LITTERFALL AND NUTRIENT INPUT IN UNDISTURBED AND ADJACENT FIRE DISTURBED FORESTS OF THE GRAN SABANA, SOUTHERN VENEZUELA

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SUMMARY

Litterfall and nutrient return were studied in a primary forest (tall forest), a slight fire-affected forest (medium forest with low abundance of charred residues) and a strong fire-affected forest (low forest with abundant burned trunks on the forest floor) in the Gran Sabana, Southern Venezuela. The purpose was to determine how old fire disturbances that affected the forest structure are affecting the return of organic matter and nutrients from the biomass to the soil surface. The results did not reveal significant differences (P>0.05) in annual litter production between tall forest (5.2Mg·ha^{-1}·year^{-1}) and medium forest (5.7Mg·ha^{-1}·year^{-1}), indicating that minor perturbations had not affected the canopy productivity. Annual litter production in low forest (3.9Mg·ha^{-1}·year^{-1}) was significantly lower than in tall and medium forests (P<0.05). The differences in the litter production of low forest compared to tall and medium forests were surprisingly small considering that low forest were largely degraded, with 74 and 79% less stem density, 91 and 90% less basal area, and 97 and 96% less aboveground biomass than tall and medium forests, respectively. This indicates that fire disturbances that considerably affected the structural attributes of the forests are not influencing substantially the canopy productivity. Inputs of nutrients were low in all the forest types with low rates of litterfall to the soil surface and low concentrations of nutrients in such litterfall. The annual input of N and P followed the same trend as the annual input of litterfall, while the annual inputs of Ca, K and Mg were very variable.

RESUMEN

La caída de hojarasca y el retorno de nutrientes fueron estudiados en un bosque primario (bosque alto), un bosque ligeramente afectado por el fuego (bosque medio con baja abundancia de residuos carbonizados) y un bosque fuertemente afectado por el fuego (bosque bajo con abundantes troncos carbonizados sobre el suelo) en la Gran Sabana, al sureste de Venezuela. El propósito de este estudio fue determinar si antiguas perturbaciones por fuego que afectaron la estructura de los bosques están afectando el retorno de hojarasca y nutrientes desde la biomasa hacia la superficie del suelo. Los resultados no mostraron diferencias significativas (P>0,05) en la producción anual de hojarasca entre el bosque alto (5,2Mg·ha^{-1}·año^{-1}) y el bosque medio (5,7Mg·ha^{-1}·año^{-1}), indicando que perturbaciones menores no afectan la productividad del dosel. La producción anual de hojarasca en el bosque bajo (3,9Mg·ha^{-1}·año^{-1}) fue significativamente mas baja que en los bosques alto y medio (P<0,05). Las diferencias en la producción de hojarasca entre el bosque bajo y los bosques alto y medio fueron sorprendentemente pequeñas si se considera que el bosque bajo estaba muy degradado, con 74-79% menos árboles y 96-97% menos biomasa que los bosques alto y medio, respectivamente. Esto sugiere que perturbaciones por fuego que afectaron considerablemente los atributos estructurales del bosque, no están influenciando sustancialmente la productividad del dosel. Las entradas de nutrientes a través de la hojarasca fueron bajas en todos los tipos de bosque, con bajas tasas de retorno de la hojarasca a la superficie del suelo y bajas concentraciones de nutrientes en esa hojarasca. Las entradas anuales de N y P siguieron la misma tendencia que la entrada anual de hojarasca, mientras que las entradas anuales de Ca, K y Mg fueron bastante variables.

Introduction

Litter production constitutes an important process controlling nutrient cycling within forest ecosystems, and is considered to be the main mechanism of transfer of dead organic matter and nutrients from the living biomass to soils (Meentmeyer *et al*., 1982; Vitousek and Sanford, 1986; Herbohn and Congdon, 1998; Arunachalam *et al*., 1998). Litter is particularly important in forests that grow in infertile soils, where the amount of nutrients entering through atmospheric deposition or weathering is disproportionately small to the amount of nutrients contained in above-ground litterfall (Brouwer, 1996; van Dam, 2001). In these forests, below-ground litter also makes a major contribution of nutrients to the soils (Burke and Raynal, 1994) and in some cases represents a very important fraction of total litterfall production and can exceed the quantity of leaf litter (Röderstein *et al*., 2005).

