaf area index

Litter production was measured using 75 leaf litter traps (5 litter traps per plot) from July 2006 to July 2008. One litter trap was located near each corner and one in the center of the plot. The leaf- litter traps had

a square opening of 50 cm×50 cm and were placed at 40 cm above the ground. All trap contents were collected monthly, placed in a plastic bag, and transferred to IBGE's laboratory and oven-dried at 65°C for 96 h. After drying, the litter samples were separated into: 1) leaves, 2) reproductive structures, and 3) other materials, which included stems, twigs and pieces of bark, and then weighed. Small particles less than 1 mm were discarded.

Leaf area index (LAI) was measured in July 2004, September and October 2007 using an AccuPAR line-integrating ceptometer (*Accupar, Decagon Devices*, Pullman, WA, USA). All measurements were performed only during clear sky days within one hour of solar noon. We subsampled LAI at 13 locations within each plot on each sample date.

Statistical analyses

We tested the differences among treatments in soil water content, litter decomposition rates, soil nutrient, aluminum and carbon contents and soil pH using one-way analysis of variance (ANOVA). To test the effect of litter addition and removal on soil respiration and tree growth we used mixed-effect models in R, version 2.6.2 (R Development Core Team 2008) with the package "nlme" version 3.1-86 (Pinheiro and Bates 2000). When we had two consecutive days of measurements for the same plot, two models with temporal pseudo-replication were tested; both models had treatment as a fixed factor and day as an intercept. Model 1 had subplot nested within treatment plot and model 2 had plot-subplot concatenated. We used the Aikake's information Criterion (AIC) as a measure of model fit to select the model with greater explanatory power of the two models. We tested the differences in soil temperature among treatments using one-way analysis of variance (ANOVA). The differences reported are after a pairwise t-test with $p < 0.05$.

To analyze tree growth, three models with different fixed-effects structures were tested. Model 1 had treatment as a main effect, model 2 had treatment as a main effect and initial circumference as a covariate as well as initial circumference by treatment interaction, and model 3 had treatment as main effect and initial circumference as covariate. All the models had plot as a random factor. Aikake's information Criterion was used as a measure of model fit.

Results

Soil water content and temperature

Soil water content in the upper 5 cm soil layer of the litter removal plots was significantly lower ($p<0.05$) compared to natural litter and double litter plots (Fig. 2). Soil water content did not differ significantly among treatments at 30 or 60 cm depth. Daily maximum soil temperature was significantly lower ($p<0.05$) at all depths in litter addition plots as compared to natural and litter removal plots (Fig. 3). Maximum soil temperature at 1 cm depth in the litter removal plot was approximately 10°C higher than in the litter addition plot. Significant difference ($p<0.05$) in average soil temperature was restricted to the surface layer (1 cm depth) although there was a general tendency for lower temperature in litter addition plot.

Rate of litter decomposition and soil nutrients

The percent of leaf mass remaining in decomposition bags decreased exponentially with time (Fig. 4). The decomposition rates differed among species. Leaves of *S. macrocarpa* decomposed four times faster than leaves of *S. paniculatum* and *O. hexasperma*. However, litter manipulation affected the decomposition rates of only *S. paniculatum* leaves, with lower decomposition rates in the litter removal plots ($p<0.05$).
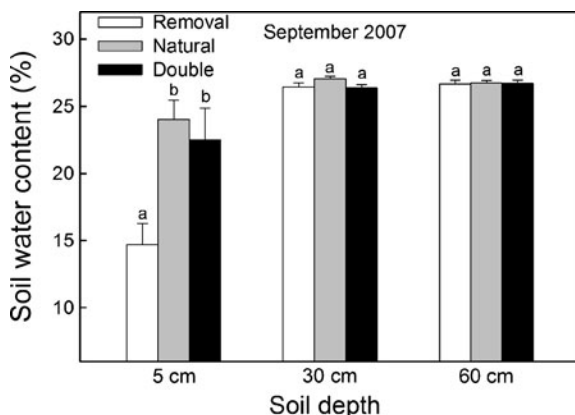

