

## SMALL LITTERFALL CHEMISTRY IN A TROPICAL RAIN FOREST IN MEXICO

### Analyse chimique des apports à la litière dans une forêt tropicale humide au Mexique

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#### RESUME

*Pour étudier la composition chimique des apports à la litière d'une forêt tropicale humide dans le Sud-Est du Mexique, 12 échantillons recueillis de 1995 à 1997 dans 132 trappes (21,0 m<sup>2</sup>) sur 0,75 ha ont été analysés. Les concentrations de P et K dans la litière pendant la saison sèche furent supérieures (1,8 à 9,2 mg g<sup>-1</sup>) à celles de la saison des pluies (1,3 à 5,9 mg g<sup>-1</sup>). En comparaison avec d'autres forêts analogues, la production de litière fut similaire, mais les concentrations en substances nutritives ont été supérieures, particulièrement en ce qui concerne le Mg. Il en résulte un apport important de minéraux pour le sol, principalement à travers les feuilles et ceci dans l'ordre décroissant Ca > N > K > Mg > P.*

#### ABSTRACT

*Small litterfall chemistry of a lowland tropical rain forest in southeastern México was analysed. Twelve samples of litterfall were collected from 1995 through 1997, from 132 traps (21.0 m<sup>2</sup>) in 0.75 ha. Litterfall P and K concentrations were higher in the dry (1.8, 9.2 mg g<sup>-1</sup>) than in the wet (1.3, 5.9 mg g<sup>-1</sup>) season. Compared to similar forests elsewhere, small litterfall production was in the mid-range and nutrient concentrations were higher, especially Mg. This gave relatively high nutrient additions to the soil in the order Ca > N > K > Mg > P, and chiefly through the leaf litterfall.*

## INTRODUCTION

Litterfall is the most important source of nutrient input into the forest soil, thus playing a fundamental role in the transfer of energy between plants and soil (BRAY & GORHAM 1964, CUEVAS & MEDINA 1986, HERRERA *et al.* 1978, VITOUSEK 1984). On weathered nutrient-poor soils, the vegetation may depend on the recycling of the nutrients contained in the litterfall (SINGH 1969, PROCTOR *et al.* 1983). Nutrients are also returned to the forest in atmospheric depositions, throughfall and rainfall (BRASELL & SINCLAIR 1983). In a mixed forest in Guyana for example, of the total mineral input of N, P, K, Ca and Mg, 1.8% was returned in atmospheric depositions, 4.8% in throughfall, 7.3% in coarse litterfall, 33.8% in small litterfall, and 52.3% in the root-mat litter production (BROUWER 1996).

Los Tuxtlas forest is distributed upon a nutrient-rich top soil relatively rich in total nitrogen (0.5%), extractable phosphorus (4.11 µg g<sup>-1</sup>), and exchangeable cations (K<sup>+</sup>, 0.62 Cmol<sub>c</sub> kg<sup>-1</sup>; Na<sup>+</sup>, 0.54 Cmol<sub>c</sub> kg<sup>-1</sup>; Ca<sup>2+</sup>, 14.2 Cmol<sub>c</sub> kg<sup>-1</sup>; Mg<sup>2+</sup>, 8.6 Cmol<sub>c</sub> kg<sup>-1</sup>) (MARTÍNEZ-SÁNCHEZ 1999). Compared to tropical lowland rain forests elsewhere, it has a medium small litterfall production of 10.6 t ha<sup>-1</sup> yr<sup>-1</sup> (MARTÍNEZ-SÁNCHEZ 2001). Nutrient contents of the small litterfall from this forest are unk-

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noun, but from the soil chemistry and the small-litterfall productivity it is expected that nutrients return to the soil may be high. Small litterfall has a marked seasonality in most tropical lowland rain forests, but not their litterfall nutrient-elements (BERNHARD 1970, BRASELL *et al.* 1980, CORNFORTH 1970, CUEVAS & MEDINA 1986, LUIZÃO 1989).

The aim of the present paper was to analyse the nutrient contents of the small litterfall of Los Tuxtlas forest to estimate the rates of nutrient-elements input to the soil, as well as to describe the seasonality of the concentrations of the small litterfall nutrients.

