

Litterfall dynamics in a iron-rich rock outcrop complex in the southeastern portion of the Iron Quadrangle of Brazil

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ABSTRACT

Ecosystems on *cangas* (duricrust) present considerable heterogeneity of habitats due to microtopographic variations, soil accumulation and a variety of plant functional groups. Therefore, spatial and temporal ecosystem processes such as litterfall are to be expected to be large, and the absence of a level of productivity represents all the facets of iron-rich landscapes. We investigated litterfall in a iron-rich rock complex in the Iron Quadrangle of Brazil, with habitats formed on different evolutionary stages of the soil, resulting in a gradient of biomass, canopy cover and community structure. The measurements were made in open field areas, dominated by herb-shrub vegetation and interspersed with islands of dense vegetation in which there were individual trees, as well as in areas of semideciduous forest. The litterfall, especially that of leaf litter, followed the gradient of woody cover and was approximately two times greater in the forest formation. However, the spatial and temporal variations in deposition were greatest in the herb-shrub areas and least in the semideciduous forest area, intermediate values being obtained for the tree island areas. The peaks in litterfall also varied among habitats, occurring in some periods of the rainy season and during the transition from rainy to dry in the herb-shrub and tree island areas, whereas they occurred at the end of the dry season in the semideciduous forest area. The results show significant differences in the patterns of litterfall among different physiognomies within the same iron-rich rock complex, indicating the need for expanded studies, focusing on the flow of matter and energy in such environments.

Key words: Canga, iron duricrust, ferruginous fields, litter production, ecosystem productivity

Introduction

Vegetation on rock outcrops over iron duricrust constitute unique ecosystems that occur exclusively in that type of landscape (Rizzini 1979; Secco & Mesquita 1983). In Brazil, duricrust are known as *cangas* and the associated vegetation formations are referred to as *canga* ecosystems, which occur mainly in the so-called Iron Quadrangle and Serra de Carajás regions of the states of Minas Gerais and Pará, respectively (Castro 2008). Microtopographic variations influence soil volume, microclimate conditions and the local accumulation of organic matter (Benites *et al.* 2007), resulting in environmental heterogeneity, which might explain the high alpha and beta diversity of the flora in such ecosystems (Jacobi *et al.* 2007, Viana & Lombardi 2007; Mourão & Stehman 2007; Vincent & Meguro 2008). Despite the fact that the number of studies describing the flora and edaphic parameters of these ecosystems has grown considerably in the last decade, virtually nothing is known about

their functioning. The lack of information on productivity and nutrient cycling, for example, is a limiting factor for the planning of reclamation activities on lands previously used for mining iron ore and bauxite in Brazil. Over the last 50 years, mining was responsible for a > 40% reduction in the area of *canga* ecosystems in the Iron Quadrangle alone (Carmo 2010). Because the purpose of environmental restoration is the renewal of the degraded system to its original level of functioning, it is first necessary to understand the ecosystem processes in vegetation formations on iron-rich rock outcrops, which present of various physiognomies, in order to establish reference standards (Grant *et al.* 2007).

Jacobi *et al.* (2007) presented a number of ecological criteria for habitat differentiation and distribution of plant functional groups on iron-rich rock outcrops. Physical characteristics such as lithology, rock fractures, permeability, porosity and crevices would lead to heterogeneity in soil accumulation and, consequently, in the distribution of plant functional groups within these ecosystems. The combinations of plant

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functional groups, together with the creation of differentiated edaphic and microclimatic conditions should cause spatial variation in productivity within these ecosystems, especially with regard to the dynamics of litter production.

Litter deposition is the major route of nutrient return to soil in terrestrial ecosystems (Spain 1984). Litter production and decomposition restore and maintain soil fertility (Ewel 1976); determine ecosystem productivity; and regulate the balance of the nutrient cycling process as a whole (Pallardy 2008). Although tropical ecosystems exhibit continuous litter production throughout the year, there can be seasonal, cyclical variations (Spain 1984, Chave *et al.* 2010). In addition, litter production is not spatially homogeneous within a given ecosystem. The presence of gaps (Martins & Rodrigues 1999), as well as variations in soil depth and fertility (Dent *et al.* 2006, Jacobi *et al.* 2007), influence the pattern of vegetation cover, resulting in heterogeneous litterfall (Prescott 2002). Spatial and temporal variations in substrate water availability (Lawrence 2005), floristic composition (Costa *et al.* 2004), successional stage (Martius *et al.* 2004, Chave *et al.* 2010) and photoperiod (Lei 1999), together with the mechanical action of rain and wind (Cianciaruso *et al.* 2006; Terror *et al.* 2011), affect the amount of deciduous components lost by plants, as well as the dynamics and structure of the community of decomposers in the soil, and, consequently, the productivity of the ecosystem (Prescott 2002; Martius *et al.* 2004, Fisk *et al.* 2010).

The *canga* ecosystems in the Iron Quadrangle show marked seasonality in terms of rainfall. In seasonal ecosystems, the tree-shrub plant community has anatomical and physiological mechanisms that facilitate reproduction and survival during the period of highest water restriction (Franco *et al.* 2005). In the *cerrado* (savanna), where rainfall patterns are also markedly seasonal, woody plants species have different phenological strategies that allow them to overcome seasonal stress. Whereas evergreen species keep the foliage throughout the year, other species drop their foliage completely (deciduous species) or partially (semi-deciduous species), predominantly during the dry season (Lenza & Klink 2006), typically showing a pattern of greater litterfall deposition in the late dry season (Nardoto *et al.* 2006, Kozovits *et al.* 2007). Therefore, *canga* and *cerrado* ecosystems would both be expected to present a markedly seasonal pattern of litterfall.

