



## Spatial-temporal variation in litterfall in seasonally dry tropical forests in Northeastern Brazil

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(With 2 figures)

### Abstract

The production of litterfall is essential for nutrient cycling in terrestrial ecosystems. From November 2009 to October 2011, analyzed the monthly litterfall production in two areas of Caatinga, a type of Seasonally Dry Tropical Forest located in the Cariri Paraibano, in the semiarid region of the Paraíba, Northeastern Brazil. One of the areas, Private Natural Heritage Reserve (RPPN) Fazenda Almas, is legally protected, and the other, Fazenda Moreiras, does not. The aims were to evaluate the effects of precipitation, evapotranspiration and vegetation structure on the temporal and spatial dynamics of litterfall production. Eight sampling points were randomly chosen at each site, and two 1 m<sup>2</sup> collectors were installed 50 m apart from each other. The collected material was sorted, dried and weighed. Additionally, the characteristics (density, species richness, height and mean basal area) of the tree-shrub stratum in plots with a 10 m radius surrounding each collector. Total litterfall production was 4,500 kg ha<sup>-1</sup> yr<sup>-1</sup> for Fazenda Almas and 3,300 kg ha<sup>-1</sup> yr<sup>-1</sup> for Fazenda Moreiras; these values were within the expected range for Seasonally Dry Tropical Forests. The inter- and intra-annual variation in litterfall production was positively correlated with precipitation and evapotranspiration rates, and four months after the highest precipitation rates, there was a marked decrease in litterfall occurred during the dry season. Furthermore, the contributions of the material fractions were distinct with the leaf fraction representing for more than 60% of the litterfall, and the vegetation structure explained 75% of the variation in litterfall production. Therefore, climatic factors and vegetation structure affect the temporal and spatial dynamics of litterfall production and consequently influence nutrient dynamics in the semiarid region of Brazil.

**Keywords:** biomass, Caatinga, evapotranspiration, rainfall, semiarid, vegetation.

### Variação espaço-temporal da serapilheira em uma floresta tropical sazonalmente seca no Nordeste do Brasil

#### Resumo

A produção de serapilheira é essencial para a ciclagem de nutrientes em ecossistemas terrestres. De Novembro de 2009 a Outubro de 2011, foi analisada a produção de serapilheira em duas áreas de Caatinga, um tipo de Floresta Tropical sazonalmente Seca localizada no Cariri Paraibano, na região do semiárido da Paraíba, Nordeste do Brasil. Uma das áreas, Reserva Particular do Patrimônio Natural - RPPN - Fazenda Almas, é legalmente protegida, ao contrário da outra, Fazenda Moreiras. Os objetivos foram avaliar o efeito da precipitação, evapotranspiração e estrutura da vegetação sobre a dinâmica temporal e espacial da produção de serapilheira. Oito pontos de amostragem foram escolhidos aleatoriamente em cada localidade, e dois coletores de 1 m<sup>2</sup> foram instalados a 50 m um do outro. O material coletado foi triado, secado e pesado. Adicionalmente, foram registradas as características (densidade, riqueza de espécies, altura e área basal média) das espécies arbóreo-arbustivas na parcela com um raio (r) de 10 m ao redor de cada coletor. A produção total de serapilheira foi 4,500 Kg ha<sup>-1</sup> yr<sup>-1</sup> para a Fazenda Almas e 3,300 kg ha<sup>-1</sup> yr<sup>-1</sup> para a Fazenda Moreiras; estes valores estão dentro da faixa esperada para as Florestas Tropicais sazonalmente secas. A variação inter e intranual na produção de serapilheira foi positivamente correlacionada com as taxas de precipitação e evapotranspiração, e quatro meses depois das maiores taxas de precipitação, houve uma diminuição acentuada na serapilheira coletada durante a estação seca. Além disso, as contribuições das frações de material foram distintas com a fração de folha representando mais que 60% da serapilheira, e a estrutura da vegetação explicou 75% da variação na produção de serapilheira. Portanto, os fatores climáticos e a estrutura da vegetação afetam a dinâmica temporal e espacial da produção de serapilheira e, consequentemente, influenciam a dinâmica de nutrientes na região semiárida do Brasil.

**Palavras-chave:** biomassa, Caatinga, evapotranspiração, pluviosidade, semiárido, vegetação.

## 1. Introduction

Litterfall production is considered one of the main routes of nutrient transfer from the vegetation to the soil (Vitousek, 1984; Búrquez et al., 1999; Vital et al., 2004). Therefore, quantifying litterfall pools is essential to properly understand the structure and function of tropical forests (Bray and Gorham, 1964; Vital et al., 2004). In semiarid terrestrial ecosystems, litterfall production provides important information about the phenological cycles of plants and their influence on the return of nutrients to the soil (Proctor et al., 1983). Thus, understanding the dynamics of litterfall production can provide insight into nutrient cycling, forest growth, successional patterns, carbon fluxes, ecological disturbances and the interactions among environmental variables in forest ecosystems (Vasconcelos and Luizão, 2004; Zhou et al., 2007; González-Rodríguez et al., 2011).

In Seasonally Dry Tropical Forests (SDTF), primary productivity is largely controlled by the amount and duration of rainfall, so seasonal variations in rainfall constrain and control the productivity and nutrient dynamics of these ecosystems (Lugo and Murphy, 1986; Dirzo et al., 2011). In arid and semiarid environments, variations in vegetation structure, caused by edaphic factors and distribution of rainfall, can also lead to spatial changes in litterfall production (Archer et al., 1988; Facelli and Pickett, 1991; Alvarez et al., 2009; Bisigato et al., 2009).