## MATERIALS AND METHODS

The study site, as well as the materials and methods on sampling of the small litter used for this study, was described in detail in the preceding paper on small litterfall of Los Tuxtlas Forest (Martínez-Sánchez 2001).

The study site was located in Veracruz, México (18° 34' - 18° 36' N, 95° 04' - 95° 09' W). Soils are classified as well drained, coarse textured, vitric Andosols mixed with volcanic ash (FAO/UNESCO 1975). The mean annual temperature is 25.1 °C. The mean annual rainfall is 4,487 mm and 48% (2,154 mm) falls from August to November. The dry season spans March (115 mm) through May (105 mm). The forest is a tropical lowland evergreen rain forest with a preponderance of mesophyllic and simple leaves, and its structure has been well described by BONGERS *et al.* (1988) and MARTÍNEZ-SÁNCHEZ (2001).

Three anthropogenic undisturbed forest plots were located within the forest. In each forest plot of 0.25 ha, 44 litter traps of 0.159 m<sup>2</sup> each were randomly placed to give a litterfall sampling area of 7.0 m<sup>2</sup> plot<sup>-1</sup>.

The sampling period was from 8 December 1995 to 19 November 1997. From 8 January to 8 May 1996 litter collections from the traps were made monthly, and henceforth biweekly until November 1997. Litter from the 44 traps of each plot was bulked and dried for 15 days at 20 - 40 °C before sorting. The litterfall was sorted into five categories: small wood ( $\leq 2$  cm diameter); leaves including petioles; fruits and seeds; miscellaneous (3 - 20 mm diameter); and trash (debris under 3 mm). Flowers were all small and were included in the miscellaneous fraction. Most workers have not considered a miscellaneous category, however in this study there was too much material in this size range containing pieces of leaves, reproductive parts, wood, bark, moss, invertebrate remains and feces which were difficult to sort.

The analyses of the leaf litterfall nutrient-contents were made on 16 woody species which represented 68% of the total leaf-litter production (MARTÍNEZ-SÁNCHEZ 1999). Samples of 5 g of freshly (< 3 days) fallen leaves were collected during September 1997 (rainy season) from the forest floor under each of three trees ( $\geq 10$  cm d.b.h.) of each species, and dried at 40 °C. For *Forsteronia viridescens* (vine) leaves were collected in one site only. Only one sample of the leaf-litter fraction was collected and hence there is no information on its temporal variation. Leaf fraction concentrations were calculated using a weighed mean to reflect the contribution from each of the 16 species. For small wood, fruits, and trash, a sample of 5 g dry weight was obtained from the bulked material of the 44 litter-traps from each plot. For each litter fraction, samples from six months from each year, April and May (dry season), and June, August, October and December (wet season), were obtained and kept until chemical analysis. August and October constituted the wettest months.

A Student-t test and a one-way ANOVA with a Tukey means comparison test were used to compare the small litter nutrient concentrations between the dry and the wet season, and among the litter fractions. When data did not match the assumptions for parametric tests, log<sub>e</sub> transformations, Mann-Whitney, and Kruskal-Wallis tests were used. In the latter case a Tukey medians com-

parison test was applied (ZAR 1984). In all cases sample sizes were equal (balanced design). Minitab (Version 10.2) was used.

## CHEMICAL ANALYSIS

Chemical analysis was conducted in the Laboratorio de Edafología from Colegio de Postgraduados at Montecillos, México. All material was oven-dried at 105°C before analysis. Nitrogen was analysed by microkjeldahl digestion, followed by titration with sulphuric acid (0.01 N) using methyl orange as an indicator (BREMNER 1975, CHAPMAN & PRATT 1979). Phosphorus, K, Ca and Mg were analysed by digestion with nitric acid (HNO<sub>3</sub>) and perchloric acid (HClO<sub>4</sub>) (2:1). The determination of P was done in a 7.5 ml complex of vanadomolybdenum-phosphorus by photometry at 470 nm, and by atomic absorption spectrophotometry for the rest of the elements (CHAPMAN & PRATT 1979).

