

**Comparative study of the litterfall in a primary and secondary
terra firme forest in the vicinity of Manaus,
State of Amazonas, Brazil***

by

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Abstract

The present study was performed for 23 consecutive months (1974) in two adjacent plots in the Ducke Forest Reserve ($02^{\circ}35' S$; $60^{\circ}00' W$), Manaus-Itacoatiara road, km 26, to the NE of Manaus, Amazonas. A brief description of the vegetation of both inventoried study plots is presented, including all trees alive measuring 20 cm or more in diameter at the breast height (DBH). This primary terra firme forest is very similar in its structure, physiognomy and floristic composition to the forest that generally is found surrounding Manaus. Its basal area was estimated in about $27 \text{ m}^2 \text{ ha}^{-1}$ and its bole volume in about $230 \text{ m}^3 \text{ ha}^{-1}$. Floristically the vegetation is very heterogeneous with no genera or species truly dominant. The Leguminosae *sensu lato* is the richest family in species and abundance followed by the Sapotaceae and Lecythidaceae. *Sclerolobium melanocarpum* DUCKE (about 24 %) and *Enterolobium schomburgkii* BENTH. (about 22 %) were the most important species with their respective Species Importance Values. The secondary vegetation originated from a primary forest that was cut 14 years ago and unburned. It mainly contained *Cecropia sciadophylla* MART. (about 115 %), *Vismia cayennensis* (JACQ.) PERS. (about 42 %) and *Tapirira guianensis* AUBL. (about 32 %), which are typical floristic elements of the late secondary vegetation. They compete only temporarily with other representative species of Amazon flora. The basal area was estimated in about $10 \text{ m}^2 \text{ ha}^{-1}$ and the bole volume in $62 \text{ m}^3 \text{ ha}^{-1}$. In the present study, it was found that leaves are the most prominent fraction of the litterfall in both communities and that there is relatively little interannual variation, particularly of the leaf-fall and the of total litter fall. Great variation of the annual amounts of non-leaf-litter was observed, which shows a clear seasonality of the leaf-fall. The fall of the other fine litter fractions shows a peaking which falls in the leaf-fall peak.

*Dedicated to Prof. Dr. Harald Sioli on the occasion of his 90th anniversary.

Comparing the available data from the two types of vegetation studied, it was observed that both the total litterfall and the leaf-fall are obviously greater in the secondary forest. The apparent seasonality of the litterfall and particularly of the leaf-fall in the terra firme forest of Manaus area, both primary and secondary vegetation, agree well with the both previous results. The leaf-fall is generally greater in months that received relatively little precipitation. This study registered the maximum leaf-fall in both vegetation types in November and the flower-fruit fraction was greater in the months of maximum leaf-fall. An hypothesis is tested that the monthly leaf-fall is correlated with the monthly evaporation expressed as percent of the monthly rainfall. The annual average litterfall in primary forest was $7.9 \text{ t ha}^{-1} \text{ yr}^{-1}$, consisting of 6.0 t of leaves and 1.6 t of non-leaf matter (woody material, flowers, fruits etc.) and in the secondary vegetation was $9.0 \text{ t ha}^{-1} \text{ yr}^{-1}$, being 7.5 t ha^{-1} of leaves and 1.6 t of non-leaf matter. The annual average percentage of fine litter fractions in the primary forest was 78.4 % of leaves, 15.7 % of woody matter and 5.9 % of flower+fruits and in the secondary vegetation was 81.7 % of leaves, 10.5 % of woody matter and 7.8 % of flowers+fruits.

Keywords: Flora, floristic composition, saisonality, litter, phytosociology, Amazon.

Resumo

Realizou-se o presente estudo em dois tipos de vegetação próximos um do outro, localizados na Reserva Florestal Ducke ($2^{\circ}25'S$, $60^{\circ}00'W$) e na estrada Manaus-Itacoatiara, km 26, a NE da cidade de Manaus, Amazonas, os quais estavam assentados sobre solos classificados como latosolo amarelo de textura muito pesada. Essas vegetações consistiam respectivamente em uma floresta densa de terra firme e em uma mata secundária nunca queimada, com 14 anos de idade. Uma curta descrição dessas vegetações foi apresentada, baseada especialmente em dados obtidos dos inventários dessas duas comunidades, abrangendo todas as árvores vivas de 20 cm ou mais de diâmetro acima do peito (DAP). A área de 0,5 ha de floresta primária demarcada para o presente estudo era muito semelhante às outras florestas de terra firme que ocorrem nas cercanias de Manaus. A área amostrada de 0,35 ha de vegetação secundária em sucessão tardia tinha inúmeras espécies próprias desse tipo de vegetação, mas como nunca havia sido queimada, apresentava também um número relativamente grande de outras espécies próprias da flora amazônica em sua composição. Floristicamente, a floresta primária era muito heterogênea, sem um gênero ou espécie propriamente dominante, sendo, no entanto, as Leguminosas s.l., com suas três famílias: Fabaceae, Caesalpiniaceae e Mimosaceae, o grupo taxonômico mais importante pelo número de espécies e indivíduos seguidas das Sapotáceas e Lecitidáceas. Pelo Valor de Importância das Espécies, *Sclerolobium melanocarpum* Ducke (aprox. 24 %) e *Enterolobium schomburgkii* Benth. (aprox. 22 %) foram as espécies que mais se realçaram dentre as 74 espécies encontradas na área inventariada (0,35 ha). A vegetação secundária se distinguiu claramente pela dominância de *Cecropia sciadophylla* Mart. (aprox. 115 %), *Vismia cayennensis* (Jacq.) Pers. (aprox. 42 %) e *Tapirira guianensis* Aubl. (aprox. 32 %), espécies próprias da vegetação em sucessão tardia, na ocasião em vantajosa competição temporária com espécies típicas da flora amazônica. A área basal foi calculada em cerca de $10 \text{ m}^2 \text{ ha}^{-1}$ e o volume de madeira em cerca de $62 \text{ m}^3 \text{ ha}^{-1}$. No estudo do ciclo biogeocímico das duas comunidades durante 2 anos seguidos (1974-75) e com coletas semanais, verificou-se que o folhado foi a fração mais importante de uma serapilheira em ambas as vegetações estudadas, sendo a variação interanual relativamente pequena. Verificou-se, também, que houve uma maior variação da produção anual de serapilheiras sem as folhas, que mostrou uma clara periodicidade anual da produção de folhado enquanto a produção de outros componentes da serapilheira pode mostrar um pico que cai no pico da produção de folhado. A aparente periodicidade anual da produção de serapilheira e em especial de folhado na floresta de terra firme de Manaus é muito semelhante ao que se tem obtido em outros estudos anteriores. A maior produção de folhado em ambas as vegetações estudadas se deu em geral nos meses de pouca chuva (estaçao seca), culminando em novembro, enquanto a fração flor+fruto tendeu para maior produção nos meses da queda máxima das folhas. Levantou-se uma hipótese de que a queda mensal de folhagem está correlacionada com a evaporação mensal expressa em porcentagem de chuva,

mensal. Observou-se também que a produção total de serapilheira e de folhado foi maior na vegetação secundária que na floresta primária. A produção média anual de serapilheira na floresta primária foi de $7.9 \text{ t ha}^{-1} \text{ ano}^{-1}$, sendo 6,0 t de folhado e 1,6 t de outras matérias (material lenhoso, flores, frutos etc.) e na vegetação secundária, a produção média anual foi de $9.0 \text{ t ha}^{-1} \text{ ano}^{-1}$, consistindo em 7,5 t ha⁻¹ de folhado e 1,6 t de outras frações de serapilheira. A percentagem anual média das frações de serapilheira foi de 78,4 % de folhado, 15,7 % de material lenhoso e 5,9 % de flores+frutos na floresta primária e de 81,7 % de folhado, 10,5 % de material lenhoso e 7,8 % de flores+frutos na vegetação secundária.

