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CLIMATIC INFLUENCES ON LEAF FALL SEASONALITY IN THE ATLANTIC FOREST (SERRA DOS ÓRGÃOS NATIONAL PARK – RJ- BRAZIL)

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Abstract: We compare temporal variations in leaf fall among three sites of evergreen Atlantic Forest and analyze how climatic variables influence it. Sites were located at Serra dos Órgãos National Park at different altitudes. Litter was collected monthly, from September 1997 to September 2005. Leaves were separated from other litter elements, oven-dried and weighted. Differences in leaf fall mass among grids and how they correlated with temporal variations were analyzed. Climatic variables were obtained from a nearby station and deviations from climatological normals were analyzed. We grouped climatic variables using Principal Component Analyses (PCA) and the highest scores of the two main factors were selected to construct regression models for different time lags. Leaf fall represented 50.5-70 percent of the total litter fall and mean leaf fall differed significantly among grids. However, leaf fall seasonality in the three areas were correlated. Leaf fall increased at the end of dry periods, when temperature and precipitation started to increase. Climatic variables were classified into two groups: seasonal and anomaly. Models constructed with lag variation from 0 and 6 months show that leaf fall was best explained by an anomaly in the maximum mean temperature, with lag 0, and by precipitation, with a six-month lag. We conclude that plant species respond immediately to drastic deviations from climatic factors, while regular climatic conditions are responsible for the seasonality of leaf fall, most likely as a late response to water shortage at the end of the dry season.

Key words: climatic anomalies; temporal variation; time lag; tropical forest.

INTRODUCTION

Litterfall, an important process in the functioning of forests, provides basic clues to understand and to estimate forest productivity (Misra & Nisanka 1997, Clark *et al.* 2001). In forest ecosystems, about 90 % of the net primary production may return to the soil as litter, which is an important reservoir of organic matter and mineral nutrients (Moraes *et al.* 1994). The quantitative aspects of litterfall remain an important part of forest ecology, since litterfall represents a major pathway for both energy and nutrient transfer in this type of ecosystem (Bray & Gorham 1964, Raimundo *et al.* 2008). Litterfall also has important implications for animal life, providing habitat and resources even for mammals (Freitas 1998, Gentile *et al.* 2004).

Seasonal and spatial variations in litterfall occur in many types of tropical rain forests (Bray & Gorham 1964, Oliveira & Lacerda 1993, Vitousek *et. al.* 1995, Wieder & Wright 1995, Louzada *et al.* 1995, Pendry & Proctor 1996, Burghouts *et. al.* 1998, Smith *et al.* 1998, Martins & Rodrigues 1999, Morellato *et al.* 2000, Saharjo & Watanabe 2000, Vasconcelos & Luizão 2004, Lu & Liu 2012, Vendrami *et al.* 2014, Ferreira & Uchiyama 2015). When considering total literfall, temperature and precipitation are the most frequent factors influencing these variations (Bray & Gorham 1964, Moraes *et al.* 1994, Lopes *et al.* 1994, Morellato *et al.* 2000, Scheer *et al.* 2009, Chave *et al.* 2010, Lu & Liu 2012, Sloboda *et al.* 2017). Seasonal variations in litter production are strong in temperate and some Neotropical environments where dry and wet periods are clearly defined, showing more litterfall in dry season (Kunkel-Westphal & Kunkel 1979, Reich 1995, Stocker *et al.* 1995, Triparthi *et al.* 2006, Machado *et al.* 2015). In semidecidous forest sites within the Atlantic forest domain, peaks in litterfall occur in the dry season (Morellato 1992b), and seem to result from the hydric stress caused by water deficit and decreasing solar radiation (Oliveira & Lacerda 1993, Louzada *et.al.* 1995, Scheer *et al.* 2009, Ferreira *et al.* 2014).

It is important to highlight that the results described above are the coupled variation of different litter components. Litter components itself presents specific responses to climatic variables, differing on its contribution on total litterfall. Leaf fall represents 60-76 % of the total litter amount (Bray & Gorham 1964, Smith *et al.* 1998, Chave *et al.* 2010, Dickow *et al.* 2012, Bianchin *et al.* 2016), presents a stronger correlation with precipitation and temperature, and the fall periodicity has less spatial variation when compared with the other main components of litter, as twigs and reproductive organs (Staelens *et al.* 2011, Siqueira *et al.* 2016). Reproductive fall dynamics are highly influenced by the different and complex species responses to the same climatic variations (Gurevitch *et al.*, 2009) and largely depends on the plant species composition of the vegetal community and their structural characteristics (Werneck *et al.*, 2001). Abiotic variables as wind speed can influence twigs fall, as well as phenological characteristics (Siqueira *et al.* 2016).

Seasonality in leaf fall and leaf flush are very marked at many types of Atlantic Forest sites (Morellato *et al.* 2000, Vidal *et al.* 2007, Ferreira *et al.* 2014, Ferreira & Uchiyama 2015, Sloboda *et al.* 2017), occurring at the end of dry season or middle of the wet season, when temperatures and precipitations are lower or starting to increase. However, many studies on tropical forest sites also shows just a weak seasonality and a less clear correlation between litterfall and climatic factors (Luizão & Schubart 1986, Morellato 1992b, Oliveira & Lacerda 1993, Sampaio *et. al.* 1993, Ramos & Pellens 1994, Louzada *et al.* 1995, Portes *et al.* 1996, Domingos *et al.* 1997, Martins & Rodrigues 1999, Vasconcelos & Luizão 2004, Chave *et al.* 2010). Leaf fall seasonality may represent the result of physiological responses of trees to prolonged soil water shortage or to changing climatic conditions (Morellato *et al.* 2000, Mendel *et al.* 2008, Scheer *et al.* 2009). It is possible that plants display delayed response to changes in environmental conditions when no large and immediate water deficit is occurring, as it is the case of many tropical forests (Chaves *et al.* 2003). In the Coastal Atlantic Forest, for example, there is mild seasonality with no real dry season (*i.e.*, without water deficit) (Salazar *et al.* 2007). In such cases, more extreme deviations from the climatic usual seasonal variations would represent an unusual degree of stress, resulting in stronger physiological responses, particularly from leaves.

An analysis of a large data set that includes old growth and secondary forests, from tropical South American forest types showed a significant correlation between litterfall and rainfall across all types of forest, but a great portion of the litterfall variation in their data remained unexplained (Chave *et al.* 2010). The authors suggested that one explanation could be unusual variations in climate in some years, which are not representative of long-term seasonality, might have played a role in their results. Therefore, besides the influence of seasonal variation on leaf fall, deviations from usual climatic variation (anomalies) can have some influence on unexplained leaf fall variation.