## RESULTS

Table I shows the mean element concentrations of the freshly fallen leaves, and Table II the mean element concentrations and the estimated rate of addition of the four small litterfall fractions. Nitrogen and P concentrations (mg g<sup>-1</sup>) were higher in trash and lower in small wood; K was higher in fruits and lower in small wood; and Ca and Mg were higher in leaf and trash litter, and lower in fruit litterfall. Calcium was particularly high in small wood. With the exception of K, the estimated rate of addition (kg ha<sup>-1</sup> yr<sup>-1</sup>) to the soil for all the elements was largest in leaf litterfall and smallest in fruit litterfall. They ranked as follows: Ca>N>K>Mg>P.

Temporal variation of the mineral-element concentrations in the litter fractions was varied. Nitrogen varied significantly only in the fruit litter with a peak in June (Figure 1). Phosphorus seemed to change only in the trash litter and decreased towards the end of the year. Potassium concentrations in fruit and trash litter showed several indistinct peaks, and small wood did not show any significant change. Calcium had higher concentrations in small wood in the dry season, the fruits had a peak concentration in June, and the trash litter did not show any significant change. Magnesium showed a peak in March for small wood and fruit litter, and only trash litter seemed to decrease consistently with the advance of the year (Figure 1). In the total small litterfall, P and K concentrations were higher during the dry than the wet season (Table III).

## DISCUSSION

There was a maximum of 15 days between litterfall collections during the study. In a sub-humid tropical forest in Nigeria, SWIFT *et al.* (1981) found a quick release of K by leaching, and a slow release of Ca during leaf litterfall decomposition. Since trash is small fragmented material it is more prone to leaching and may be one reason for showing larger seasonal differences in element concentrations.

Many workers have not found seasonal differences of litterfall nutrient elements (BERNHARD 1970, BRASELL *et al.* 1980, CORNFORTH 1970, CUEVAS & MEDINA 1986, LUIZÃO 1989). SCOTT *et al.* (1992) in Brazil, noticed a dry-season peak for K concentrations and to a lesser extent for leaf N. Leaf litterfall P seemed to peak in the wet season and early dry season. In Los Tuxtlas, GONZÁLEZ-ITURBE (1988) found only higher.

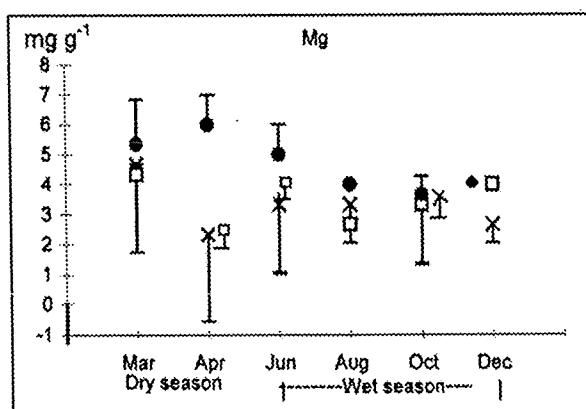
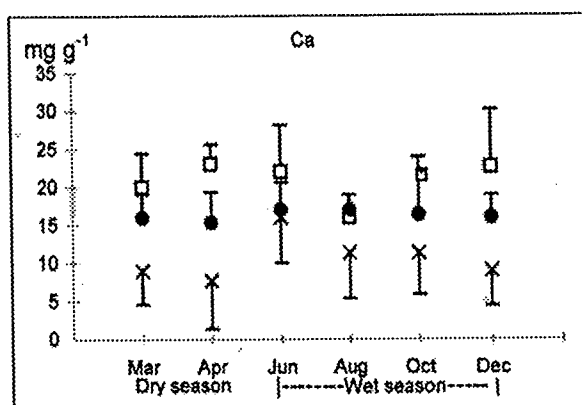
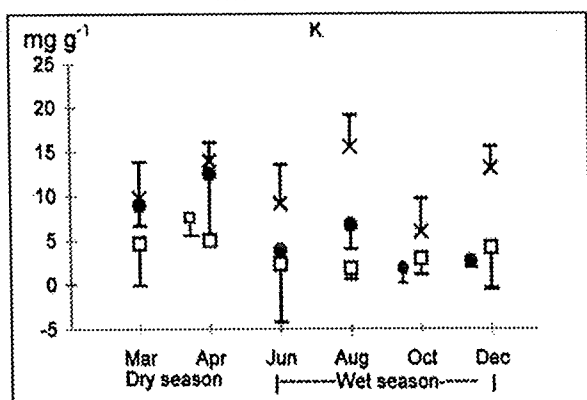
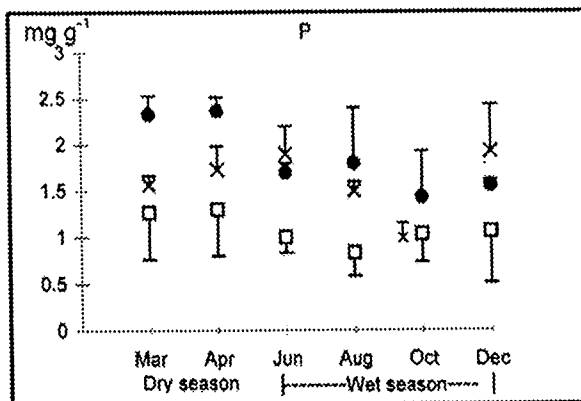
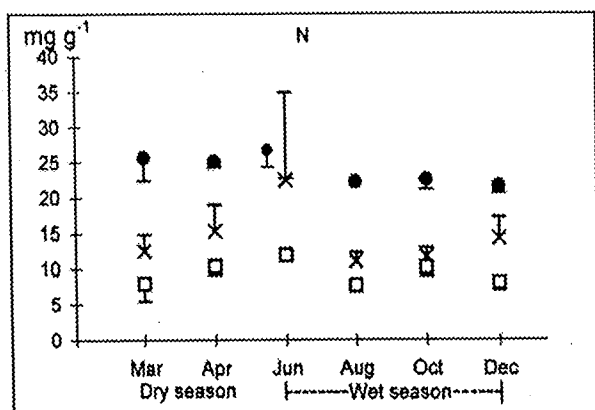