Fig. 2 Soil gravimetric water content in the experimental plots: removal, natural and double litter. Three soil samples were collected on September 17, 2007 at different depths (5, 30 and 60 cm) in all treatment plots. Bars are averages + 1SE. Bars marked with the same letter are not significantly different as determined by Tukey's pairwise comparison ($\alpha=0.05$)
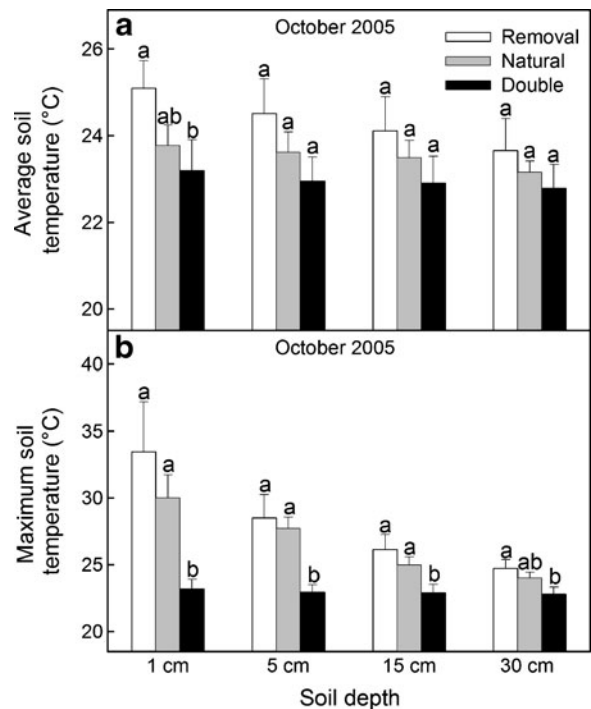

Fig. 3 Average and maximum soil temperatures at different depths (1, 5, 15 and 30 cm) in the experimental plots ($n=3$ per depth): removal, natural and double litter, measured from October 18 to 21, 2005, in the middle of the dry season. Bars are averages + 1 SD. Bars marked with different letter are significantly different at $p<0.05$

Total carbon, pH and nutrient availability in the first 5 cm of soil were not significantly different among plots before litter manipulation began on July 2004 (Fig. 5). After 4 years of litter manipulation Ca and Mn levels were significantly higher ($p<0.05$) in double litter compared to natural litter and litter removal plots. Magnesium, carbon and nitrogen tended to be higher ($p=0.06$, 0.07 and 0.08 respectively) in the addition treatment (double litter plots) compared to the natural litter and litter removal treatments. Phosphorus levels tended to be higher in the double litter plots on the fourth year since the litter manipulation began. On the other hand, pH was marginally lower ($p=0.06$), in the double litter treatment compared to the natural litter and removal treatments by July 2008 (Fig. 5). Aluminum availability did not differ among treatments.

Soil respiration and stem growth

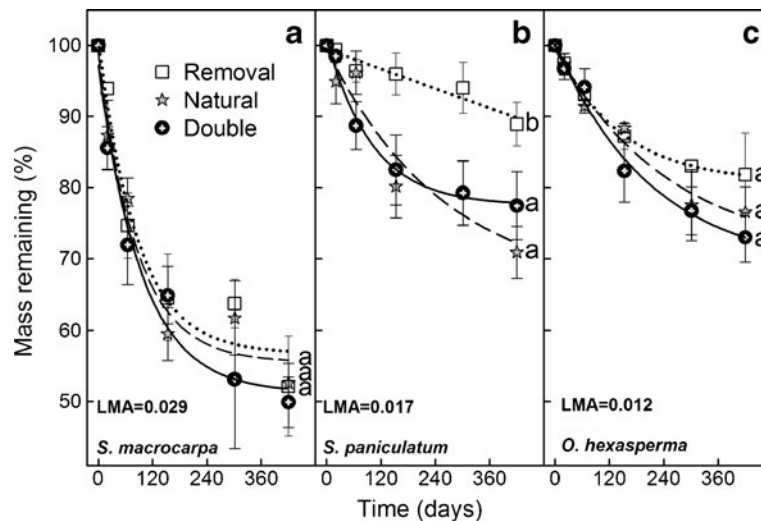Soil respiration was higher ($p<0.001$) in the double litter plots compared to litter removal and natural litter