Here we analysed leaf fall variation at 3 Atlantic forest sites and correlate it with the climatic variables, considering time lag responses of leaf fall to seasonal variation and deviation from climatic anomalies. We hypothesized that besides the immediate response to seasonal climatic variation, a lagged response and a response to anomalies are influencing leaf fall and, so, the primary productivity of the Atlantic Forest sites studied.

MATERIAL AND METHODS

Study site

The study sites were located at the Iconha River Valley, Serra dos Órgãos National Park, municipality of Guapimirim, state of Rio de Janeiro, Brazil, in an area locally known as Garrafão (22°28’ S and 42°60’ W) (PELD nº 441.589/2016-2). The climate is classified as *Cfa* by Köeppen classification, with a hot and very rainy period from October to March and a cold and drier period from April-June to September (Alvares *et al.* 2013), but real water deficit is rare (Salazar *et al.* 2007). Mean monthly temperature is 20.37 ± 2.52 °C and mean monthly precipitation is 134 ± 113 mm with a weak marked dry season, could be classified by Kopen climatic classification as *CFb*. Although there is no really dry season at this work we will call “dry” season the period between April and September when temperature and precipitation are lower. The vegetation is typical of Tropical Evergreen Atlantic Forests, with high closed canopy and many forms of woody lianas and epiphytes. Lianas, palm trees, epiphytes, ferns, and bromeliads are frequent. Common tree species belong to the genera *Sloanea*, *Ficus*, *Cedrela*, *Cariniana*, *Vochysia*, *Cecropia*, among others. Common species of the sub canopy and understory include tree ferns belonging to the genera *Alsophila*, *Cyathea*, and *Hemitelia*, and the palm heart tree *Euterpe edulis* (Rizzini 1979). The topography is irregular. We quantified and analysed the litterfall of the three sites, which differ in altitude (A, 748 m; B, 652 m; and C, 522 m), all along the Iconha River Valley (Figure 1). These sites were used simultaneously in a study of small mammal populations (Gentile *et al.* 2004). The vegetation in the three locations is Atlantic Evergreen Montane Formation, which begins nearly 500 m and goes up to 1,500 m according to the IBGE (1992). The three locations were on the northeast slope of the valley, and represent a range variation in habitat structure among sites of Atlantic Evergreen Montane Formation. For example, the lower location, C, did not have any bamboo species, and location B had the highest density of bamboos (Freitas 1998). The three locations are in an area of continuous forest, but small vacation homes and dirt roads are present, with low human population density.

Sampling method

The study on litter fall occurred from April 1997 to February 2005. In each location, we set five litter traps within a 0.64 ha square area, also used as trapping grid to capture-recapture of small mammals (Gentile *et al.* 2004). Litter traps were spaced 28 m, and set along a transect crossing the 0.64 square diagonally. We used a bootstrapping method devised by us to determine the number of litter traps per location. This number is sufficient to detect the temporal and spatial variation in litterfall (Finotti *et al.* 2003). Litter was collected monthly and taken to the laboratory, where we separated leaves from other litter categories: twigs, reproductive structures, bamboo, and residues. All litter components were oven-dried at 80 °C during 24 h and then weighted to the nearest 0.01 g. We estimated the leaf fall as monthly and annual litterfall for each location (t/ha/mo, and t/ha/yr, respectively).

Data analyses

We used Kruskal-Wallis non-parametric ANOVA (H) and Mann-Whitney (U) *a posteriori* test to test for differences in total and monthly leaf fall mass among sites, and the differences between years for each area.

Time series analyses require series to be stationary. This means that the mean and variance need to be constant through the series (Hipel & McLeod 1994), and that mean and variance are not correlated. To test the assumption of stationarity, leaf fall was divided into subsets of one year, and the significance of the differences in their means and variances was tested with ANOVA and Brown-Forsythe test of homogeneity of variances (HOV). We used linear regression to test the relationship between mean and variance in the subsets. If we found a correlation, the magnitude of the correlation coefficient can be used to determine the appropriate data transformation to make the series stationary (Pankratz 1983, Legendre & Legendre 2012). Leaf fall mass did not need transformation to meet the assumption of stationarity. We performed autocorrelation functions (Davis 1986) with a 12-month lag in each leaf fall series using the program Past3 (version 3.02) for analyses of leaf

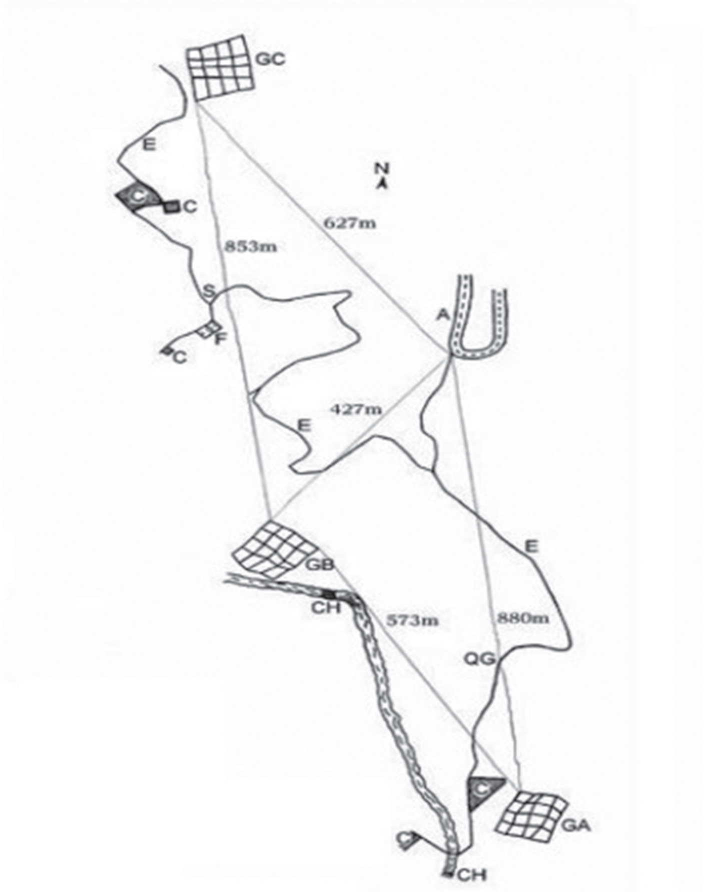

Figure 1. Position of the three study sites in the area. E=roads, GA=location A, GB = location B, GC = location C, C = house; S = road bifurcation; F = soccer pitch; A = Rio-Teresópolis highway; CH = waterfall; QG = laboratory.

fall seasonality. The correlation between leaf fall among the three locations was tested by Pearson correlations using 0 to 12 months lag (Zar 1996).

