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LEAF LITTERFALL COMPOSITION IN A TROPICAL RAIN FOREST IN MEXICO

Composition des apports à la litière dans une forêt dense humide tropicale au Mexique

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RESUME

La masse et la composition des apports foliaires et de matière organique de faibles dimensions à la litière ont été analysées pendant 22 mois à partir de 132 pièges (21,0 m^2) situés dans 0,75 ha d'une forêt dense humide tropicale du Sud-Est du Mexique. En comparaison avec d'autres forêts similaires, les apports moyens à la litières de faibles dimensions (10,6 $t.ha^{-1}.an^{-1}$) et les apports foliaires (6,3 $t.ha^{-1}$, an^{-1}) présentent des valeurs moyennes. Les échantillons présentant une valeur mensuelle toujours > à 1 g. de matière sèche concernent 119 espèces relevant de 51 familles dont 49 espèces où le diamètre des tiges à 1,3 m de hauteur est < à 10 cm. Les arbres, les lianes, les épiphytes et semi-épiphytes représentent respectivement 86,3%, 11,4% et 1,9%. Quant aux arbres, 75% concernent la strate arborée dominante, 19,6% la strate arborée intermédiaire et 5,4% la strate arborée inférieure.

ABSTRACT

Los Tuxtlas mean values of small litterfall (10.6 t ha^{-1} yr^{-1}) and leaf litterfall (6.3 t ha^{-1} yr^{-1}) are in the mid-range. Samples having a dry weight > 1 g any month included a total of 119 leaf litter species from 51 families, including 49 species not present as stems ≥ 10 cm d.b.h. Trees contributed 86.3% of the leaf litterfall, vines 11.4%, epiphytes and hemi-epiphytes 1.9%. From the trees, 75% was leaf-litter from high canopy species, 19.6% from mid-canopy species, and 5.4% from low canopy species.

Key words: Leaf litterfall, Los Tuxtlas, México, seasonality, small litterfall, species composition, tropical rain forest.

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INTRODUCTION

The net primary production of an ecosystem is distributed in four ways. Some is stored as biomass, some secreted as soluble organic matter, some consumed by animals, and some is shed as plant litter, including roots. The root litter is very difficult to quantify. Lowland tropical evergreen rain forests are characterized by their large production of small litterfall (PROCTOR 1984). Small litterfall comprise leaves, flowers, fruits, small branches and trash including animal material (PROCTOR 1983). Leaves comprise the largest portion, about 60% of the small litterfall (PROCTOR 1984). Leaf-litter quantity, quality and time of shedding affect accumulation of the litter layer, litter decomposition, humus formation, and hence nutrient cycling (BURGHOUTS 1993). Seedling establishment may also be affected (SYDES & GRIME 1981).

The total and sorted small litterfall productivity as well as their seasonality, have been studied already at Los Tuxtlas forest. ALVAREZ & GUEVARA (1993) have reported a total small litterfall of 7.26 t ha^{-1} yr^{-1} studying one hectare plot, and SÁNCHEZ & ALVAREZ-SÁNCHEZ (1995) 6.44 t ha^{-1} yr^{-1} studying two plots. In another study, ALVAREZ-SÁNCHEZ & GUEVARA (1999) found that small litterfall can be highly underestimated in this forest, since the canopy of the palm *Astrocaryum mexicanum* retained 48% of the total litterfall in one year of study. In addition, CARABIAS & GUEVARA (1985) conducted a five-year study of leaf, flower and fruit phenology in the same study site. Few studies are available which describe the leaf-litter composition. ALVAREZ & GUEVARA (1993) and SÁNCHEZ & ALVAREZ-SÁNCHEZ (1995) described the contribution to the leaf litterfall of the dominant tree species, and BURGHOUTS (1993) in Malaysia described the contribution of the canopy strata. The aim of the present study is to describe the species composition of the leaf litterfall at Los Tuxtlas, México, and to discuss several aspects of the small litterfall productivity.

THE STUDY SITE

The study site (BS) was the Biological Station 'Los Tuxtlas' belonging to the Institute of Biology of the Universidad Nacional Autónoma de México. It is located in the southeastern portion of the state of Veracruz, México (18° 34' - 18° 36' N, 95° 04' - 95° 09' W) (Figure 1).