Fig. 1. Mean  $\pm$  S.D. concentrations of N, P, K, Ca and Mg in small wood (□), fruits (x), and trash (●) from the three forest plots. Values are average from 1996 and 1997.

Concentrations moyennes et écart-types pour N, P, K, Ca et Mg des catégories petit bois (□), fruits (x), et débris (●) pour les trois placeaux forestiers. Les valeurs sont des moyennes pour la période 1996-1997.

Tab. I. Mean leaf litterfall element concentrations (mg g<sup>-1</sup>) for 16 species collected during September 1997. The range for three replicates is shown in parenthesis. Maximum and minimum mean values for each element are in bold.

Concentrations moyennes en éléments (mg g<sup>-1</sup>) des apports foliaires à la litière pour 16 espèces récoltées en septembre 1997. Les valeurs extrêmes pour trois répétitions sont fournies entre parenthèses. Les valeurs moyennes maximale et minimale pour chaque élément sont en gras.

	N	P	K	Ca	Mg
<i>Nectandra ambigens</i>	10.1 (9.1-11.9)	1.6 (1.2-2.0)	11.6 (7.3-16.3)	28.7 (25.0-35.0)	3.3 (2.0-5.0)
<i>Spondias radlkoferi</i>	10.4 (9.3-11.1)	0.9 (0.8-1.0)	4.8 (4.0-6.0)	26.7 (25.0-30.0)	5.3 (4.0-6.0)
<i>Vatairea lundelli</i>	11.8 (11.0-12.7)	0.9 (0.8-1.0)	7.5 (6.7-8.0)	14.0 (9.0-17.0)	5.7 (4.0-7.0)
<i>Pseudolmedia oxyphyllaria</i>	12.8 (12.0-13.3)	0.8 (0.7-0.85)	11.0 (8.3-12.7)	15.3 (14.0-40.0)	5.7 (5.0-6.0)
<i>Forsteronia viridescens</i>	12.6 (10.1-15.2)	0.8 (0.7-0.9)	18.7 (17.7-20.7)	19.3 (18.0-21.0)	4.3 (4.0-5.0)
<i>Ficus tecolutensis</i>	8.6 (7.1-10.2)	0.8 (0.7-0.9)	8.0 (7.7-8.7)	18.7 (18.0-19.0)	4.3 (4.0-5.0)
<i>Poulsenia armata</i>	9.5 (8.4-10.1)	1.2 (1.0-1.3)	13.8 (10.0-16.3)	31.7 (30.0-35.0)	6.3 (6.0-7.0)
<i>Pterocarpus rohrii</i>	13.9 (12.2-16.0)	1.5 (0.8-2.0)	8.0 (4.0-10.0)	25.3 (25.0-26.0)	6.7 (5.0-8.0)
<i>Ficus yoponensis</i>	9.9 (7.9-11.2)	0.5 (0.1-0.8)	9.4 (6.0-11.3)	51.7 (35.0-80.0)	13.7 (12.0-15.0)
<i>F. petenensis</i>	7.7 (7.2-8.3)	0.6 (0.5-0.7)	5.0 (3.0-8.0)	38.3 (30.0-45.0)	2.2 (1.9-2.5)
<i>Orthion oblanceolatum</i>	22.7 (22.1-23.2)	1.9 (1.6-2.3)	12.7 (12-13.3)	23.3 (18.0-30.0)	7.0 (6.0-8.0)
<i>Faramea occidentalis</i>	12.4 (11.3-13.6)	0.8 (0.7-0.9)	4.9 (2.7-7.3)	24.0 (21.0-26.0)	3.0 (1.0-4.0)