The aim of the present study was to characterize and compare the litter production in vegetation formations on different types of duricrust in a iron-rich rock complex in Brazil. This area offers an interesting opportunity for study, because it presents a mosaic of habitats: one dominated by herbaceous plants; one composed of herbaceous plants interspersed with islands of trees and shrubs; and a semi-deciduous forest formation (at one end of the area). These three environments, all under the same climate, represent a gradient of biomass, vegetation cover and community structure associated with variations in soil and microcli-

matic parameters. Would such environmental variations be sufficient to produce distinct patterns of litterfall?

Materials and methods

Study area and climate

The study was carried out between October 2009 and December 2010 in a iron-rich rock outcrop complex in the Serra da Brígida (20°21'S; 43°30'W; elevation, 1470-1500 m), near the city of Ouro Preto, in the Iron Quadrangle, which lies within the state of Minas Gerais. Detritus from duricrust fragments, *in situ* or upstream, is commonly observed. It is known that microtopographic variations on laterite soil lead to heterogeneity in the accumulation of debris (Castro 2008). For this reason and based on *in situ* observations of the physiognomies, we defined three different vegetation habitats: herb-shrub areas (HSAs), characterized by a matrix of herbaceous-shrubby vegetation in areas where the duricrust is more exposed; tree island areas (TIAs), comprising islands of woody, arboreal, plant encroachment, presenting greater vegetation cover and a more evident litter layer on the substrate; and a semideciduous forest area (SFA), which is semideciduous seasonal forest on colluvial deposits. In the HSAs and TIAs, the soils range from entisols to humic entisols, with severely morphogenetic conditions. In the SFA, soils range from cambisols at higher altitudes, evolving to oxisols along the topographic gradient (IEF/UFV/IBAMA 2005).

Monthly precipitation was measured over a one-year period with three pluviometers, each located in an area without vegetation cover, as was the case for 300-500 m of the area sampled. During 2010, the accumulated rainfall was 1204.8 mm, with marked seasonality: 1150.9 mm (95.5%) of the yearly precipitation accumulated during the rainy season (October to April), compared with only 53.8 mm (4.5%) during the dry season (May to September). Once a month (always between 9 and 11 am), we measured air temperature and relative air humidity, as well as relative soil water content (at a depth of ≤ 5 cm). The average temperature was approximately 30.9 °C in the rainy season and 24.9°C in the dry season (Fig. 1). The annual values of relative soil water content varied: 2.3-19.6% in HSAs; 5.0-35.4% in TIAs; and 20.5-34.7% in the SFA. The mean values for relative air humidity ranged from 34.2% (in August) to 82.1% (in June).

Experimental design

Two 100-m transects were established, one in the SFA and the other within the HSA/TIA physiognomy. We designated one sampling point every 10 m, approximately 3 m from and perpendicular to the transect line, alternating between the left and right sides of the line. In the TIAs, it was not always possible to mark a point within 3 m of the transect line; and in this case, the sampling point was marked as close as possible to the line.

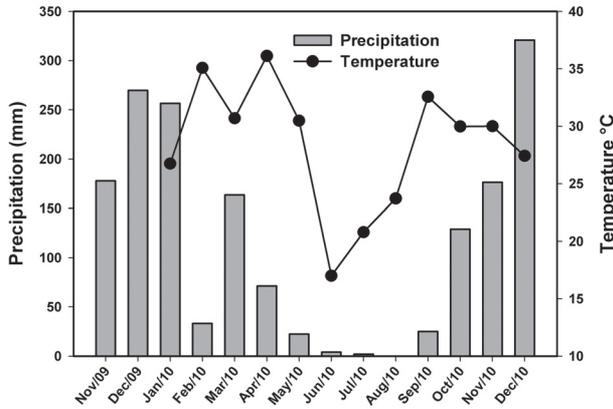


Figure 1. Cumulative monthly precipitation and mean air temperature measured monthly between 9 and 11 am, in the study area.

Litterfall production

Every two weeks, between October 2009 and December 2010, litter production was quantified at the community level. Litter collectors (0.5 × 0.5 m, 2-mm mesh) were placed at each sampling point. A total of 30 collectors were put in place, some in the HSA/TIA physiognomy (in the soil, to a depth of 10 cm) and some in the SFA (suspended at a height of 30 cm). In the laboratory, litter samples were dried (at 40°C for 72 h) and the dry weights were determined separately for leaves and for miscellaneous litter (flowers, fruits, stalks, seeds, bark), excluding animal tissues and grasses.

Statistical analysis

The data were submitted to a normality test (Kolmogorov-Smirnov test). To confirm differences in litterfall between habitats and months, we used repeated measures ANOVA. Student's t-test was used in order to detect differences in litter production between the dry and rainy seasons. For each habitat, the coefficient of variation (CV) was calculated in order to estimate the variation in litterfall among months and among sampling points. For each habitat, relationships between the monthly total rainfall and miscellaneous litter fraction were assessed using linear regression.