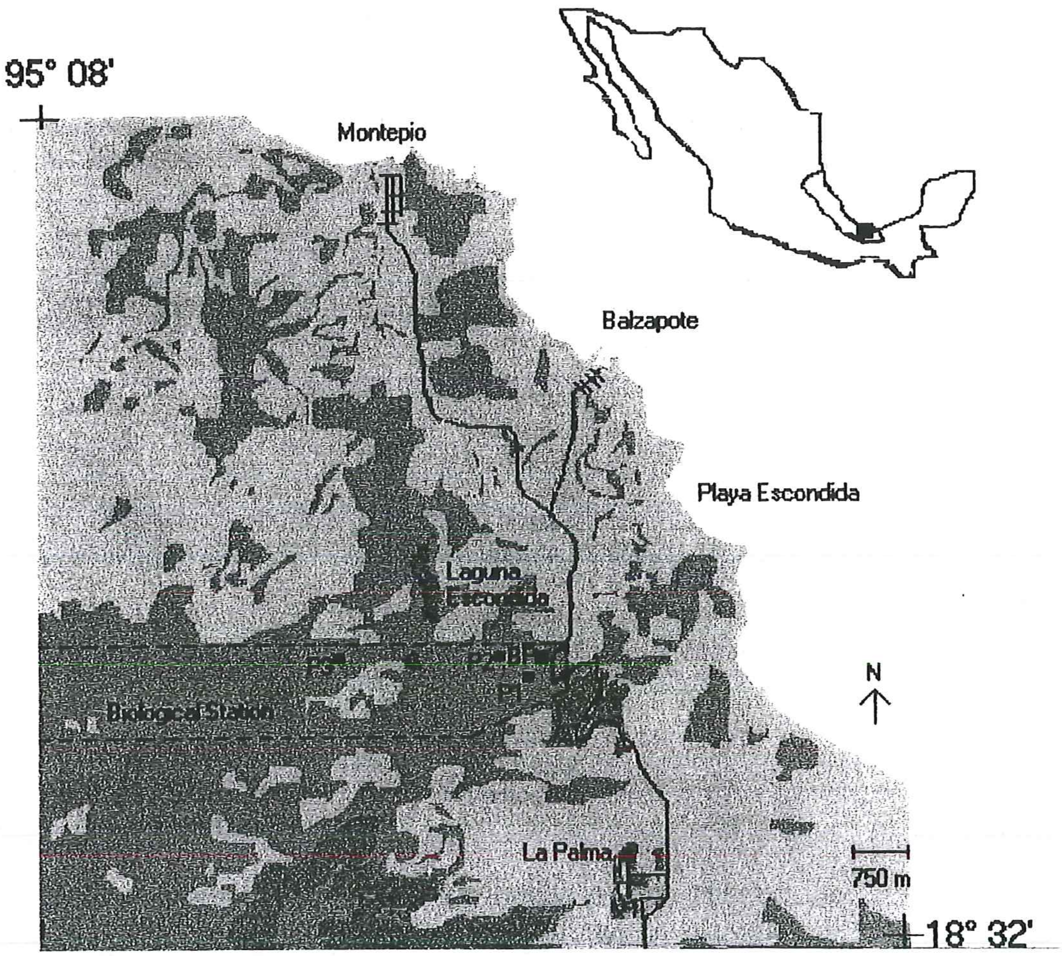

Fig.1. – Location of the study site at the biological station "Los Tuxtlas" (BS). Plot 1 (P1), Plot 2 (P2),Plot 3 (P3), and the building (BP)
Situation du site d'étude à la station biologique "Los Tuxlas"

Soils in the area of the study site are classified as well drained, coarse textured, vitric andosols mixed with volcanic ash (FAO/UNESCO 1975). Unpublished weather records from the BS show a mean annual temperature of 25.1 °C. The hottest month is May with a mean of 28.3 °C, and the coldest months are January and February with a mean of 21.5 °C. The absolute highest and lowest temperatures have been 39.0 °C and 12.0 °C. Mean annual rainfall (23 years from 1972 to 1997) is 4,487 mm; 48% (2,154 mm) falls from August to November, occasionally exceeding 1,000 mm per month. A drier season spans March (115 mm) through May (105 mm). Evaporation data from a government weather station in Sontecomapan (*c.* 10 km SE from the BS) from 1976 to 1997 had an annual mean of 1,390 mm. There is a mean of 157.4 rainless (0 mm) days per year, with the lowest mean of 5.7 rainy days in May and the highest mean of 18.8 rainy days in August (BS, unpublished data). This location, like most of the coast of the gulf of México, is characterized by northern lies strong-cold winds called 'nortes' from October to February. Their speeds up to 100 km h^{-1}, exert a major roll in branch and tree falls (BONGERS *et al.* 1988). The vegetation is classified as 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).

MATERIALS AND METHODS

Three anthropogenic undisturbed forest plots of 0.25 ha each, were located in the BS within 2.3 km from the buildings at the following orientation and altitudes above sea level: plot 1, NE, 120 m; plot 2, NW, 170 m; plot 3, NE, 200 m (Figure 1). The plots were located in accessible areas and have been disturbed only by natural tree and branch falls. Previous to conduct the litterfall study, the forest structure of each plot was described. All trees, palms and lianas were measured for their d.b.h. when this was ≥ 10 cm, and their species recorded.

SMALL LITTERFALL

Forty-four litter traps of 0.159 m^2 each were randomly placed within each plot including the edges. This gave a total of 7.0 m^2 of litterfall sampling area per plot. The traps were cone-shaped, 45-cm diameter at the rim, and made with a well drained nylon-cloth of *c.* 0.5-mm holes. They were attached to the top of a buried plastic pole at 50 - 100 cm in height. A plastic plate was placed on the poles to prevent terrestrial frugivores from reaching the litterfall (Figure 2).