<i>Rheedia edulis</i>	7.9 (7.6-8.3)	0.5 (0.4-0.6)	5.0 (4.3-6.0)	11.7 (11.0-13.0)	1.7 (1.0-2.0)
<i>Cecropia obtusifolia</i>	11.9 (10.3-13.3)	1.7 (1.2-3.0)	9.6 (7.7-11.3)	21.0 (20.0-23.0)	5.0 (3.0-7.0)
<i>Trichospermum galeottii</i>	7.1 (6.0-8.9)	0.4 (0.3-0.6)	6.4 (4.3-8.7)	19.7 (19.0-21.0)	8.3 (7.0-11.0)
<i>Heliocarpus appendiculatus</i>	10.3 (9.2-11.7)	2.3 (1.6-3.0)	16.7 (12.7-22.3)	23.7 (19.0-27.0)	9.0 (5.0-12.0)

Tab. II.- Mean nutrient concentrations (mg g<sup>-1</sup>) and estimed rate of addition (kg ha<sup>-1</sup> yr<sup>-1</sup>) of the small-liter fractions. One-way ANOVA<sup>1</sup> (means) and Kruskal-Wallis<sup>2</sup> (medians) tests for nutrient concentrations. Different superscript letters indicate a significant difference between means and medians within a column (Tukey test, p ≤ 0.05). n = 3 being each replicate the plot's average of six monthly samples bulked from 1996 and 1997.

*Teneurs moyennes en nutriments (mg g<sup>-1</sup>) et rapports estimés de l'apport (kg ha<sup>-1</sup> an<sup>-1</sup>) de la fraction "petite litière".*

	Litter-fall <sup>(1)</sup>	N		P		K		Ca		Mg	
	t ha <sup>-1</sup> yr <sup>-1</sup>	mg g <sup>-1</sup>	kg ha <sup>-1</sup> yr <sup>-1</sup>	mg g <sup>-1</sup>	Kg ha <sup>-1</sup> Yr <sup>-1</sup>	mg g <sup>-1</sup>	kg ha <sup>-1</sup> yr <sup>-1</sup>	mg g <sup>-1</sup>	kg ha <sup>-1</sup> yr <sup>-1</sup>	mg g <sup>-1</sup>	kg ha <sup>-1</sup> yr <sup>-1</sup>
Leaf <sup>(2)</sup>	6.29	11.0 <sup>ab</sup>	69.2	1.14 <sup>a</sup>	7.2	10.1 <sup>a</sup>	63.5	24.6 <sup>a</sup>	154.7	4.8 <sup>a</sup>	30.2
Small wood	1.33	9.1 <sup>a</sup>	12.1	1.08 <sup>a</sup>	1.4	2.5 <sup>b</sup>	3.3	20.0 <sup>ab</sup>	26.6	3.0 <sup>bc</sup>	4.0
Fruits and seeds	0.79	13.2 <sup>bc</sup>	10.4	1.59 <sup>b</sup>	0.95	12.4 <sup>a</sup>	9.8	11.0 <sup>c</sup>	6.7	3.0 <sup>bc</sup>	2.4
Trash	0.90	22.9 <sup>c</sup>	20.6	1.87 <sup>b</sup>	1.7	4.5 <sup>b</sup>	4.0	16.5 <sup>bc</sup>	14.9	4.0 <sup>ac</sup>	3.6
Miscellaneous <sup>3</sup>	1.26	-	28.9	-	2.4	-	5.7	-	20.8	-	5.0
P		< 0.0001 <sup>2</sup>		<0.0001 <sup>1</sup>		= 0.0001 <sup>2</sup>		<0.0001 <sup>2</sup>		<0.0001 <sup>2</sup>	