Introduction

Terra firme forest is the predominant woody vegetation in the Amazonian region where it occupies the dry ground above the river levels (PIRES 1973; PRANCE 1978). Terra firme forest NE of Manaus area has been studied for its floristic composition by LECHTHALER (1956), SOARES (1957, 1961), TAKEUCHI (1960), AUBRÉVILLE (1961), RODRIGUES (1964, 1967), ARAUJO (1967), PRANCE et al. (1976), SOÁREZ (1984), RANKIN-DE-MÉRONA et al. (1992), TELLO (1995), RIBEIRO et al. (1999), AMARAL et al. (2000) and for its biomass and nutrient contents by KLINGE & RODRIGUES (1973, 1974), KLINGE (1976), FITTKAU & KLINGE (1973), GOLLEY et al. (1980).

The dominant plant family of this forest type is, in terms of biomass, the Leguminosae s.l. (KLINGE 1973a), no genus or species of this or any other plant family being dominant *per se*.

According to the distribution of precipitation in Manaus area (SALATI et al. 1978; HERRERA et al. 1978), during the dry season individual trees of the terra firme forest of Manaus area may be leafless for some days. The canopy of the forest, however, is never completely leafless. Terra firme forest of Manaus area is therefore evergreen forest.

The litterfall in some adjacent plots of primary terra firme forest in Manaus area has already been studied by KLINGE & RODRIGUES (1968), STARK (1971), KLINGE (1977a) and FRANKEN et al. (1979).

Investigations on litter production and nutrient cycles in some other Amazonian communities are available in STARK (1971), KLINGE (1977a, b), FURCH & KLINGE (1978), ADIS et al. (1979), FRANKEN (1979), FRANKEN et al. (1979), HERRERA (1981), KLINGE et al. (1983), KLINGE 1985.

The present study was performed in order to compare the litterfall in the undisturbed equatorial rainforest with secondary vegetation which was 14 years old when the litterfall studied was started early in 1974. The study plots, both of the primary and the secondary vegetation, are located at Ducke Forest Reserve ($2^{\circ}25'S$, $60^{\circ}00'W$), near Manaus, on the Manaus-Itacoatiara highway, Km 26.

Geologically, this area pertains to Barrier series, Manaus formation, Tertiary-Pliocene, and the soil where this study occurred is classified in yellow latosol, with a very heavy texture (FALESI et al. 1969).

Litterfall collection technique

Ten litter traps of size 50 x 50 cm (0.25 m²) each were installed in a 0.5 ha rectangular plot of primary forest and 14 litter traps of equal size were set out in 0.35 ha rectangular plot of secondary vegetation. The traps were emptied weekly from March 1974 until January 1976. The samples were air-dried and shipped to Plön.

The samples were then divided into leaves, fruits plus flowers, and the remaining woody material consisting mainly of twigs and bark fragments. The 4 to 5 weekly leaf-litter samples from the 10 and 14 litter traps, respectively, corresponding to each of the 23 consecutive months, were lumped, except for 3 individual months (November 1974, April and October 1975). The 10 to 14 litter monthly samples were kept separately in order to study the spatial variation of the leaf-fall in both types of vegetation.

The samples of the two other fractions were separately lumped per month. Their monthly dry weights were converted into g m⁻² 30 days⁻¹, as were the monthly dry weights of the leaf-litter samples. For ulterior chemical analysis, the monthly samples of all fractions were lumped, separately for each fraction, up to 5 consecutive months in order to reduce the load of analytical work, ground in a commercial mill, dried at 105 °C and stored in sealed plastic bags.

Family Importance Values (FIV) and Species Importance Values (SIV) were calculated based in statistical formula adoted by MORI et al. (1983), including the sum of relative abundance, relative frequency, relative basal area and relative bole volume of all living woody plants measured on the study sites.

Vegetation

Floristic cover of the primary terra firme forest at Ducke Forest Reserve

This terra firme (upland non-flooded ground) primary forest is a typical and complex dense ombrophilous forest of Central Amazonia on yellow latosol soil with a very heavy texture. The mean height of the main canopy is about 25-28 m. Floristically and physiognomically it may be considered the same forest bioma type generally found surrounding Manaus, already studied before by LECHTHALER (1956), SOARES (1957), TAKEUCHI (1960), RODRIGUES (1966), KLINGE & RODRIGUES (1968), PRANCE et al. (1976), RANKIN-DE-MERONA et al. (1992), AMARAL et al. (2000) and others.

In a 0.5 ha plot subdivided into 5 rectangular 0.1 ha subplots, 119 trees (about 238 ha⁻¹) with a diameter of ≥20 cm at breast height (DBH) were recorded, representing 74 species (Table 2), 49 genera and 27 families (Table 1). Leguminosae s.l. were the most important by the number of species: Caesalpiniaceae and Mimosaceae with five species each and Fabaceae with three species, followed by Sapotaceae with thirteen species. The families Sapotaceae with thirteen species and nineteen individuals sampled represented the most Family Importance Value (FIV) with 56 %. In decreasing order of FIV (see Table 1) that last family was followed by Caesalpiniaceae (55 %), Lecythidaceae (46 %), Mimosaceae (36 %), Moraceae (28 %) and Lauraceae (26 %). The remaining 21 families had a low FIV which ranked between 15 and 2 %. No genera or species were considered dominant or truely so in the inventoried forest. Forty six species (see Table 2) were only represented by a single individual. The diameter of the most trees ranged from 20 to 54 cm, rare over this size as observed in some single individuals of

