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Effect of seasonal flooding cycle on litterfall production in alluvial rainforest on the middle Xingu River (Amazon basin, Brazil)

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(With 3 figures)

Abstract

The assumption for this study was that litterfall in floodplain environments of the middle Xingu river follows a pattern of seasonal variation. According to this view, litterfall production (total and fractions) was estimated in four alluvial rainforest sites on the middle Xingu River over an annual cycle, and examined the effect of seasonal flooding cycle. The sites included two marginal flooded forests of insular lakes (Ilha Grande and Pimentel) and two flooded forests on the banks of the Xingu itself (Boa Esperança and Arroz Cru). Total litterfall correlated with rainfall and river levels, but whereas the leaf and fruit fractions followed this general pattern, the flower fraction presented an inverse pattern, peaking in the dry season. The litterfall patterns recorded in the present study were consistent with those recorded at other Amazonian sites, and in some other tropical ecosystems.

Keywords: alluvial rainforest, fractions of litter production, middle Xingu River.

Efeito da variação da inundação sazonal na produção de serrapilheira numa floresta aluvial do médio Rio Xingu (bacia do Amazonas, Brasil)

Resumo

O pressuposto para este estudo foi que a produção de serrapilheira nos ambientes inundáveis do médio rio Xingu, segue um padrão de variação sazonal. Assim, se quantificou durante um ciclo anual a produção de serapilheira total e de suas frações, e se indagou a correlação entre o regime do nível do rio e a produção de serapilheira. Quatro ambientes de floresta ombrófila aluvial foram estudados: duas florestas inundáveis de lagoas insulares (Ilha Grande e Pimentel) e dois ambientes de floresta marginal no canal principal do rio Xingu (Boa Esperança e Arroz Cru). A produção de serapilheira total nos quatro ambientes mostrou um padrão sincrônico com a variação do nível do rio e com a inundação das áreas marginais. Por sua vez, foi evidente um aumento da produção de frutos durante a inundação local e de forma inversa uma maior produção de flores com o regime de seca. Os padrões registrados para os componentes de serapilheira do médio rio Xingu, confirmam os achados para outros ambientes amazônicos e tropicais.

Palavras-chave: floresta ombrófila aluvial, produção de serrapilheira, médio Rio Xingu.

1. Introduction

Litterfall in a forest ecosystem is constituted of all the organic material, including leaves, twigs, flowers, fruits, bark, and other plant parts, that fall to the forest floor (Randazzo et al., 2006). This material functions primarily as a route for the transfer of nutrients from vegetation to the soil, maintaining its fertility, which is essential for the sustainability of forest systems (Sayer and Tanner, 2010; Ge et al., 2013; Silver et al., 2014; Zhang et al., 2014). Given this function, the amount of litterfall in a forest is an important index of the productivity of the ecosystem (Lonsdale, 1988; Grant et al., 2007).

Plant detritus falls to the forest floor at varying rates (Kramer and Kozlowski, 1960), depending on the physiology of each plant species in the forest and the effects of environmental factors, such as the photoperiod, temperature, and hydrological stress. Given this, each type of soil will support different plant species, adapted to its specific nutritional conditions. Figueiredo Filho et al. (2003) concluded that the litter found in a forest ecosystem is an index of its reproductive capacity, balancing the availability of nutrients with the ecological requirements of the species found in the forest.

Litter is considered the principal source of organic matter for the soil (Selle, 2007; Zheng et al., 2014). A number of studies have shown that leaves make up the majority of the litterfall – approximately 70%, on average – deposited over the course of the year (Andrade et al., 2000; Toledo et al., 2002; König et al., 2002; Schumacher et al., 2003, 2004; Ferreira et al., 2007).

A number of studies have attempted to relate spatial and temporal variations in litterfall production to factors such as latitude and climatic factors, including precipitation, temperature, light availability, and soil humidity (Dias and Oliveira Filho, 1997; Chave et al., 2010). Litterfall production and the transfer of nutrients to the soil are closely related to the region's seasonality. The climate, successional stage of the forest, and the fertility of the soil are the principal factors determining the variation observed in the deposition of litter (Vitousek and Sanford Junior, 1986), as well as all other aspects of nutrient cycling in forest ecosystems.