Because leaf fall of grids A, B and C show similar patterns of seasonal variation and are correlated, we grouped these data to analyse the general annual trend in the temporal variation of monthly leaf fall by autocorrelations series analyses and correlations with climatic variables using Cross-Correlations Analyses (Legendre & Legendre 2012).

We obtained meteorological data from the meteorological station of Teresópolis (Rio de Janeiro – RJ) (Instituto Nacional de Meteorologia - INMET). We tested the association between leaf fall and the following climatic variables: mean monthly temperature (TMEAN), maximum absolute temperature (TMAXAB), minimum absolute temperature (TMINABT), mean minimum temperature (TMMIN), mean maximum temperature (TMMAX), and precipitation (PREC) and Thornwhite Potential Evapotranspiration (PET) (Ometto 1981). Additionally, the normal climatic data of the Nova Friburgo Station, a nearby station and the one available for this mountain region, localized in the same mountain chain and at equivalent altitude, were included to evaluate the monthly anomalies of the mean (ANOMMEAN), mean maximal temperature (ANOMTMAX), mean minimal temperature (ANOMTMIN), and precipitation (ANOMPREC). These anomalies were simply the deviation of the observed monthly values of these variables from climatological normals (World meteorological organization 1996).

Climatic variables are often correlated to some degree, being such correlations variable among different sites. To overcome this problem, we conducted a Principal Component Analysis (PCA) of the correlation matrix of climatic variables (Manly 1994) to reduce the number of variables and to analyse the factors responsible for their variation.

The factor scores of the principal components selected were correlated with mean monthly leaf fall mass of the next month by Cross-Correlation Analyses (Statistica, Stat Soft. Inc. 1997).

We tested for correlations of leaf fall with monthly climatic factors, and with their anomalies (deviations from historical means) using an information criterion approach. We also examined the relative weights of immediate and delayed (time lag series) responses of leaf fall to climatic factors.

Results of cross-correlation analyses were considered to choose the time lags. We used General Linear Model (GLM) with a Gaussian distribution, considering as independent variables the climatic factors more correlated with PCA axes and the mean monthly leaf fall as a dependent variable using STATISTICA 10.0 (Stat Software INC.). The null model considered that all correlations with independent variables are zero, and variation in this model is from the mean and variances of the data itself, with no relationship with the independent variables. We used null model as reference for other goodness-of-fit models. These models were classified using Akaike Information Criterion (AIC; Burnham and Anderson, 2002). We considered equally plausible models that had delta AIC values less than 2.0.

RESULTS

Total litterfall varied from 6.68 to 8.55 t/ha/yr. and leaf represented from 50.6 percent to 72 % of total litterfall mass (Table 1). Grids did not presented significant differences in mean leaf fall between years (Grid A: H = 4.42, p = 0.72, Grid B: H = 8.93, p = 0.26, Grid C: H = 10.19, p = 0.18) (Table 2). There were significant differences in leaf mass between grids (H = 25.03, p < 0,01). Leaf mass of Grid B was significantly less than Grid A (U = 2683.5, p = 0.000003) and Grid C (U = 2977, p = 0.00016), Grid A and Grid C did not differed significantly (U = 3890, p = 0.19).

Table 1. Mean year litterfall and leaf fall production for the three sites (t/ha/yr). Total ± SD: mean of total annual production (t/ha/yr) ± standard deviation (SD) and Mean ± SD: mean monthly production (t/ha/mo) ± standard deviation (SD), Between brackets the proportion of leaf on litter. Sample size for all sites was 93.

	SITES	TOTAL ± SD	MEAN ± SD
LITTER	A (748 m)	8.55 ± 1.03	0.68 ± 0.48
	B (652 m)	6.97 ± 0.95	0.57 ± 0.29
	C (522 m)	6.68 ± 0.88	0.54 ± 0.23
LEAVES	A (748 m)	4.43 ± 0.5 (67.7%)	0.46 ± 0.37
	B (652 m)	3,53 ± 0.73 (50.6%)	0.28 ± 0.16
	C (522 m)	4,81 ± 0.85 (72%)	0.39 ± 0.17

Table 2. Annual production (t/ha) of leaf fall at each site. Sum is expressed as t/ha/yr and change t/ha/yr at mean for t/ha/mo, SD = standard deviation and CV = confidence of variation.

SITE	YEAR	SUM	MEAN±SD	CV
A	1997	5.19	0.58 ± 0.57	99.63
	1998	4.50	0.37 ± 0.20	52.81
	1999	4.47	0.37 ± 0.18	47.41
	2000	3.82	0.32 ± 0.18	57.17
	2001	4.65	0.42 ± 0.24	55.98
	2002	5.37	0.45 ± 0.29	64.39
	2003	3.26	0.27 ± 0.12	45.05
	2004	4.27	0.39 ± 0.27	70.32

Table 2. Continue on next page...

Table 2. ...Continued

SITE	YEAR	SUM	MEAN±SD	CV
B	1997	3.04	0.34 ± 0.26	76.22
	1998	3.17	0.26 ± 0.07	25.46
	1999	3.09	0.26 ± 0.14	54.95
	2000	2.73	0.23 ± 0.14	63.26
	2001	1.08	0.13 ± 0.04	32.87
	2002	3.35	0.28 ± 0.16	57.14
	2003	2.79	0.23 ± 0.17	72.81
	2004	2.67	0.22 ± 0.15	66.96
C	1997	2.94	0.33 ± 0.24	72.82
	1998	4.70	0.39 ± 0.14	34.83
	1999	4.28	0.36 ± 0.15	43.04
	2000	3.00	0.25 ± 0.15	60.97
	2001	3.26	0.27 ± 0.11	42.46
	2002	3.92	0.33 ± 0.13	41.39
	2003	3.03	0.25 ± 0.12	48.86
	2004	3.74	0.31 ± 0.16	50.70

Table 3. Autocorrelation coefficients of leaf fall temporal variation for each grid.