Note: Nutrient rates of addition of each litterfall fraction were estimated by multiplying their production (t ha<sup>-1</sup> yr<sup>-1</sup>) by their nutrient concentrations (mg g<sup>-1</sup>)

- <sup>(1)</sup> Taken from MARTINEZ-SANCHEZ (2001).
- <sup>(2)</sup> The mean nutrient concentrations of the leaf fraction comes from 16 species with three replicates each (Table I), and was estimated by multiplying the leaf litter mass of each species by its element concentration, and then the total was divided by the total litterfall mass of the 16 species.
- <sup>(3)</sup> Nutrient rates of addition of Miscellaneous were estimated with the nutrient concentrations of the trash fraction.

Tab. III. Student-t <sup>1</sup> (means) and Mann-Whitney <sup>2</sup> (medians) tests for element concentrations (mg g<sup>-1</sup>) of small litter fractions (n = 3) and total small litter (n = 9) between dry (March and April) and wet (August and October) seasons. For each season, replicates were the plots and values constituted the monthly and yearly average for that plot.

*Tests de Student-t (moyennes) et de Mann-Whitney (médianes) pour les concentrations en éléments (mg g<sup>-1</sup>) des fractions "petite litière" (n=3) et "petite litière totale" (n=9) entre saisons sèche (mars et avril) et humide (août et octobre). Pour chaque saison, les répétitions sont constituées par les placeaux et les valeurs par les moyennes mensuelles et annuelles pour chaque placeau.*

		N	P	K	Ca	Mg
Small wood	Dry	9.16	1.28	4.83	21.5	3.0
	Wet	8.86	0.93	2.43	18.0	3.0
	p	N.S. <sup>1</sup>	N.S. <sup>1</sup>	N.S. <sup>1</sup>	<0.05 <sup>1</sup>	N.S. <sup>2</sup>
Fruits & seeds	Dry	13.9	1.65	11.9	8.33	3.0
	Wet	11.4	1.21	10.8	11.3	3.0
	p	N.S. <sup>1</sup>	<0.02 <sup>1</sup>	N.S. <sup>1</sup>	N.S. <sup>1</sup>	N.S. <sup>2</sup>
Trash	Dry	25.4	2.35	10.7	15.6	5.5
	Wet	22.4	1.61	4.28	16.6	4.0
	p	<0.01 <sup>1</sup>	<0.003 <sup>1</sup>	<0.02 <sup>1</sup>	N.S. <sup>1</sup>	<0.01 <sup>2</sup>
Total	Dry	11.1	1.76	9.18	15.16	3.5
	Wet	13.2	1.25	5.86	15.3	3.0
	p	N.S. <sup>2</sup>	<0.005 <sup>1</sup>	<0.05 <sup>1</sup>	N.S. <sup>1</sup>	N.S. <sup>2</sup>

K concentrations for the leaf litterfall in the dry season. In the present study, element concentrations were highest in the dry season (Table III); Ca in the small wood, P in fruits and trash litterfall, and N, K and Mg in the trash litterfall. The lower nutrient concentrations in the wet season than in the dry season could be partly owing to leaching of the nutrients by rain water (BRASELL & SINCLAIR 1983, LARCHER 1977). Potassium particularly is a highly mobile element since it is not strictly fixed to any molecule (MEDINA 1984).