The period during which most litter is produced and decomposed has been related primarily to the climate (Spain, 1984), although a number of other factors have also been implicated, such as the availability of nutrients, the successional stage of the community, and the deciduousness of the tree species (Vogt et al., 1986; Villela and Proctor, 1999). César (1991) observed a correlation between the production of leaf litter and the humidity of the soil in a number of different forest ecosystems, with litterfall increasing considerably during the dry season.

A number of studies have estimated litterfall production in both temperate and tropical forests in different regions of the world (e.g., Bray and Gorham, 1964; Adis et al., 1979; Vitousek, 1984; Vogt et al., 1986; Vitousek and Sanford Junior, 1986; Celentano et al., 2011; Negash and Starr, 2013; Gawali, 2014; León and Osorio, 2014; Silver et al., 2014;). However, few data are available on the alluvial forests of the Amazonian ecosystems associated with clear water rivers such as the Xingu River. Given this, the present study quantified litterfall production and its different fractions over an annual cycle at four sites in the alluvial forests of the middle Xingu.

2. Material and Methods

2.1. Study area

The present study was conducted on a 180 km stretch of the middle Xingu River in Pará, in the eastern Brazilian Amazon basin (Figure 1). This region is characterised by numerous waterfalls and river rapids, as well as extensive areas of alluvial rainforest (Camargo et al., 2004).

The climate of the study area is of Köppen's A type, varying between Aw and Am (Critchfield, 1968). Annual temperature in the study area oscillates between 17.5°C and 24.5°C, with relative humidity of 84-86%. Mean annual precipitation varies between 2066.8 mm and 2379.4 mm (Camargo et al., 2004).

Four areas of alluvial rainforest were monitored in the present study. Two were located beside lakes on river islands (Ilha Grande and Pimentel) and the other two (Boa Esperança and Arroz Cru) on the banks of the Xingu River. The vegetation that borders Ilha Grande (3°34'47" S, 52°23'42" W) and Pimentel lakes (3°25'46" S, 52º24'4" W) is a dense rainforest with large trees, such as the Arapari (*Macrolobium acaciaefolium* Benth), Louro canela (*Aniba riparia* (Nees)), and Piranheira (*Piranhea triflora* Baill). During the rainy season, the forest is flooded by the creeks that run into the area surrounding the lakes.