The sampling period was from 8 December 1995 to 19 November 1997, however the collection from May 1997 was lost giving a total of 22 months and 11 days. From 8 January to 8 May 1996, litter from the traps were collected monthly, and henceforth biweekly until November 1997. Material from all the traps of each plot was bulked altogether before sorting into litter fractions. Owing to the large amount collected, the material was dried in a drying room for 15 days at 20 - 40 °C, and a sub-sample was oven-dried at 105 °C to obtain a moisture correction factor. The litterfall was sorted into five categories: small wood (≤ 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 with 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. HERBOHN & CONGDON (1993) had similar problems sorting the small litterfall including the floral fragments. Leaf litterfall taxa with a dry weight over 1 g in any month in any plot were determined to species level. For each plot, the total dry weight (g) of each litter fraction was divided by the trap area (7.0 m^2) and then by 710 days of sampling to obtain a value of g m^{-2} d^{-1}, which was extrapolated to t ha^{-1} yr^{-1}. The means' confidence limits of the small litterfall production for each plot were estimated from three consecutive bi-weekly collections only. For this, it was weighed the total mass from each single trap (n=44), during the windy season (January and February 1997). Minitab (Version 10.2) was used to run a one-way ANOVA with a Tukey test for means comparison, a regression model (r^2), and a Pearson point-moment correlation model (r).

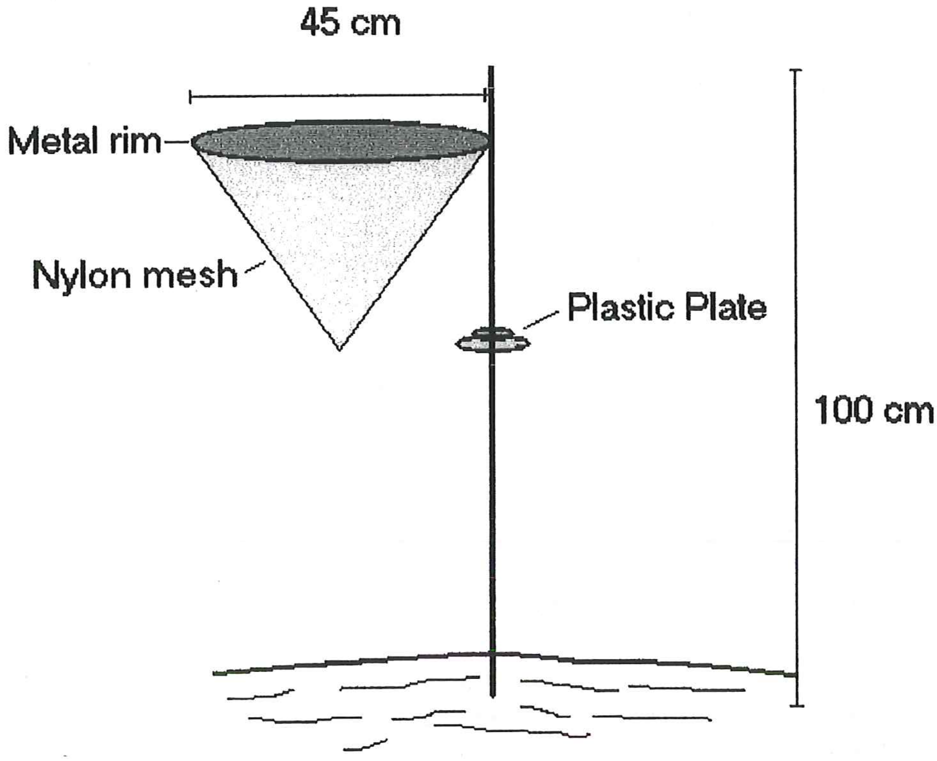

Fig.2. – Design of the litterfall trap used in the study.
Croquis de la trappe à litière utilisée dans l'étude.

RESULTS

FOREST STRUCTURE OF THE STUDY PLOTS

Table I gives the values of tree density and basal area of the study plots. For trees ≥ 10 cm d.b.h. in 0.75 ha, the forest had a relatively low species richness (81 species), low density (306 trees), and low basal area (24.9 m^2) (BONGERS *et al.* 1988). Only 2% of the individuals from the three plots were lianas, the rest were trees (Table I). Major tree families were the Lauraceae, Moraceae, Fabaceae, Anacardiaceae and Euphorbiaceae. Plot 1 was considered as the most mature plot with the least stem density, highest basal area $tree^{-1}$ and absence of obligate gap species. Plots 2 and 3 were considered less mature with a higher stem density, higher proportion of trees in the smallest diameter class, and the presence of obligate gap species. Difference in structure among the plots may be owing to plot's altitude and orientation, being plot 2 and plot 3 more exposed to the typical strong and cold winds.

Tab.I. - Forest structure description of the three 0.25-ha study plots at Los Tuxtlas, México. Number of individuals (≥ 10 cm d.b.h.) and basal area (BA).

Description de la structure forestière dans trois sites de 0,25 ha à Los Tuxtlas, (Mexique). Nombre d'individus(≥10 cm d.b.h.) et surface terrière (BA).

		Plot 1	Plot 2	Plot 3	Total
Total	Individuals	70	127	109	306
	BA (m^2)	8.0	8.1	8.8	24.9
Mean BA (m^2)	Individuals^{-1}	0.11	0.06	0.08	0.08
Trees	% Individuals	100	98.4	96.2	98.0
	% BA	100	99.6	99.3	99.7
Lianas	% Individuals	0	1.6	3.8	2.0
	% BA	0	0.4	0.7	0.3

TOTAL SMALL LITTERFALL

A mean total of 10.6 t ha^{-1} yr^{-1} of litterfall dry weight was estimated.