Data compilations indicate that so far much emphasis has been placed in determining nutrient flux through litterfall and decomposition in undisturbed tropical rain forests (Bray and Gorham, 1964; Proctor, 1983, 1984; Clark *et al*., 2001) and there are limited data related with the response of litterfall dynamics to disturbances (Hall and Okaly, 1979; Lodge *et al*., 1991; Herbohn and Congdon,

KEYWORDS / Forest Disturbance / Litter Nutrient Content / Litter Production / Nutrient Return / Tropical Forest /

Received: 05/31/2006. Modified: 11/22/2006. Acepted: 11/23/2006.

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RESUMO

A queda de serapilheira e o retorno de nutrientes foram estudados em uma floresta primária (floresta alta), uma floresta ligeiramente afetada pelo fogo (floresta média com baixa abundância de resíduos carbonizados) e uma floresta fortemente afetada pelo fogo (floresta baixa com abundantes troncos carbonizados sobre o solo) na Gran Sabana, ao sudeste da Venezuela. O propósito deste estudo foi determinar se antigas perturbações por fogo, que afetaram a estrutura das florestas, estão afetando o retorno de serapilheira e nutrientes desde a biomassa para a superfície do solo. Os resultados não mostraram diferenças significativas (P>0,05) na produção anual de serapilheira entre a floresta alta (5,2Mg·ha^{-1}·año^{-1}) e a floresta média (5,7Mg·ha^{-1}·año^{-1}), indicando que perturbações menores não afetam a produtividade do dossel. A produção anual de serapilheira na floresta baixa (3,9Mg·ha^{-1}·año^{-1}) foi significativamente mais baixa que nas florestas alta e média (P<0,05). As diferenças na produção de serapilheira entre a floresta baixa e as florestas alta e média foram surpreendentemente pequenas si consideramos que a floresta baixa estava muito degradada, com 74-79% menos árvores e 96-97% menos biomassa que as florestas alta e média, respectivamente. Isto sugere que perturbações por fogo que afetaram consideravelmente os atributos estruturais da floresta, não estão influenciando substancialmente a produtividade do dossel. As entradas de nutrientes através da serapilheira foram baixas em todos os tipos de floresta, com baixas taxas de retorno da serapilheira à superfície do solo e baixas concentrações de nutrientes nessa serapilheira. As entradas anuais de N e P seguiram a mesma tendência que a entrada anual de serapilheira, enquanto que as entradas anuais de Ca, K e Mg foram bastante variáveis.

1993; Arunachalam *et al*., 1998; Vogt *et al*., 1986).

Disturbances influence the composition and structure of tropical forests (Lodge *et al*., 1991; Dezzeo *et al*., 2004) and therefore change the nutrient cycling patterns, changing the equilibrium between production of biomass, accumulation of organic matter and decomposition and absorption of nutrients (Jordan, 1985; Barnes *et al*., 1998). Forest disturbances and savannization are critical environmental issues associated with forest fires in the Gran Sabana, Southern Venezuela. In this region the vegetation cover is characterized by a mosaic of primary forests, secondary forests and savanna. This vegetation mosaic represents a transitional stage in a long term savannization process, which is originally triggered by fires but is essentially conditioned by soil chemical stress and episodic drought stress (Fölster, 1986; Dezzeo *et al*., 2004). High acidity, low base cations and a high amount of toxic elements in the soils limit the microbial activity and are responsible for the accumulation of organic matter on the soil surface (Fölster *et al*., 2001; Priess and Fölster, 2001), making the forests highly susceptible to fire, especially during exceptionally dry years.