SITE	LAG	r	SE	p
A	0	0.23	0.10	0.02
	1	0.13	0.10	0.04
	4	-0.18	0.10	0.05
B	0	0.38	0.10	0.0001
	1	0.15	0.10	0.0003
	5	-0.18	0.10	0.0006
	6	-0.22	0.10	0.0002
	10	0.16	0.09	0.0005
	11	0.18	0.09	0.0002
C	0	0.32	0.10	0.001
	1	0.19	0.10	0.001
	5	-0.13	0.10	0.006

Significant autocorrelations were found at the three areas showing an annual seasonality of leaf fall (Table 3). It was significantly correlated between the three locations for lag 0 (A x B r = 0.78, A x C r = 0.83, B x C r = 0.89, all comparison $p < 0.01$) and for Lag 1 (A x B r = 0.40, p = 0.02, A x C r = 0.35, p = 0.01, B x C r = 0.34, p = 0.02). Total monthly leaf fall varied from 1.59 t/ha/mo in September 1997 to 0.034 t/ha/mo in December 1999 for grid A, from 0.59 t/ha/mo in September 1997 to 0.035 t/ha/mo in May 2001 for grid B and from 0.73 t/ha/mo in December 1997 to 0.0015 t/ha/mo in October 2001 for grid C.

Climatic factors were grouped into two principal components (PC) that together explained 67.41 percent of the variance. The first component (PC1) explained 41.27 percent of the total variation. It can be interpreted as the seasonal factor of the climatic variation, with a high load for most variables and where all the standard climatic variables were grouped. The second component (PC2), explaining 26.14 percent of total variation, was interpreted as the anomaly factor, representing deviations from the normal seasonal variation, grouping all anomaly values. The highest loadings on PC1 were mean temperature, mean maximal temperature, mean minimal temperature (0.99, 0.95 and 0.95, respectively) and the highest loads on PC2 were maximal and mean temperature anomalies (0.81 and 0.94, respectively) (Table 4).

Mean Leaf fall was positively correlated with the seasonal factor, with lags 0 and 11. It was negatively correlated with time lags 4 and 5 and positively correlated with the anomaly factor with time lag 6 (Table 5).

Based on that we selected three climatic variables, the variable with the highest load on PC1, mean temperature (TMEAN), and also two others with high loads representing water availability, Precipitation (PREC) and Potential Evapotranspiration (PET). We also selected the two variables with the highest loads on PC2, precipitation anomaly (ANOMPREC) and mean maximum temperature anomaly (ANOMTMAX). Regression models selected by AIC were constructed with lag 0 and lag 6 using TMEAN, PREC, PET, ANOMPREC and ANOMTMAX as independent variables, and mean monthly leaf fall as dependent variable.

The variables that better explained the temporal variation in leaf fall was the maximum temperature anomaly (ANOMTMAX) with lag 0 and PRECIPITATION with lag 6, but models with TMED and PET were better than the null model. Therefore, we can say that leaf fall is an immediate response to deviations in maximum temperatures from the historical mean, and that seasonality of leaf fall is a lagged response to variations in climatic variables, mainly rainfall, with higher leaf fall at the end of dry periods (Figure 2 and Table 6).

Table 4. Correlation coefficients of each climatic variable with the factors, explained variance and total proportion explained for the Principal Component Analysis. PREC = precipitation, TMMA= Mean Maximal Temperature, TMMI = Mean Minimum Temperature, TMAXAB = Maximal Absolute Temperature, TMINAB = Minimum Absolute Temperature, TMEAN = Mean temperature, ANOMTMEAN = Mean Temperature Anomalie, ANOTMAX = Maximal Temperature Anomalie, ANOTMIN = Minimal Temperature Mean, ANOMPREC = Mean Precipitation Temperature, PET = Potencial EvapoTranspiration. * *p*<0.05.

	FACTORS	
	1	**2**
PREC	0.75*	-0.32
TMMA	0.91*	0.27
TMMI	0.96*	0.11
TMAXAB	0.78*	0.31
TMINAB	0.94*	0.09
TMEAN	0.99*	0.05
ANOMTMEAN	0.70	-0.23
ANOMTMAX	0.21	0.92*
ANOMTMIN	-0.77*	0.11
ANOMPREC	0.15	0.75*
PET	0.93*	0.04
EXPLAINED VARIANCE	9.15	2.47
TOTAL PROPORTION	0.61	0.16

Table 5. Correlation coefficients of cross-correlation analyses between climatic factors scores and Mean leaf fall values. Only significant values ($p < 0.05$) are shown. R = coefficient of correlation, SE = standard error.

Factors	timelag	r	SE
1	0	0.33	0.10
	4	-0.36	0.11
	5	-0.38	0.11
	11	0.36	0.11
2	6	0.26	0.11