In the second year there was a higher production (13.2 t ha^{-1} yr^{-1}) compared to the previous year (7.9 t ha^{-1} yr^{-1}). This was owing to a wind storm in October 1997 which dislodged 1.42 t ha^{-1} of small wood, fruits and miscellaneous litterfall, and a higher leaf-fall during the dry season. The confidence limits for the total small litterfall from the three consecutive collections varied depending on the collection itself: plot 1, 12% - 20%; plot 2, 15% - 26%; plot 3, 14% - 19%. Plot 1 had a higher total small litterfall production than plot 2 or plot 3 ($p = 0.003$, $n = 132$; Table II). With 6.3 t ha^{-1} yr^{-1}, leaves were the preponderant fraction (around 60% of the total small litterfall) while small wood was 12.7%, miscellaneous plus trash 20.4%, and fruits were only 7.5%. SPAIN (1984) found an overall mean of 8.2% analysing fruitfall in 22 studies world-wide. Total, leaf, miscellaneous and trash litterfall trends over the 22 months of sampling were similar. There was a peak in the dry season, and a smaller peak in the windy season (September-November). Figure 3 shows the relationship between leaf litterfall and climate; 43% of the annual production fell during the dry season. Small wood was very variable and did not show any seasonal pattern with the exception of the high value after the wind storm. The fruit litter peaked twice a years, having a small peak from April to June (dry season) and a large peak from August to November (rainy and windy season). Miscellaneous production was significantly higher than trash production during the wind storm. No flowers bigger than 2 cm were found in most of the samples.

Tab. II. - Production (t ha^{-1} yr^{-1}) of the small litterfall fractions (with the 95% confidence limits for the total production from three collections; n = 44) from three 0.25-ha plots during 710 days at Los Tuxtlas, México. Different superscript letters indicate a significant difference among the plots (Tukey test, $p \leq 0.05$).

Production (t.$ha^{-1}an^{-1}$) de fraction de petites chutes de litière (limite de confiance à 95 % pour la production totale des 3 collections; n=44), pour trois sites de 0.25 ha pendant 710 jours à Los Tuxtlas, au Mexique. Les lettres en exposant indiquent des différences significatives suivant les sites (Test de Tukey), avec p= ≤0.05).

	Plot 1	Plot 2	Plot 3	Mean
Leaves	6.39	6.19	6.30	6.29
Small wood	1.28	1.35	1.37	1.33
Fruits	1.02	0.91	0.44	0.79
Miscellaneous	1.41	1.02	1.36	1.26
Trash	0.97	0.78	0.95	0.90
Total	11.07 [a]	10.25 [b]	10.42 [b]	10.58
	± 1.75	± 1.93	± 1.64	±1.77

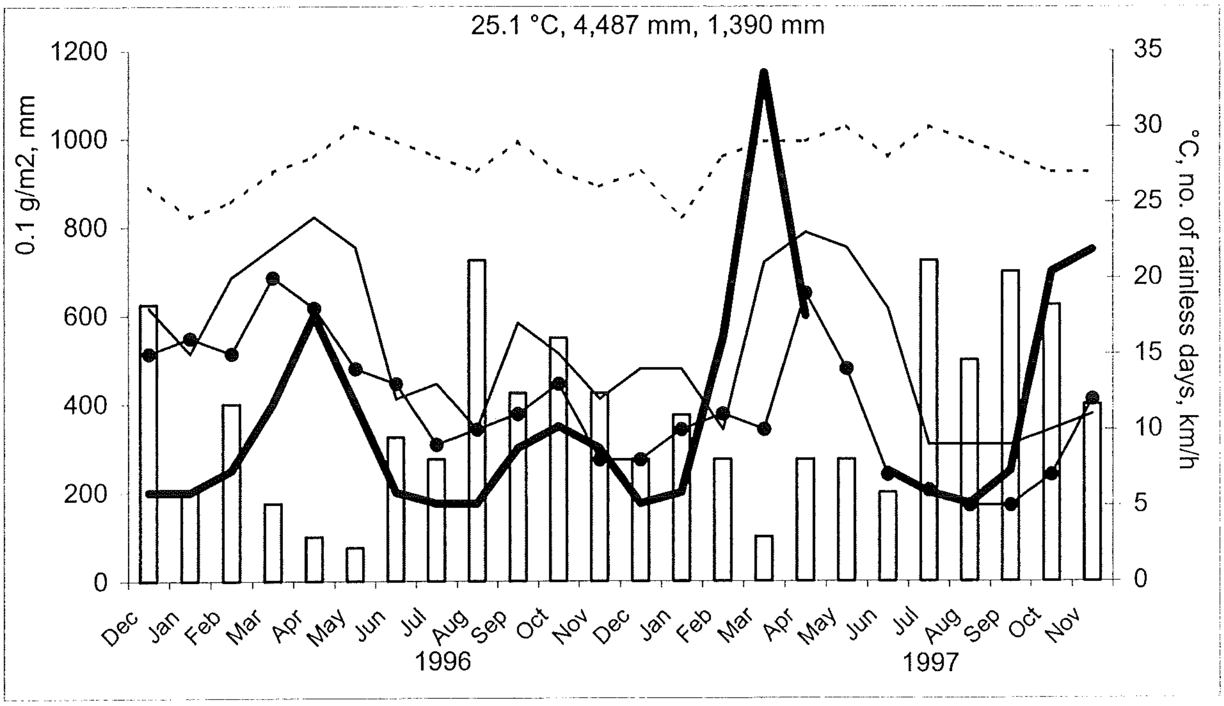

Fig.3. – Leaf litterfall (—— ,g m^{2}), rainfall (open bar, mm), monthly mean maximum température(---, °C), number of rainless days (—), and mean wind speed (•, km h^{-1}). Annual mean temperature, rainfall and evaporation are also shown. Leaf litterfall data for May 1997 are missing.