plots (Fig. 6) in August 2006, November 2006 and October 2007, but only marginally significant (*p*=0.08) in August 2007. Based on model selection, plots and subplots were treated separately as random factors only for the data collected in November 2006. For the remaining three data sets the analysis was carried out at the subplot level. Soil respiration was 2 mmol m^{-2} s^{-1} higher during the wet season compared to the dry season (Fig. 6), perhaps reflecting in part the higher activity of the decomposing organisms and shallow roots.

Cumulative stem growth for the six most abundant species, four evergreen (*M. pohliana*, *S. macrocarpa*, *O. hexasperma* and *S. paniculatum*) and two deciduous (*Q. grandifloria* and *C. brasiliense*), in the removal, natural litter and litter addition plots are shown in Fig. 7. Only one of the evergreen species, *S. paniculatum*, exhibited greater growth in the litter addition plots (*p*=0.01) than in natural litter or the removal plots.

Litter production and leaf area index

The amount of litterfall in the three litter treatments exhibited seasonal changes from July 2006 until July 2008. Leaf fall was highest at the end of the dry seasons (July to September, Fig. 8 A). Litter fall was similar among litter treatments in terms of seasonal patterns and in terms of average values, with standard errors overlapping at each collection time. The branches, twigs, and reproductive structures components of litter fall did not show consistent seasonal changes (Fig. 8 B, C). Leaf area index, that was measured to provide an index of alterations in tree canopy cover as a result of the treatments, was not affected by the litter treatments. For example, in October 2007, LAI averages ± SE were 1.19±0.10, 1.2±0.13, and 1.39±0.19 for the removal, control and double litter plots respectively.

Discussion

The long term litter manipulation in the experimental study site influenced soil properties and ecosystem processes and had an effect on tree growth in one of the six species investigated. Litter addition significantly decreased maximum soil temperature in all soil layers and increased soil water content in the uppermost soil layer. These changes in soil temperature and water content likely enhanced the activity of decomposing organisms and superficial root systems,

Fig. 5 Total carbon, pH and soil nutrient concentration for the first 5 cm of soil in the experimental plots (removal, natural and double litter). Results are shown for the initial conditions (July 2004) and during four years of treatment, from July 2005 until July 2008. Values are averages ± 1SE ($n=5$ per treatment). Values for 2008 with the same letter are not significantly different as determined by pairwise t test comparison ($\alpha=0.05$). Holm adjustment method was used to control for the family-wise error rate
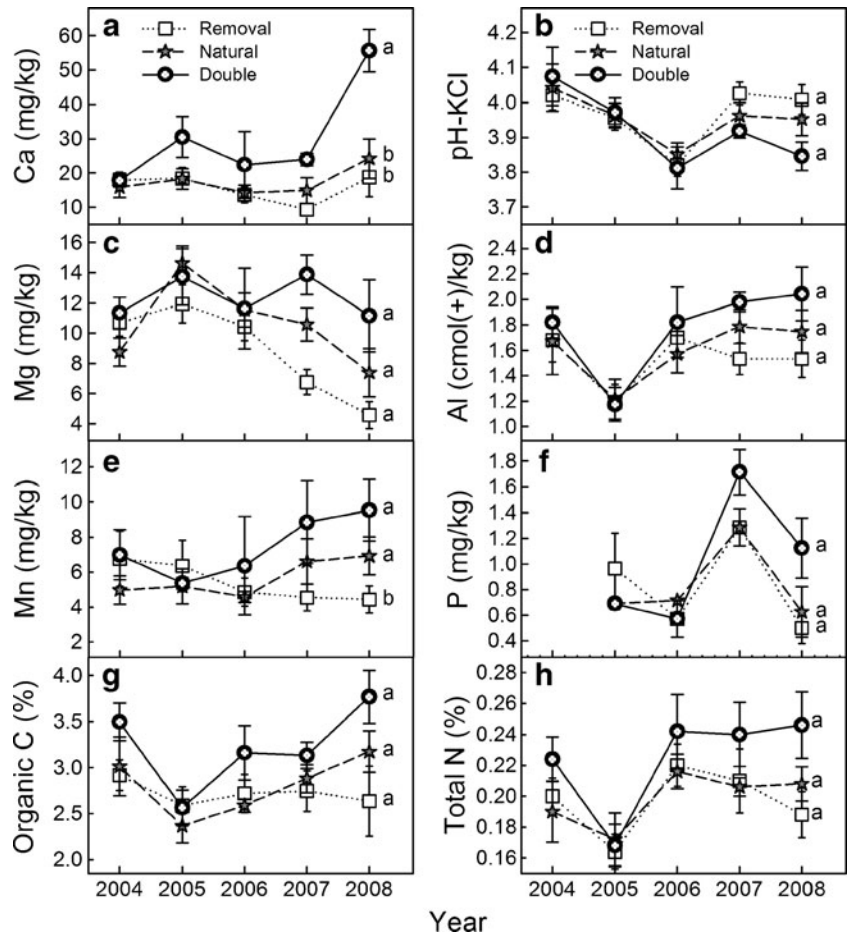
as soil respiration was higher in the double litter plots, particularly during the wet season. Litter addition also

