ECOLOGY

Seasonality of litterfall and leaf decomposition in a cerrado site

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(With 4 figures)

Abstract

We investigated annual litterfall and leaf decomposition rate in a cerrado site. We collected woody plant litter monthly from April 2001 to March 2002 and from July 2003 to June 2004. We placed systematically 13 litter traps (0.5 x 0.5 m) in a line, 10 m one from the other. We sorted litter into 'leaves', 'stems', 'reproductive structures', and 'miscellanea' fractions, oven-dried them at 80 °C until constant mass and weighed the dry material. To assess leaf decomposition rate, we packed leaves recently shed by plants in litter bags. We placed seven sets of nine litter bags in a line, 10 m one from the other, on the soil surface and collected nine bags each time after 1, 2, 3, 4, 6, 9, and 12 months. Total and leaf litter productions showed a seasonal pattern. Leaf litterfall was the phenological attribute that showed the strongest response to seasonality and drought. Decomposition was slower in the cerrado that we studied compared to a more closed cerrado physiognomy, reflecting their structural and environmental differences. Thus, decomposition rates seem to increase from open to closed cerrado physiognomies, probably related to an increase of humidity and nutrients in the soil.

Keywords: cerrado, savanna, litterfall, leaf decomposition.

Estacionalidade da produção de serapilheira e decomposição foliar em um sítio de cerrado

Resumo

Investigamos a produção de serapilheira e a taxa de decomposição foliar em uma área de cerrado sensu stricto. Coletamos mensalmente a serapilheira do componente arbustivo-arbóreo de abril de 2001 a março de 2002 e de julho de 2003 a julho de 2004. Dispusemos sistematicamente 13 coletores (0,5 x 0,5 m) em uma linha, com distância de 10 m entre eles. Separamos a serapilheira nas frações 'folhas', 'galhos', 'estruturas reprodutivas' e 'miscelânea'; as secamos em estufa a 80 °C até atingirem massa constante; e pesamos o material seco. Para analisar a taxa de decomposição foliar, acondicionamos folhas caídas recentemente em sacos de decomposição. Dispusemos sete conjuntos de nove sacos de decomposição em uma linha, distantes 10 m um do outro, sobre a superfície do solo e retiramos nove sacos a cada coleta depois de 1, 2, 3, 4, 6, 9 e 12 meses. As produções totais e de folhas apresentaram um padrão estacional. A queda de folhas foi o atributo fenológico que melhor respondeu à estacionalidade e à seca. A decomposição foi mais lenta no cerrado sensu stricto que estudamos do que em um fragmento de cerradão, o que refletiu em suas diferenças estruturais e ambientais. Portanto, as taxas de decomposição devem aumentar das fisionomias de cerrado abertas para as fechadas, provavelmente devido ao aumento da umidade e dos nutrientes do solo.

Palavras-chave: cerrado, decomposição foliar, savana, serapilheira.

1. Introduction

Litterfall transfers organic matter, nutrients, and energy from vegetation to soil and is a dominant link in the biogeochemical cycling of matter (Facelli and Pickett, 1991; Delitti, 1998; Liu et al., 2004). Litter production depends on the vegetation form and the climate (Bray and Gorham, 1964; Leitão Filho, 1993; Liu et al., 2004). Its accumulation changes the physical and chemical environments, affecting plant community structure (Facelli and Pickett, 1991). The quantification of the foliage, flower, and fruit amounts in litter allows direct measurements of year-to-year variation in phenology as a reaction to natural factors and anthropogenic actions, including global climate changes (ICP Forests, 2004).

Litter production and decomposition are processes linked through a positive feedback (Kitayama et al., 2004). Decomposition provides nutrients necessary for primary productivity by recycling organic matter, whereas the increase in plant biomass is positively related to litterfall, providing substrate for decomposition (Swift et al., 1979). Therefore, the rate of decomposition may regulate the cycle of matter in the plant community, and litterfall measurement may be an indirect way to estimate net primary productivity (Clark et al., 2001).