Caatinga, a type of SDTF in South America (Prado and Gibbs, 1993), covers an area of approximately 735,000 km<sup>2</sup>, in Northeastern Brazil. This region is characterized by high temperatures and water deficits that exacerbate the effects of poorly distributed low rainfall (Reis, 1976; Andrade-Lima, 1981). The landscape is dominated by a mosaic of physiognomic forms, particularly with xerophytic plant species (Medeiros et al., 2009). The aerial biomass ranges between 30,000 and 50,000 kg ha<sup>-1</sup> (Menezes et al., 2012). In the Caatinga, the vegetation cover and litterfall are important for soil protection because the soil is usually shallow with low infiltration capacity, high surface runoff and reduced natural drainage (Sampaio et al., 1981; Lopes et al., 2009).

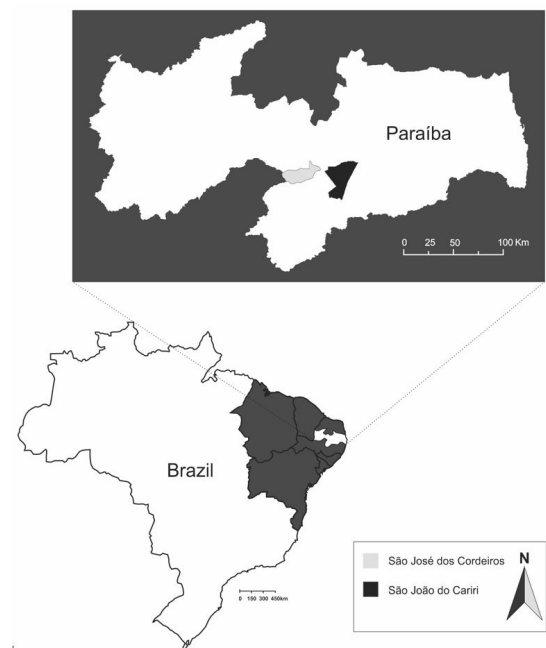
There are only a few studies on the production and accumulation of litter in the caatinga (Andrade et al., 2008; Costa et al., 2010; Santos et al., 2011; Silva et al., 2015b), as well as about its degradation rate (Sampaio, 1995; Dantas, 2003; Alves et al., 2006; Lopes et al., 2009; Santana and Souto, 2011; Menezes et al., 2012; Bauer et al., 2016). Our hypothesis is that variations in litter production in the Caatinga could occur due to variations in climatic factors and variations in the structures of natural ecosystems. Areas more impacted by anthropogenic action would have less plant diversity and less litter production. The present study sought to evaluate the effect of precipitation, evapotranspiration and vegetation structure on the spatial-temporal dynamics of litterfall production in one of the driest region of SDTF in Northeastern Brazil.

## 2. Materials and Methods

This study was conducted between November 2009 and October 2011 in two localities in the Cariri Paraíba: Fazenda Moreiras and a Private Natural Heritage Reserve (RPPN) Fazenda Almas, both in the semiarid region in northeastern Brazil. Fazenda Almas (07°28'15"S and 36°52'51"W) is one of the best-preserved areas in the region, with approximately 3,505 ha extending between 600 and 720 m above sea level, and it is located in the municipality of São José dos Cordeiros (Barbosa et al., 2007). Fazenda Moreiras (07°23'51"S and 36°24'49.1"W), with an area of ca. 499 ha and approximately 460 m above sea level, is a private property, which is representative of the land use reality in the region, presents a comparatively more altered vegetation, on the banks of the Taperoá River in the municipality of São João do Cariri (Carvalho and Carvalho, 1985) (Figure 1).

The climate in the region is BSh, according to the Köppen classification (Albuquerque et al., 2005); rainfall is concentrated in three or four months, and ranges between 250 and 900 mm per year. Average annual temperatures are relatively high, surface temperature values ranged between 21.8 and 34.7 °C, net radiation ranged from 532.22 to 732.66 W/m<sup>2</sup> and potential evapotranspiration from 3.99 to 6.64 mm/day (Silva et al., 2015a). Relative humidity rarely exceeds 75% (Barbosa et al., 2007). Soils are shallow and rocky (Sampaio et al., 1981).

Eight sampling points were randomly chosen at each site, and two 1 m<sup>2</sup> collectors were installed 50 m apart from



**Figure 1.** Map of Northeast Brazil showing the municipalities of São José dos Cordeiros (Fazenda Almas) and São João do Cariri (Fazenda Moreiras), in the Cariri Paraíba.

each other at each point. Collectors were wooden frames covered with 1 mm nylon mesh suspended approximately 20 cm above the ground. The litterfall gathered in each collector was removed once a month (between November 2009 and October 2011) and manually sorted in the laboratory into four fractions: leaves (including leaflets and petioles), branches (including bark and other woody parts), reproductive structures (flowers, fruits and seeds) and miscellaneous material that could not be precisely identified. The different fractions were dried in a forced-air oven at 60 °C for 72 h and then weighed to an accuracy of four decimal places using a precision balance.