The quantification of litterfall rates and the analysis of the quality of litterfall are potential keys to describing any change which might occur in a forest when it is disturbed (Sizer *et al*., 2000). The purpose of this study was to compare the litter and nutrient inputs in an undisturbed forest and adjacent fire disturbed forests in the north of Gran Sabana, in order to determine how fire disturbances that affected the forest structure may affect the return of nutrients in litterfall.

Study area

The Gran Sabana is located in Southeastern Venezuela, 04º45'-05º30'N and 60º30'-61º22'W, forming a plateau between 800 and 1500masl. The area belongs to the Central Guayana Province of the Guayana Region (Huber, 1994) and its potential vegetation has been defined as evergreen montane forest (Huber, 1995). The actual vegetation is dominated by savannas with irregularly interspersed fragments of forest and bush vegetation. The parent material consists of quartzitic sandstone of the Roraima Group, an assemblage of Precambrian Formations with radiometric ages of 1600-1700 million years (Schubert *et al*., 1986).

The climate has been classified as tropical premontane very humid (Galán, 1984). According to the climatic diagram of Kavanayén, the closest meteorological station to the study site, a mean of 2548mm of annual precipitation is distributed unevenly, with mean monthly rainfall >60mm the dry season (Dec-Mar; Hernández, 1994). Chacón (2002) measured the monthly precipitation in a savanna adjacent to the studied forests from Jan 2000 to Apr 2001, and reported a precipitation peak in November and an annual value (2233mm) which does not differ from the mean annual value registered for Kavanayén.

Field work was carried out in a site of approximately 30ha which was impacted by uncontrolled fires occurring at least 5 years before the beginning of this study. According to Dezzeo *et al*. (2004), the site is covered, by a vegetation gradient consisting of 1) tall primary forest dominated by *Dimorphandra macrostachya* Benth. and *Euterpe* sp. (tall forest); 2) slight fire affected secondary forest dominated by *D. macrostachya* and *Euceraea nitida* Martius (medium forest); 3) strong fire affected secondary forest dominated by *Vismia guianensis* (Aubl.) Choisy, *Myrcia* sp. and *Clusia* sp. (low forest); and 4) open savanna with few, scattered trees (savanna). Dezzeo *et al*. (2004) found large differences in stem density, basal area and species richness between the forests (Table I), and concluded that these differences could not be explained by differences in soil characteristics but only by fire which triggered the conversion. All soils along the vegetation gradient show similar charac-

TABLE I
STRUCTURAL ATTRIBUTES OF VEGETATION IN THE STUDIED FORESTS

Variable	Tall forest	Medium forest	Low forest
Number of species >2.5cm dbh / 0.1ha *	45	47	28
Number of trees 2.5-10cm dbh / ha *	3400	4530	1030
Number of trees >10cm dbh / ha *	1060	950	130
Maximal height of trees (m) *	30	24	16
Basal area >10cm dbh (m^2·ha^{-1}) *	40	29.7	2.0
Basal area <10cm dbh (m^2·ha^{-1}) *	7.0	9.2	2.0
Number of dead standing trees >5cm dbh / ha	320	860	360
Total biomass (Mg·ha^{-1}) **	411	313	13
Organic surface layer (Mg·ha^{-1}) *	227	140	0

* From Dezzeo *et al*. (2004). ** From Dezzeo and Chacón (2005).

TABLE II
ANNUAL LITTER PRODUCTION (Mg·ha^{-1}·year^{1})
AND NUTRIENT INPUT (kg·ha^{-1}·year^{1})
IN THE STUDIED FORESTS

Parameter	Tall forest	Medium forest	Low forest
Annual litterfall	5.19 a	5.65 a	3.93 b
N	45.87 a	45.15 a	29.88 b
P	0.55 a	0.52 a	0.39 b
Ca	33.78 a	20.35 b	38.14 a
K	10.73 a	9.38 a	16.72 b
Mg	9.82 a	11.88 a	10.52 a

Different letters in columns indicate significant differences between vegetation types (ANOVA, P<0.05).