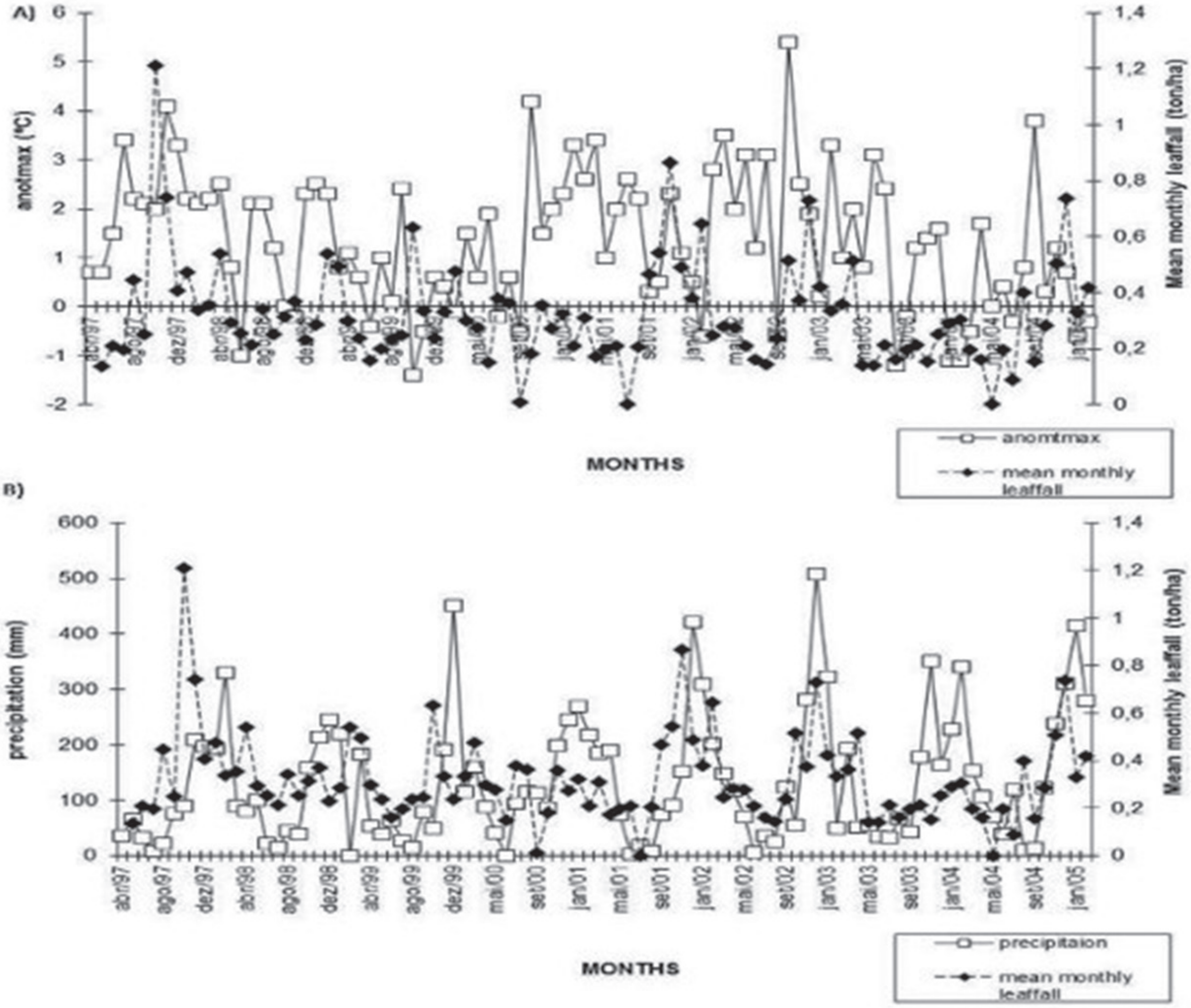

Figure 2 – Mean monthly leaf fall (t/ha/mo) in relation to: A) the mean maximum temperature anomaly (ºC) and B) monthly precipitation (mm).

Table 6. Models for climatic variables and mean leaffall mass, where: null = 1 (the reference model); k = number of parameters; w_i = Akaike weights (based on AIC corrected for small sample sizes). ANOMTMAX = Mean Maximal Temperature Anomalie, PET = Thornwhite Potential Evapotranspiration, TMEAN = Mean Monthly Temperature, ANOMPREC = Mean Precipitation Anomalie, PREC = Precipitation.

Models	***k***	***n***	**ΔAICc**	**w_i**
MEANLEAFFALL x ANOMTMAX	3	95	0	0.535
Null	2	95	2.59	0.147
MEANLEAFFALL x PET	3	95	2.78	0.133
MEANLEAFFALL x TMEAN	3	95	4.07	0.07
MEANLEAFFALL x ANOMPREC	3	95	4.45	0.058
MEANLEAFFALL x PREC	3	95	4.5	0.056

Models	***k***	***n***	**ΔAICc**	**w_i**
MEANLEAFFALL x PREC	3	95	0	0.957
MEANLEAFFALL x TMEAN	3	95	6.39	0.039
MEANLEAFFALL x PET	3	95	11.79	0.003
Null	2	95	14.46	0.001
MEANLEAFFALL x ANOMPREC	3	95	15.91	0
MEANLEAFFALL x ANOMTMAX	3	95	15.91	0

DISCUSSION

The values found for total litterfall in this study are within the means found for other tropical forests, 8.61 ± 1.91 Mg/ha/yr (Chave *et al.* 2010) and within the range found for other Atlantic Forest sites, which varied from 4.91 t/ha/yr to 9.8 /ha/yr in most studies (Meguro *et al.* 1979, Varjabedian & Pagano 1988, Morelatto 1992a, Oliveira & Lacerda 1993, Sampaio *et al.* 1993, Louzada *et al.* 1995, Moraes & Delitti 1996, Pinto *et al.* 2008, Calvi *et al.* 2009, Menezes *et al.* 2010). The proportion of leaves in the total litterfall was also within the range of other tropical forests.

The high autocorrelation coefficients in leaf fall demonstrate the effects of seasonality on the three areas, with high peaks of leaf fall at the end of the ”dry” season (September), and at the beginning of wet season (October) and lowest leaf fall peaks in the middle of wet season. Studies conducted at Deciduous Atlantic Forest Formations that have more marked seasonal variation also show an increase in leaf fall in the drier periods of the year, when water availability is reduced and temperatures are lower (Morellato 1992b, Louzada *et al.* 1995, Martins & Rodrigues 1998, Lopes *et al.* 1994, Portes *et al.* 1996, Morellato 2000). However, in some humid forests, the largest litterfall usually coincides with the period of greatest rainfall (Moraes *et al.* 1999, Pinto & Marques 2003, Schumacher *et al.* 2003, Dickow *et al.* 2012). In our study, leaf fall increased at the end of “dry” season, but its response to climatic factors was delayed as the higher leaf falls occurs after 3 or 4 months after lower precipitations. It is possible that leaf fall will happen faster in dryer forests with stronger water deficits. South American forests can have very different litterfall peaks, varying from June to October, with a weak correlation between litterfall seasonality and rainfall seasonality, probably due to years of unusual climatic variations (Chave *et al.* 2010). Here we are suggesting that leaf fall can happen as a delayed and also as an immediate response to changes in rainfall. In forests with less marked seasonality, leaf fall is probably a delayed response to water deficit, to temperature and solar radiation decrease. During the dryer period, trees draw upon the moisture preserved in the soil to have new foliage ready for the next growing season (Hopkins 1995, Martins & Rodrigues 1999).