To analyze temporal variation, was correlated litterfall production, accumulated rainfall and actual evapotranspiration in both localities. Climatic data were provided by the Programa de Monitoramento Climático em Tempo Real da Região Nordeste (Northeastern Region Real-time Climate Monitoring Program – PROCLIMA, 2011). To analyze spatial heterogeneity, the relationship between litterfall production and vegetation structure (density, species richness, medium height and mean basal area of tree and shrubby species) at each sampling point was investigated. Plots with radii ( $r$ ) of approximately 10 m were installed around each collector, and within that all living plants with a stem diameter at ground level (DGL)  $\geq 3$  cm and total height (TH)  $\geq 1$  m were sampled and measured (Barbosa et al., 2007). Density, species richness, height and mean basal area of the plots were calculated using FITOPAC software (Shepherd, 2008).

### 3. Statistical Analysis

Two sampling periods denominated year 1 (November 2009 to October 2010) and year 2 (November 2010 to October 2011) were considered. The annual litterfall production for each sampling point was calculated with the average obtained from the two collectors.

Repeated measures ANOVA were used to analyze the temporal variation in litterfall production between years and months, and Spearman's correlations between litterfall production and climatic data (precipitation and evapotranspiration) recorded 30, 60, 90 and 120 days prior to the sampling events were estimated. A General Linear Models (GLM) analysis was performed to evaluate the relationship between spatial variability of litter production and vegetation structure. To meet the assumption of normality, the data were  $\log(x + 1)$  transformed. The analyses were performed using STATISTICA 5.0 (StatSoft, 1995).

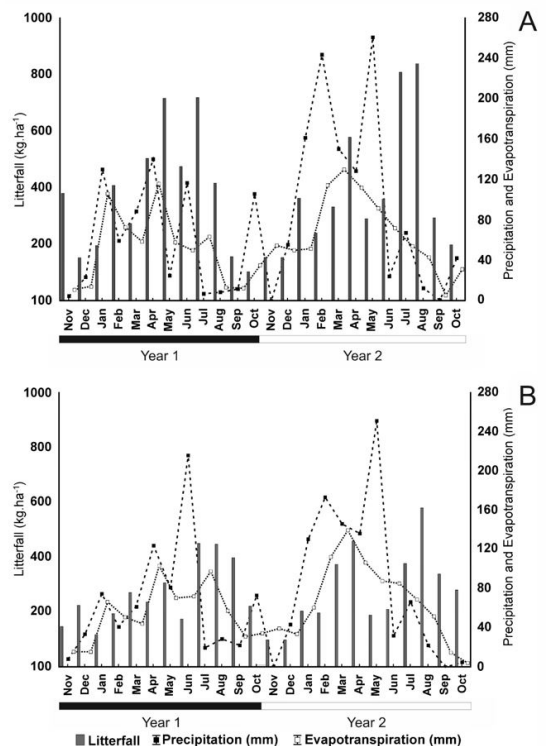
### 4. Results

Litterfall production at RPPN Fazenda Almas totaled approximately 4,580 kg ha<sup>-1</sup> yr<sup>-1</sup> with a monthly average ( $\pm$  standard error) of 380  $\pm$  40 kg ha<sup>-1</sup>. The highest rates of production occurred in July 2011 (860 kg ha<sup>-1</sup>) and August 2011 (846 kg ha<sup>-1</sup>), and the lowest rates were in December 2009 and October 2010 (151 kg ha<sup>-1</sup> and 103 kg ha<sup>-1</sup>, respectively) (Table 1). At Fazenda Moreiras, the annual production was approximately 3,320 kg ha<sup>-1</sup> yr<sup>-1</sup>

with a monthly average of 280  $\pm$  30 kg ha<sup>-1</sup>. The highest production rates occurred in April 2011 and August 2011 (458 and 577 kg ha<sup>-1</sup>, respectively), and the lowest in November 2010 and December 2010 (90 and 100 kg ha<sup>-1</sup>, respectively) (Table 1).

The accumulated annual rainfall was greater than 700 mm at both sites during the year 1 (November 2009 to October 2010), with precipitation greater than 60 mm month<sup>-1</sup> for four consecutive months (January–April 2010). In the year 2 (November 2010–October 2011), annual rainfall was greater than 1,000 mm with five consecutive months exceeding 100 mm month<sup>-1</sup> (January–May 2011) (Figure 2A and 2B). There was significant variation in the total production of litterfall between months but not between years for both RPPN Fazenda Almas (Month:  $F_{11,180} = 14.18$ ,  $p < 0.001$ ; Year:  $F_{1,180} = 0.05$ ,  $p > 0.05$ ) and Fazenda Moreiras (Month:  $F_{11,180} = 4.48$ ,  $p < 0.001$ ; Year:  $F_{1,180} = 1.54$ ,  $p > 0.05$ ). However, the temporal heterogeneity in litterfall production responded to variations between years and months (Year x Month – Fazenda Almas:  $F_{11,180} = 7.13$ ,  $p < 0.001$ ; Fazenda Moreiras:  $F_{11,180} = 1.91$ ,  $p < 0.05$ ) (Table 2).

The rate of litterfall production correlated most strongly with rainfall in the fourth month prior to sampling ( $r_{s60\text{ days}} = 0.32$ ,  $n = 48$ ,  $p < 0.05$ ;  $r_{s90\text{ days}} = 0.36$ ,  $n = 48$ ,  $p < 0.05$ ;



**Figure 2.** Temporal variations in litterfall production, evapotranspiration and rainfall between November 2009 and October 2011 at RPPN Fazenda Almas (A), São José dos Cordeiros and Fazenda Moreiras (B), São João do Cariri, Paraíba state, Brazil. The values are the means.