Results

The mean annual production of litterfall was 112.8 ± 45.7 g.m⁻² in the HSAs, 330.3 ± 108.5 g.m⁻² in the TIAs and 461.0 ± 110.8 g.m⁻² in the SFA, differing significantly among habitats (F_{2,18} = 28.501, p<0.001) and among months (F_{11,99} = 3.023, p=0.002) (Fig. 2). In addition, in all three habitats, the total litter production was significantly higher during the rainy season than during the dry season: by 76.1% in the HSAs (t₁₈ = 4.367, p<0.001); by 61.0% in the TIAs (t₁₈ = 2.206, p=0.041); and by 60.9% in the SFA (t₁₈ = 3.203, p=0.005) (Fig. 3). On average, leaf litter accounted for 59.8%

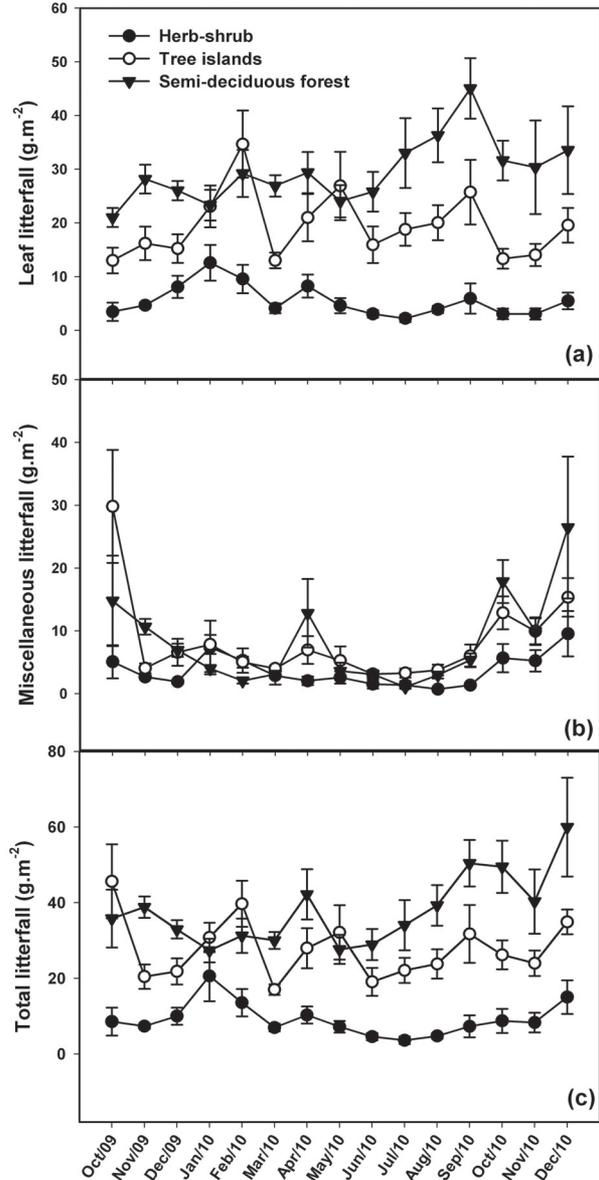


Figure 2. Mean monthly litterfall (in gm⁻²)—leaf litter (a); miscellaneous litter (b); and total litter (c)—between October 2009 and December 2010 in the open areas (herb-shrub habitats and tree islands) and in the semideciduous forest. Bars represent the standard error.

of the total annual production of litterfall in the HSAs (67.5 ± 35.1 g.m⁻²), 74.7% of that observed for the TIAs (246.8 ± 94.3 g.m⁻²) and 80.0% of that observed for the SFA (368.6 ± 96.4 g.m⁻²). As can be seen in Fig. 2, the quantity of leaf litter also differed significantly among habitats (F_{2,18} = 30.737, p<0.001) and among months (F_{11,99} = 2.041, p=0.012).

Comparing the dry and rainy seasons, we found that leaf litter production differed significantly between the two seasons only in the HSAs (T₁₈ = 2.625, p=0.017). Nevertheless, the mean production of leaf litter was higher during the rainy season in all three habitats, rainy season leaf litter