Apport de feuilles, précipitations, moyennes mensuelles des maximum de températures, nombre de jours sans pluie et vitesse moyenne du vent. La valeur des apports à la litière du mois de mai 1997 est manquante.

LEAF LITTERFALL BY SPECIES

A total of 119 species from 51 plant families which contributed at least 1 g $month^{-1}$ were determined (Table III, Appendix). It was possible to determine to species level 80% (94 species) of the total leaf litter from plot 1, 75% (80 species) from plot 2, and 69% (88 species) from plot 3. The leading families were Lauraceae > Moraceae > Fabaceae > Anacardiaceae > Apocynaceae. The leaves from ten tree species recorded as stems on the sampling plots were not found in the litterfall. This was chiefly because no litter traps were near these individual trees. For the case of the compound-leaved species *Acacia hayesii* and *Albizia purpusii* (Mimosaceae), leaflets were too small (< 2 cm long) to be sorted, and hence were included with the miscellaneous fraction. On the other hand, 49 leaf-litter species were not censused in the forest plots (Appendix). These species contributed 9.8% of the total leaf litterfall and came from stems (< 10 cm d.b.h.) of trees, palms, and vines; epiphytes; and from stems adjacent to the plots.

Among the 20 most important species, seven accounted for 58.2% of the total leaf litterfall (Table IV). The vine *Forsteronia viridescens* (one stem ≥ 10 cm d.b.h. and perhaps some others < 10 cm d.b.h.) is ranked fifth. Species contribution to the total leaf litterfall clearly had an exponential decay ($F = 3{,}759.3$, $P < 0.0001$, $r^2 = 0.97$, $n = 119$) as follows: *Nectandra ambigens,* the species with the highest basal area, contributed 22.6% followed by *Spondias radlkoferi* which contributed 8.5%, and so on down to a contribution of 2% by the 10th ranked-species (Table III). Ninety-eight species contributed 19.5% all together. Trees (83 species) provided 86.3% of the total leaf litterfall, vines (27 species) 11.4%, epiphytes (4 species) 1.2%, hemi-epiphytes (3 species) 0.7%, and palms (2 species) 0.3%. Concerning the trees, 27 canopy species (> 20 m tall) represented 74.9% of the leaf litterfall mass, 32 mid-canopy species (10 - 20 m) represented 19.6%, and 18 understorey species (0 - 10 m) 5.4%. At family and species level, leaf litterfall was better correlated to tree basal area ($r = 0.94$, $r = 0.89$) than to tree density ($r = 0.5$, $r = 0.34$).
(Table III, Table IV)

DISCUSSION

TOTAL SMALL LITTERFALL

Small litterfall production in lowland evergreen tropical rain forests around the world ranges from 5.7 t ha^{-1} yr^{-1} in a heath forest in Venezuela to 12.4 t ha^{-1} yr^{-1} in Zaïre (PROCTOR 1984). The values of the total (10.6 t ha^{-1} yr^{-1}) and leaf-litter (6.3 t ha^{-1} yr^{-1}) production for Los Tuxtlas are around the mid-range. Small wood is in the lower limit, flowers and fruits in the mid-range, and trash and miscellaneous in the higher limit. In this study, mean confidence limits for the total small litterfall were wide (16 - 20% depending on the plot) possibly due to the small trap size and variability in forest structure.

Tab.III. - Percentage of leaf litter dry weight (%LL) contributed by families in three 0.25-ha plots at Los Tuxtlas, México. S = number of species.

Pourcentage de poids sec de litière (% LL) par famille dans trois sites de 0.25 ha à Los Tuxtlas au Mexique. S= nombre d'espèces.

	Family	%LL	S		Family	%LL	S
1	Lauraceae	24.41	5	27	Flacourtiaceae	0.29	2
2	Moraceae	18.51	10	28	Capparaceae	0.29	1
3	Fabaceae	12.01	5	29	Dilleniaceae	0.23	1
4	Anacardiaceae	7.75	2	30	Cecropiaceae	0.21	1
5	Apocynaceae	5.97	3	31	Malvaceae	0.18	1
6	Sapotaceae	3.75	7	32	Verbenaceae	0.17	2
7	Meliaceae	2.45	3	33	Mimosaceae	0.16	1
8	Euphorbiaceae	2.18	3	34	Staphylaceae	0.15	1
9	Nyctaginaceae	2.17	2	35	Aquifoliaceae	0.15	1
10	Araceae	1.98	6	36	Malphigiaceae	0.10	2
11	Araliaceae	1.74	2	37	Menispermaceae	0.10	1
12	Asteraceae	1.56	3	38	Hippocrateaceae	0.09	2
13	Ulmaceae	1.49	2	39	Convolvulaceae	0.08	1
14	Bignoniaceae	1.44	7	40	Chrysobalanaceae	0.06	1
15	Rubiaceae	1.39	4	41	Polygonaceae	0.04	1
16	Clusiaceae	1.30	5	42	Solanaceae	0.04	1
17	Burseraceae	1.16	1	43	Rhamnaceae	0.03	1
18	Violaceae	1.04	2	44	Piperaceae	0.03	1
19	Annonaceae	0.97	2	45	Celastraceae	0.03	1
20	Sapindaceae	0.88	4	46	Myrtaceae	0.02	1
21	Bombacaceae	0.80	2	47	Urticaceae	0.02	2
22	Caesalpiniaceae	0.54	2	48	Hernandiaceae	0.02	1
23	Tiliaceae	0.45	2	49	Amaranthaceae	0.01	1
24	Connaraceae	0.41	1	50	Loranthaceae	0.01	1
25	Boraginaceae	0.33	1	51	Aristolochiaceae	0.007	1
26	Arecaceae	0.33	2		Total	100.00	119