teristics. They are shallow soils (<50cm depth) with high percentage of sand, low pH, base saturation and P concentration, and with high concentration of Al (Chacón and Dezzeo, 2004; Dezzeo *et al*., 2004). Tall forest shows no evidences of fire damage and therefore can be considered as an undisturbed primary forest. In low forest, the large and still standing charred stumps, the abundance of burned trunks on the forest floor and the absence of the organic surface layer (typical of mature forest in the region) signal a strong impact of fire. In medium forest, the presence of an organic surface layer and the low abundance of charred residues of trees indicate a slight fire impact. In both medium and low forests the impact of fire was not recent enough so as to affect the soil chemical properties through ash inputs (Dezzeo *et al*., 2004).

Methods

Litterfall sampling

The vegetation types identified as tall, medium and low forests are not considered defined types of a regular pattern, but were selected as transitional stages to characterize the gradient as such (Dezzeo *et al*., 2004). At each forest type one rectangular plot of 10×100m (0.1ha) was delimited to sample litter production. Each plot was divided in 10 subplots of 10×10m each. In the centre of subplots 1 to 8 a litter trap of 70×70cm was installed (8 replicate traps per forest plot). The litter traps were made from plastic material with a well draining 3mm mesh. Each trap was supported on four legs so that the top was 50cm above the soil.

Unreplicated forest sampling was used because it was very difficult to delimit more plots for each forest type presenting exactly the same characteristics. It is acknowledged that pseudo-replications can be a limitation of the present study, as in many other published studies related to litter production (Proctor *et al*., 1983; Dantas and Phillipson, 1989; Lisanework and Michelsen, 1994; Arunachalam *et al*., 1998; Burghouts *et al*., 1998; Morães *et al*., 1999; Cutini, 2002; Rogers, 2002). However, the absence of forest replications should not be a serious problem since the plots were delimited for the purpose of identifying major vegetation types and, furthermore, spatial and temporal replications within each plot were obtained for analysis of litter mass and nutrient inputs. Hurlbert (1984) recognized that the most common type of controlled experiment in field ecology involves a single replicate per treatment, and indicated that this is neither surprising nor bad.

Aboveground litterfall was collected every two weeks from Nov 1999 to Oct 2000. The material that fell in the traps included leaves, flowers fruits and twigs (<2cm), and was therefore equivalent to the fine litter of Vitousek (1984) and the small litter of Proctor *et al*. (1983). At each collection date the content of each trap was placed in paper bags, brought to the field laboratory and dried at 65°C to a constant weight. All oven dried samples were weighed, milled and digested with a mixture of H_2SO_4-H_2O_2, according to Tiessen and Moir (1993). The extracts were colorimetrically analyzed for total N and total P with a Technicon Auto-Analyzer. Ca, Mg and K were determined in the same extract by atomic absorption spectrophotometry. At each collection date, nutrient pools in litterfall were calculated by multiplying the mass of each trap by its corresponding nutrient concentration.

Mean values and their standard deviation are provided for mass and elemental pools of litterfall by each forest types. Statistical differences were tested using one-way analysis of variance (ANOVA). A Tukey honest significant difference (HSD) test was used when statistical differences at P<0.05 were obtained.

Results

Total annual litterfall (Table II) was 5.19Mg·ha^{-1}·year^{-1} in the tall forest (tall primary forest), 5.65Mg·ha^{-1}·year^{-1} in the medium forest (slight fire affected forest) and 3.93Mg·ha^{-1}·year^{-1} in the low forest (strong fire affected forest). The annual litterfall values of the tall and medium forests did not differ significantly between them, but were significantly higher than the annual litterfall value for the low forest (P<0.05).