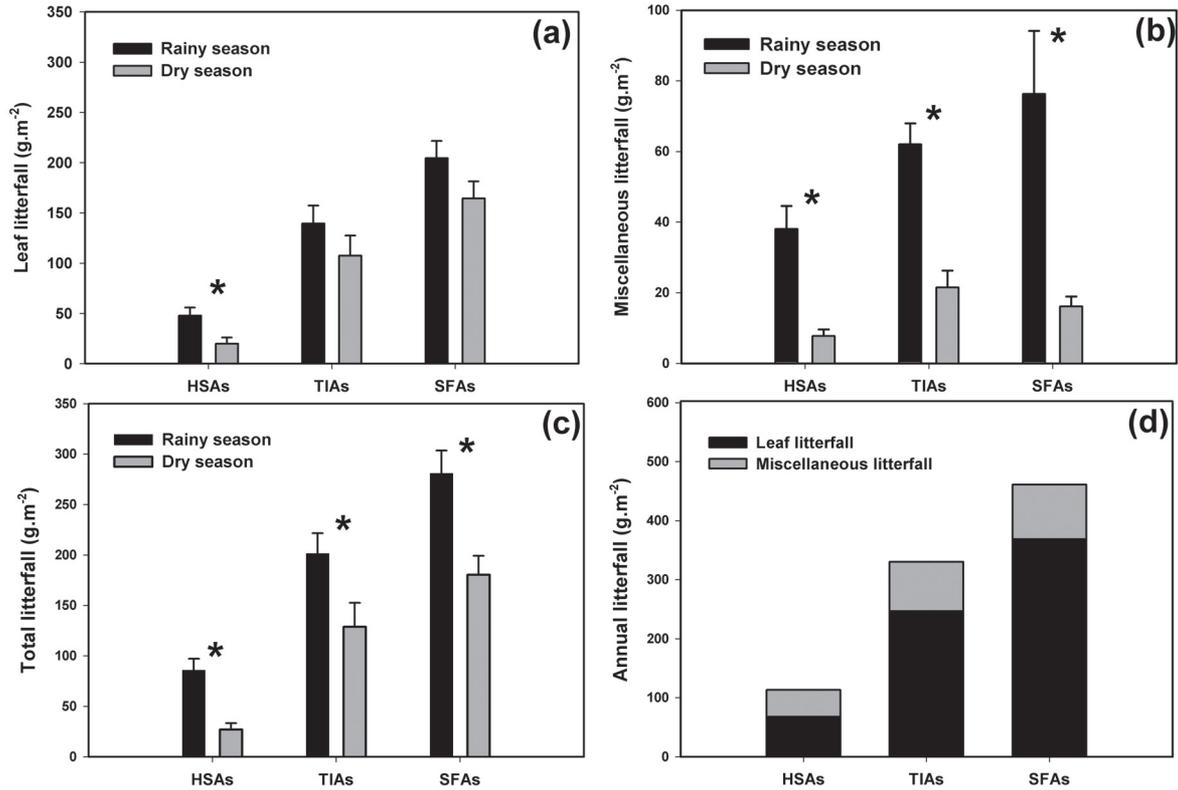


Figure 3. Litterfall—rainy and dry season leaf litter (a); miscellaneous litter (b); and total litter (c), as well as their proportional contributions to the annual total litterfall (d)—in herb-shrub areas (HSAs), tree island areas (TIAs) and semideciduous forest area (SFA). Asterisks (*) indicate significant differences between seasons (t-test, $p < 0.05$).

accounting for 70.7% of the annual litterfall in the HSAs ($47.7 \pm 25.4 \text{ g.m}^{-2}$), 56.5% in the TIAs ($139.3 \pm 56.5 \text{ g.m}^{-2}$, $p > 0.27$) and 55.3% in the SFA ($204.4 \pm 54.4 \text{ g.m}^{-2}$, $p > 0.13$), as shown in Fig. 3.

The production of miscellaneous litterfall typically peaked at the beginning of the rainy season. For example, such production was higher in October than in September—by 314.6%, 108.5% and 232.2% in the HSA, TIAs and SFA, respectively (Fig. 2). The analysis of linear regressions showed significant relationships between monthly accumulated rainfall and monthly miscellaneous litter production in all three of the habitats studied ($p < 0.001$ for all; Fig. 4).

In the HSAs, leaf litter production peaked twice during the rainy season—in January ($12.6 \pm 10.5 \text{ g.m}^{-2}$) and February ($9.6 \pm 8.4 \text{ g.m}^{-2}$)—and again during the transition between the rainy and dry seasons, in April ($8.3 \pm 6.7 \text{ g.m}^{-2}$). In the TIAs, peaks in leaf litter production occurred in February ($34.7 \pm 19.7 \text{ g.m}^{-2}$); in the early dry season, in May ($26.9 \pm 20.1 \text{ g.m}^{-2}$) and at the end of the dry season, in September ($25.7 \pm 19.1 \text{ g.m}^{-2}$). In the SFA, leaf litter production peaked during the dry season—in July ($33.0 \pm 20.5 \text{ g.m}^{-2}$) and in August ($36.3 \pm 15.9 \text{ g.m}^{-2}$), the highest peak ($45.0 \pm 17.8 \text{ g.m}^{-2}$) occurring in September, at the end of the dry season (Fig. 2a).

The seasonality of total litter production was higher in the HSAs (range, $3.6\text{--}20.2 \text{ g.m}^{-2}$; $\text{CV} = 52\%$) than in the TIAs (range, $17.0\text{--}39.7 \text{ g.m}^{-2}$; $\text{CV} = 23\%$) and the SFA (range, $27.7\text{--}60.0 \text{ g.m}^{-2}$; $\text{CV} = 26\%$). The variation in the production of leaf litter appeared to follow a gradient that is the inverse of that of woody biomass, for which the coefficients were also higher in the HSAs (range, $2.2\text{--}12.9 \text{ g.m}^{-2}$; $\text{CV} = 57\%$) than in the TIAs (range, $13.0\text{--}34.7 \text{ g.m}^{-2}$; $\text{CV} = 30\%$) and the SFA (range, $23.3\text{--}45.0 \text{ g.m}^{-2}$; $\text{CV} = 19\%$).

When analyzing the spatial variation in litterfall, i.e., comparing the averages values among collectors in each physiognomy, higher heterogeneity was found for the HSAs and TIAs (range, $49.4\text{--}498.5 \text{ g.m}^{-2}$; $\text{CV} = 62\%$) than for the SFA (range, $197.4\text{--}621.2 \text{ g.m}^{-2}$; $\text{CV} = 25\%$).