Although there are many papers on litterfall in South American rain forests, there are few focused on Neotropical savannas (Peres et al., 1983; Schiavini, 1983; Guerra-Filho, 1985; Pompéia, 1989; Delitti, 1998; Wilcke and Lilienfein, 2002; Nardoto et al., 2006; Cianciaruso et al., 2006). The largest Neotropical savanna region is the Brazilian cerrado, which is one of the world's biodiversity hotspots (Myers et al., 2000). Nowadays, it covers about 45% of its original area (Machado et al., 2004). In São Paulo State, for instance, 99% of the cerrado has been cleared or transformed for human uses (Kronka et al., 1998). Only small areas remain, which are important in the context of landscape ecology and represent refuges of savanna fauna and flora (Bitencourt and Mendonça, 2004). So, studies on the structure and function of these communities are essential and urgent for their conservation, since investigating litter production and decomposition may provide key descriptors to environmental impact assessment and management decisions (Leitão Filho, 1993; Clark et al., 2001; Kushwaha and Singh, 2005). Here, we analyzed litterfall production and leaf decomposition rate in a disjunct cerrado site and looked for climatic variables that would predict litterfall dynamics. We expected higher production of litter in the dry season and significant relationships with climatic variables. In addition, we compared the decomposition rate to that in a more closed cerrado physiognomy (Cianciaruso et al., 2006). We expected that the decomposition rate would be higher in cerradão, since it is a tall woodland.

2. Material and Methods

We carried out this study in a 32 ha disjunct cerrado site, classified as cerrado sensu stricto (a woodland) according to Coutinho (1990), located in the Federal University of São Carlos, São Paulo State, southeastern Brazil (21° 58' 12" S and 47° 52' 01" W), at 850 m above sea level. The regional climate is warm temperate with dry winter, or Cwa (Köppen, 1931). The dry season goes from April to September, and the wet season, from October to March. Mean temperature is around 21 °C, and the annual precipitation lies between 1.138 and 1.593 mm. The soil of the study site is a dystrophic Oxisol on a flat topography (Damascos et al., 2005). The soil water content from 0 to 3 m deep follows the seasonal pattern of rainfall, and the water-table is located 10 m below the soil surface (Damascos et al., 2005).

In the study site, we placed systematically 13 litter traps (0.5 x 0.5 m), made with 1.0 mm^2 nylon mesh, at 30 cm above the ground. Litter traps were 100 m distant from the fragment edge and distributed in a line, 10 m one from the other. We collected woody plant litter monthly, in two years, from April 2001 to March 2002 and from July 2003 to June 2004. We sorted litter into 'leaves', 'stems', 'reproductive structures', and 'miscellanea' fractions, oven-dried them at 80 °C for 24 hours (or until constant mass), and weighed the dry material.

We also used 63 litterbags, made with 1.0 mm^2 nylon mesh, to estimate leaf decomposition. We collected leaves recently shed by plants in the study site and cleaned them with a soft brush to avoid contamination by soil, roots, animals, or other materials. Then, we oven-dried the leaves at 80 °C for 24 hours and packed 5.0 g in each litter bag. We exposed the leaves to decomposition, placing seven sets of nine bags in a line, 10 m one from the other, on the soil surface of study site. We collected nine bags each time after 1, 2, 3, 4, 6, 9, and 12 months. After each gathering, we gently cleaned the material with a soft brush to remove all elements that were not leaf material, oven-dried the leaves at 80 °C for 24 hours and weighed them to obtain the difference between initial and final dry weights.

We used one-way repeated measures analyses of variance and the Tukey multiple comparison test (Zar, 1999) to test for differences (α = 0.05) among monthly litter productions. We obtained climate data from Embrapa Meteorological Station (21° 55' S and 47° 48' W), which is located near the studied site. We tested for relationships between monthly litterfall (and fractions) and climatic factors (monthly total precipitation – P, monthly mean air relative humidity – ARH, and monthly maximum, minimum, and mean temperatures – T_{max}, T_{min}, and T_{mean}, respectively) with multiple regression analyses (Jongman et al., 1995). We used backward elimination to find the best model. We considered monthly maximum temperature as the average daily maximum air temperature, for each month; monthly minimum temperature as the average daily minimum air temperature, for each month; and monthly mean temperature as the average air temperature, for each month (Smith, 2006). As the independent variables were correlated with each other, we used simple linear regression analyses (Zar, 1999).