Tab.IV. - Percentage of leaf litterfall for the 20 species with most production in three 0.25-ha plots at Los Tuxtlas, México during 22 months. n = number of individuals (≥ 10 cm d.b.h.) present in the plots.

Pourcentage de litière pour 20 espèces avec la production la plus importante dans trois sites de0.25 ha à Los Tuxtlas (Mexique pendant 22 mois: n=nombre d'individus (≥10 cm d.b.h) présents dans le site.)

	Species	%	n		Species	%	n
1	*Nectandra ambigens*	22.58	15	11	*Clarisia biflora*	1.84	1
2	*Spondias radlkoferi*	8.48	13	12	*Guarea glabra*	1.59	10
3	*Vatairea lundellii*	8.39	2	13	*Omphalea oleifera*	1.57	10
4	*Pseudolmedia oxyphyllaria*	6.28	29	14	*Ficus petenensis*	1.51	1
5	*Forsteronia viridescens*	5.80	1	15	*Tuxtla pittieri*	1.46	0
6	*Ficus tecolutensis*	3.74	1	16	*Pouteria sapota*	1.41	1
7	*Poulsenia armata*	2.93	4	17	*Ampelocera hottlei*	1.38	2
8	*Pteropcarpus rohrii*	2.71	2	18	*Bursera simaruba*	1.26	2
9	*Ficus yoponensis*	2.16	2	19	*Oeropanax obtusifolius*	1.17	0
10	*Neea psychotroides*	2.07	2	20	*Pouteria reticulata*	1.06	1

Confidence limits for each single litterfall fraction could not be obtained from these data but they are usually wider (VILLELA & PROCTOR 1999).

The higher number of sampling plots set up over a wider area in this study than in previous studies confined to the east side of the BS (ALVAREZ & GUEVARA 1993, SÁNCHEZ & ALVAREZ-SÁNCHEZ 1995), did not give substantial difference in small litterfall estimation. The higher total small litterfall value from this study resulted partly from a pronounced dry-season and partly from small wood and fruits dislodged after a wind storm. The pattern of fruit litterfall during the study period was not consistent in this study, and like the flower fraction, was prone to vary by several months from one year to another (ALVAREZ & GUEVARA 1993, SÁNCHEZ & ALVAREZ-SÁNCHEZ 1995). However, lower values tend to be during the dry season and higher peaks in the wet and windy season.

There is an apparent relationship between litterfall and the yearly weather pattern (CARABIAS & GUEVARA 1985, GONG & ONG 1983, LUIZÃO 1989, SANCHEZ & ALVAREZ-SANCHEZ 1995, WILLIAMS-LINERA 1997, Figure 3), however this relationship may not be statistically significant, owing to the non-independent and non-random nature of the phenological events. For example, in deciduous species, and to some extent in evergreen species, it is not possible to observe leaf litterfall soon after the leaf shedding season, and fruiting is dependent on flowering.

LEAF LITTERFALL AND SPECIES TEMPORAL PATTERNS

The 15 days collecting period was frequent enough to avoid serious deterioration of the leaves. Thirty-four species of vines, epiphytes, and hemi-epiphytes were found, which suggests that litterfall analysis could be a method of sampling the species richness of these life forms. The palm fraction was not sampled adequately by the trap size and hence was underestimated (VILLELA & PROCTOR 1999).

Similar patterns in the species contribution to the total leaf litterfall have previously been found. ALVAREZ & GUEVARA (1993) reported that depending on the year, *Nectandra ambigens* contributed 12.3% and 28.6%; *Pseudolmedia oxyphyllaria* 3.4% and 10.3%; and *Poulsenia armata*, 4.0% and 5.9% in this forest. The five most important species provided between 26% and 55% leaf litterfall. SÁNCHEZ & ALVAREZ-SÁNCHEZ (1995) reported that seven species provided 60% of leaf litterfall in one site and six species 47% in another site. In my study, seven species accounted for 58% of the total leaf litterfall. In Sabah, Malaysia the six and 16 most productive species in two plots, contributed 36% and 58% from the total leaf litterfall (BURGHOUTS 1993).

Like this study, in Malaysia BURGHOUTS (1993) found correlations between leaf litterfall and basal area (0.8), and tree density (0.71) at a family level. Species-specific timber exploitation in the tropics should take into account the possible impact on litter production and hence nutrient cycling. However, if this is unrealistic, harvesting of many small trees would seem to be better than few large trees. Considering the leaf litterfall from trees at Los Tuxtlas, 75% fell from the canopy species, 19.6% from the mid-canopy and 5.4% from the understory species. In Sabah, Malaysia, 39% leaf litterfall was from the emergent trees, 37% from the canopy species, 10% from the understory and 13% from climbers (BURGHOUTS 1993).