Discussion

The mean annual litter production in the HSAs and TIAs, collectively, was 219 g.m^{-2} , a value comparable to those found for vegetation formations composed of higher biomass, such as the *cerrado sensu stricto*, for which it has been reported to be, variously, 230 g.m^{-2} (Nardoto *et al.* 2006), 210 g.m^{-2} (Peres *et al.* 1983) and 151 g.m^{-2} (Kozovits *et al.* 2007). Although the mean annual litter production in

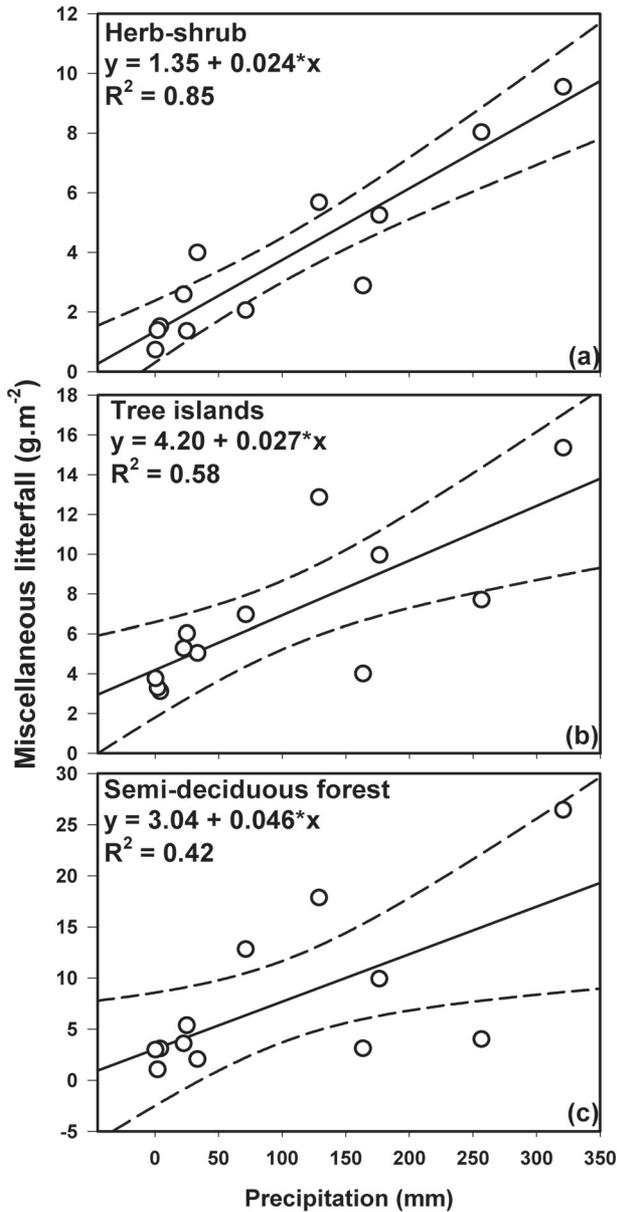


Figure 4. Relationship between monthly rainfall and the mean monthly miscellaneous fraction produced in the herb-shrub areas (a), tree island areas (b) and semideciduous forest area (c). Solid lines represent the regression line and dotted lines represent the 95% confidence intervals.

the SFA (461 g.m^{-2}) was more than double that observed for the HSAs and TIAs, it was much lower than the 861 g.m^{-2} and 801 g.m^{-2} , respectively, estimated for primary and secondary tropical forests in South America (Chave *et al.* 2010). It was also lower than the 568 g.m^{-2} and 509 g.m^{-2} reported by Terror *et al.* (2011) and Werneck *et al.* (2001), respectively, for other semideciduous forests in the Ouro Preto region, as well as the 560 g.m^{-2} and 565 g.m^{-2} reported by Valenti *et al.* (2008) and Cianciaruso *et al.* (2006), respectively, for the *cerradão* (woodland savanna), although it was comparable to the 470 g.m^{-2} and 433 g.m^{-2} reported by Chave *et al.* (2010)

and Röderstein *et al.* (2005), respectively, for upland forest formations on cambisols.

Monthly variations in litterfall throughout the year were much less pronounced for the SFA and the TIAs than for the HSAs (CV = 26% and 23% vs. 52%). The HSAs also showed higher annual variability and lower values of relative soil water content (range, 2.3-19.6%, data not shown). Soil water content ranged from 5.0% to 35.4% in the TIAs and from 20.5% to 34.7% in the SFA. Such differences in soil water availability dynamics among the studied areas are in accordance with results of other studies that investigated the effects of woody plant encroachment in open landscapes on hydrological and biogeochemical parameters (Hibbard *et al.* 2001; Huxman *et al.* 2005). Although the initial distribution of trees and shrubs in the herbaceous matrix is affected by soil conditions, trees and shrubs affect the spatial and temporal litterfall, nutrient cycling, due to changes in soil structure, water availability, fertility, and microbial biomass beneath their canopies (Reich & Borchert 1984; Hibbard *et al.* 2001, Lawrence 2005).

Despite this variability, the seasonal variation of litterfall found in the SFA was not as pronounced as that reported for other seasonal forests (Lawrence 2005; Köhler *et al.* 2008; Terror *et al.* 2011). At the ecosystem level, a greater diversity of plant species and functional groups with different phenological patterns can lead to more uniform litter deposition throughout the year (Köhler *et al.* 2008). In tropical forests, pulses of litterfall, with a high proportion deposited in a short time, can occur in formations with one or a few dominant species, reflecting the phenological pattern of these species (Villela & Proctor 1999; Köhler *et al.* 2008; Terror *et al.* 2011). Pulses of litter deposition can also occur in forests with high species diversity, such as semideciduous and deciduous forests, in response to changing environmental conditions. Lower variability in these conditions can delay the occurrence or reduce the intensity of deposition pulses (Reich & Borchert 1984, Martins & Rodrigues 1999; Lawrence 2005). A phytosociological survey in the seasonal forest studied has not yet been finalized, but field observation indicates the occurrence of evergreen species belonging to the genera *Eremanthus* and *Byrsonima*.