increased litter decomposition rates of leaves of one of the three studied species. It is possible that

Fig. 6 Soil respiration measured in all experimental plots (removal, natural and double litter) at the end of the dry season (August 2006 and 2007) and during the wet season (November 2006 and October 2007). Bars are averages + 1SE ($n=20$ per treatment). Bars marked with the same letter are not significantly different as determined by treatment contrast analysis ($\alpha=0.05$)
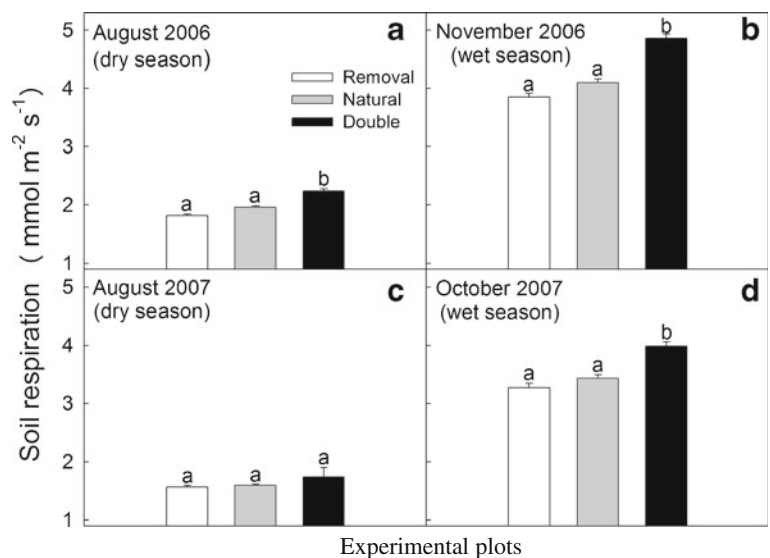
Fig. 7 Cumulative stem growth (percentage growth normalized to the initial stem circumference) of six dominant woody species, from August 2006 until May 2008 in removal, natural and double litter plots for 4 evergreen (*Miconia pohliana, Schefflera macrocarpa, Ouratea hexasperma* and *Sclerolobium paniculatum*) and 2 deciduous (*Qualea grandifloria* and *Cariocar brasiliense*) tree species. Values represent stem growth averages of 5 to 14 individuals depending on species and treatments. Lines with the same letter are not significantly different as determined by treatment contrast analysis ($\alpha = 0.05$). Error bars ($\pm$1SE) were included only for the last date of measurements
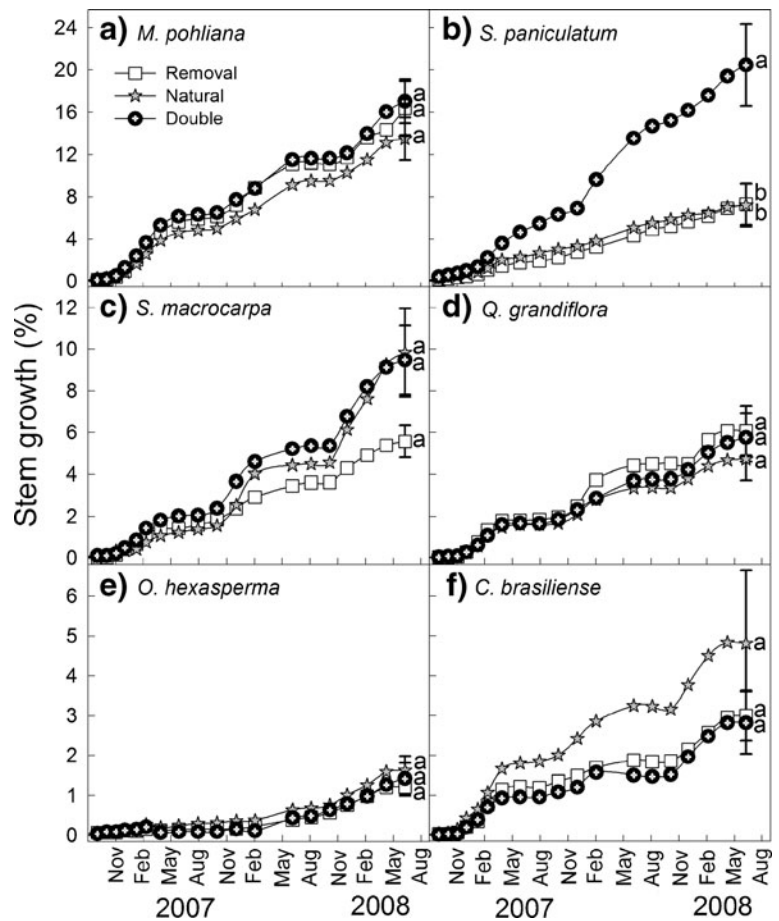
mineralization of nutrients in the double litter plots as a result of faster litter decomposition, increased the uptake of nutrients by trees having relatively shallow root systems.