Sclerolobium melanocarpum DUCKE (Caesalpiniaceae, 94 cm DBH) *Parkia multijuga* BENTH. (Mimosaceae, 82 cm DBH) and *Enterolobium schomburgkii* BENTH. (Mimosaceae, 80 cm DBH), *Minquartia guianensis* AUBL. (76 cm DBH) and *Chimarrhis barbata* (DUCKE) BREMEK. (72 cm DBH). The most abundant species sampled were *Croton lanjouwensis* JABLONSKI, *Tachigali paniculatum* DUCKE, *Corythophora alta* KNUTH, *Chrysophyllum pomiferum* (EYMA) T.D. PENN., *Trichilia septentrionalis* DC. The total basal area was about 27 m² ha⁻¹ and the total bole volume was about 230 m³ ha⁻¹. Species with highest bole volumes per hectare were found mainly in *Enterolobium schomburgkii* (about 24 m³), *Sclerolobium melanocarum* (about 22 m³), *Parkia multijuga* (about 14 m³) and in *Minquartia guianensis* (12 m³). The highest basal area per species was 1.10 m² for *Sclerolobium melanocarpum* (Caesalpiniaceae), 0.92 m² for *Enterolobium schomburgkii* (Mimosaceae) and 0.52 m² for *Parkia multijuga* (Mimosaceae). The most important species, with their respectives Species Importance Values (SIV), were: *Sclerolobium melanocarpum* (23%) and *Enterolobium schomburgkii* (21%). The remaining species had a low SIV which varied between 13 and 2 %. The family Arecaceae was present in the study site with many palms not inventoried such as *Astrocaryum acaule* MART., *Astrocaryum sciophilum* (MIQ.) PULLE, *Attalea attaleoides* (BARB. RODR.) WESS. BOER, *Attalea microcarpa* MART. and *Oenocarpus bacaba* MART. (immature), *Oenocarpus minor* MART. (immature). Many lianas were also seen in the area, but not counted, including *Desmoncus polyacanthos* MART., *Abuta* spp., various species of Bignoniaceae, Dilleniaceae, Convolvulaceae, Araceae (*Philodendron* spp., *Heteropsis* sp.), Fabaceae (*Machaerium* spp., *Derris* spp.). Mimosaceae (*Piptadenia minutiflora* DUCKE, *Mimosa* spp., *Acacia* spp.) etc., and in the understory a large abundance of shrubs, small trees, seedlings as *Gouania glabra* AUBL., *Zygia racemosa* (DUCKE) BARNEBY & J.W. GRIMES, *Scleronema micranthum* DUCKE, *Eperua glabriflora* (DUCKE) R.S. COWAN, *Piper* sp., *Lacistema grandiflorum* (BERG) RUSBY, *Psychotria* sp., *Palicourea* spp., *Miconia* spp., *Rinorea racemosa* (MART.) KUNTZE, *Cassipourea guianensis* AUBL. and herbs of the families Marantaceae (*Ischnosiphon* sp. and *Monotagma* sp.), Zingiberaceae (*Renealmia* sp.), Costaceae (*Costus* sp.), Heliconiaceae (*Heliconia psittacorum* L.f.) etc. Epiphytes were very rare.

Table 1: Plant families in a 0,5 ha plot of primary terra firme forest at Reserva Florestal Ducke near Manaus, with trees DBH ≥20 cm. No. spp. = number of species; Rel. no. of spp. = relative number of species; Rel. B.A. = relative basal area; FIV = family importance value.

Family	No. spp.	No. of trees	Rel. no. of spp. (%)	Rel. no of trees (%)	Rel. B.A. (%)	Rel. bole vol. (%)	FIV
Sapotaceae	13	19	17.57	15.96	14.47	8.38	56.38
Caesalpiniaceae	5	14	6.76	11.76	18.35	18.07	54.94
Lecythidaceae	7	13	9.45	10.92	13.47	12.46	46.30
Mimosaceae	5	8	6.76	6.72	3.09	19.02	35.59
Moraceae	6	8	8.11	6.72	7.40	6.22	28.45
Lauraceae	6	8	8.11	6.72	6.52	4.81	26.16
Euphorbiaceae	2	7	2.70	5.88	4.45	2.44	15.47
Fabaceae	3	4	4.05	3.36	3.63	3.71	14.75
Meliaceae	3	6	4.05	5.04	2.56	1.40	13.05
Olacaceae	2	3	2.70	2.52	5.29	1.23	11.74
Elaeocarpaceae	3	3	4.05	2.52	2.43	2.06	11.06
Memecylaceae	2	3	2.70	2.52	0.28	3.02	8.52
Melastomataceae	2	2	2.70	1.68	3.53	0.46	8.37
Bombacaceae	1	3	1.35	2.52	2.50	1.92	8.29
Rubiaceae	1	2	1.35	1.68	0.87	4.25	8.15
Anacardiaceae	1	1	1.35	0.84	2.61	2.80	7.60
Apocynaceae	2	2	2.70	1.68	0.92	1.95	7.25
Celastraceae	1	1	1.35	0.84	1.48	1.72	5.39
Annonaceae	1	2	1.35	1.68	1.31	0.79	5.13
Vochysiaceae	1	1	1.35	0.84	1.19	1.38	4.76
Myrtaceae	1	2	1.35	1.68	0.70	0.29	4.02
Chrysobalanaceae	1	2	1.35	1.68	0.65	0.30	3.98
Nyctaginaceae	1	1	1.35	0.84	0.80	0.43	3.42
Myristicaceae	1	1	1.35	0.84	0.61	0.33	3.13
Rhizophoraceae	1	1	1.35	0.84	0.33	0.20	2.72
Cecropiaceae	1	1	1.35	0.84	0.28	0.19	2.66
Sapindaceae	1	1	1.35	0.84	0.28	0.17	2.64
Total	74	119	99.96	99.96	100	100	399.92
Total hectare⁻¹	-	238	99.96	99.96	100	100	399.92

Table 2: Plant species composition in a 0.5 ha plot of primary terra firme forest at Ducke Forest Reserve near Manaus, with trees DBH ≥20 cm. Rel. freq. = relative frequency; Rel. B.A. = relative basal area; SIV = species importance value.