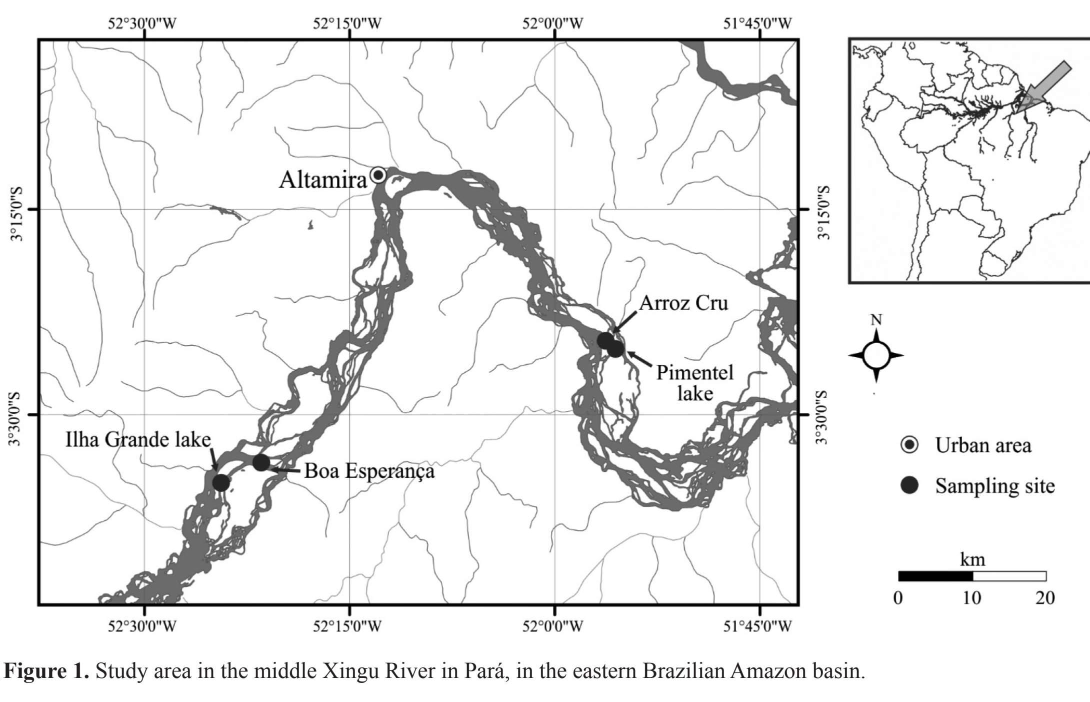

Figure 1. Study area in the middle Xingu River in Pará, in the eastern Brazilian Amazon basin.

The river margin site Boa Esperança (3°34'12" S, 52°22'46" W) is located in the vicinity of Ilha Grande, while Arroz Cru (3°19'48" S, 52°06'00" W) is near Pimentel Island. The vegetation at these sites varies considerably in structure, ranging from pioneer forests to dense swamp (Estupinãn and Camargo, 2009).

2.2. Collection and analysis of leaf litter samples

The leaf litter samples were collected at each of the four study sites in eight randomly-distributed collectors separated by a mean distance of 200 m. The collectors have an area of 1 m^2 and a base made of nylon mesh. At each site, the collectors were set at heights above the maximum level of the flood water.

The plant detritus collected each month between August, 2006, and July, 2007, was separated into leaf, twig, flower, fruit, and bark fractions. These fractions were stored in number-coded paper bags and maintained in a stove kept at a mean temperature of 65°C until they reached a constant weight, based on measurements taken using a balance with a precision of 0.001 g.

The possible relationship between the monthly biomass of each fraction of the litterfall and the level of the river was tested using the Pearson correlation coefficient (r) for the four sites, with the results being presented as the mean ± standard deviation of the r values obtained. Differences in the production of litter among months and sites were evaluated using a factorial ANOVA once the data had been normalised using the logarithmic function. Fisher's exact test was used to verify the significance of differences in the production of litter between sites and months (Zar, 1999).

3. Results

The variation in the level of the Xingu River recorded during the period of the present study was typical of the average value recorded in previous years (Figure 2). Between 1961 and 1990, the rainy season in the region normally began in December, and peaked between January and May (INMET, 1992).

The total weight of the litter collected during the study period varied from 4,900 kg.ha^{-1}.year^{-1}, at Arroz Cru on the banks of the Xingu, to 10,300 kg.ha^{-1}.year^{-1} at Pimentel Lake (Table 1). Monthly values followed a systematic seasonal pattern, with the highest mean weights being recorded during the rainy season, and the lowest in the dry season (Figure 3A).

A similar pattern of variation in the different fractions was recorded at all the study sites. Leaves and twigs provided the majority of the biomass throughout the study period. The annual production of the leaf fraction was 5745.7 kg.ha^{-1} for Pimentel Lake, 3760.3 kg.ha^{-1} for Ilha Grande Lake, 2481.6 kg.ha^{-1} for Arroz Cru, and 6599.4 kg.ha^{-1} for Boa Esperança. The peak in leaf biomass was recorded in April, 2007 (high water), with a marked reduction over the course of the dry season, being reflected in a positive correlation ($r_{med} = 0.47 \pm 0.088$) between the production of this fraction and the level of the river (Figure 3B). In the case of the bark fraction, while there was a positive correlation with the level of the river ($r_{med} = 0.18 \pm 0.061$), the relationship was much weaker (Figure 3C).