In agreement with SÁNCHEZ & ALVAREZ-SÁNCHEZ (1995) three main groups of species can be defined at Los Tuxtlas with respect to their peak time of leaf litterfall: dry season, wet season and windy season. Depending on the site, they found that between 40% and 52% of the species produced leaf litter during the dry season, around 5% during the wet season, and less than 10% during the windy season. Some species in my study fell within Sánchez & Alvarez-Sánchez's groups: *Guarea glabra*, *Ficus yoponensis*, *Nectandra ambigens*, *Pseudomedia oxyphyllaria*, and *Pterocarpus rohrii*. Others did not: *Bursera simaruba*, *Cymbopetalum bailloni*, *Forsteronia viridescens* and *Rheedia edulis*. Additionally, similar to ALVAREZ & GUEVARA (1993) there are species like *Ficus yoponensis* and *Spondias radlkoferi* with a main peak in the dry season and a second peak in the wet and windy season. Species with a continuous leaf fall were also recorded, including understory tree species (*e.g. Cymbopetalum bailloni* and *Rheedia edulis*). Shrubs tend to have more regular patterns from year to year than trees (CARABIAS & GUEVARA 1985). VILLELA (1995) found very small temporal and spatial variation in palm leaf litterfall in Brazil.

Phenology within the same species has been found to vary greatly at different sites, and in the same site (CARABIAS & GUEVARA 1985, SÁNCHEZ & ALVAREZ-SÁNCHEZ 1995). Cycles of leaf renewal can be of variable length and are not necessarily synchronized among individuals (BURGHOUTS 1993, CHABOT & HICKS 1982), such that species rankings in leaf litterfall production change easily among annual periods and sites. BURGHOUTS *et al.* (1992) found high variation in litter fall in a 4-ha plot as a result of the variable composition and structure of the vegetation emphasizing the importance of spatial variation in litterfall. Spatial effect on total small litterfall at a scale of 0.25-ha plots (Table II) was seen in my study.

Currently, looking at nearly six years of small litterfall analysis in the same location at Los Tuxtlas during the period 1984 – 1997 (ALVAREZ & GUEVARA 1993, SÁNCHEZ & ALVAREZ-SÁNCHEZ 1995, and this study) litterfall seasonality appears consistent at the community level, but not at species level. This is exemplified by CARABIAS & GUEVARA (1985) who found a consistency in seasonal patterns of community leaf and flower shedding during five years in Los Tuxtlas, and WILLIAMS-LINERA (1997) who did not find regular seasonality in single evergreen-species leaf litterfall during five years too in a tropical lower montane forest in Mexico. Phenological patterns of tropical forest trees and species have been derscribed as diverse and complex, as well as the factors that regulate these patterns (see BAWA & HADLEY 1990).

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APPENDIX.

List of species from a 22-month study of leaf litterfall in three 0.25-ha plots in Los Tuxtlas, México. Nomenclature follows Ibarra-Manriquez & Sinaca (1995, 1996a, 1996b).

Amaranthaceae
Iresine arbuscula Uline et W.L. Bray

Anacardiaceae
Spondias radlkoferi Donn. Sm.
\+ *Tapirira mexicana* Marchand

Annonaceae
Cymbopetallum baillonii R.E.Fr.
Guamia sp.

Apocynaceae
Aspidosperma megalocarpon Mull. Arg.
Forsteronia viridescens S.F. Blake
Stemmadenia donnell-smithii (Rose) Woodson

Aquifoliaceae
Ilex valeri Standl.

Araceae
\+ *Philodendron guttiferum* Kunth
\+ *Philodendron sagittifolium* Liebm.
\+ *Philodendron scandens* K. Koch et Sell
\+ *Rhodospatha aff. wendlandii* Schott
\+ *Syngonium*
\+ *Syngonium podophyllum* Schott

Araliaceae
Dendropanax arboreus (L.) Ecne. et Planch.
\+ *Oeropanax obtusifolius* L. O. Williams

Arecaceae
\+ *Astrocaryum mexicanum* Liebm. ex Mart.
\+ *Chamaedorea alternans* H. Wendl.

Aristolochiaceae
\+ *Aristolochia ovalifolia* Duch.

Asteraceae
Eupatorium galeottii B.L. Rob.
\+ *Mikania*
\+ *Tuxtla pittieri* (Greenm.) Villaseñor et Strother

Bignoniaceae
Amphitecna tuxtlensis A.H. Gentry
\+ *Anemopaegna chrysanthum* Dugand
\+ *Arrabidaea verrucosa* (Standl.) A.H. Gentry
\+ *Callichlamys latifolia* (Rich.) Schum.
\+ *Mansoa hymenaea* (DC.) A.H. Gentry
Mansoa verrucifera (Schtdl.) A.H. Gentry
\+ *Paragonia pyramidata* (Rich.) Bur.

Bombacaceae
Quararibea funebris (La Llave) Vischer
Quararibea yunckeri Standl. subsp. *sessiliflora* Miranda ex W.S. Alverson

Boraginaceae
Cordia megalantha S.F. Blake

Burseraceae
Bursera simaruba (L.) Sarg.