To analyze the decomposition through time, we obtained the mean mass of the nine bags of each sampled period and adjusted these values to an exponential equation ($y = ae^{kt}$), in which k was the coefficient of decomposition. This coefficient was multiplied by 12 to obtain the annual decomposition coefficient (t = 12 months). The exponential model describes best the loss of mass over time during litter decomposition (Wieder and Lang, 1982). We compared the decomposition equation obtained in the present study to that obtained in a nearby tall woodland cerrado site, in Luiz Antônio, São Paulo State (Cianciaruso et al., 2006). In that study, the mean weight values were obtained from twenty litter bags gathered after 1, 2, 3, 6, 11, and 12 months of decomposition. We compared slope parameters of the linearized regressions (after log-transformation of the independent variable) with a test for difference of slopes using the t statistics (Zar, 1999).

3. Results

Annual litterfall was 5.8 $t.ha^{-1}$ in the first year and 5.4 $t.ha^{-1}$ in the second year. The total production was not uniformly distributed throughout the year ($F = 6.39$ and $F = 10.03$, respectively; $P < 0.001$; Figure 1). We found 41.30% and 41.87% of litterfall in the first and in the second years, respectively, concentrated in only three months (July, August, and September). Total litter production was negatively related to ARH ($R^2 = 0.48$; $F = 22.00$; $P < 0.01$, Table 1).

The 'leaves' fraction was the most representative one. Leaf litterfall was 3.90 $t.ha^{-1}$ per year in the first year and 4.07 $t.ha^{-1}$ per year in the second year, corresponding to 67.23% and 75.38% of total production, respectively. In both studied periods, the amount of leaves was high during all months, but not uniformly distributed throughout the year ($F = 9.14$ and $F = 12.90$, $P < 0.001$; Figure 2a and Figure 3a, respectively). The highest leaf productions were in July, August, and September and the lowest from October to May. We found a significant negative relationship between leaf litterfall and ARH and P ($R^2 = 0.62$; $F = 19.38$; $P < 0.01$, Table 1).

In the first year, 'stems', 'reproductive structures', and 'miscellanea' corresponded to 17.51%, 13.53%, and

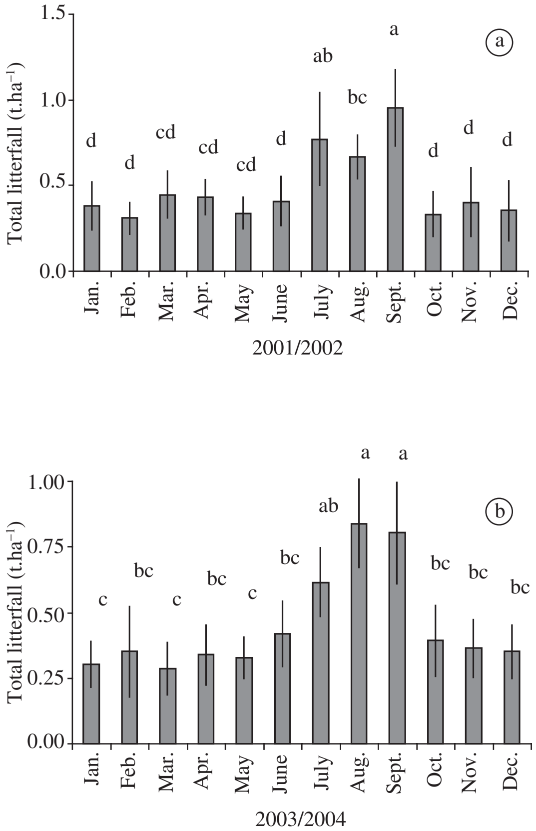

Figure 1. Total litterfall production ($t.ha^{-1}$) throughout the year in a disjunct cerrado site in São Carlos, São Paulo State, southeastern Brazil (approximately, 21° 58' 12" S and 47° 52' 01" W). a) first year (from April 2002 to March 2002), and b) second year (from July 2003 to June 2004). Different letters indicate significant differences among months ($\alpha = 0.05$).