Small-litterfall element concentrations in Los Tuxtlas were all in the higher parts of the ranges of those described from around the world (Table IV). Magnesium was the highest, even compared to a relatively Mg-rich soil in Maracá Island, Brazil (VILLELA & PROCTOR 1999). Leaf litterfall concentrations (mg g<sup>-1</sup>) of P, K, Ca and Mg in Los Tuxtlas (Table IV) were also higher than the values collated by Scott et al. (1992) for a range of several Amazonian forests (N, 6 - 18; P, 0.20 - 0.71; K, 1.3 - 6.6; Ca, 1.5 - 7.7; Mg, 0.7 - 3.5). Richest fractions in nutrient are trash, flowers and fruits, and leaf litterfall; and small wood litter for Ca (Table IV).

Tab. IV. Mean element concentrations (mg g-1) for small litterfall fractions in lowland tropical forests around the world. - = no data. FF = flowers and fruits.

*Concentrations moyennes en éléments (mg g-1) pour les catégories "petite litière" en forêts tropicales de basse altitude au travers du monde. - = pas de données, FF = fleurs et fruits.*

	Forest type	N	P	K	Ca	Mg	Reference
Leaf	Alluvial forest	9.0	0.27	2.62	24.4	1.96	Proctor <i>et al.</i> (1983), Sarawak, Malaysia
	Dipterocarp forest	9.5	0.10	4.47	1.51	1.07	
Branches	Alluvial forest	7.1	0.17	1.30	28.8	1.22	
	Dipterocarp forest	6.2	0.04	1.82	1.32	0.66	
FF	Alluvial forest	11.9	0.72	4.00	13.8	1.60	
	Dipterocarp forest	11.6	0.50	4.82	1.33	1.12	
Trash	Alluvial forest	14.2	0.75	2.10	23.8	1.61	
	Dipterocarp forest	13.1	0.41	3.43	2.07	1.27	
Total	Alluvial forest	10.5	0.48	2.50	22.7	1.59	
	Dipterocarp forest	10.1	0.26	3.63	1.55	1.03	
Leaf	Plateau	13.7	0.2	1.5	3.8	1.8	Luizão (1989), Brazil
	Valley	17.8	0.3	3.3	7.7	2.1	
Branches	Plateau	12.5	0.3	1.9	6.5	1.4	
	Valley	16.7	0.4	2.2	10.1	1.6	
FF	Plateau	16.7	0.9	3.7	3.3	1.7	
	Valley	18.5	-	4.2	4.6	2.0	
Trash	Plateau	20.0	0.7	2.2	4.5	1.6	
	Valley	22.9	0.8	3.0	7.2	1.7	
Total	Plateau	15.7	0.5	2.3	4.5	1.6	
	Valley	18.9	0.5	3.1	7.4	1.8	
Leaf	Lowland rain forest	12.6	0.57	4.67	7.36	2.66	Scott <i>et al.</i> (1992), Brazil
Branches	" "	9.74	0.71	2.71	9.31	2.05	
FF	" "	14.6	1.30	10.7	4.81	2.63	
Trash	" "	19.3	1.12	6.13	8.03	2.55	
Total	" "	12.4	0.64	5.05	7.21	2.46	
Leaf	Lowland rain forest	11.4	0.33	6.1	5.9	3.0	Pendry & Proctor (1996), Brunei
Branches	" "	7.9	0.22	3.7	7.0	2.7	
FF	" "	17.8	1.02	7.3	4.7	2.7	
Trash	" "	20.8	0.85	3.7	5.5	2.2	
Total	" "	14.5	0.60	5.2	5.7	2.6	
Leaf	Lowland tropical forest	14.2	1.33	10.9	20.9	4.5	Songwe <i>et al.</i> (1997), Cameroon
Branches	" "	0.9	1.22	5.8	23.8	1.9	
Fruits	" "	15.0	2.50	19.7	9.8	2.7	
Total	" "	10.0	1.68	12.1	18.2	3.0	
Leaf *	Lowland rain forest	23.8	1.05	4.35	20.9	4.8	González-Iturbe (1988)
Leaf	Lowland rain forest	11.0	1.14	10.1	24.6	4.8	This study, México
Branches	Lowland rain forest	9.1	1.08	2.5	20.0	3.0	
Fruits	" "	13.2	1.59	12.4	11.0	3.0	
Trash	" "	22.9	1.87	4.5	16.5	4.0	
Total	" "	14.1	1.42	7.4	18.0	3.7	

\*= Mean of two years, México.