The tendencies in the monthly litterfall variation were relatively similar in the tall, medium and low forests (Table III). These forests showed evidences of seasonality, with a 2.9 fold difference between maximum and minimum values in the tall forest, a 2.8 fold in the medium forest and a 3.5 fold in the low forest. Tall and medium forests exhibited production peaks in July and October, while the low forest showed a slight fall in the litter production in July and only one peak in October (Table III). The litterfall peaks seem to have

TABLE III
MEAN MONTHLY VARIATION IN THE LITTERFALL OF UNDISTURBED AND DISTURBED FORESTS IN THE GRAN SABANA, AND MEAN AND MONTHLY RAINFALL DURING THE STUDY PERIOD

	Litterfall (g·m^{-2})			
Month	Tall forest	Medium forest	Low forest	Rainfall (mm) *
November 1999	43.0 ±16.2	48.7 ±15.5	31.7 ±22.8	-
December 1999	37.9 ±13.5	44.7 ±15.6	27.3 ±18.4	-
January 2000	34.6 ± 9.7	33.8 ± 8.9	19.0 ±14.7	117.5
February 2000	33.1 ± 7.6	34.4 ±16.0	25.4 ±11.5	67.6
March 2000	36.2 ±11.8	36.6 ±18.9	33.9 ± 9.7	125.8
April 2000	27.0 ± 8.3	29.5 ± 9.8	31.7 ±21.1	239.0
May 2000	32.2 ± 9.2	35.3 ±15.7	34.8 ±22.5	211.3
June 2000	40.3 ±25.8	48.5 ±31.3	35.4 ±22.0	275.8
July 2000	59.4 ±38.7	81.8 ±50.5	22.9 ±16.9	265.2
August 2000	39.5 ±15.9	45.4 ±39.1	26.2 ±21.2	211.8
September 2000	57.3 ±27.3	58.9 ±15.5	37.9 ±27.3	128.9
October 2000	78.5 ±29.8	66.8 ±24.0	66.8 ±50.9	160.1

According to Chacón (2002).

no relation with the monthly rainfall variation.

All the studied forests showed a high spatial heterogeneity in litterfall production, which is evidenced in Table III by the high standard deviations of the mean values. High spatial variance in litterfall is common in tropical forests (Clark *et al.*, 2001) and indicates a great natural variability in the production of the different components of the small litterfall (leaves, reproductive parts and small woody material).

Between tall and medium forests, the annual input of nutrients was statistically similar (Table II) with the exception of Ca, which was significantly higher ($P<0.05$) in the tall forest. Compared to the tall and medium forests, the low forest showed significantly lower annual inputs of N and P, and a significantly higher input of K ($P<0.05$). In all studied forests large variations in the monthly content of nutrients in the litterfall were observed (Figure 1). With few exceptions, the highest values in nutrient content were observed in October, the month with the higher litter production (Table III). Like litterfall mass, peaks in the nutrient content (Figure 1) seem to have no relation with the monthly rainfall variation (Table III).

Discussion

Measurements of litterfall were made in order to determine how fire disturbances that affected the structural attributes of the forest are affecting the return of organic matter and nutrients from the biomass to the soil surface. Statistical comparisons of the annual litterfall revealed that tall forest (primary forest) and medium forest (slight fire affected forest) produced similar litter amounts, while low forest (strong fire affected forest) produced significantly less litter than tall and medium forests. It has been mentioned that crowns and canopies seem to be more sensitive to disturbances than other structural components of the forest (Cutini, 2002). In the present case, however, the similarity between the tall and medium forests in annual litter production indicates that minor perturbations do not affected the canopy productivity. On the other hand, the differences in the litter production (Table I) of the low forest compared to the tall and medium forests (24 and 30% less production in the low forest than in the other two, respectively, were surprisingly small considering the intensity of the fire perturbation occurred in the low forest. According to Dezzeo *et al.* (2004) and Dezzeo and Chacón (2005; Table I) the low forest showed 74 and 79% less stem density, 91 and 90% less basal area, and 97 and 96% less aboveground biomass than the tall and medium forests, respectively. These results indicate that fire perturbations that have considerably affected the structural attributes of the forests are not influencing substantially the canopy productivity.