By contrast, the flower fraction correlated negatively ($r_{med} = -0.61 \pm 0.021$) with the level of the river (Figure 3D), with a peak in October, 2006, and a marked reduction during the flood period. The fruit fraction was relatively important in both seasons (Figure 3E), but especially during the flooding of the forest, with a peak in biomass being recorded in April, 2007, and a positive correlation overall ($r_{med} = 0.48 \pm 0.32$). Twigs followed a similar pattern (Figure 3F), also peaking in the flood period ($r_{med} = 0.43 \pm 0.26$).

The ANOVA revealed significant differences in the production of litter among sites (ANOVA test: F = 2.73; p = 0.04) and months (ANOVA test: F = 9.63; p < 0.001).

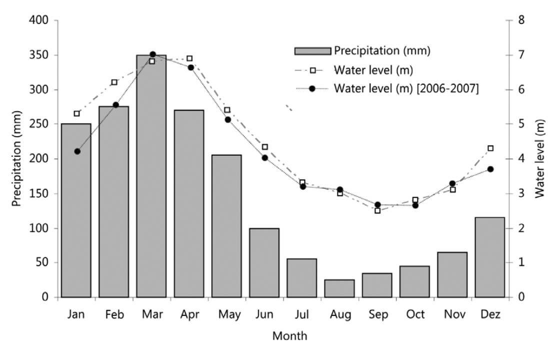

Figure 2. Hydrological data (precipitation and water level) in the middle Xingu River in Pará, in the eastern Brazilian Amazon basin.

Table 1. Production of litter (kg.ha^{-1}.year^{-1}) in four alluvial rainforest sites on the middle Xingu River over an annual cycle (August, 2006 – July, 2007).

Fraction	Marginal forest - Insular lakes		Banks of the Xingu River	
	Pimentel	Ilha Grande	Arroz Cru	Boa Esperança
Leafs	5,745.7 (55.5%)	3,760.3 (65.6%)	2,481.6 (49.8%)	6,599.4 (66.9%)
Flowers	330.8 (3.2%)	198.6 (3.5%)	175.4 (3.5%)	299.4 (3%)
Fruits	1,095.6 (10.6%)	266.5 (4.6%)	885.3 (17.8%)	788.4 (8%)
Twigs	2,962.8 (28.6%)	1,465.7 (25.6%)	1,363.9 (27.4%)	2,003.2 (20.3%)
Barks	213.0 (2.1%)	41.0 (0.7%)	76.9 (1.5%)	174.3 (1.8%)
Total production	10,347.9	5,732.1	4,983.0	9,864.7