Soil water content and temperature

The litter layer acts as an interface between the soil surface and the atmosphere, providing some protection to the soil surface by intercepting rain (Benkobi et al. 1993), solar radiation and buffering the soil surface against large temperature fluctuations (Ponge et al. 1993). Litter's buffering effect is particularly important in savannas because canopy interception of rain and shading by trees is relatively low compared to tropical rain forests. Depending on the type of savanna, sometimes less than 40% of the ground is covered by trees. At the end of the dry season some amount of the herbaceous vegetation dies-back, thereby exposing a higher percentage of the soil surface. At this time of the year the buffering effect of litter should be even more important for maintaining ecosystem functions.

In this study, litter removal resulted in maximum soil temperature increases and in a decrease of soil water content. The effects of litter manipulation on soil water content and soil temperature have been reported for other ecosystems (Sayer 2006). For example, it was observed that litter removal increases water content immediately after precipitation and decreases it during dry periods (e.g. Lunt 1951; Ginter et al. 1979). Similar to results obtained by Gill (1969) and Poser (1990) for other ecosystems, we found little effect on soil water content in the double litter treatment. In our study, the presence of a thick layer of litter in the double litter plots buffered maximum soil temperatures in the first centimeter of the soil profile by approximately 10°C in the double litter plots, compared to the removal plots.