**Table 1.** Monthly litterfall production between November 2009 and October 2011 at RPPN Fazenda Almas, São José dos Cordeiros, and Fazenda Moreiras, São João do Cariri, Paraíba state, Brazil. The values are the means  $\pm$  SE.

Sampling period	Month	Leaves			Branches			Flowers			Miscellaneous			Total		
		kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE	%
Year 1	Nov/09	260	( $\pm$ 73)	69	85	( $\pm$ 49)	23	29	( $\pm$ 6)	4	( $\pm$ 1)	1	378	( $\pm$ 88)	1	
	Dec/09	56	( $\pm$ 18)	37	36	( $\pm$ 11)	24	48	( $\pm$ 18)	11	( $\pm$ 4)	7	151	( $\pm$ 30)	7	
	Jan/10	68	( $\pm$ 11)	35	32	( $\pm$ 7)	16	84	( $\pm$ 26)	9	( $\pm$ 8)	5	193	( $\pm$ 33)	5	
	Feb/10	190	( $\pm$ 26)	47	124	( $\pm$ 41)	31	74	( $\pm$ 21)	17	( $\pm$ 5)	4	405	( $\pm$ 59)	4	
	Mar/10	156	( $\pm$ 29)	57	38	( $\pm$ 10)	14	63	( $\pm$ 27)	15	( $\pm$ 7)	5	272	( $\pm$ 44)	5	
	Apr/10	278	( $\pm$ 44)	55	34	( $\pm$ 8)	7	177	( $\pm$ 66)	13	( $\pm$ 3)	3	502	( $\pm$ 85)	3	
	May/10	564	( $\pm$ 75)	79	117	( $\pm$ 62)	16	23	( $\pm$ 9)	10	( $\pm$ 5)	1	714	( $\pm$ 117)	1	
	Jun/10	395	( $\pm$ 45)	84	45	( $\pm$ 9)	9	29	( $\pm$ 8)	4	( $\pm$ 1)	1	473	( $\pm$ 47)	1	
	Jul/10	572	( $\pm$ 77)	80	71	( $\pm$ 13)	10	69	( $\pm$ 28)	5	( $\pm$ 1)	1	717	( $\pm$ 76)	1	
	Aug/10	335	( $\pm$ 71)	80	34	( $\pm$ 8)	8	46	( $\pm$ 14)	2	( $\pm$ 1)	0	417	( $\pm$ 72)	0	
Year 2	Sep/10	103	( $\pm$ 26)	67	22	( $\pm$ 8)	14	28	( $\pm$ 11)	1	( $\pm$ 0)	1	154	( $\pm$ 34)	1	
	Oct/10	36	( $\pm$ 8)	35	34	( $\pm$ 9)	33	20	( $\pm$ 7)	13	( $\pm$ 3)	12	103	( $\pm$ 18)	12	
	Nov/10	59	( $\pm$ 8)	39	42	( $\pm$ 14)	28	6	( $\pm$ 3)	4	( $\pm$ 11)	30	152	( $\pm$ 25)	30	
	Dec/10	59	( $\pm$ 8)	39	42	( $\pm$ 14)	28	6	( $\pm$ 3)	4	( $\pm$ 11)	30	152	( $\pm$ 25)	30	
	Jan/11	141	( $\pm$ 21)	39	150	( $\pm$ 102)	41	56	( $\pm$ 32)	15	( $\pm$ 6)	4	362	( $\pm$ 108)	4	
	Feb/11	108	( $\pm$ 18)	45	47	( $\pm$ 18)	20	79	( $\pm$ 34)	5	( $\pm$ 1)	2	239	( $\pm$ 46)	2	
	Mar/11	205	( $\pm$ 31)	62	32	( $\pm$ 9)	10	88	( $\pm$ 34)	6	( $\pm$ 2)	2	331	( $\pm$ 46)	2	
	Apr/11	434	( $\pm$ 67)	75	67	( $\pm$ 16)	12	71	( $\pm$ 25)	4	( $\pm$ 1)	1	576	( $\pm$ 64)	1	
	May/11	239	( $\pm$ 34)	83	41	( $\pm$ 16)	14	27	( $\pm$ 9)	2	( $\pm$ 1)	1	309	( $\pm$ 42)	1	
	Jun/11	292	( $\pm$ 36)	81	62	( $\pm$ 18)	17	28	( $\pm$ 9)	0	( $\pm$ 0)	0	382	( $\pm$ 48)	0	
Total (24 months)	Jul/11	721	( $\pm$ 145)	89	66	( $\pm$ 18)	8	70	( $\pm$ 24)	3	( $\pm$ 2)	0	860	( $\pm$ 150)	0	
	Aug/11	724	( $\pm$ 108)	86	68	( $\pm$ 18)	8	53	( $\pm$ 13)	1	( $\pm$ 0)	0	846	( $\pm$ 123)	0	
	Sep/11	216	( $\pm$ 38)	75	45	( $\pm$ 21)	15	22	( $\pm$ 6)	7	( $\pm$ 2)	3	290	( $\pm$ 54)	3	
	Oct/11	106	( $\pm$ 23)	54	41	( $\pm$ 14)	21	50	( $\pm$ 22)	1	( $\pm$ 1)	0	198	( $\pm$ 33)	0	
			<b>6,317</b>	<b>69</b>	<b>1,375</b>		<b>15</b>	<b>1,246</b>		<b>238</b>		<b>3</b>	<b>9,176</b>		<b>3</b>	

SE: Standard Error of the mean.