It is not possible to generalize the effects of longer cycles and the influence of great deviations from mean climatic conditions on litter/leaf fall in the Atlantic Forest, since most studies are based on data from one or two years (Lopes *et al.* 1994, Morelatto 1992a, Ramos & Pellens 1994, Martins & Rodrigues 1999, Morellato 2000). However, the extremely high litterfall peak that was recorded by us (September 1997) seems also seems to have occurred in other Atlantic forest sites (Martins & Rodrigues 1999, Morellato 2000), that was a year of high El Ninõ anomaly (http://enos.cptec.inpe.br/artigos/pt), which suggests which suggest that anomalies could be an important influence on increasing leaf fall.However, as the majority of litterfall studies were done in a time period of one or two years, it is not possible to analyse this. This highlights the very importance of long-term studies for the detection and analyses of ecological patterns and process. As frequency and amplitude of plant ecology phenomena’s can largely vary, depending on the plants physiological response to stress conditions (Chaves *et al.* 2003), long-term studies are the way to detect and analyse these variations, studies of 1 or 2 years, although valuable, probably, are only detecting a small frame of a greater picture, what make difficult to compare and generalize patterns for Atlantic Forest formations.

Litterfall is directly associated with other aspects of the dynamics of tropical forests, such as nutrient cycling (Lu & Liu 2012) and soil richness (Chave *et al.* 2010), but deviations from the climatological normals are rarely considered in studies of the dynamics of tropical forests. Great deviations from normal seasonal variations can increase organic matter input and the organic matter decomposition (Sayer *et al.* 2011). This changes CO_2 atmospheric inputs from the soil, adding more carbon to the atmosphere and promoting the loss soil organic carbon (Sayer *et al.* 2007), having a significant impact on the dynamics of tropical forests (Saura-Mas *et al.* 2012) mainly considering the potential effects in plant communities related to long-term climate changes (Salazar *et al.* 2007).

In this study we indicate that there are not only immediate and lagged leaf fall responses related to seasonal regular climatic variations but also a lagged response related to greater deviations to these seasonal variations. Litterfall, mainly leaf fall, long-term studies could be a good tool to monitor possible changes on forest function on a climate change scenario, where these deviations become wider and/or more frequent.

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REFERENCES

Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes, G., Leonardo, J., & Sparovek, G. 2013. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift, *22*(6), 711–728.

Bianchin, J.E., Marques, R., Britez, R.M. & Capretz, R.L. 2016. Deposição de fitomassa em formações secundárias na Floresta Atlântica do Paraná. Floresta e Ambiente, 23(4), 524–533. http://dx.doi.org/10.1590/2179-8087.134015.

Bray, J. R., & Gorham E. 1964. Litter production in forests of the world. Advances in Ecological Research, 2, 101–157.

Burghouts, T.B.A., Van Straalen, N.M. & Bruijnzeel, L.A. 1998. Spatial heterogeineity of element and litter turnover in a Borean rain forest. Journal of Tropical Ecology, 14, 477–506. https://doi.org/10.1017/S0266467498000352.

Burnham, K. P., & Anderson D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York: p. 485

Calvi, G.P., Pereira, M.G., & Espíndula A.Jr. 2009. Produção de serapilheira e aporte de nutrientes em áreas de floresta atlântica em Santa Maria de Jetibá, ES. Ciência Florestal, 19(2),131–138. http://dx.doi.org/10.5902/19805098404.

Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L.E.C., Bonal D., Chatelê, P., Silva-Espejo, J. E., Goret, J.-Y., von Hildebrand, P., Jiménez, E., Patiño, S., Peñuela, M. C., Phillips, O. L., Stevenson, P., & Malhi, Y. 2010. Regional and seasonal patterns of litterfall in tropical South America. Biogeosciences, 7, 43–45.

Chaves, M.M., Maroco, J.P., & Pereira, J.S. 2003. Understanding plant responses to drought — from genes to the whole plant. Functional Plant Biology, 30, 239–264.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., & Holland, E.A. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecological Applications, 11, 371–384.

Davis, J.C. 1986. Statistics and Data Analysis in Geology. John Wiley & Sons. New York.

Dickow, K.M.C., Marques, R., Pinto, C.B., & Höfer H. 2012. Produção de serapilheira em diferentes fases sucessionais de Floresta Atlântica secundária, em Antonina, PR. Cerne, 18(1), 75–86. http://dx.doi.org/10.1590/S0104-77602012000100010

Domingos, M., Moraes, R.M., Vuono, Y.S. & Anselmo, C.E. 1997. Produção de serapilheira e retorno de nutrientes em um trecho de Mata Atlântica secundária, na Reserva Biológica de Paranapiacaba, SP. Revista Brasileira de Botânica. 20(1), 91–96.

Ferreira, M.L., Silva, J.L., Pereira, E.E., & Lamano-Ferreira A.P.M. 2014. Litter fall production and decomposition in a fragment of secondary Atlantic Forest of São Paulo, SP, Southeastern Brazil. Revista Árvore, 38 (4), 591–600. http://dx.doi.org/10.1590/0100-67622015000500002

Ferreira, M.L., & Uchiyama E.A. 2015. Litterfall assessement in a fragment of secondary tropical forest, Ibiúna, SP, Southeastern Brazil. Revista Árvore, 39(5), 791–799.

Finotti, R., Freitas, S. R., Cerqueira, R., & Vieira, M. V. 2003. A Method to Determine the Minimum Number of Litter Traps in Litterfall Studies1. Biotropica, 35(3), 419–421.

Freitas, S.R. 1998. Variação espacial e temporal na estrutura do habitat e preferência de microhabitat por pequenos mamíferos na Mata Atlântica. Master thesis. Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 168 p. Available at https://www.researchgate.net/publication/337063454

Gentile, R., Finotti, R., Rademaker, V., & Cerqueira, R. 2004. Population dynamics of four marsupials and its relation to resource production in the Atlantic forest in southeastern Brazil. Mammalia, 68, 5–15.

Gurevitch, J.; Scheiner, S. M., & Fox, G. A. 2009. Ecologia vegetal. Porto Alegre: Artmed. P. 592.

Hipel, K.W., & McLeod., A.I. 1994. Time series modelling of water resources and environmental systems. Elsevier Science, Amsterdam. p. 1013.

Hopkins, W.G. 1995. Introduction to Plant Physiology. Jonh Wiley & Sons Inc. New York-USA. p. 464.

IBGE. 1992. Manual Técnico da Vegetação Brasileira. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro: p. 91.

Kunkel-Westphal, I. & Kunkel, P. 1979. Litter fall in a

Guatemalan primary forest, with details of leaf-shedding by some common tree species. Journal of Ecology, 67, 665–686.

Legendre, P. & Legendre, L. 2012. Numerical Ecology. 3rd ed. New York, Elsevier: p. 1006.

Lopes, M.I.M.S., Teixeira, C.B., Compte, V.X., Liess, S. & Mayer, R. 1994. Litter production in the Atlantic Forest vegetation of Serra do Mar, Cubatão Region, Brazil. III Simpósio de Ecossistemas da Costa Brasileira. Volume II: Mata Atlântica e Ecossistemas Marinhos. ACIESP, São Paulo: p. 323.