Caesalpiniaceae
\+ *Cynometra retusa* Britton et Rose
Dialium guianense (Aubl.) Sandwith.

Capparaceae
Crataeva tapia L.

Cecropiaceae
Cecropia obtusifolia Bertol.

Celastraceae
Maytenus schippii Lundell

Chrysobalanaceae
Couepia polyandra (Kunth) Rose

Clusiaceae
Calophyllum brasiliense Cambess.
\+ *Clusia flava* Jacq.
\+ *Clusia lundellii* Standl.
\+ *Clusia minor* L.
Rheedia edulis (Seem.) Triana et Planch.

Connaraceae
\+ *Connarus schultesii* Standl. ex R.W. Schult.

Convolvulaceae
\+ *Ipomoea phillomega* (Vell.) House

Dilleniaceae
\+ *Tetracera volubilis* L.

Euphorbiaceae
\+ *Alchornea latifolia* Sw.
Croton schiedeanus Schltds.
Omphaleae oleifera Hemsl.

Fabaceae
\+ *Dussia mexicana* (Standl.)
\+ *Lonchocarpus cruentus* Lundell
Machaerium floribundum Benth.
Pterocarpus rohrii Vahl.
Vatairea lundellii (Standl.)

Flacourtiaceae
Lunania mexicana Brandegee
Pleuranthodendron lindenii (Turez.) Sleumer

Hernandiaceae
\+ *Sparattanthelium amazonum* Mart.

Hippocrateaceae
\+ *Hippocratea*
\+ *Salacia megistophylla* Standl.

Lauraceae
Licaria velutina van der Werff
Nectandra ambigens (S.F. Blake) C.K. Allen
Nectandra globosa (Aubl.) Mez
Nectandra salicifolia (Kunth) Mez
Ocotea dendrodaphne Mez

Loranthaceae
\+ *Phorandendron piperoides* (Kunth)

Malphigiaceae
\+ *Hiraea fagifolia* (DC.) A. Juss.
Mascagnia rivularis C.V. Morton et Standl.

Malvaceae
\+ *Robinsonella mirandae* Gómez Pompa

Meliaceae
Guarea glabra Vahl ('raza' bijuga (DC.) T.D. Penn., sensu Pennington 1981)
Guarea grandifolia A. DC.

Trichilia moschata Sw.

Menispermaceae

\+ *Abuta panamensis* (Standl.) Krukoff et Barneby

Mimosaceae
Inga acrocephala Steud.

Moraceae

Brosimum alicastrum Sw.
Clarisia biflora Ruiz et Pav. subsp. *mexicana* (Liebm.) W.C. Burger
\+ *Ficus cotinifolia* aff. *cotinifolia*
\+ *Ficus lundellii* Standl.
\+ *Ficus pertusa* L.f.
Ficus petenensis Lundell
Ficus tecolutensis (Liebm.) Miq.
Ficus yoponensis Desv.
Poulsenia armata (Miq.) Standl.
Pseudolmedia oxyphyllaria Donn. Sm.

Myrtaceae
\+ *Eugenia mexicana* Steud.

Nyctaginaceae
Neea psychotrioides Donn. Sm.
Pisonia aculeata L. var. *aculeata*

Piperaceae
Piper amalago L.

Polygonaceae
\+ *Coccoloba*

Rhamnaceae
\+ *Gouania lupuloides* (L.) Urb.

Rubiaceae
\+ *Genipa Americana* L.
Faramea occidentalis (L.) A. Rich.
\+ *Psychotria chiapensis* Standl.
Psychotria faxlucens Lorence et Dwyer
Psychotria simiarum Standl.

Sapindaceae
\+ *Paullinia fuscescens* Radlk.
Sapindus saponaria L.
Serjania goniocarpa Radlk.
\+ *Thinouia myriantha* Triana et Planchón

Sapotaceae
Crysophyllum mexicanum Brandegee ex Standl.
Pouteria campechiana (Kunth) Baehni
Pouteria durlandii (Standl.) Baehni subsp. *durlandii*
Pouteria aff. *reticulata* (Engl.) Eyma subsp. *reticulata*
Pouteria rhynchocarpa T.D. Penn.
Pouteria sapota (Jacq.) H. Moore et Stearn
\+ *Sideroxylon portoricense* Urb. subsp. *minutiflorum* (Pittier) T.D. Penn.

Solanaceae
\+ *Juanulloa mexicana* (Schltdl.) Miers

Staphylaceae
Turpinia occidentalis (Sw.) G. Don. subsp. *breviflora*

Tiliaceae

Heliocarpus appendiculatus Turcz.
Mortoniodendron guatemalense Standl. et Steyerm.

Ulmaceae
Ampelocera hottlei (Standl.) Standl.
\+ *Celtis iguanaea* (Jacq.) Sarg.

Urticaceae
\+ *Urera caracasana* (Jacq.) Griseb.
Urera elata (Sw.) Griseb.

Verbenaceae
Aegiphila costaricensis Moldenke
Citharexylum affine D. Don

Violaceae
Orthion oblanceolatum Lundell
Rinorea guatemalensis (S. Watson) Barlett

\+= species not present as individuals > 10 cm d.b.h. in the forest plots.