The distribution of nutrient-elements in the litterfall fractions reflected to a great extent the distribution of nutrient-elements in the living mass fractions for a montane forest (GRUBB & EDWARDS 1982).

DANTAS & PHILLIPSON (1989) gave wide ranges of nutrient-element additions of the total small litterfall to the soil ( $\text{kg ha}^{-1} \text{ yr}^{-1}$ ) for tropical rain forests from Africa, Asia, Central and South America: N (28 - 224), P (0.8 - 14), K (8 - 130), Ca (8 - 290), Mg (1 - 64). The estimated rate of small litterfall production for Los Tuxtlas forest is similar to the mid-range from lowland tropical forests elsewhere (MARTINEZ-SANCHEZ 2001), but concentrations in the litterfall of some elements like P, Ca and Mg are high (Table IV), giving a relatively high addition of these nutrients to the soil, particularly for phosphorus ( $13.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) (Table V).

This location provides another example of how small litterfall chemistry may be tightly bounded to the forest soil chemistry in a forest ecosystem. An opposite example to Los Tuxtlas forest can be the highly productive dipterocarp forest in Malaysia ( $57 \text{ m}^2 \text{ ha}^{-1}$  of basal area) on nutrient-poor soil (PROCTOR *et al.* 1983) with very low nutrient inputs to the soil by small litterfall (Table V).

Table V. Estimated rates of addition ( $\text{kg ha}^{-1} \text{ yr}^{-1}$ ) of nutrient-elements of total small litterfall in lowland tropical forests around the world. - = no data.

*Rapports estimés des apports ( $\text{kg ha}^{-1} \text{ an}^{-1}$ ) de nutriments de la petites litière totale en forêts tropicales de basse altitude au travers du monde. - = pas de données.*

Forest type	N	P	K	Ca	Mg	
Alluvial forest, Malaysia	111.0	4.1	26.1	286.0	20.1	Proctor <i>et al.</i> (1983)
Leaf	59.0	1.80	17.0	160.0	13.0	
Branches	17.0	0.42	3.1	70.0	3.0	
Flowers and Fruits	4.8	0.30	1.6	5.6	0.6	
Trash	30.0	1.60	4.4	50.0	3.4	
Dipterocarp forest,	81.0	1.20	33.0	13.0	8.9	Proctor <i>et al.</i> (1983)
Malaysia	51.0	0.56	24.0	8.1	5.8	
Leaf	13.0	0.08	3.7	2.7	1.4	
Branches	3.1	0.13	1.3	0.3	0.3	
Flowers and Fruits	14.0	0.45	3.7	2.3	1.4	
Trash						
Lowland rain forest,	118.0	6.7	48.5	63.7	23.8	Scott <i>et al.</i> (1992)
Brazil	79.1	3.6	29.4	46.4	16.8	
Leaf	13.1	1.0	3.6	12.5	2.7	
Branches	17.6	1.6	12.9	5.8	3.2	
Flowers and Fruits	8.1	0.5	2.6	2.6	1.1	
Trash						
Lowland rain forest,	122.0	3.9	60.0	64.0	31.0	Pendry & Proctor (1996)
Brunei	90.0	2.6	48.4	46.1	23.5	
Leaf	14.4	0.4	6.7	13.0	4.9	
Branches	8.5	0.5	3.5	2.3	1.3	
Flowers and Fruits	9.2	0.4	1.7	2.4	1.0	
Trash						
Lowland rain forest,	141.2	13.7	86.3	223.7	45.2	This study
México	69.2	7.2	63.5	154.7	30.2	
Leaf	12.1	1.4	3.3	26.6	4.0	
Branches	10.4	0.95	9.8	6.7	2.4	
Flowers and Fruits	49.5	4.1	9.7	35.7	8.6	
Trash*						

\* The trash fraction includes the miscellaneous fraction from Table II



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