The seasonality of litterfall has been shown to be lower in montane forests than in primary and secondary lowland forests (Chave *et al.* 2010). Minor variations in soil moisture and atmospheric evaporative demand, possibly favored by constant fog events (Dawson 1998), might also contribute to reducing the seasonality of litterfall. In fact, fog events are common in the area evaluated, accounting for 54.6 mm (70%) of the wet deposition during the dry season (Baêta, unpublished data). Unlike the SFA, the high litterfall seasonality in the HSAs is in accordance with what has been observed in savanna formations (Nardoto *et al.* 2006; Kozovits *et al.* 2007). Ecosystems with marked seasonality of rainfall or low soil water retention often have high proportions of deciduous and semideciduous species in their

communities (Reich & Borchert 1984, Williams *et al.* 1997; Lenza & Klink 2006). However, in the TIAs evaluated here, the variation in leaf litterfall was intermediate to those of the other habitats studied. Larger soil volume accumulated in microtopographic depressions in the HSAs, coupled with the consequent creation of mesic microenvironments (with higher soil fertility, higher relative soil water content, etc.) might favor the coexistence of species with different phenological strategies and promote tree establishment. A phytosociological survey performed in the HSA/TIA physiognomy (Vale, unpublished data) indicates that the importance value is high for shrubby semideciduous species, such as *Periandra mediterranea* Taub. and *Tibouchina heteromalla* Cong. Evergreen trees species belonging to the *Eremanthus* genus were also found to have a high importance value but mainly occupied the TIAs. As a result, the relative contribution of different plant functional groups to the monthly or annual litterfall in the HSA/TIA physiognomy should change over time, seasonal fluctuations coming to be comparable to those observed for the SFA. In turn, the gradual occupation of the open landscape by shrubs and woody plants should gradually accelerate changes in physicochemical properties of the soil, increasing its fertility, cationic exchange capacity and water retention, as well as improving its texture, thereby increasing the productivity of the TIAs (Prescott 2002; Hobbie *et al.* 2007; Cardelús *et al.* 2009). In fact, our results indicate that the TIAs are at an intermediate stage of litter production and decomposition (data not shown), approaching the patterns found in the SFA. The spatial variation of litterfall being larger in the HSAs (CV = 62%) than in the SFA (CV = 25%) is, in fact, a pattern similar to that found by Mlambo & Nyathi (2008) in a semi-arid savanna, in which it was also related to variation in vegetation cover in the landscape, a mosaic of microenvironments characterized by variable productivity.

The studied habitats showed different peaks of leaf and total litterfall throughout the year. As previously mentioned, two and three peaks of deposition were observed in the HSAs and TIAs, respectively, some during the rainy season and some during the transition from the rainy season to the dry season, as well as (in the TIAs only) during the transition from the dry season to the rainy season. High litter production during the rainy season might be related to the intensity and frequency of rain events, the mechanical action of which leads to abscission of plant parts (Terror *et al.* 2011). This factor seems to provide a reasonable explanation for the litter production peak in the HSAs in January (during the rainy season), given that the cumulative rainfall for that month was 257 mm. However, it does not explain the peak in litter production in the TIAs in February, when the cumulative monthly rainfall was only 33 mm.

In 2010, at the end of January and during February, there were some periods of drought affecting the study site. Those periods were characterized not only by a lack of precipitation but also by high temperature (35.1°C) and

low relative humidity (39.9%). Such conditions can cause major physiological restriction, leading to a decline in photosynthesis rates and requiring water balance adjustments (Mattos *et al.* 2002), and can be even more severe for plants on shallow soils (Nobel & Zutta 2007). In a deciduous forest in Mexico, litter production peaks during the rainy season were also found when there were dry periods lasting for 11-18 days, as reported by Lawrence (2005). We showed that the miscellaneous fraction of litter production was correlated with rainfall in all habitats ($R^2 > 0.42$) and that the peaks in that fraction occurred mainly at the beginning of the rainy season (in October, November and December). After the leaf fraction, fragments of branches and trunks are the largest contributor to total litterfall in an ecosystem (Martins & Rodrigues 1999, Dent *et al.* 2006; Cianciaruso *et al.* 2006, Köhler *et al.* 2008, Valenti *et al.* 2008). During the dry season, twigs and branches can show xylem cavitation, which results in death from embolism (Tyree & Sperry 1989). With the onset of rainy season, the mechanical action of rain will facilitate the abscission of these organs which, in most cases, were already decomposing.

Conclusion

The habitats studied showed differences in litter production and in its spatial and temporal variation. The annual litter production was highest in the SFA and lowest in the HSAs, which also showed the highest seasonality. The presence of semideciduous plants in HSAs, of evergreen species in the SFA, and of soil conditions that promote the formation of a habitat with intermediate characteristics between the two other extremes in vegetation cover are factors possibly related to the patterns observed. Therefore, in the TIAs, the coexistence of plant species with different phenological strategies, together with the fact that, over the year, the microclimatic conditions were better and less variable in the TIAs than in the HSAs, resulted in intermediate seasonality of leaf litter production in the former. The litterfall in the TIAs seems to behave more like that observed for the SFAs. These results demonstrate the role of microtopography in the differentiation of soil sites into those that are more favorable to the establishment of different functional groups and those that are less favorable to such establishment, which would therefore make different contributions to the flow of matter within the ecosystem.

