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Da cooperação entre Max-Planck-Institut für Limnologie, Abteilung Tropenökologie, Plön, Alemanha, e Instituto Nacional de Pesquisas da Amazônia, Manaus–Amazonas, Brasil

Preliminary data on nutrient release from decomposing leaf litter in a neotropical rain forest.

by

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Introduction

In a steady state system in a climax community, the rate of production should equal the rate of decay, and nutrient input should balance nutrient output.

It has been pointed out (KIRA & SHIDEI 1967, GREENLAND & KOWAL 1960, RICHARDS 1973, ODUM 1971) that biogeochemical pathways in tropical forests are of the form where the bulk of the mineral nutrients is bound up in the biomass and relatively little occur in the soil. Data for the Amazon rain forest (KLINGE 1976 a) show that this view is also true for the central Amazonian rain forest which was described as a filtering system (KLINGE & FITTKAU 1972). In a climax system of this nature, one would expect that the rate at which nutrients are added through litter fall would equal the rate of nutrient release by decomposition.

Litter includes fine litter (leaves, bud scales, twigs, pieces of bark, small flowers and fruits, etc.), and coarse litter (branches, stems, large and heavy fruits) (KLINGE 1974). Coarse litter represents a high proportion of the total standing crop of litter (KLINGE 1973 a). It decomposes relatively slowly and supplies on the long run the forest with considerable amounts of nutrients. In a short period, however, the relatively small amount of fine litter which decomposes easier and quicker, will release appreciable amounts of nutrients. Considering that it is virtually impossible to study adequately the nature and fate of the coarse litter fall, and considering the relative importance of the fine litter fall and its decomposition for the release of nutrients, the estimation of the coarse litter production and its nutrient release due to decomposition was therefore not considered practicable, in the present study.

This paper attempts to show the rate at which individual elements were released from the leaf litter accumulated on the soil of the seasonal evergreen rain forest near Manaus/Amazonas, and to investigate any differences in the rates of release between individual elements.

Full details of the study site are given in FITTKAU & KLINGE (1973). The vegetation in the plot was inventoried and sampled for the determination of structure and phytomass (KLINGE & RODRIGUES 1971, 1973, 1974, KLINGE 1973 a, 1973 b, 1973 c, 1976 b, KLINGE et al. 1975). Fine litter fall in a neighbouring stand of comparable composition and structure had been measured previously during two consecutive years (KLINGE & RODRIGUES 1968).

Material and methods

A method of litter sampling was devised whereby the amount of fine litter produced, and the amount decomposed during the sampling period could be calculated. Fine litter fall (P) was measured by regularly collecting litter from 10 litter traps of size 0.25 m^2 each. A number of 10 traps of that size was found to be sufficient to give an acceptable average of fine litter production in Amazon rain forests (KLINGE 1976 c, KLINGE & PIRES, in preparation). The traps were spaced at regular intervals around a 50 x 50 m plot in the forest during the dry season from July 6 to November 10, 1970. The plot was choosen at a site where structure and composition of the forest could be considered typical for the area which had been inventoried previously by RODRIGUES (1967). The traps were emptied weekly to keep the loss of litter weight within acceptable limits (KIRITA & HOZUMI 1969). In order to assess changes in the standing crop of fine litter during this period, the biomass of the fine litter (B_1) was estimated on June 17, using a metal frame 50 x 50 cm which was pressed on the soil surface, at 9 of the 10 litter fall sampling sites. All litter material inside the frame was carefully removed. It was impossible to start the sampling of both fine litter fall and fine litter at the same time, since the litter traps arrived late at the forest camp. There is an unfortunate non-coincidence by 3 weeks of the start of litter fall measurement and first harvest of standing crop of litter. On November 9 the biomass sampling was repeated in 4 quadrats immediately adjacent to the June sampling quadrats (B_2), and in 2 additional localities. The amount of decomposition during this period (D) is equal to $P + B_1 - B_2$.