Species	Family	No. of trees	Rel. no. of trees (%)	Rel. freq. (%)	Rel. B.A. (%)	Rel. vol. (%)	SIV (%)
<i>Sclerolobium melanocarpum</i> DUCKE	Caesalpiniaceae	3	2.52	2.85	8.02	10.07	23.46
<i>Enterolobium schomburgkii</i> BENTH.	Mimosaceae	2	1.68	1.90	6.71	11.24	21.53
<i>Minquartia guianensis</i> AUBL.	Olacaceae	2	1.68	1.90	4.28	5.04	12.90
<i>Tachigali paniculata</i> DUCKE	Caesalpiniaceae	4	3.36	3.80	2.80	2.85	12.81
<i>Parkia multijuga</i> BENTH.	Mimosaceae	1	0.84	0.95	3.82	6.42	12.03
<i>Corythophora alta</i> KNUTH	Lecythidaceae	4	3.36	2.85	2.84	2.35	11.40
<i>Pouteria petiolata</i> T.D. PENN.	Sapotaceae	3	2.52	2.85	4.45	1.28	11.10
<i>Eperua glabriflora</i> (DUCKE) S.R. COWAN	Caesalpiniaceae	3	2.52	2.85	2.40	2.69	10.46
<i>Corythophora rimosa</i> W. RODR. subsp. <i>rimosa</i>	Lecythidaceae	2	1.68	1.90	3.00	3.78	10.36
<i>Chimarrhis barbata</i> (DUCKE) BREMEK.	Rubiaceae	2	1.68	0.95	3.40	4.00	10.03
<i>Croton lanjouwensis</i> JABLONSKY	Euphorbiaceae	5	4.20	1.90	2.35	1.21	9.66
<i>Chrysophyllum pomiferum</i> T.D. PENN.	Sapotaceae	4	3.36	2.85	1.87	1.19	9.27
<i>Eschweilera grandiflora</i> SANDWIITH	Lecythidaceae	2	1.68	1.90	2.46	2.99	9.03
<i>Scleronema micranthum</i> DUCKE	Bombacaceae	3	2.52	1.90	2.18	1.82	8.42
<i>Tachigali myrmecophylla</i> DUCKE	Caesalpiniaceae	3	2.52	2.85	1.57	1.30	8.24
<i>Trichilia septentrionalis</i> DC.	Meliaceae	4	3.36	1.90	1.24	0.68	7.18
<i>Astronium lecointei</i> DUCKE	Anacardiaceae	1	0.84	0.95	2.27	2.66	6.72
<i>Platymiscium duckei</i> HUBER	Fabaceae	1	0.84	0.95	1.94	2.59	6.32
<i>Brosimum rubescens</i> TAUB.	Moraceae	3	2.52	1.90	1.00	0.51	5.93
<i>Eschweilera coriacea</i> S.A. MORI	Lecythidaceae	2	1.68	1.90	1.35	0.84	5.77
<i>Mouriri angulicosta</i> MORLEY	Memecylaceae	1	0.84	0.95	1.60	2.10	5.49
<i>Guatteria scytophylla</i> DIELS	Annonaceae	2	1.68	1.90	1.16	0.75	5.49
<i>Ocotea</i> sp.	Lauraceae	2	1.68	1.90	0.91	1.00	5.49
<i>Pogonophora schomburgkiana</i> MIERS	Euphorbiaceae	2	1.68	0.95	1.54	1.11	5.28
<i>Micropholis guyanensis</i> (A.DC.) PIERRE	Sapotaceae	2	1.68	0.95	1.22	1.35	5.20
<i>Mouriri huberi</i> COGN.	Memecylaceae	2	1.68	1.90	0.84	0.77	5.19
<i>Brosimum parinarioides</i> DUCKE subsp. <i>parinarioides</i>	Moraceae	1	0.84	0.95	1.50	1.86	5.15
<i>Clarisia racemosa</i> RUIZ & PAV.	Moraceae	1	0.84	0.95	1.55	1.80	5.14
<i>Mezilaurus duckei</i> VAN DER WERFF	Lauraceae	1	0.84	0.95	1.89	1.26	4.94
<i>Ocotea minor</i> VICENTINI	Lauraceae	1	0.84	0.95	1.44	1.57	4.80
<i>Gouipa glabra</i> AUBL.	Celastraceae	1	0.84	0.95	1.32	1.63	4.74
<i>Swartzia recurva</i> POEPP. & ENDL.	Fabaceae	2	1.68	1.90	0.66	0.44	4.68
<i>Ficus paraensis</i> (MIQ.) MIQ.	Moraceae	1	0.84	0.95	1.77	1.04	4.60
<i>Myrciaria</i> sp.	Myrtaceae	2	1.68	1.90	0.61	0.27	4.46
<i>Ocotea canaliculata</i> MEZ	Lauraceae	2	1.68	1.90	0.63	0.24	4.45
<i>Licania octandra</i> subsp. <i>pallida</i> PRANCE	Chrysobalanaceae	2	1.68	1.90	0.57	0.28	4.43

Table 2: Continuation.

Species	Family	No. of trees	Rel. no. of trees (%)	Rel. freq. (%)	Rel. B.A. (%)	Rel. bole vol. (%)	SIV
<i>Pouteria eugeniifolia</i> BAEHNI	Sapotaceae	1	0.84	0.95	1.13	1.23	4.15
<i>Erisma</i> sp.	Vochysiaceae	1	0.84	0.95	1.05	1.30	4.14
<i>Aspidosperma marcgravianum</i> WOODSON	Apocynaceae	1	0.84	0.95	0.77	1.53	4.09
<i>Peltogyne catingae</i> subsp. <i>glabra</i>							
M.F. SILVA	Caesalpiniaceae	1	0.84	0.95	1.30	0.87	3.96
<i>Zygia racemosa</i> BARNEBY & GRIMES	Mimosaceae	2	1.68	0.95	0.66	0.39	3.68
<i>Pithecellobium</i> sp.	Mimosaceae	2	1.68	0.95	0.57	0.45	3.65
<i>Sloanea floribunda</i> BENTH.	Elaeocarpaceae	1	0.84	0.95	1.07	0.71	3.57
<i>Eschweilera collina</i> EYMA	Lecythidaceae	1	0.84	0.95	0.76	0.96	3.51
<i>Sloanea latifolia</i> (RICH.) K. SCHUM.	Elaeocarpaceae	1	0.84	0.95	0.70	0.88	3.37
<i>Pouteria manaosensis</i> T.D. PENN.	Sapotaceae	1	0.84	0.95	0.64	0.80	3.23
<i>Lecythis gracieana</i> S.A. MORI	Lecythidaceae	1	0.84	0.95	0.80	0.59	3.18
<i>Pouteria guianensis</i> AUBL.	Sapotaceae	1	0.84	0.95	0.71	0.59	3.09
<i>Trichilia pallida</i> SW.	Meliaceae	1	0.84	0.95	0.68	0.45	2.92
<i>Neea</i> sp.	Nyctaginaceae	1	0.84	0.95	0.71	0.41	2.91
<i>Geissospermum argenteum</i> WOODSON	Apocynaceae	1	0.84	0.95	0.77	0.32	2.88
<i>Andira parvifolia</i> DUCKE	Fabaceae	1	0.84	0.95	0.58	0.48	2.85
<i>Pradosia schomburgkii</i> (A.DC.)							
CRONQUIST subsp. <i>schomburgkii</i>	Sapotaceae	1	0.84	0.95	0.77	0.20	2.76
<i>Eschweilera tessmannii</i> KNUTH	Lecythidaceae	1	0.84	0.95	0.53	0.35	2.67
<i>Virola michelii</i> HECKEL	Myristicaceae	1	0.84	0.95	0.54	0.31	2.64
<i>Pouteria caimita</i> (RUIZ & PAV.) RADLK.	Sapotaceae	1	0.84	0.95	0.37	0.37	2.53
<i>Sloanea guianensis</i> BENTH.	Elaeocarpaceae	1	0.84	0.95	0.37	0.37	2.53
<i>Stryphnodendron guianense</i> subsp. <i>floribundum</i> FORERO	Mimosaceae	1	0.84	0.95	0.44	0.20	2.43
<i>Naucleopsis glabra</i> SPRUCE ex BAILL.	Moraceae	1	0.84	0.95	0.40	0.20	2.39
<i>Pouteria retinervis</i> T.D. PENN.	Sapotaceae	1	0.84	0.95	0.42	0.17	2.38
<i>Licaria chrysophylla</i> KOSTERM.	Lauraceae	1	0.84	0.95	0.29	0.29	2.37
<i>Pouteria</i> sp.	Sapotaceae	1	0.84	0.95	0.29	0.28	2.36
<i>Miconia regelii</i> COGN.	Melastomataceae	1	0.84	0.95	0.33	0.24	2.36
<i>Pourouma palmata</i> POEPP. & ENDL.	Cecropiaceae	1	0.84	0.95	0.25	0.31	2.35
<i>Mezilaurus synandra</i> KOSTERM.	Lauraceae	1	0.84	0.95	0.33	0.22	2.34
<i>Miconia argyrophylla</i> subsp. <i>gracilis</i> WURDACK	Melastomataceae	1	0.84	0.95	0.33	0.19	2.31
<i>Trichilia micrantha</i> BENTH.	Meliaceae	1	0.84	0.95	0.30	0.20	2.29
<i>Cassipourea peruviana</i> ALSTON	Rhizophoraceae	1	0.84	0.95	0.29	0.19	2.27
<i>Chrysophyllum prieurii</i> A.DC.	Sapotaceae	1	0.84	0.95	0.32	0.16	2.27
<i>Aptandra tubicina</i> (POEPP.) BENTH. ex MIERS	Olacaceae	1	0.84	0.95	0.33	0.14	2.26

Table 2: Continuation.