A single productivity value might not adequately express the functioning of the different physiognomies in a iron-rich rock outcrop complex. The productivity values found in the present study are within the ranges reported for other upland tropical ecosystems and savanna woodlands, showing the relevance of litterfall for nutrient cycling at the tops of hills and the need to expand such studies in order to cover other iron-rich rock outcrop landscapes. The results presented here, although not derived from a long-term study, are the first to characterize the nutrient cycling and

productivity processes in these ecosystems and provide an information base to be used as a reference for the evaluation of reclamation status in degraded areas after bauxite mining in the state of Minas Gerais.

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References

- Benites, V.M.; Simas, F.N.B.; Schaefer, C.E.G.R.; Santos, H.G.; Mendonça, B.A.F. 2007 Soils associated to rock outcrops in the highlands of Serras da Mantiqueira and Espinhaço, southeastern Brazil. *Revista Brasileira de Botânica* 30: 569-577.
- Cardelús, C.L.; Mack, M.C.; Woods, C.; DeMarco, J.; Treseder, K.K. 2009. The influence of tree species on canopy soil nutrient status in a tropical lowland wet forest in Costa Rica. *Plant Soil* 318: 47-61
- Carmo, F.F. 2010. **Importância Ambiental e Estado de Conservação dos Ecossistemas de Cangas no Quadrilátero Ferrífero e Proposta de Áreas-Alvo para a Investigação e Proteção da Biodiversidade em Minas Gerais**. Dissertação de mestrado. Universidade Federal de Minas Gerais, Brasil
- Castro, P.T.A. 2008. Cangas: A influência da geodiversidade na biodiversidade. Pp. 30-51. In: Jacobi, C.M.; Stehman, J.R.; Antonini, Y.; Carmo, F.F.; Oliveira-Neves, A.C.; Mourão, F.A.; Silva, E.S. **Afloramentos Ferruginosos no Quadrilátero Ferrífero: Biodiversidade, Conservação e Perspectivas de Sustentabilidade**. I Simpósio: Afloramentos ferruginosos no Quadrilátero Ferrífero.
- Chave, J.; Navarrete, D.; Almeida, S.; Alvarez, E.; Aragão, L.E.O.C.; Bonal, D.; Châtelet, P.; Silva-Espejo, J.E.; et al. 2010. Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences* 7: 43-55
- Cianciaruso, M.V.; Pires, J.S.R.; Delitti, W.B. C.; Silva, E.F.L.P. 2006. Produção de serapilheira e decomposição do material foliar em um cerrado na Estação Ecológica de Jataí, município de Luiz Antônio, SP, Brasil. *Acta Botânica Brasileira* 20(1): 49-59.
- Costa, G.S.; Franco, A.A.; Damasceno, R.N.; Faria, S.M. 2004. Aporte de nutrientes pela serapilheira em uma área degradada e revegetada com leguminosas arbóreas. *Revista Brasileira de Ciência do Solo* 28: 919-927.
- Dawson, T.E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* 117: 476-485
- Dent, D.H.; Bagchi, R.; Robinson, D.; Majalap-Lee, N.; Burslem, D.F.R.P. 2006. Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in a lowland tropical rain forest. *Plant Soil* 288: 197-215.
- Ewel, J.J. 1976. Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *Journal of Ecology* 64: 293-308
- Fisk, M.C.; Fahey, T.J.; Groffman, P.M. 2010. Carbon resources, soil organisms, and nitrogen availability: Landscape patterns in a northern hardwood forest. *Forest Ecology and Management*. 260: 1175-1183
- Franco, A.C.; Bustamante, M.M.C.; Caldas, L.S.; Goldstein, G.; Meinzer, F.C.; Kozovits, A.R.; Rundel, P.; Coradin, V.T.R. 2005. Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees* 19: 326-335
- Grant, C.D.; Ward, S.C.; Morley, S.C. 2007. Return of ecosystem function to restored bauxite mines in Western Australia. *Restoration Ecology* 15(4): 94-103
- Hibbard, K.A.; Archer, S.; Schimel, D.S.; Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82: 1999-2011
- Hobbie, S.E.; Ogdahl, M.; Chorover, J.; Chadwick, O.A.; Oleksyn, J.; Zytowski, R.; Reich, P.B. 2007. Tree species effects on soil organic matter dynamics: the role of soil cation composition. *Ecosystems* 10: 999-1018.
- Huxman, T.E.; Wilcox, B.P.; Breshears, D.D.; Scott, R.L.; Snyder, K.A.; Small, E.E.; Hultine, K.; Pockman, W.I.; Jackson, R.B. 2005. Ecophysiological implications of woody plant encroachment. *Ecology* 86(2): 308-319
- IEF/UFV/IBAMA. 2005. **Zoneamento Ecológico da Área de Proteção Ambiental Estadual Cachoeira da Andorinhas, Ouro Preto, Minas Gerais: Relatório do meio físico: geologia, solos e geomorfologia**. Universidade Federal de Viçosa.
- Jacobi, C.M.; Carmo, F.F.; Vincent, R.C.; Stehmann, J.R. 2007. Plant communities on ironstone outcrops – a diverse and endangered Brazilian ecosystem. *Biodiversity and Conservation* 16: 2185-2200.
- Köhler, L.; Hölscher, D.; Leuschner, C. 2008. High litterfall in old-growth and secondary upper montane forest of Costa Rica. *Plant Ecology* 199: 163-173.
- Kozovits, A.R.; Bustamante, M.M.C.; Garofalo, C.R.; Bucci, S.; Franco, A.C.; Goldstein, G.; Meinzer, F.C. 2007. Nutrient resorption and patterns of litter production and decomposition in a Neotropical Savanna. *Functional Ecology* 21: 1034-1043.
- Lawrence, D. 2005. Regional-Scale Variation in Litter Production and Seasonality in Tropical Dry Forests of Southern Mexico. *Biotropica* 37(4): 561-570
- Lei, S.A. 1999. Phenological events and litterfall dynamics of Blackbrush in Southern Nevada. *USDA Forest Service Proceedings* 11: 113-118.
- Lenza E, Klink C.A. 2006. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. *Revista Brasileira de Botânica* 29(4): 627-638
- Martins, S.V. & Rodrigues, R.R. 1999. Produção de serapilheira em clareiras de uma floresta estacional semidecidual no município de Campinas, SP. *Revista Brasileira de Botânica* 22(3): 405-412
- Martius, C.; Höfer, H.; Garcia, M.V.B.; Bömbke, J.; Hanagarth, W. 2004. Litter fall, litter stocks and decomposition rates in rainforest and agroforestry sites in central Amazonia. *Nutrient Cycling in Agroecosystems* 68: 137-154.
- Mattos, E.A. de.; Lobo, P.C.; Joly, C.A. 2002. Overnight rainfall inducing rapid changes in photosynthetic behaviour in a cerrado woody species during a dry spell amidst the rainy season. *Australian Journal of Botany* 50(2): 241-246
- Mlambo, D. & Nyathi, P. 2008. Litterfall and nutrient return in a semi-arid southern African savanna woodland dominated by *Colophospermum mopane*. *Plant Ecology* 196: 101-110
- Mourão, A. & Stehman, J.R. 2007. Levantamento da flora do campo rupestre sobre canga hematítica couraçada remanescente na Mina do Brucutu, Barão de Cocais, Minas Gerais, Brasil. *Rodriguésia* 58 (4): 775-786.
- Nardoto, G.B.; Bustamante, M.M.C.; Pinto, A.S.; Klink, C.A. 2006. Nutrient use efficiency at ecosystem and species level in savanna areas of Central Brazil and impacts of fire. *Journal of Tropical Ecology* 22: 1-11
- Nobel, P.S. & Zutta, B.R. 2007. Carbon dioxide uptake, water relations and drought survival for *Dudleya saxosa*, the 'rock live-forever', growing in small soil volumes. *Functional Ecology* 21: 698-704
- Pallardy, S.G. 2008. **Physiology of woody plants**. 3 ed. Elsevier.
- Peres, J.R.R., Suhet, A.R., Vargas, M.A.T., Drozdowicz, A. 1983. Litter production in areas of Brazilian "cerrados". *Pesquisa. Agopecuária Brasileira* 18(9): 1031-1036.
- Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiology* 22: 1193-1200
- Reich, P.B. & Borchet, R. 1984. Water Stress and Tree Phenology in a Tropical Dry Forest in the Lowlands of Costa Rica. *Journal of Ecology* 72(1): 61-74
- Rizzini, C.T. 1979. **Tratado de fitogeografia do Brasil. Aspectos sociológicos e florísticos**. HUCITEC/EDUSP, São Paulo.