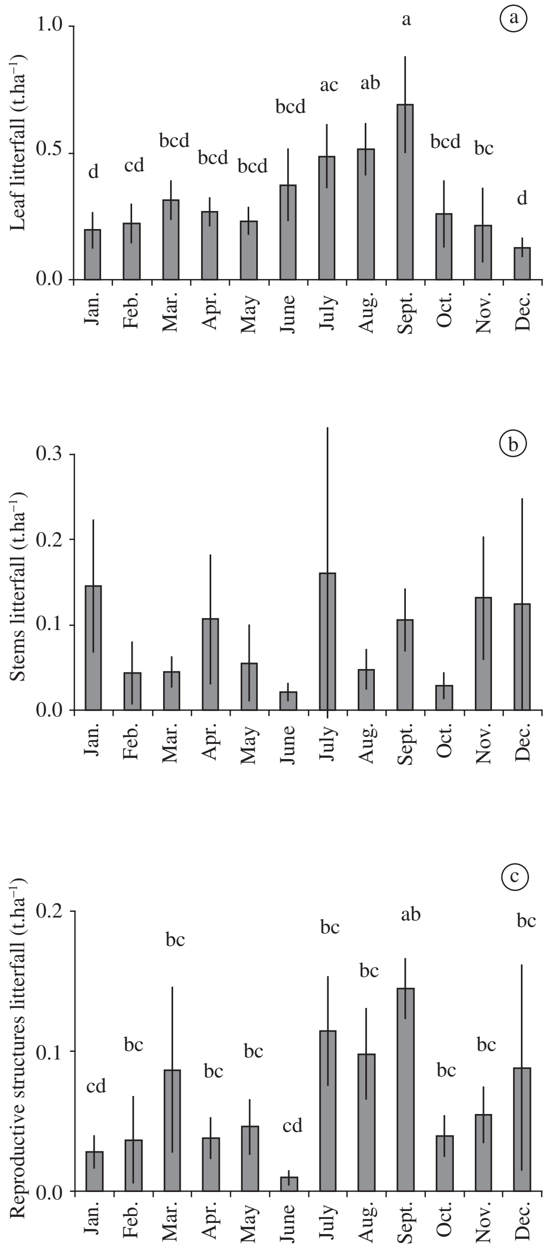

Figure 2. a) Leaf, b) stem, and c) reproductive structure litterfall production ($t.ha^{-1}$) throughout the year, from April 2002 to March 2002, in a disjunct cerrado site in São Carlos, São Paulo State, southeastern Brazil (approximately, 21° 58' 12" S and 47° 52' 01" W). Different letters indicate significant differences among months ($\alpha = 0.05$).

1.73% of total litterfall, respectively. In the second year, these fractions corresponded to 14.94, 9.35, and 0.33% of total litterfall, respectively. In both studied years, stem production was uniform (F = 1.60 and F = 1.10, P > 0.005; Figure 2b and 3b, respectively). In the first year, reproductive structure production was not uniformly distributed (F = 4.97, P < 0.05; Figure 2c), but we found significant differences between the most productive month (September) and the two least productive ones (January and June). In the second year, reproductive structure litterfall was uniform (F = 1.05, P > 0.05; Figure 3c). We did not find significant relationships between these fractions and climatic elements.

During one year, 28% of the leaf material was decomposed. Leaf biomass decreased throughout time exponentially in the cerrado sensu stricto (F = 137.72; P < 0.001; r^2 = 0.96) and in the cerradão (F = 100.44; P < 0.001; r^2 = 0.95). The annual decomposition coefficient k was 0.36 and 0.52, respectively. The slopes of linear regression for decomposition in the cerrado sensu stricto and cerradão were significantly different (t = 2.71; P < 0.05; Figure 4).