Species	Family	No. of trees	Rel. no. of trees (%)	Rel. freq. (%)	Rel. B.A. (%)	Rel. bole vol. (%)	SIV
<i>Micropholis venulosa</i> (MART. ex EICHL.) PIERRE	Sapotaceae	1	0.84	0.95	0.29	0.17	2.25
<i>Trymatococcus amazonicus</i> POEPP. & ENDL.	Moraceae	1	0.84	0.95	0.25	0.18	2.22
<i>Talisia cupularis</i> RADLK.	Sapindaceae	1	0.84	0.95	0.25	0.16	2.20
<i>Pouteria cladantha</i> SANDWITH	Sapotaceae	1	0.84	0.95	0.25	0.16	2.20
Total		119	99.96	99.75	100	100	399.71

Secondary vegetation including trees with DBH ≥ 20 cm at Ducke Forest Reserve
The chosen plot was situated about 50 m behind and away from the Metereological Station at Ducke Forest Reserve and in front and adjacent to the primary forest plot. Its soil is classified in yellow latosol with a very heavy texture according to FALESI & al. (1969).

The original forest was cut down and the site cleaned without use of fire and the vegetation was left in natural regeneration (ARAUJO, n.d.). The composition of this same vegetation is also briefly treated by RODRIGUES (1995), ARAUJO (n.d.) and AGUIAR SOBRINHO (n.d.). When this litterfall study started, its vegetation was a late secondary forest 14 years old. The size of this study plot was of 70 x 50 m (0.35 ha) subdivided into 10 rectangular 50 x 7 m subplots. Seventy one trees (about 202 trees ha⁻¹) with diameter 20 cm or more at breast height were found, which represented 20 species (Table 4), 15 genera and 13 families (Table 3). Mimosaceae were also the most important in number of species (4 species). Cecropiaceae with a highest percentage of Family Importance Value (134 %) were the most prominent family followed by behind by the Mimosaceae (70 %) and other families in the site. *Cecropia sciadophylla* MART. was dominant with 22 samples, followed by *Vismia cayennensis* (JACQ.) PERS. and *Tapirira guianensis* AUBL. These species, typical floristic elements of late secondary vegetation, were in temporary competition with other representative primary species of the Amazonian flora (see Table 4). Eight species were only represented by a single sample. The diameter of the trees varied from 20 to 30 cm DBH, trees over this diameter were rare: a single sample of *Inga thibaudiana* DC. (44 cm), *I. paraensis* DUCKE (35 cm) and *Cecropia sciadophylla* MART. (33 cm). The tallest trees in the main canopy of this vegetation ranged between 25 to 28 m, as observed in a single sample of *Vismia cayennensis* (28 m), *Tapirira guianensis* AUBL. (27 m), *Byrsonima duckeanaum*

W.A. ANDERSON (26 m) and of *Inga thibaudiana* DC. (25 m). Total basal area was 3.59 m² (10 m² ha⁻¹) and total bole volume was 21.76 m³ (62 m³ ha⁻¹). Species with highest bole volumes per hectare were calculated for *Cecropia sciadophylla* (about 22 m³), *Vismia cayennensis* (about 8 m³), *Tapirira guianensis* (about 6 m³), *Cecropia latifolia* AUBL. (about 4 m³) and *Aegiphyllea intermedia* MOLDENKE (about 3 m³). Based on the study of RODRIGUES & SILVA (1995) and RODRIGUES et al. (unpubl.), with plants of ≥2 m height, some of the most important species of the understory strata are *Siparuna guianensis* AUBL. (Siparunaceae), *Mabea speciosa* MÜLL. ARG. (Euphorbiaceae), *Rinorea racemosa* KUNTZE (Violaceae), *Miconia elaeagnoides* COGN. (Melastomataceae), *M. regelii* COGN. (Melastomataceae), *Rudgea fissistipula* MÜLL. ARG. (Rubiaceae), *Casearia* sp. (Flacourtiaceae), *Protium* sp. (Burseraceae), *Pseudima frutescens* (AUBL.) RADLK. (Sapindaceae), *Erythroxylon macrophyllum* Cav. (Erythroxylaceae), *Cordia cf. tachyphylla* MART. (Boraginaceae), *Astrocaryum acaule* MART. (Arecaceae), *Attalea attaleoides* (BARB. RODR.) WESS. BOER (Arecaceae), *Bactris* sp. (Arecaceae). Many species of lianes occur in the area as *Memora flava* (DC.) BUREAU & K. SCHUM. (Bignoniaceae), *Desmoncus polyacanthus* MART. (Arecaceae), *Memora adenophora* SANDWITH (Bignoniaceae), *Arrabidaea trailii* Sprague (Bignoniaceae), *Memora longilinea* A. SAMPAIO (Bignoniaceae), *Combretum laxum* AUBL. (Combretaceae), *Davilla kunthii* A. ST.-HIL. (Dilleniaceae), *Sparathanthelium cf. acreanum* PILG. (Hernandiaceae), *Maripa glabra* CHOISY (Convolvulaceae), *Salacia* spp. (Hippocrateaceae), *Machaerium hoehnianum* DUCKE (Fabaceae), *Strychnos* spp. (Loganiaceae), *Abuta grandifolia* (MART.) SANDWITH (Menispermaceae), *Passiflora auriculata* KUNTH (Passifloraceae), *Bredemeyera* sp. (Polygalaceae), *Paullinia* sp. (Sapindaceae). The species of the ground stratum were represented mainly by *Heliconia acuminata* RICH. (Heliconiaceae), *Ischnosiphon* sp. (Marantaceae), *Monotagma plurispicatum* (KÖRN.) K. SCHULM. (Marantaceae) and *Renealmia floribunda* K. SCHUM. (Zingiberaceae). Epiphytes were very rare or not noted in the area. *Coussapoa* sp. (Cecropiaceae) is a hemiepiphyte rarely present in that area. Many of the forest tree species produced shoots sprouting from stumps as observed in some individuals of *Tapirira guianensis* AUBL., *Pourouma guianensis* AUBL., *Inga thibaudiana* DC., *Inga rubiginosa* (RICH.) DC., *Vismia cayennensis* PERS., *Byrsonima duckeana* W.A. ANDERSON, *Siparuna guianensis* AUBL., *Caryocar villosum* (AUBL.) PERS., *Eschweilera* spp., *Mabea speciosa* MÜLL. ARG. and others.

Table 3: Plant families in a 0.35 ha plot of secondary vegetation at Ducke Forest Reserve near Manaus, with trees DBH ≥20 cm. FIV = family importance value.