Fig. 8 Litter fall in the removal, natural and double litter plots from July 2006 until July 2008. Litter was subdivided into (A) leaves, (B) branches and twigs, and (C) reproductive parts (e.g. flowers and fruits). Values are averages ± 1SE (*n*=25 per treatment)
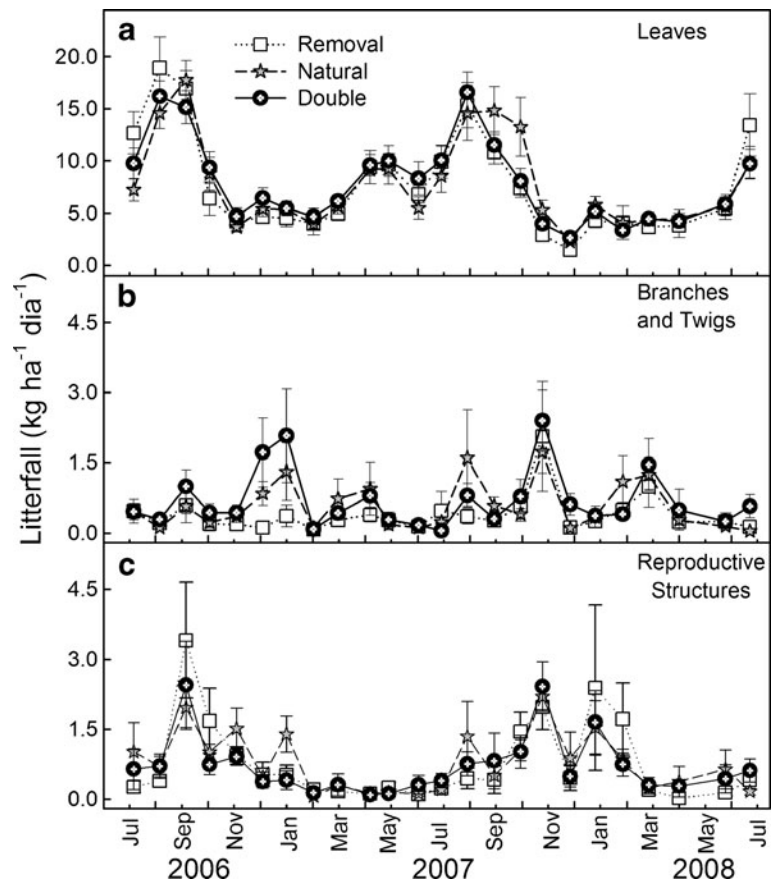
Litter decomposition

Reports in literature regarding the effects of liter manipulation on microbial activity are not consistent. Some studies showed that litter removal decreases active microbial biomass (e.g. Anderson and Domsch 1978; Peng et al. 2003; Nilsson et al 1999), while others showed no decrease in microbial biomass (Nadelhoffer et al. 2004). In the present study litter manipulation affected the decomposition rate of the leaves of only one (*S. paniculatum*) out of three species investigated, for which the decomposition was faster in the double litter plots than in the removal plots.

Soil respiration and soil nutrients

Litter removal may affect microbial communities in the soil because of decreases in the amount of fresh decaying organic matter, which should result in lower soil respiration rates (e.g. Bowden et al. 1993; Li et al.

2004). Litter itself posses an important microbial community growing on the senescent leaves, so litter removal is not only a removal of substrate to decomposers but also a removal of decomposers. Most studies have found that litter removal decreases soil respiration from 7–60% depending on the vegetation type and the duration of the litter removal period (Sayer 2006). In our study, litter removal resulted in a decrease in soil respiration of about 7 to 15% during both the wet and dry seasons.

The increase of both leaf decomposition rates in one species and the larger amount of litter in the double litter plots resulted in partial increases in soil nutrient concentrations compared to the litter removal plots. After 4 years of litter manipulation a significant increases in one important soil nutrient (Ca) and a trend of increase in other soil nutrients was observed. Manganese, Magnesium, carbon and nitrogen tended to be higher and significant at $p=0–05$, 0.06, 0.07 and 0.08 respectively, in the addition treatment (double litter plots) compared to the litter removal treatments.