No direct relationships between annual litterfall and structural attributes of the forests (basal area, density or biomass) have been reported for tropical moist deciduous forests (Kumar and Deepu, 1992), evergreen tropical forests (Sundarapandian and Swamy, 1999) and premontane tropical forests (Priess *et al.*, 1999). However, for regrowing forests in India, Arunachalam *et al.* (1998) reported direct correlations between basal area and annual litter production.

It is difficult to compare litterfall production in the studied sites with other tropical forests, because the different methods used in the published studies limit the comparison. However, it should be noted that annual litterfall in the studied forests (3.9 to 5.7ton·ha^{-1}·year^{-1}) can be considered low when compared with the mean values (also in ton·ha^{-1}·year^{-1}) compiled by Dantas and Phillipson (1989) for Amazonian forests (8.0), Central and South America forests (7.2), African forests (11.7) and Asian forests (7.8), and also with the values reported by Brouwer (1996) by sandy soils in Guyana (7.7 and 9.1) and with the range of values compiled by Morães *et al.* (1999) for Amazonian and non Amazonian forests of Brazil (6.3 to 9.9). The values of litterfall in tall and medium forests are comparable with the mean value of 5.6 reported by Priess *et al.* (1999) for primary forests on clayed soils in the southern

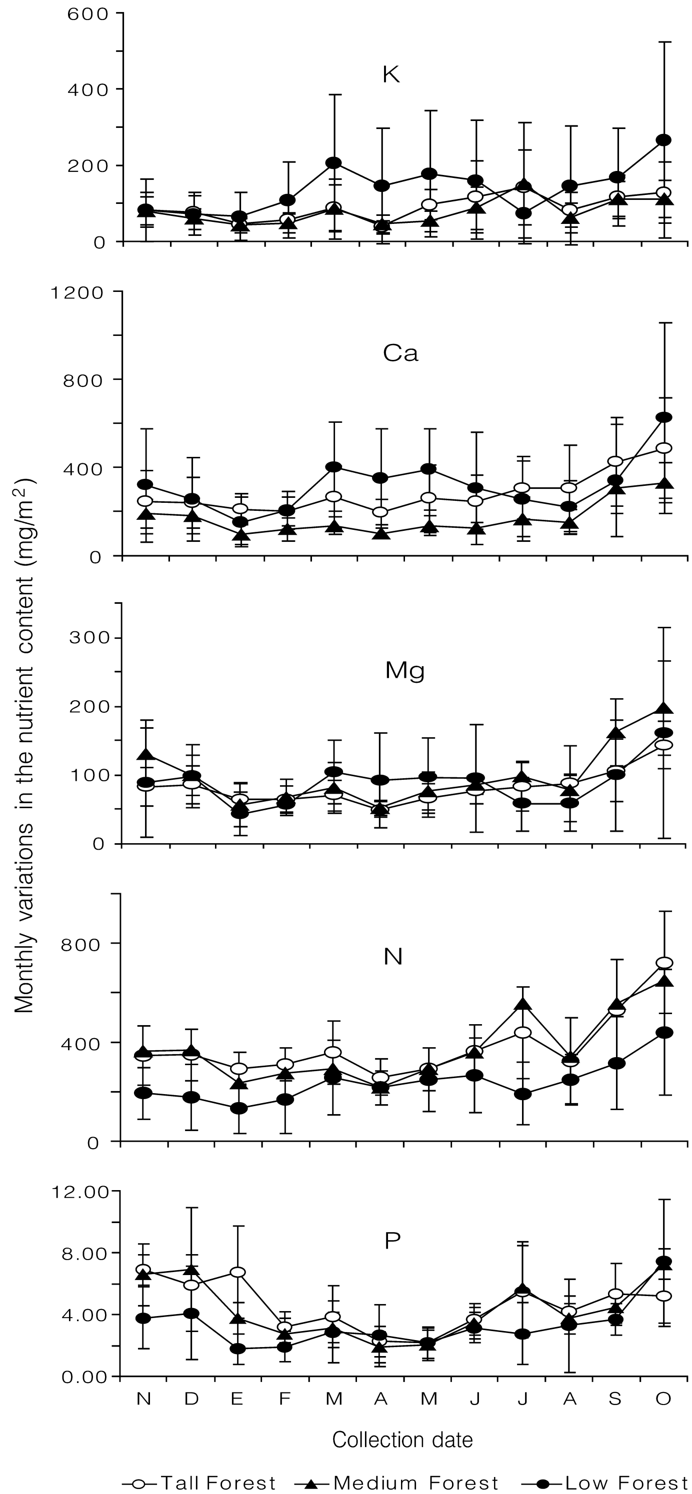

Figure 1: Mean monthly variation in the content of nutrients (mg/m^2) in the litterfall of undisturbed and disturbed forests in the Gran Sabana.

part of Gran Sabana, with the value reported by Cuevas and Medina (1986) for Amazonian Caatinga on sandy soils (5.6) and with that of 5.0 reported by Dantas and Phillipson (1989) for a three year old secondary forest in the Amazon. The low values of annual litterfall found in the present study indicate low productivity, which is probably associated with the strong acidification and nutrient impoverishment reported for the sandy soils of the studied forests (Dezzeo *et al*., 2004). It should be noted, however, that Scott *et al*. (1992) reported higher litterfall production (8.9-9.5ton·ha^{-1}·year^{1}) for rain forests growing on very nutrient-poor sandy soils of Roraima, Brazil, and therefore they concluded that these forest did not display nutrient limitations.