Family	No. of spp.	No. of trees	Rel. no. of spp. (%)	Rel. no. of trees (%)	Rel. basal area (%)	Rel. bole volume (%)	FIV
Cecropiaceae	3	27	15	38.57	37.72	43.19	134.48
Mimosaceae	4	11	20	15.71	21.30	13.36	70.37
Clusiaceae	1	7	5	10.00	8.36	12.58	35.94
Malpighiaceae	2	6	10	8.57	8.46	6.92	33.95
Anacardiaceae	1	6	5	8.57	8.77	9.81	32.15
Verbenaceae	1	4	5	5.71	5.00	5.20	20.91
Annonaceae	2	2	10	2.86	2.46	1.60	16.92
Simaroubaceae	1	2	5	2.86	2.61	3.07	13.54
Myristicaceae	1	1	5	1.43	1.25	1.58	9.26
Meliaceae	1	1	5	1.43	1.18	1.36	8.97
Flacourtiaceae	1	1	5	1.43	0.91	0.84	8.18
Sapotaceae	1	1	5	1.43	0.93	0.32	7.68
Burseraceae	1	1	5	1.43	1.05	0.17	7.65
Total	20	70	100	100	100	100	400

Table 4: Plant species composition in a 0.35 ha plot of secondary vegetation with trees DBH ≥ 20 cm preserved at Ducke Forest Reserve near Manaus. SIV = species importance value.

Species	Family	No. of trees	Rel. no. of trees (%)	Rel. freq. (%)	Rel. basal area (%)	Rel. bole volume (%)	SIV
<i>Cecropia sciadophylla</i> MART.	Cecropiaceae	22	30.98	19.60	29.03	35.15	114.76
<i>Vismia cayennensis</i> (JACQ.) PERS.	Clusiaceae	7	9.90	10.90	8.78	12.69	42.27
<i>Tapirira guianensis</i> AUBL.	Anacardiaceae	6	8.45	4.34	8.84	9.84	31.47
<i>Cecropia latifolia</i> AUBL.	Cecropiaceae	5	7.04	6.52	7.60	7.15	28.31
<i>Byrsonima duckeanum</i>							
W.R. ANDERSON	Malpighiaceae	4	5.63	8.69	5.60	5.05	24.97
<i>Aegiphyllea intermedia</i> MOLDENKE	Verbenaceae	4	5.63	8.69	4.96	5.25	24.53
<i>Inga thibaudiana</i> DC.	Mimosaceae	4	5.63	6.52	8.10	3.80	24.05
<i>Inga alba</i> (S.W.) WILLD.	Mimosaceae	3	4.22	4.35	5.68	3.48	17.73
<i>Inga paraensis</i> DUCKE	Mimosaceae	2	2.81	4.35	4.81	4.53	16.50
<i>Simarouba amara</i> AUBL.	Simaroubaceae	2	2.81	4.34	2.59	3.08	12.82
<i>Byrsonima crispa</i> A. JUSS.	Malpighiaceae	2	2.81	2.17	2.77	1.79	9.54
<i>Inga rubiginosa</i> (RICH.) DC.	Mimosaceae	2	2.81	2.17	2.60	1.51	9.09
<i>Iryanthera coriacea</i> DUCKE	Myristicaceae	1	1.41	2.17	1.23	1.57	6.38
<i>Guarea silvatica</i> C. DC.	Meliaceae	1	1.41	2.17	1.17	1.35	6.10
<i>Guatteria olivacea</i> R.E. FRIES	Annonaceae	1	1.41	2.17	1.14	0.99	5.71
<i>Guatteria discolor</i> R.E. FRIES	Annonaceae	1	1.41	2.17	1.30	0.60	5.48
<i>Pourouma guianensis</i> AUBL.	Cecropiaceae	1	1.41	2.17	0.93	0.85	5.36
<i>Laetia procera</i> (POEPP.) EICHLER	Flacourtiaceae	1	1.41	2.17	0.90	0.83	5.31
<i>Pouteria</i> sp.	Sapotaceae	1	1.41	2.17	0.93	0.32	4.83
<i>Trattinickia glaziovii</i> SWART	Burseraceae	1	1.41	2.17	1.04	0.17	4.79
Total		71	100	100	100	100	400

Results and discussion

Total litterfall and its composition by leaves and non-leaf matter.

The litterfall dealt with in this study does not include the fall of big branches and boles. It only comprises the fall of small-sized litter which has been termed fine litterfall (KLINGE 1974).

The total amounts of the litterfall in the years 1974 and 1975 are given in Tables 5 and 6, separately for both the total litterfall and the fractions leaf and non-leaf matter, and for the primary and the secondary vegetation. Table 5 also contains data for the litterfall which had been estimated previously in a different plot of terra firme forest of the Manaus area (KLINGE & RODRIGUES 1968), some 35 km off the present study site.

Table 5: Annual fine litterfall in primary terra firme forests near Manaus (S.D. = standard deviation).

Year	Annual fine litterfall ($t \text{ ha}^{-1} \text{ yr}^{-1}$)			Source
	Leaves	Other fine litter	Total	
1963	6.4	1.5	7.9	KLINGE & RODRIGUES 1968
1964	4.8	1.9	6.7	KLINGE & RODRIGUES 1968
1974	6.1	1.7	7.8	This study
1975	6.7	1.3	7.9	This study
Average	6.0	1.6	7.6	
S.D.	± 0.7	± 0.2	± 0.5	
S.D. in %	± 11.7	± 12.5	± 6.6	

Leaves are the most prominent fraction of the litterfall in both primary and secondary vegetation. There is relatively little interannual variation, particularly of the leaf-fall and the total litterfall. The greatest variation of the annual amounts of non-leaf-litter is also observed in figs. 1 and 2, which show a clear-cut seasonality of the leaf-fall, while the fall of the other fine litter fractions may show a peaking which, if occurring, falls in the leaf-fall peak.

When comparing the data for the primary and the secondary vegetation of the study period March 1974 – January 1976, it is obvious that both the total litterfall and the leaf-fall are greater in the secondary forest. The differences are statistically significant at the level of probability. Since the litterfall and the leaf-fall data have a diagnostic value for the estimation of the productivity of the vegetation (BRAY & GORHAM 1964; JORDAN & MURPHY 1978), the secondary vegetation was more productive during the litterfall study period than the mature primary forest.

Table 6: Annual fine litterfall in the secondary terra firme forest at Ducke Forest Reserve near Manaus
(S.D. = standard deviation).

Annual fine litterfall ($t \text{ ha}^{-1} \text{ yr}^{-1}$)			
Year	Leaves	Other fine litter	Total
1974	7.2	1.4	8.6
1975	7.7	1.7	9.4
Average	7.5	1.6	9.0
S.D.	± 0.3	± 0.2	± 0.6
S.D. in %	± 4.0	± 12.5	± 6.6

Table 7: Annual average percentages of the fine litterfall fractions in different primary terra firme forests and in the secondary vegetation near Manaus (S.D. = standard deviation).

		Annual average percentage			Source
Vegetation	Year	Leaves	Wood	Fruits+flowers	
Primary Forest	Febr.-Dec. 1963	81.0	16.5	2.5	KLINGE & RODRIGUES 1968
	Jan. 1964-Jan. 1965	71.6	20.9	7.5	" " "
	March 1974-Febr. 1975	77.7	12.9	9.4	This study
	Febr. 1975-Jan. 1976	83.4	12.6	4.0	This study
	Average	78.4	15.7	5.9	
	S.D.	± 5.1	± 3.9	± 3.2	
	S.D. in %	± 6.5	± 24.8	± 54.2	
Secondary Forest	March 1974	83.9	7.5	8.6	
	Febr. 1975	79.4	13.5	7.0	
	Average	81.7	10.5	7.8	
	S.D.	± 1.8	± 3.0	± 0.9	
	S.D. in %	± 2.2	± 28.6	± 11.5	

Percentage composition of the litterfall by litter fractions

The annual average percentages of the three fractions of the fine litterfall in both primary and secondary vegetation are given in Table 7.