- Röderstein, M.; Hertel, D.; Leuschner, C. 2005. Above- and below-ground litter production in three tropical montane forests in southern Ecuador. **Journal of Tropical Ecology** **21**: 483-492
- Secco, R.S. & Mesquita, A.L. 1983. Notas sobre a vegetação de canga da Serra Norte. I. Bol. Mus Para. Emílio Goeldi, **Nova Série Botânica** **59**: 1-13.
- Spain, A.V. 1984. Litterfall and the standing crop of litter in three tropical Australian rainforests. **Journal of Ecology** **72**: 947-961.
- Terror, V.L.; Sousa, H.C.; Kozovits, A.R. 2011. Produção, decomposição e qualidade nutricional da serapilheira foliar em uma floresta paludosa de altitude. **Acta Botânica Brasileira** **25**(1): 113-121
- Tyree, M.T. & Sperry, J.S. 1989. Vulnerability of xylem to cavitation and embolism. **Annual Review of Plant Physiology and Plant Molecular Biology** **40**: 19-38
- Valenti, M.W.; Cianciaruso, M.V.; Batalha, M. A. 2008. Seasonality of litterfall and leaf decomposition in a cerrado site. **Brazilian Journal of Biology** **68**(3): 459-465.
- Viana, P.L. & Lombardi, J.A. 2007. Florística e caracterização dos campos rupestres sobre canga na Serra da Calçada, Minas Gerais, Brasil. **Rodriguésia** **58**: 159-177.
- Villela, D.M. & Proctor, J. 1999. Litterfall mass, chemistry and nutrient retranslocation in a monodominant forest on Maracá Island, Roraima, Brazil. **Biotropica** **31**(2): 198-211.
- Vincent, R.C. & Meguro, M. 2008. Influence of soil properties on the abundance of plant species in ferruginous rocky soils vegetation, southeastern Brazil. **Revista Brasileira de Botânica** **3**: 377-388.
- Werneck, M.S.; Pedralli, G.; Gieseke, L.E. 2001. Produção de serapilheira em três trechos de uma floresta semidecídua com diferentes graus de perturbação na Estação Ecológica do Tripuí, Ouro Preto, MG. **Revista Brasileira de Botânica** **24**(2): 195-198
- Williams, R.J.; Myers, B.A.; Muller, W.J.; Duff, G.A.; Eamus, D. 1997. Leaf phenology of woody species in a North Australian Tropical Savanna. **Ecology** **78**(8): 2542-2558.