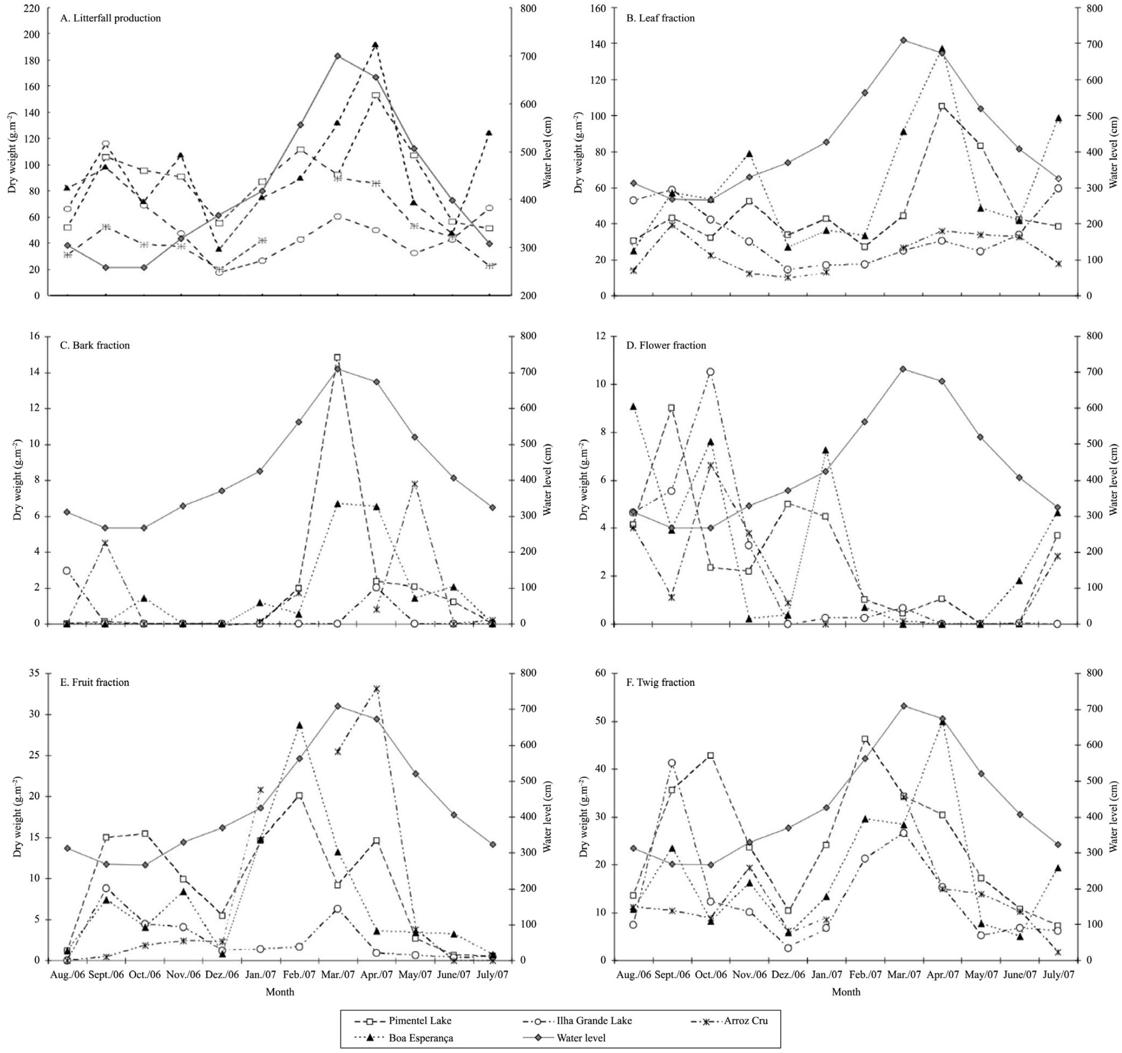

Figure 3. Mean total weight of the litterfall production (A), leafs (B), barks (C), flowers (D), fruits (E), and twigs (F) fractions in alluvial rainforest on the middle Xingu River in the eastern Brazilian Amazon basin between August, 2006 and July, 2007.

While no significant differences in dry weight were found between sites at the two river margins, the two lakes were significantly different from one another and from the other sites. Similarly, significant differences were found in the production of leaf litter among the months of the study period.

4. Discussion

The results of the present study contrast with those of Jackson (1978), Delitti (1984), Pagano (1991), Gisler (1995), and Martins and Rodrigues (1999), who all recorded increased litterfall in tropical forests during the dry season, and interpreted the loss of leaves as a strategy for the avoidance of excessive water loss during this period. However, in a semi-deciduous forest in southeastern Brazil, Dias and Oliveira Filho (1997) recorded a pattern similar to that observed in the present study, that is, a higher rate of litterfall during the rainy season, when the hydrological deficit was at its lowest.

As the present study focussed on forests adjacent to bodies of water, it seems likely that the hydrological potential of the soil may have varied little over the course of the year, maintaining relatively high levels of humidity even during the dry season. This may have meant that the humidity of the soil was not a factor determining leaf fall in the trees, although the forest may have responded to the seasonal flooding occurring during the rainy season by losing leaves.

The total litterfall recorded over the course of the year at the four study sites on the middle Xingu River were consistent with the estimates obtained for other Amazonian forests, including *terra firme* habitats, and *igapó* and *várzea* swamps (Klinge, 1977; Adis et al., 1979; Silva and Lobo, 1982; Silva, 1984; Worbes, 1986b; Scott et al., 1992). The leaf fraction accounted for more than 50% of

Table 2. Production of the litter (total and fraction) in different Amazon sites.