Periodicity of litterfall is largely influenced by annual climatic variations (Jackson, 1978; Proctor *et al*., 1983; Dantas and Phillipson, 1989; Scott *et al*., 1992; Kumar and Deepu, 1992; Liu *et al*., 2003). However, the results of this study seem to indicate that litterfall peaks do not have any relation with the rainfall variation (Table III). This emphasizes the need for long-term litterfall studies to confirm seasonal periodicity and establish relations between rainfall and litterfall peaks.

Nutrient inputs through litterfall (kg·ha^{-1}·year^{1}) at each studied forest are in the lower part of the spectrum of values compiled by Barbosa and Fearnside (1996) for upland tropical forests (34.2-158.0 N, 1.9-6.7 P, 12.7-59.3 K, 17.4-114.2 Ca, and 7.2-26.8 Mg), and by Liu *et al.* (2003) for tropical montane forests (25-90 N, 1.1-6.1 P, 5-59 K, 16-136 Ca, and 9-90 Mg). P inputs in the studied sites are quite low, particularly in the low forest, and can therefore be considered as the lowest P inputs recorded for tropical forests (see also Vitousek and Sanford, 1986; Danta and Phillipson, 1989; Veneklaas, 1991). Low inputs of nutrients through litterfall in the studied forests were due to a combination of low rates of return of litter to the soil surface and low concentrations of nutrients in the fallen material. Such results are consistent with the low concentration of nutrients, particularly P, in the sandy soils of these forests (Chacón and Dezzeo, 2004).

The annual input of N and P in the studied forests followed the same trend as the annual input of litterfall, while the annual inputs of Ca, K and Mg were quite variable. Nutrient content of litterfall may vary between perturbed and unperturbed forests as a result of the differing floristic compositions (Herbohn and Congdon, 1993). According to Dezzeo *et al*. (2004), the three studied forest have low floristic affinity, probably because they have a different successional status. It is probably, therefore, that differences in the phenology of the species have affected the fall of reproductive material and have influenced the nutrient input through litterfall between the forests. It is concluded that fire disturbances that did not change considerably the forest structure do not affect the return of organic matter and nutrients from the biomass to the soils, while disturbances that affected considerably the structural attributes of the forest influence the annual litter production but not in a substantial way.

ACKNOWLEDGMENTS

This study is a contribution to the research project Atmosphere-Biosphere Interactions in the Gran Sabana, Southern Venezuela. The work was supported by grant G-98001124 of FONACIT, Venezuela.

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