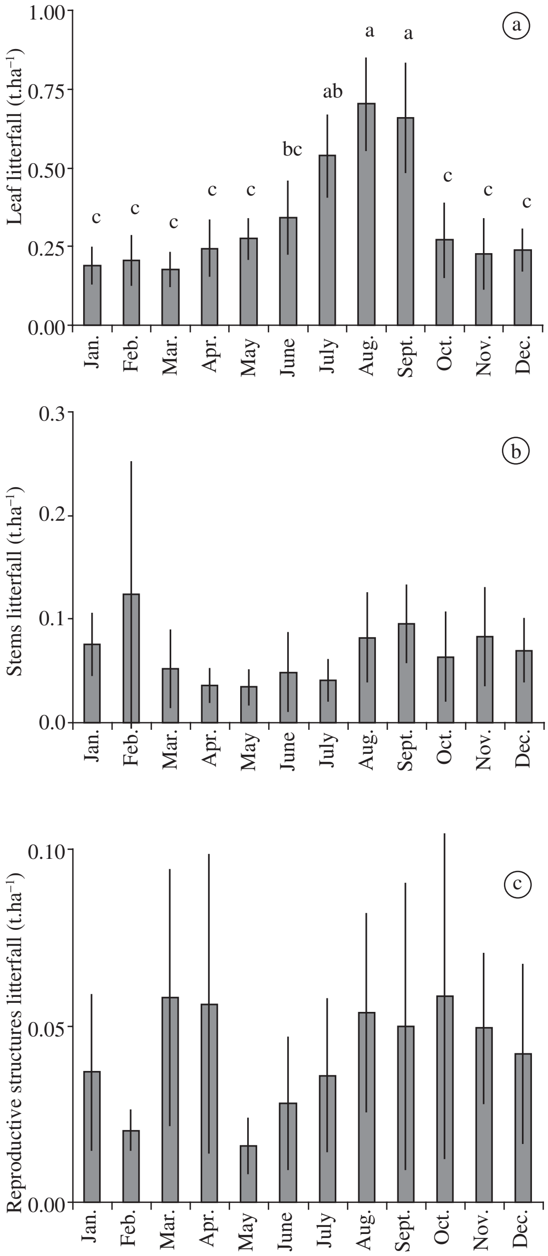

Figure 3. a) Leaf, b) stem, and c) reproductive structure litterfall production ($t.ha^{-1}$) throughout the year (from July 2003 to June 2004) in a disjunct cerrado site in São Carlos, São Paulo State, southeastern Brazil (approximately, 21° 58' 12" S and 47° 52' 01" W). Different letters indicate significant differences among months (α = 0.05).

4. Discussion

Litterfall may be affected by physical factors such as the mechanic action of wind and rain or physiological responses of the plants to environment changes (Delitti, 1998; Moraes and Prado, 1998; ICP Forests, 2004; Santiago and Mulkey, 2005). We found a seasonal

Table 1. Parameters of the multiple regression analyses among total and leaf litterfall and monthly air relative humidity (ARH) and monthly total precipitation (P) in a disjunct cerrado site in São Carlos, São Paulo State, southeastern Brazil (approximately, 21° 58' 12" S and 47° 52' 01" W).

Litterfall	Parameter estimates	T	P	β	±SD
Total	intercept	6.690	<0.001	-	-
	ARH	–4.690	<0.001	–0.707	0.151
Leaf	intercept	6.240	<0.001	-	-
	ARH	–3.890	<0.001	–0.585	0.150
	P	–2.201	0.039	–0.331	0.150

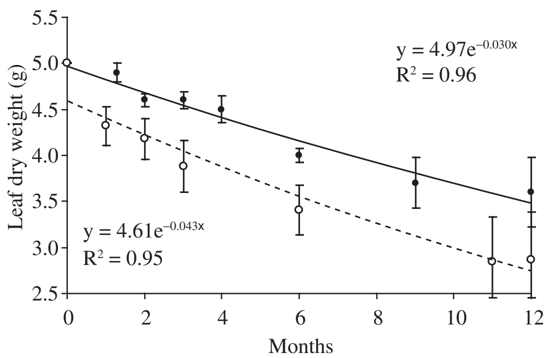

Figure 4. Leaf decomposition throughout the year in a cerrado sensu stricto site in São Carlos (black circles; equation and R^2 on the upper right side) and in a cerradão site in Luiz Antônio (white circles; equation and R^2 on the lower left side), both in São Paulo State, southeastern Brazil.

pattern of litter production, which increased in the dry season, indicating that the physiological response to drought plays a major role in this process. Similar results were obtained by Pompéia (1989), Delitti (1998), and Cianciaruso et al. (2006), in other cerrado disjunct sites, and by Morellato (1992) and Werneck et al. (2001), in semideciduous forests. This pattern, found in vegetation forms under seasonal climates, is different from those found in vegetation forms under climates without dry seasons, such as the Atlantic rain forest, where the production peak occurs in the rainy season, indicating an effect of mechanical factors (Moraes et al., 1999).