Along topographic gradients in the cerrado, vegetation varies from open savannas with relatively few small trees in the lower portions of the topographic gradients to closed savannas or woodlands with a relatively high density of taller trees in the upper portions of the gradient (Goodland and Pollard 1973; Hoffmann et al., 2005). We did not find variation in soil nutrient availability along these topographic/tree density gradients at the IBGE's Ecological Reserve (R. Villalobos-Vega, unpublished information). Other studies have shown inconsistent changes in nutrient concentrations along these topographic/physiognomic gradients (e.g. Askew et al. 1970; Gibbs et al. 1983; Ribeiro 1983; Haridasan 1992; Bucci et al. 2006). The reasons for not finding consistent differences in soil nutrient availability along these gradients may reside in the nature of the carbon and nutrient cycling of the oligotrophic cerrado soils. Litter decomposes faster, and mineralized nutrients are rapidly absorbed by roots at the onset of the rainy season (Garofalo 2001). Even though litterfall increases along the tree density gradient, differences in litter production across savanna physiognomies are not as large as the differences caused by the experimental manipulation of litter in this study. We have found that litter accumulated at the end of the dry season ranged from 103 g m^{-2} in open savannas to 282 g m^{-2} in closed savannas. In contrast the average difference in the amount of litter between litter addition and removal plots in this study was approximately 440 g m^{-2}, which was substantially larger than differences observed along the topographic/physiognomic gradients. At a soil depth of 50 cm nutrient concentrations is extremely low, and only traces of nutrients are found in the water table located at 1 to12 m below the soil surface, depending on the topographic position and season (results not shown). In natural litter plots the amount of soil nutrients in the upper soil layers remained fairly constant during the 4 years of our study. Thus it is likely that nutrient cycling in the cerrado savannas is in a closed loop with most of the nutrients released by decomposition and mineralization being rapidly absorbed and utilized by plants, minimizing nutrient leakage. Preliminary results indicate that litter accumulation in double litter plots contributed to increased availability of essential nutrients, especially of Ca, in the upper soil layers. Such an increase in soil fertility suggests that the additional nutrients were not utilized immediately by the plants. A new equilibrium point in the nutrient circulation pathway may be reached once new growth take place as a consequence of higher soil fertility.

Tree growth

Among the six tree species studied, stem growth was significantly higher for only one species, *S. paniculatum,* growing in the double litter compared to removal and natural litter plots. This is a fast growing pioneer species (Pires and Marcati 2005; Felfili et al. 2004) with shallow root systems (Jackson et al. 1999; Scholz et al. 2002) which have associations with mycorrhizal fungi and nitrogen fixing bacteria (Quintanilha de Albuquerque and Dias 1999; Franco et al. 1996). Such associations would enable this species to quickly absorb the larger amount of nutrients released by the decomposing litter in the litter addition plots, competing successfully with herbaceous plants in their ability to exploit limiting resources. Despite being adapted to chronic nutrient limitations, *S. paniculatum* appears to be able to exploit increases in nutrient availability. It is possible that the other species do not have sufficiently shallow roots to absorb upper soil nutrients or that they allocate the newly acquired nutrients to leaf or root growth instead of stem growth or reproduction. Longer treatment periods probably will result in enhanced stem growth in some of the other species (Bucci et al. 2006).

Conclusions

The removal as well as the addition of litter significantly affected ecosystem-level processes and properties such as soil temperature, soil water content, availability of some nutrients and soil respiration. Nutrient uptake by roots, tree growth, litter production and soil nutrient availability are in steady state equilibrium in natural communities (natural litter plots). Such equilibrium is important for nutrient conservation and to minimize nutrient leakage in a highly nutrient limited ecosystem, such as the Neotropical savannas. Altering the amount of litter on the savanna floor, one component of this interlocked system, resulted in a substantial changes of maximum soil temperature, soil water content and soil

respiration, stem growth of *S. paniculatum* and the decomposition rates for one of three studied species. After 4 years of continuous litter manipulation, the addition of litter tended to increased organic soil carbon as well as some soil nutrients, including nitrogen and phosphorus (two of the most limiting nutrients in the cerrado). Only one essential nutrient (Ca) increased significantly with respect to the other two treatments. Opposite trends were found for the removal treatment.

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