Table 1. Continued...

Fazenda Moreiras															
Litterfall															
Sampling period	Month	Leaves			Branches			Flowers			Miscellaneous			Total	
		kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE	%	kg ha <sup>-1</sup>	SE
Year 1	Nov/09	104	(±69)	71	22	(±6)	15	13	(±8)	9	8	(±2)	5	147	(±81)
	Dec/09	32	(±20)	14	167	(±120)	75	30	(±24)	14	8	(±6)	4	237	(±116)
	Jan/10	31	(±10)	26	43	(±16)	36	38	(±25)	32	6	(±2)	5	118	(±39)
	Feb/10	93	(±26)	48	58	(±15)	30	20	(±8)	10	22	(±11)	12	193	(±55)
	Mar/10	85	(±24)	31	54	(±31)	20	89	(±62)	33	43	(±32)	16	271	(±146)
	Apr/10	83	(±24)	35	28	(±10)	12	99	(±48)	42	26	(±7)	11	236	(±71)
	May/10	176	(±41)	58	60	(±34)	20	58	(±17)	19	10	(±5)	3	304	(±61)
	Jun/10	133	(±22)	77	20	(±6)	12	17	(±7)	10	2	(±1)	1	172	(±27)
	Jul/10	360	(±47)	80	35	(±9)	8	48	(±12)	11	5	(±1)	1	448	(±53)
	Aug/10	430	(±104)	96	36	(±10)	8	42	(±18)	9	2	(±1)	1	510	(±107)
Year 2	Sep/10	315	(±87)	80	34	(±10)	8	43	(±25)	11	4	(±1)	1	396	(±104)
	Oct/10	158	(±96)	72	33	(±11)	15	19	(±5)	9	10	(±3)	5	220	(±103)
	Nov/10	31	(±6)	32	21	(±6)	22	5	(±1)	5	40	(±23)	41	97	(±28)
	Dec/10	31	(±6)	32	21	(±6)	22	5	(±1)	5	40	(±23)	41	97	(±28)
	Jan/11	72	(±18)	35	42	(±24)	20	84	(±29)	41	6	(±2)	3	204	(±44)
	Feb/11	56	(±15)	29	11	(±3)	6	122	(±84)	63	6	(±2)	3	195	(±93)
	Mar/11	155	(±29)	42	115	(±76)	31	101	(±31)	27	2	(±0)	0	373	(±100)
	Apr/11	320	(±60)	70	68	(±33)	15	41	(±11)	9	29	(±25)	6	458	(±91)
	May/11	150	(±30)	80	12	(±3)	6	24	(±9)	13	2	(±1)	1	188	(±32)
	Jun/11	164	(±31)	78	28	(±8)	13	16	(±4)	8	2	(±1)	1	210	(±34)
Total (24 months)	Jul/11	323	(±58)	86	27	(±10)	7	24	(±5)	6	2	(±1)	1	376	(±61)
	Aug/11	479	(±83)	83	31	(±10)	5	65	(±18)	11	2	(±1)	0	577	(±87)
	Sep/11	287	(±67)	85	18	(±6)	5	27	(±5)	8	6	(±1)	2	338	(±67)
	Oct/11	214	(±120)	77	22	(±12)	9	36	(±15)	13	3	(±1)	1	275	(±136)
				<b>64</b>	<b>1,006</b>		<b>15</b>	<b>1,066</b>		<b>16</b>	<b>286</b>		<b>4</b>	<b>6,640</b>	

SE: Standard Error of the mean.



**Table 2.** Results of repeated measures ANOVA for the monthly and annual variation in litterfall production between November 2009 and October 2011 at RPPN Fazenda Almas, São José dos Cordeiros, and Fazenda Moreiras, São João do Cariri, Paraíba state, Brazil.

	Fazenda Almas					Fazenda Moreiras				
	SS	df	MS	F	p	SS	df	MS	F	p
<b>Intercept</b>	6.306	1	6.306	897.271	0.000 *	3.346	1	3.346	317.294	0.000 *
<b>Months</b>	1.096	11	0.100	14.179	0.000 *	0.520	11	0.047	4.481	0.000 *
<b>Error</b>	1.265	180	0.007			1.898	180	0.011		
<b>Years</b>	0.000	1	0.000	0.053	0.818	0.007	1	0.007	1.547	0.215
<b>Year x Month</b>	0.315	11	0.029	7.127	0.000 *	0.097	11	0.009	1.909	0.041 *
<b>Error</b>	0.723	180	0.004			0.834	180	0.005		

\* significant difference with  $p < 0.05$ . SS: Sum of squares; df: Degrees of freedom; MS: Mean square; F: F-test; p: Statistical significance.

$r_{s120\text{ days}} = 0.52$ ,  $n = 48$ ,  $p < 0.001$ ), while evapotranspiration correlated most strongly with rainfall in the second and third months prior to sample collection ( $r_{s60\text{ days}} = 0.53$ ,  $n = 48$ ,  $p < 0.001$ ;  $r_{s90\text{ days}} = 0.53$ ,  $n = 48$ ,  $p < 0.001$ ;  $r_{s120\text{ days}} = 0.43$ ,  $n = 48$ ,  $p < 0.005$ ) (Figure 2A and 2B).