The interannual and intervegetation variations are relatively small in the case of the leaf fraction. For both other fractions a considerably greater variation between i) the individual years and ii) the primary and secondary vegetation are observed.

For the period July – November 1970 (the dry season) additional litterfall data of the primary terra firme forest are available (KLINGE 1977). They refer to a site immediately adjacent to the one in which the litterfall was studied in 1963 and 1964. Cumulative litterfall data for this period of four individual years are given in table 8 which also presents the percentage composition of the litterfall by the three fractions. While there is a relatively great variation of the total amounts of leaf-fall and total fine litter, there is almost no variation of the leaf percentages which agree well with the respective values of table 7. The variations of the other two fractions are considerably greater, as they are greater in the annual litterfall (Table 7).

Table 8: Cumulative leaf and total litterfall data for primary terra firme forests near Manaus, in the period July-November (dry season); 1 = KLINGE & RODRIGUES (1968); 2 = KLINGE (1977); 3 = this study (S.D. = standard deviation).

Year	Leaves	Total litterfall	Source	$t \text{ ha}^{-1}$			% of total		
				Leaves	Wood	Fruits + flowers	Leaves	Wood	Fruits + flowers
1964	2.8	3.6	1	77.0	20.1	2.9	80.1	14.7	5.1
1970	3.6	5.2	2	80.6	17.6	1.6	80.1	14.7	5.1
1974	3.6	4.7	3	75.4	11.1	13.5	80.1	14.7	5.1
1975	4.5	5.1	3	87.5	10.0	2.5	80.1	14.7	5.1
Average	3.6	4.7		80.1	14.7	5.1	80.1	14.7	5.1
S.D.	± 0.6	± 0.7		± 2.0	± 2.0	± 2.0	± 2.0	± 2.0	± 2.0
S.D. in %	± 16.7	± 14.9		± 2.5	± 13.6	± 39.2	± 2.5	± 13.6	± 39.2

For the months November 1974 and April and October 1975 of the present litterfall study it was possible to calculate the spatial variation of the litterfall, since the respective samples of the leaf-fall in the primary and secondary vegetation were kept separately. These individual months were selected because they are periods of i) low rainfall and high leaf-fall (October, November) or ii) low leaf-fall and high rainfall (April). As expected the variation is much less for the leaf fraction (Table 9). Table 9 also presents data of the spatial variation of the litterfall in April, October and November 1964. For unknown reasons, the variations were generally smaller in 1964.

Table 9: Spatial variation of the litterfall in April, October and November, in both primary and secondary terra firme forests near Manaus.

Month	Year	Litterfall ($\text{g m}^{-2} \text{ month}^{-1}$)					
		Leaves		Wood		Fruits+flowers	
		Average	S.D. (%)	Average	S.D. (%)	Average	S.D. (%)
Primary forest							
April	1964	24.3	17.1	6.5	50.9	3.6	57.3
October	1964	39.7	20.7	4.0	27.9	3.2	67.9
November	1964	30.9	19.2	4.2	42.3	6.0	56.9
Average		31.6	19.0	4.9	40.4	4.3	60.7
November	1974	52.6	33.8	29.7	284.8	6.8	207.7
April	1975	41.6	30.7	10.6	101.5	2.6	98.5
October	1975	87.7	33.5	21.2	79.7	6.1	276.5
Average		60.7	32.7	20.5	155.3	5.2	194.2
Secondary forest							
November	1974	53.5	33.5	1.7	183.7	7.0	128.6
April	1975	51.8	33.9	6.0	79.6	2.4	224.6
October	1975	47.1	29.8	45.2	72.9	8.1	125.5
Average		50.8	32.4	17.6	112.1	5.8	159.6

Seasonality of litterfall

The apparent seasonality of the litterfall and particularly of the leaf-fall in the terra firme forest of Manaus area, both primary and secondary vegetation (Figs. 1 and 2), agree well with both previous results (KLINGE & RODRIGUES 1968) and the results of litterfall studies in different forest types of Manaus area, including forests growing on wet and periodically flooded sites (FRANKEN 1979; FRANKEN et al. 1979; IRMLER & FURCH 1979). Comparing the monthly leaf-fall, it is generally greater in months which received relatively little precipitation. The maximum leaf-fall in both vegetation types occurred in November. The tendency was observed that the fruit + flower fraction is greater in the months of maximum leaf-fall. The same is true for the wood fraction in 1975.

The observations on the seasonality of the litterfall, in connection with the seasonal distribution of the rainfall in the study area, point to the climatic seasonality as the reason for the seasonality of the litterfall. If this supposition is true, then a water stress of the vegetation should occur in the period of low rainfall. Such a water stress can be minimized by the vegetation, by reducing its transpiration through reduction of the transpiring leaf area, i.e. by shedding the leaves in a much greater amount than is observed in the rainy season for which it can be assumed that no water deficit in the soil occurs.

We not have any data proving the existence of water deficit in the soil during the dry season. However, ARAUJO (1970), ALENCAR et al. (1979) and FRANKEN et al. (1979) were able to show for the primary terra firme forest of Manaus area, among others, that a correlation exists between the monthly leaf-fall and the monthly insolation which is involved in producing the water stress of the dry season.

Looking for a parameter which might represent perhaps more directly the low water availability in the soil during the dry season, we have tested the hypothesis that the monthly leaf-fall is correlated with the monthly evaporation expressed as percent of the monthly rainfall. We proceeded in the way that the leaf-fall of a given month was plotted against the evaporation in this month and the preceding one as percent of the cumulative rainfall in both months. The result is presented in fig. 3. The figure shows a statistically significant correlation between the chosen parameters in the sense that the leaf-fall is the greater, the higher the percentage of the precipitation which is evaporated, i.e. the smaller the potential water availability in the soil.

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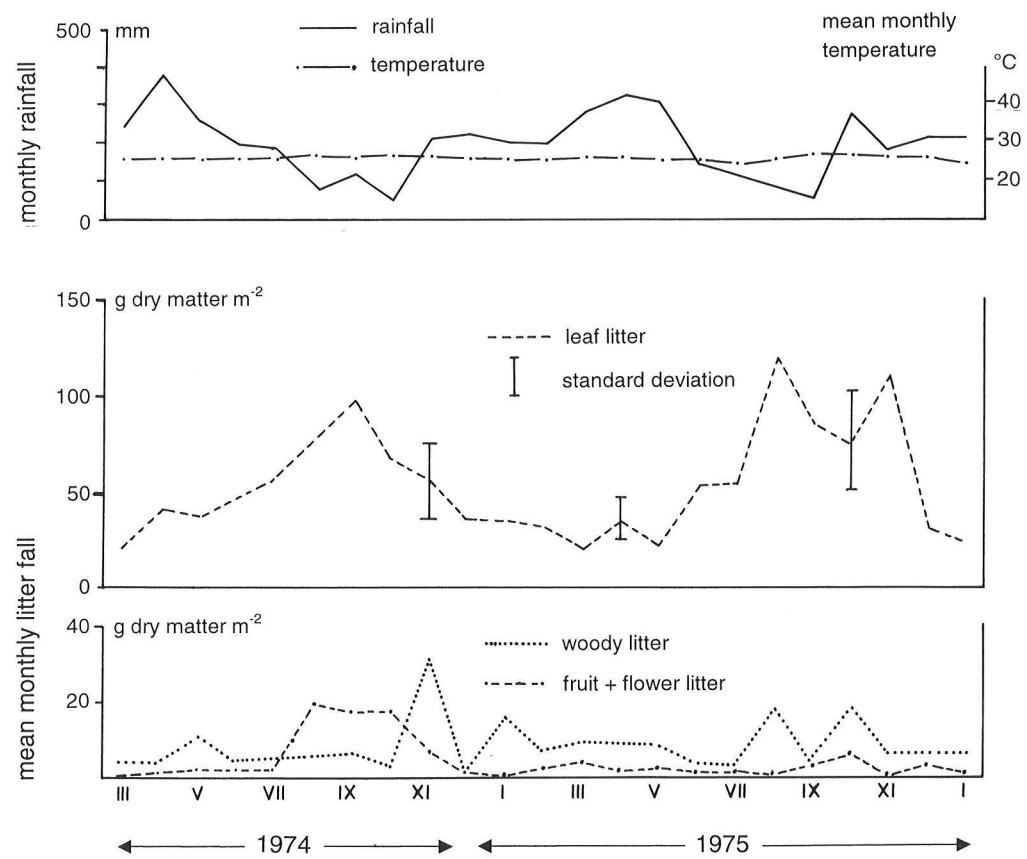