Louzada, M.A.P., Quintela, M.F.S. & Penna, L.P.S. 1995. Estudo comparativo da produção de serrapilheira em áreas de Mata Atlântica: a floresta secundária "antiga" e uma floresta secundária (capoeira). In: F.A. Esteves (Ed.). Estrutura, funcionamento e manejo de ecossistemas brasileiros, pp. 61–74. Oecologia Brasiliensis, PPGE, UFRJ, Rio de Janeiro. 1.

Lu, S-W., & Liu, C-P. 2012. Patterns of litterfall and nutrient return at different altitudes in evergreen hardwood forest of Central Taiwan. Annals of Forest Science, 69, 877–886. ff10.1007/s13595-012-0213-4ff.

Luizão, F.J. & Schubart, H.Q.R. 1986. Produção e decomposição de liteira em floresta de Terra Firme da Amazônia Central. Acta Limnológica Brasiliensis I, 575–600.

Machado, D.L., Pereira, M.G., Correia, M.E.F., Diniz, A.R., Santos. L.L., & Menezes, C.E.G. 2015. Ciclagem de nutrientes em diferentes estádios sucessionais da Mata Atlântica na bacia do rio Paraíba do Sul, RJ. Bioscience Journal, 31(4), 1222–1237. http://dx.doi.org/10.14393/BJ-v31n1a2015-23092.

Manly, B.F.J. 1994. Multivariate statistical methods: a primer. 2nd edition. Ed. Chapman & Hall, London: p. 215.

Martins, S.V., & Rodrigues, R.R. 1999. Produção de serrapilheira em clareiras de uma floresta estacional semidecidual no município de Campinas, SP. Revista Brasileira de Botânica, 22(3), 405–412.

Meguro, M., Vinueza, G.N., & Delitti, W.B.C. 1979. Ciclagem de nutrients minerais na mata mesófila secundária – São Paulo. I: Produção e conteúdo de nutrientes minerais no folhedo. Boletim de Botânica, Universidade de São Paulo, 7, 11–31.

Mendel, S.M., Vieira, M.V., & Cerqueira, R. 2008. Precipitation, litterfall, and the dynamics of density and biomass in the black-eared opossum, *Didelphis aurita*. Journal of Mammalogy, 89.1, 159–167.

Menezes, C.E.G., Pereira, M.G., Correia, M.E.F., Anjos, L.H.C., Paula, R.R., & Souza, M.E. 2010. Aporte e decomposição da serapilheira e produção de biomassa radicular em florestas com diferentes estágios sucessionais em Pinheiral, RJ. Ciência Florestal, 20(3), 439–452. http://dx.doi.org/10.5902/198050982059

Misra, M.K., & Nisanka, S.K. 1997. Litterfall decomposition and nutrient release in *Casuarina equifolia* plantations on the sandy coast of Orissa, India. Tropical Ecology, 38, 109–119.

Moraes, R.M., Rebelo, C.F., Delitti, W.B.C., & Struffaldi-De Vuono, Y. 1994. Serrapilheira acumulada em um trecho de Mata Atlântica de encosta, no Parque Estadual da Ilha do Cardoso (São Paulo). III Simpósio de Ecossistemas da Costa Brasileira. Volume II: Mata Atlântica e Ecossistemas Marinhos. ACIESP, São Paulo: p. 323.

Moraes, R. M., & Delitti, W. B. C. 1996. Produção e retorno de nutrientes via serrapilheira foliar de *Euterpe edulis* Mart. em Mata Atlântica de encosta, Ilha do Cardoso, SP. Naturalia, 21, 57–62.

Moraes, R.M., Delitti, W.B., & Struffaldi-Devuono, Y. 1999. Litterfall and litter nutrient content in two Brazilian Tropical Forest. Brazilian Journal of Botany, 22(1), 9–16. http://dx.doi. org/10.1590/S0100-84041999000100002.

Morelatto, L.P.C. 1992a. Nutrient cycling in two southeast Brasilian forests. I. Litterfall and litter standing crop. Journal of Tropical Ecology, 8, 205–215.

Morelatto, L.P.C. 1992b. Sazonalidade e dinâmica de ecossistemas florestais na Serra do Japi. In: L.P.C. Morelatto. História natural da Serra do Japi: ecologia e preservação de uma área florestal no Sudeste do Brasil. UNICAMP/FAPESP, Campinas: p. 321.

Morellato, P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C., & Zipparo, V.B. 2000. Phenology of Atlantic Forest Trees: A comparative study. Biotropica, 32, 811–823.

Oliveira, R.R., & Lacerda L.D. 1993. Produção e composição química da serrapilheira na Floresta da Tijuca (RJ). Revista Brasileira de Botânica, 16, 93–99.

Ometto, J.C. 1981. Bioclimatologia Vegetal. 2ª ed. Editora Agronômica Ceres. São Paulo-SP: p. 425.

Pagano, S.N. 1989. Produção de folhedo em Mata mesófila semidecídua no município de Rio Claro, SP. Revista Brasileira de Biologia, 49, 633–639.

Pankratz, A. 2012. Forecasting with dynamic regression models. V. 935. John Wiley & Sons. p. 400.

Pendry, C. A., & Proctor, J. 1996. The causes of altitudinal zonation of rain forests on Bukit Belalong, Brunei. Journal of Ecology, 84, 407–418.

Pinto, C.B. & Marques, R. 2003. Aporte de nutrientes por frações da serapilheira em sucessão ecológica de um ecossistema da Floresta Atlântica. Floresta; 33(3), 257–264. http://dx.doi.org/10.5380/rf.v33i3.2256.

Pinto, S.I.C., Martins, S.V., Barros, N.F., & Dias, H.C.T. 2008. Produção de serapilheira em dois estádios sucessionais de Floresta Estacional Semidecidual na Reserva Mata do Paraíso, em Viçosa, MG. Revista Árvore, 32(3), 545–556. http:// dx.doi.org/10.1590/S0100-67622008000300015.

Portes, M.C.G.O., Koelher, A., & Galvão, F. 1996. Variação sazonal da deposição de serrapilheira em uma floresta ombrófila densa altomontana no morro do Anhangava - PR. Floresta 26, 3–10.