Leaves constituted the predominant fraction of the litterfall, contributing for more than 60% of the total, while reproductive structures and branches represented approximately 15% each and miscellaneous materials approximately 3% (Table 1). The leaf fraction of the litterfall correlated most strongly with precipitation (Pp) and actual evapotranspiration (AE) in the fourth and the third months prior to sample collection, respectively (Pp:  $r_{s60\text{ days}} = 0.28$ ,  $n = 48$ ,  $p > 0.05$ ;  $r_{s90\text{ days}} = 0.46$ ,  $n = 48$ ,  $p < 0.005$ ;  $r_{s120\text{ days}} = 0.71$ ,  $n = 48$ ,  $p < 0.0001$ ; AE:  $r_{s60\text{ days}} = 0.53$ ,  $n = 48$ ,  $p < 0.0001$ ;  $r_{s90\text{ days}} = 0.67$ ,  $n = 48$ ,  $p < 0.0001$ ;  $r_{s120\text{ days}} = 0.62$ ,  $n = 48$ ,  $p < 0.0001$ ). The reproductive structures fraction correlated most strongly with precipitation in the month immediately preceding litterfall collection and with evapotranspiration in the same month of litterfall collection (Pp:  $r_{s30\text{ days}} = 0.32$ ,  $n = 48$ ,  $p < 0.05$ ;  $r_{s60\text{ days}} = 0.34$ ,  $n = 48$ ,  $p < 0.05$ ; AE:  $r_{s30\text{ days}} = 0.48$ ,  $n = 48$ ,  $p < 0.001$ ;  $r_{s60\text{ days}} = 0.26$ ,  $n = 48$ ,  $p > 0.05$ ). The branches fraction presented correlation with precipitation and evapotranspiration only in the month prior the sampling event (Pp:  $r_{s60\text{ days}} = 0.35$ ,  $n = 48$ ,  $p < 0.05$ ; AE:  $r_{s60\text{ days}} = 0.38$ ,  $n = 48$ ,  $p < 0.05$ ).

Species richness and density varied from 4 to 22 species (Table 3), and from 199 to 1,648 individuals per ha, respectively. The height varied between 2.8 and 5.1 m, and the mean basal area varied between 0.8 and 19.6 m<sup>2</sup> ha<sup>-1</sup> (Table 4). Together, the vegetation structure explained 75% of the annual litterfall production in both localities (Table 5).

## 5. Discussion

The quantities of litterfall deposition observed in this study were within the previously recorded ranges for Seasonally Dry Tropical Forests (Medina and Zelwer, 1972; Gessel et al., 1980; Lugo and Murphy, 1986; Cintrón and Lugo, 1990; Morellato, 1992; Haase and Hirooka, 1998; Saynes et al., 2005). The litterfall production recorded in

the drier areas of the Caatinga tends to average between 1,900 and 3,000 kg ha<sup>-1</sup> yr<sup>-1</sup> (Santana, 2005; Souto, 2006), but it can reach values about 6,000 kg ha<sup>-1</sup> yr<sup>-1</sup> in relatively more humid areas (Sampaio and Silva, 1996; Dantas, 2003; Lopes et al., 2009; Menezes et al., 2012), and even 8,440 kg ha<sup>-1</sup> yr<sup>-1</sup> in Piauí (Lima et al., 2015) and 9,160 kg ha<sup>-1</sup> yr<sup>-1</sup> in Pernambuco (Santos et al., 2011). The value found for the legally protected area in this study (Fazenda Almas: 4,500 kg ha<sup>-1</sup> yr<sup>-1</sup>) was higher than the obtained for other areas of hyper-xerophytic Caatinga (between 900 and 3,700 kg ha<sup>-1</sup> yr<sup>-1</sup>) with similar amounts of annual precipitation (Santana, 2005; Alves et al., 2006; Souto, 2006; Andrade et al., 2008; Santana and Souto, 2011; Lopes et al., 2015; Silva et al., 2015b). These results indicate that other factors besides precipitation must be influencing litterfall production; including vegetation structure. Climate, topography and edaphic factors are already known to influence the productivity of arid and semiarid ecosystems (Bray and Gorham, 1964; Jaramillo et al., 2011).

In this study, litterfall production presented inter- and intra-annual variation and was correlated with precipitation and evapotranspiration rates. The average annual rainfall is responsible, at least in part, for the variability in primary net productivity between years and consequently, for the variation in litterfall production in both forests (Münster-Swendsen, 1987; Bo Pedersen and Bille-Hansen, 1999) and deserts (Strojan et al., 1979; Lauenroth and Sala, 1992; Alvarez et al., 2009; Campanella and Bertiller, 2010). In the present study, a decrease in litterfall production occurred during the dry season, approximately four months after the highest monthly precipitation rates were recorded. This delayed (two to four months) effect of precipitation and evapotranspiration on litterfall production was consistent with findings for other dry tropical forests, where the highest monthly litterfall production depends on soil water availability, rainfall distribution, natural disturbances and landscape position (Martínez-Yrizar and Sarukhán, 1990; Whigham et al., 1991; Campo and Vázquez-Yanes, 2004; Jaramillo et al., 2011).