Fig. 1:
Monthly fall of fine litter and precipitation, and mean monthly temperature from March 1974 until January 1976 in the primary terra firme forest near Manaus.

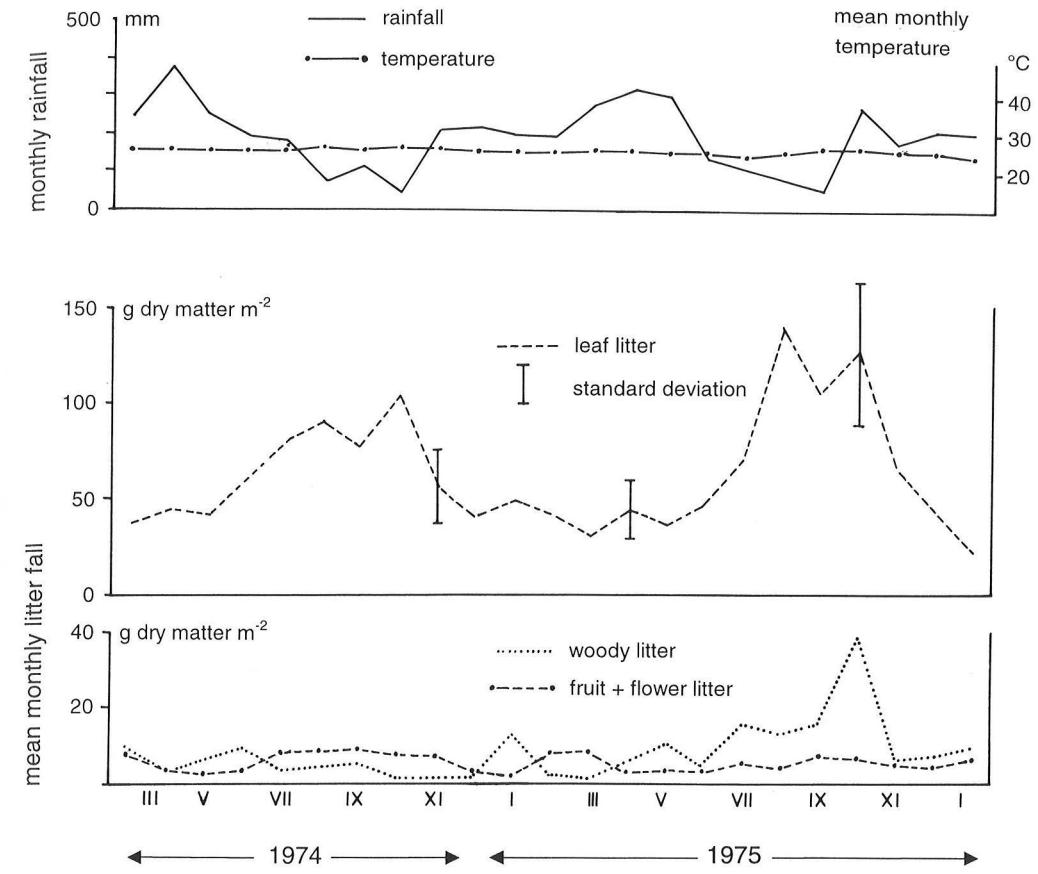


Fig. 2:
Monthly fall of fine litter and precipitation, and mean monthly temperature from March 1974 until January 1976 in the secondary terra firme forest near Manaus.

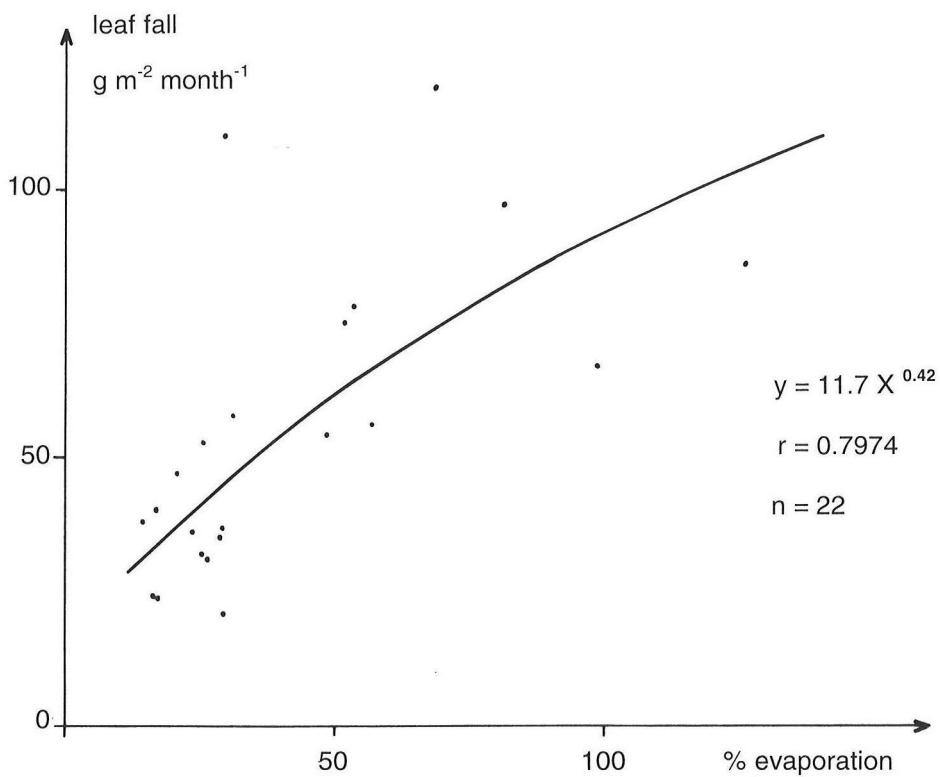


Fig. 3:

Monthly leaf-fall and bi-monthly evaporation (as percent of bi-monthly forest data) in the primary terra firme forest near Manaus (evaporation $\times 100$ precipitation $^{-1}$). See text for futher explanation.