Raimundo, F., Martins, A., & Madeira, M. 2008. Decomposition of chestnut litterfall and eight-year soil chemical changes under a no-tillage management system in Northern Portugal. Annals of Forest Science. 65, 408–419.

Ramos, M.C.L., & Pellens, R. 1994. Produção de serrapilheira em ecossistemas de restinga em Maricá – Rio de janeiro. III Simpósio de Ecossistemas da Costa Brasileira, ACIESP: p. 89–98.

Reich, P.B. 1995. Phenology of tropical forests: patterns, causes, and consequences. Canadian Journal of Botany, 73, 164–174.

Rizzini, C.T., 1979. Tratado de fitogeografia do Brasil; aspectos sociológicos e florísticos. Vol. 2 ed. Universidade de São Paulo. São Paulo, Brasil.

Saharjo, B.H., & Watanabe, H. 2000. Estimation of litter fall and seed production of Acacia mangiumina forest plantation in South Sumatra, Indonesia. Forest Ecology Management, 130, 265–268.

Salazar, L.F., Nobre, C.A., & Oyama M.D. 2007. Climate change consequences on the biome distribution in tropical South America. Geophysical Research Letters, 34, 1–6. doi:10.1029/2007GL029695.

Sampaio, E.V.S.B., Dall'olio, A., Nunes, K.S., & Lemos, E.E.P. 1993. A model of litterfall, litter layer losses and mass transfer in a humid tropical forest at Pernambuco, Brazil. Journal of Tropical Ecology, 9, 291–301.

Saua-Mas, S., Estiarte, M., Saura-Mas, S., Peñuelas, J., Lloret, F. 2012. Effects of climate change on leaf litter decomposition across post-fire plant regenerative groups. Environmental and Experimental Botany. 77, 274–282. https://doi.org/10.1016/j.envexpbot.2011.11.014.

Sayer, E.J., Powers, J.S., & Tanner E.V.J. 2007. Increased Litterfall in Tropical Forests Boosts the Transfer of Soil CO_2 **to the Atmosphere.** PLoS One, 2(12), e1299. doi: 10.1371/journal.pone.0001299

Sayer, E.J., Heard, M.S., Grant, H.K., Marthews, T.R. & Tanner, E.V.J. 2011. Soil carbon release enhanced by increased tropical forest litterfall. Nature Climate Change, 1, 304–307.

Scheer, M.B., Gatti, G., Wisniewski, C., Mocochinski, A.Y., Cavassani, A.T., Lorenzetto, A., & Putini F. 2009. Patterns of litter production in a secondary alluvial Atlantic Rain Forest in southern Brazil. Revista brasileira de Botânica, 32(4), 805–817.

Schumacher, M.V., Brun, E.J., Rodrigues, L.M., & Santos, E.M. 2003. Retorno de nutrientes via deposição de serapilheira em um povoamento de Acácia Negra (Acacia mearnsii Wild) no estado do Rio Grande do Sul. Revista Árvore, 27(6), 791–798. http://dx.doi.org/10.1590/S010067622003000600005.

Siqueira, T.M., Pinheiro, M.H.O., Silva, D.G., & Franco, T.M.. 2016. Influências climáticas na produção de serapilheira em um cerradão em Prata – MG. Biotemas, 29(2), 7–15.

Sloboda, B., Marques, R., Bianchin, J., Blum, H., Donha, C., Silveira, F., & Capretz, R. 2017. Litterfall and Nutrient Dynamics in a Mature Atlantic Rainforest in Brazil. Floresta e Ambiente, 24, e20160339. http://dx.doi.org/10.1590/2179-8087.033916.

Smith, K., Gholz, H.L., & Oliveira, F.A. 1998. Litterfall and nitrogen-use efficiency of plantations and primary forest in the eastern Brazilian Amazon. Forest Ecology and Management, 109, 209–220.

Staelens, J., Nachtergale, L., De Schrijver, A., Vanhellemont, M., Wuyts, K., & Verheyen, K. 2011. Spatio-temporal litterfall dynamics in a 60-year-old mixed deciduous forest. Annals of forest science, 68(1), 89–98.

Stocker,.G.C., Thompson, W.A.A., Irvine, K., Fitzsimon, J.D., & Thomas, P. R. 1995. Annual patterns of litterfall in Lowland and Tableland Rainforest in tropical Australia. Biotropica, 27, 412–420.

Tripathi, S., Srinivas V.V., & Nanjundiah R.S. 2006. Downscaling of precipitation for climate change scenarios: a support vector machine approach. Journal of Hydrology, 330.3, 621–640.

Varjabedian, R., & Pagano, S.N. 1988. Produção e decomposição do folhedo em um trecho de Mata Atlântica de encosta no município de Guarujá, SP. Acta Botânica Brasilica, 1, 243–256.

Vasconcelos, H.L., & Luizão, F.J. 2004. Litter production and litter nutrient concentrations in a fragmented Amazonian landscape. Ecological Applications, 14, 884–892.

Vendrami, J.L., Jurinitz, C.F., Castanho, C.T., Lorenzo, L., & Oliveira A. A. 2012. Litterfall and leaf decomposition in forest fragments under different successional phases on the Atlantic Plateau of the state of Sao Paulo, Brazil. Biota Neotropica, 12(3), 136–143.

Vidal, M.M., Pivello, V.R., Meirelles, S.T., & Metzger, J.P. 2007. Produção de serapilheira em floresta Atlântica secundária numa paisagem fragmentada (Ibiúna, SP): importância da borda e tamanho dos fragmentos. Revista Brasileira Botânica, 30(3), 521–532. DOI: 10.1590/s0100-84042007000300016

Vitousek, P.M., Gerrish, G., Turner, D.R., Walker, L.R., & Mueller-Dombois, D. 1995. Litterfall and nutrient cycling in four Hawaiian montane rainforests. Journal of Tropical Ecology, 11, 189–203.

Werneck, M.S., Pedralli, G., & Gieseke, L.F. 2001. Produção de serapilheira em três trechos de uma loresta semidecídua com diferentes graus de perturbação na Estação Ecológica do Tripuí, Ouro Preto, MG. Revista Brasileira de Botânica, 24(2), 195–198.

Wieder, R.K., & S.J. Wright. 1995. Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. Ecology, 76, 1971–1979.

World meteorological organization. 1996. Climatological normals (CLINO) for the period 1961-1990. Ed. Secretariat of the world metereological Organization, Geneva – Switzerland.

Zar, G.H. 1996. Biostatistical Analysis. Prentice-Hall, New Jersey. p. 662.

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