Leaves constituted the predominant fraction of the litterfall, accounting for more than 60% of the total, and this corroborates the results of Bray and Gorham (1964),

**Table 3.** List of plant species that occur in sampling points at RPPN Fazenda Almas, São José dos Cordeiros, and Fazenda Moreiras, São João do Cariri, Paraíba state, Brazil.

Plant species	Fazenda Almas								Fazenda Moreiras							
	Sampling points															
	I	II	III	IV	V	VI	VII	VIII	I	II	III	IV	V	VI	VII	VIII
<i>Allophylus quercifolius</i> (Mart.) Radlk.				X	X											
<i>Amburana cearensis</i> (Allemão) A.C.Sm.				X						X						
<i>Anadenanthera colubrina</i> (Vell.) Brenan	X	X	X	X		X	X	X	X							
<i>Annona leptopetala</i> (R.E.Fr.) H.Rainer		X					X				X					
<i>Aspidosperma pyriforme</i> Mart. & Zucc		X	X	X		X	X	X	X	X	X	X	X	X	X	X
<i>Bauhinia cheilantha</i> (Bong.) Steud.	X	X	X	X		X	X	X		X		X				
<i>Cereus jamacaru</i> DC.		X														
<i>Combretum glaucocarpum</i> Mart.										X						
<i>Combretum</i> sp.1	X	X	X			X	X	X								
<i>Combretum</i> sp.2	X	X	X			X	X					X				
<i>Commiphora leptophloeos</i> (Mart.) Gillet		X	X	X				X	X	X	X	X				
<i>Croton blanchetianus</i> Baill.			X	X	X		X	X			X	X			X	X
<i>Croton echinoides</i> Baill.	X	X	X	X		X	X	X		X	X					
<i>Cynophalla flexuosa</i> (L.) J.Presl					X				X							
<i>Erythrina velutina</i> Willd.			X													
<i>Eugenia</i> sp.										X						
<i>Helicteres</i> cf. <i>guazumifolia</i> Kunth	X		X													
<i>Jatropha mollissima</i> (Pohl) Baill.	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X
<i>Lantana</i> sp.						X										X
<i>Libidibia ferrea</i> (Mart. ex Tul.) L.P. Queiroz							X				X	X				X
<i>Luetzelburgia auriculata</i> (Allemão) Ducke				X												
<i>Manihot glaziovii</i> Müll. Arg.	X	X	X	X		X	X	X	X		X					
<i>Maytenus rigida</i> Mart.				X			X		X			X				
<i>Mimosa ophthalmocentra</i> Mart. ex Benth.	X	X	X	X		X	X	X	X	X		X	X	X		X
<i>Mimosa tenuiflora</i> (Willd.) Poir.			X		X	X										
<i>Myracrodruon urundeuva</i> Allemão	X	X	X	X			X	X	X		X	X				X
<i>Pilosocereus gounellei</i> (F.A.C.Weber) Byles & Rowley	X									X						
<i>Piptadenia stipulacea</i> (Benth.) Ducke			X		X		X					X				
<i>Pisonia</i> sp.	X			X								X				
<i>Poincianella pyramidalis</i> (Tul.) L.P. Queiroz	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Pseudobombax marginatum</i> (A.St.-Hil., Juss. & Cambess.) A.Robyns				X						X						
<i>Sapium glandulosum</i> (L.) Morong	X			X			X									
<i>Schinopsis brasiliensis</i> Engl.			X						X		X					
<i>Sideroxylon obtusifolium</i> (Roem. & Schult.) T.D.Penn.											X					
<i>Spondias tuberosa</i> Arruda	X	X					X	X			X					
<i>Varronia polycephala</i> Lam.									X							X
<i>Ziziphus joazeiro</i> Mart.			X		X						X					X
<i>Indeterminado 1</i>			X	X			X									
<i>Indeterminado 2</i>	X		X													
<i>Indeterminado 3</i>			X													
<i>Indeterminado 4</i>						X										
<i>Indeterminado 5</i>								X								
<i>Indeterminado 6</i>							X	X								
<i>Indeterminado 7 (Capparaceae)</i>					X	X					X					X
<i>Indeterminado 8 (Fabaceae)</i>											X					

**Table 4.** Litterfall production and vegetation structure from November 2009 to October 2011 at RPPN Fazenda Almas, São José dos Cordeiros, and Fazenda Moreiras, São João do Cariri, Paraíba state, Brazil.

	Fazenda Almas								Fazenda Moreiras							
	Sampling points															
	I	II	III	IV	V	VI	VII	VIII	I	II	III	IV	V	VI	VII	VIII
<b>Litterfall (kg ha<sup>-1</sup>)</b>	6,000	4,900	5,900	4,800	4,600	2,100	5,500	2,600	3,900	3,500	7,000	3,800	1,600	2,100	900	3,400
<b>Individuals (number)</b>	143	125	194	148	86	145	159	109	207	184	96	102	149	85	25	75
<b>Density (ind ha<sup>-1</sup>)</b>	1,139	1,011	1,377	1,178	685	1,154	1,266	860	1,648	1,465	764	812	1,186	677	199	597
<b>Species richness</b>	16	15	22	19	9	14	20	15	12	12	17	12	4	4	10	5
<b>Height (m)</b>	4.3	4.0	3.4	3.3	3.9	3.2	4.4	3.2	4.0	3.5	4.9	4.4	3.1	2.8	3.1	5.1
<b>Basal area (m<sup>2</sup> ha<sup>-1</sup>)</b>	6.0	8.5	7.1	6.1	4.9	4.5	19.6	3.7	5.7	8.0	13.2	5.3	3.2	3.0	0.8	1.8

**Table 5.** General Linear Models (GLM) to evaluate the relationship between spatial variability of litter production and vegetation structure at RPPN Fazenda Almas, São José dos Cordeiros, and Fazenda Moreiras, São João do Cariri, Paraíba state, Brazil.