Total litterfall seems to vary according to vegetation structure. Although the value obtained in the present work was slightly higher than values previously obtained in other cerrado sensu stricto sites (Peres et al., 1983; Schiavini, 1983), it was lower than values obtained in cerradão sites (Peres et al., 1983; Guerra-Filho, 1985). This suggests an increase in litterfall from open to closed cerrado physiognomies and may reflect the relationship between litterfall and primary productivity as stated by Clark et al. (2001).

Leaves are the most important component of litter and respond rapidly to climatic changes (Liu et al., 2004). On our study site, the proportion of leaf litterfall in relation to stems and reproductive structures was higher in all months. The best model to predict the relationships with climatic elements included ARH and P. In general, changes in mean climatic conditions lead to changes in community function, including productivity (Walker, 2001). On a regional scale, precipitation and temperature are the most important climatic factors controlling ecological processes (Liu et al., 2004) and are related to litterfall (Martins and Rodrigues, 1999; Liu et al., 2004; Cianciaruso et al., 2006). We found higher leaf production in the dry season, when leaf fall of most woody cerrado species occurs due to decreases in soil moisture and air temperature (Mantovani and Martins, 1988; Oliveira, 1998; Batalha and Mantovani, 2000). Seasonal variations in leaf litterfall in the cerrado may be a strategy to save water when it is scarce, since shedding decreases plant transpiration surface (Delitti, 1998; Moraes and Prado, 1998).

Although stem production usually varies considerably (Proctor, 1983), we did not find seasonality in this fraction. The differences in production of the 'reproductive structures' fraction occurred only between the most (September) and the two least productive months (January and June), and only in the first year. So, we did not identify a seasonal pattern in this fraction, contrary to what was found in other cerrado and semideciduous forest sites (Morellato, 1992; Delitti, 1998; Martins and Rodrigues, 1999; Moraes et al., 1999). Most cerrado woody species flower in late dry season and early rainy season, whereas the community as a whole, fruits throughout the year: anemo and autochorous species fruiting mainly in the dry season and zoochorous species fruiting mainly in the rainy season (Mantovani and Martins, 1988; Batalha and Mantovani, 2000; Batalha and Martins, 2004).

The decomposition rate varied during time and among different vegetation physiognomies. The process was initially faster, since the unstable nutrients are liberated first and the more stable matter remains on the leaf, decreasing the velocity through time (Swift et al., 1979). Decomposition was slower in the cerrado sensu stricto than in the cerradão. The difference of k values between the sites may reflect their structural and environmental differences. Similarly, the decomposition rate in the cerrado sensu stricto was higher than in more open physiognomies (Delitti, 1998). Therefore, decomposition rates seem to increase from open to closed cerrado physiognomies, probably due to an increase of humidity and nutrients in the soil, since moisture improves decomposers performance (Mason, 1980) and nutrients accumulated in leaves facilitates decomposition (Gartner and Cardon, 2004).

In conclusion, total and leaf productions were not uniform throughout the year. Total litterfall changed according to air relative humidity; and leaf litterfall, according to air relative humidity and precipitation. These climatic elements decreased in the dry season, while litterfall increased. This phenological response might have been selected in communities under seasonal climates, since it provides water economy by reducing leaf transpiration during the unfavorable season. In addition, our results corroborated that leaf fraction is the principal component of litter in tropical communities, as previously observed in other communities (Bray and Gorham, 1964; Morellato, 1992; Kushwaha and Singh, 2005; Cianciaruso et al., 2006). Therefore, leaf fraction rather than total litter may be used to indicate structure changes in the cerrado.

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