Amazon sites	Leafs (%)	Flowers (%)	Fruits (%)	Twigs (%)	Barks (%)	Total litterfall kg.ha^{-1}.year^{-1}	Source
Igapó	79	-	7	15	-	6,700	Adis et al. (1979)
Terra Firme - Manaus	81	-	6	13	-	7,900	Worbes (1986a)
Terra Firme - Belém	81	-	6	13	-	9,900	Klinge (1977)
Várzea	82	-	8.3	9.7	-	10,300	Worbes (1986b)
Mocambo - Belém - PA (Várzea)	76	-	-	-	-	8,500	Silva and Lobo (1982)
Terra firme Tucuruí - PA	71	-	-	-	-	6,600	Silva (1984)
Terra firme Ilha de Maracá – Roraima (Várzea)	68	-	-	-	-	9,200	Scott et al. (1992)
Pimentel Lake	55.5	3.2	10.6	28.6	2.1	10,347.9	This study
Ilha Grande Lake	65.6	3.5	4.6	25.6	0.7	5,732.1	This study
Arroz Cru marginal forest	49.8	3.5	17.8	27.4	1.5	4,983.0	This study
Boa Esperança marginal forest	66.9	3	8	20.3	1.8	9,864.7	This study

the volume of litter, even at the sites (Arroz Cru) where the lowest values were recorded. While the leaf fraction was relatively reduced at these sites, twigs were important, contributing more than 20% of the total litter (Table 2). Comparisons with other tropical sites further emphasize the importance of the leaf fraction of the litter throughout the year, albeit with values slightly lower than the mean of 70%, as observed in the studies of Andrade et al. (2000), Toledo et al. (2002), and König et al. (2002).

The close relationship between the production of different fractions of the litter and the seasonal fluctuations in river levels appears to reflect adaptations in the phenological strategies of the vegetation, and the optimisation of the vital functions of the different species in response to the variation in hydrological conditions. The increased production of litter during the flood period recorded in the present study is consistent with that recorded in other tropical environments (Klinge and Rodrigues, 1968; Klinge, 1977; Silva, 1984).

As in the present study, Cattanio et al. (2004) recorded an increase in the production of the flower fraction of the litter during the dry season in a *várzea* forest of the Amazon Estuary. The negative correlation with river levels found in both studies (r_{med} =–0.61 here, and r_{med} =-0.65 in the earlier study) reflect a flowering peak between August and October, that is, in the early dry season. A similar seasonal pattern has been recorded in other tropical forests by Janzen (1967), Araújo (1970), Frankie et al. (1974), Fournier (1976), and Jackson (1978).

While present throughout the year, the fruit fraction peaked during the flood period. The synchrony between the peak in fruit production and the river flood appears to represent an adaptation of many floodplain tree species for the dispersal of their seeds through ichthyochory (Camargo, 2009), reinforced by the abundance of frugivorous fish species found in the middle Xingu River, which depend on the resources provided by the alluvial forests during the annual flood. Seed dispersal is a fundamentally important mechanism for the maintenance of the biodiversity of tropical forests, and frugivorous fishes appear to play a major role in this process in the *várzea* and *igapó* floodplain swamps (Ayres, 1995).

The differences found in the present study between the island lakes and the sites on the river margin may be related to variations in the response of the different systems to the local characteristics of the flood pulse and hydrological cycle (César, 1991; Cattanio et al., 2004). Even though the forests of the middle Xingu may be distinct from the *várzea* habitats of the Amazon Estuary, the similar phenological patterns recorded in the present study indicate a standard response to local climatic variation and the intense oscillations in rainfall levels and the related flood pulse.

In conclusion, the total litterfall was positively correlated with rainfall and river levels. Whereas the leaf and fruit fractions followed this general pattern, the flower fraction shows the inverse pattern, peaking in the dry season.

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