	SS	df	MS	F	p	
<b>Intercept</b>	1,296	1	1,296	11,218	0.006	*
<b>Density (ind ha-1)</b>	1,818	1	1,818	15,744	0.002	*
<b>Species richness</b>	0.668	1	0.668	5,788	0.035	*
<b>Height (m)</b>	0.046	1	0.046	0.397	0.541	
<b>Basal area (m<sup>2</sup> ha-1)</b>	0.021	1	0.021	0.183	0.677	
<b>Error</b>	1,270	11	0.115			

\*significant difference with  $p < 0.05$ . SS: Sum of squares; df: Degrees of freedom; MS: Mean Square; F: F-test; p: Statistical significance.

who found that leaves constitute 58% to 79% of the organic material deposited in the soil in different macroecological zones. In areas with Caatinga vegetation, the leaf fraction has been observed to vary from 56.2% to 80.6% (Santana, 2005; Alves et al., 2006; Souto, 2006; Costa et al., 2007; Andrade et al., 2008; Lopes et al., 2009; Costa et al., 2010; Lopes et al., 2015; Silva et al., 2015b). Reproductive structures and branches represented approximately 15% of the total litterfall in this study. Martínez-Yrizar and Sarukhán (1990) reported a 17% contribution from the branch fraction in a deciduous forest in Mexico, which was very similar to the value observed by Santos et al. (2011) in the Caatinga in Pernambuco, and Lopes et al. (2015) in Rio Grande do Norte, Brazil.

The deposition of the leaf fraction was best explained by precipitation and evapotranspiration in the fourth and third months prior to the collecting events. The loss of leaves by the vegetation is due to natural senescence and the mechanical action of rain (Toledo, 2003) as well as the deciduous behavior of most Caatinga species (Souto, 2006). The deposition of reproductive structures was correlated with precipitation and evapotranspiration in the month preceding sampling as well as with the phenology of the dominant species (Lampe et al., 1992; Martínez-Yrizar et al., 1999; Alvarez et al., 2009). The peak

of reproductive structures in the litterfall during the rainy season observed in this study agreed with the findings of Quirino (2006), who reported that most individuals at RPPN Fazenda Almas were developing flower buds during this period. Studies in other tropical regions have also indicated that a greater number of species present flower buds during the wet season (Talora and Morellato, 2000; Zipparro, 2004).

The variation in litterfall production rates between the study areas resulted, at least in part, from the effects of species richness, density, average height and basal area of the woody species. It is known that litterfall production is related to vegetation structure (Schlittler et al., 1993; Werneck et al., 2001), age (Leitão-Filho et al., 1993) and floristic composition (Sundarapandian and Swamy, 1999), but the degree of influence of each factor depends on the unique characteristics of each plant community (Pires et al., 2006). According to Delitti (1989), litterfall composition also varies according to the ecosystem and its successional stage. Therefore, the litterfall production in the study areas reflected the characteristics of each habitat (such as the presence of mountainous areas and the proximity to rocky outcrops or temporary water courses) and the different land-use histories.



Biodiversity loss, especially of large tree species, and the predominance of a few species in sites previously used for agriculture and livestock are characteristics of Caatinga ecosystems (Pereira et al., 2001; Pereira et al., 2003; Alves et al., 2009). In this study, the woody vegetation structure accounted for 75% of the litterfall production, which indicates that disturbances that interfere with the Caatinga structure can affect litterfall production and, consequently, the dynamics of nutrient cycling. Several authors have proposed that woody species promote soil heterogeneity through the differential accumulation of litterfall under their canopies, thus acting as “ecosystem engineers” (Schlesinger, 1997; Reynolds et al., 1999). There is evidence that climatic seasonality and microhabitat heterogeneity greatly influence plant biological cycles and the dynamics of plant populations in the Caatinga (Araújo, 2005; Lima et al., 2007).

In conclusion, climatic factors (precipitation and evapotranspiration) indirectly influence the annual rate of litterfall production in the semi-arid region of Northeastern Brazil, since they directly influence the species and the structure of the vegetation in the region. Sites with greater plant density and species richness, as well as taller individuals and greater basal areas and, thus, greater aerial biomass produce greater amounts of litterfall. Plant cover also influences quantitatively and qualitatively litterfall production throughout the year because this process is directly related to plant phenology. Therefore, climate and vegetation structure affect the temporal and spatial dynamics of litterfall production in the Caatinga and consequently influence the return of nutrients to the soil. Thus, the pathways of nutrient transfer from plants to the soil in the Caatinga are closely associated with climatic and phenological factors (Schumacher, 1992; Poggiani and Schumacher, 2000; Santana, 2005; Souto, 2006) as well as with environmental aspects such as the preservation status and land-use history of an area. Knowledge about these pathways is highly important, both for understanding ecosystem function and for improving forest management practices and restoration of degraded areas (Souza and Davide, 2001). So, data on nutrient cycling in the Caatinga are fundamental for the conservation of its biodiversity and for the design of adequate management plans for this ecosystem.

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