Litter samples were pre-dried in the forest camp and oven-dried in the laboratory of Instituto Nacional de Pesquisas da Amazônia (I.N.P.A.) at Manaus during the weekend following each sampling data. Leaf matter, flowers and fruits, and woody matter in the samples were carefully separated by hand in the laboratory at Plön.

The three litter fractions were ground in an electric mill, and analyses for Ca, Mg, Na, K, and P were made after ignition of the ground material at 450°C and subsequent solution in dilute HCl (ANON. 1969 a). Na, K,and Mg were estimated by flame photometry, and Ca by EDTA titration. Nitrogen was determined by the Kjeldahl method. P was estimated colorimetrically.

Results

a) Fine litter fall and decomposition

The amounts of fine litter produced weekly in the period July to November (dry season) of the years 1963, 1964, and 1970 are shown in Fig. 1. Rain fall data for these periods are also given. Patterns of the fine litter fall in the dry season for the three years are fairly similar as are the totals of both fine litter fall (3.62 in 1963, 4.13 in 1964, and 4.41 t/ha in 1970) and rainfall. In August and October 1970 much larger litter amounts were recorded than in the corresponding months of 1963 and 1964. This deviation in apparantly due to a greater proportion of wood in the total fine litter fall in 1970. The period of intensive litter fall normally occurs from July to September (KLINGE & RODRIGUES 1968), in the dry season (WALTER & LIETH 160-67).

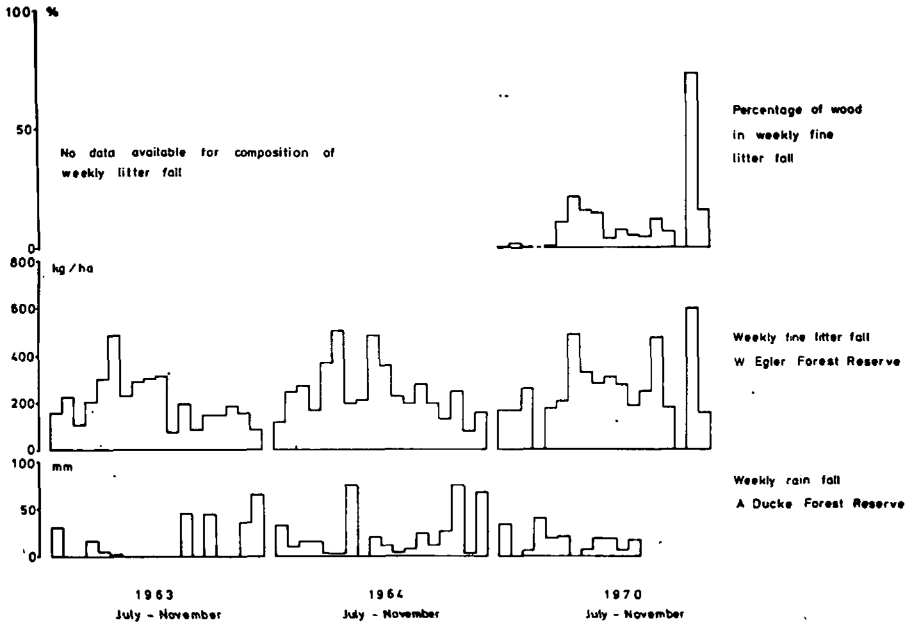

Fig. 1: Weekly fall of fine litter and rain in the seasonal evergreen rainforest at Manaus, during the period July - November in 1963, 1964 and 1970, respectively.

As already mentioned, coarse litter fall was not measured. Occasional observations during field work suggest that coarse litter fall occurs very unevenly. This view is supported by the distribution of branches on the soil within 40 plots of 50 m^2 each, which varied from 2 to 91 kg/50 m^2. A single occurrence of coarse litter production was observed between June and November when the crown of a large Lecythidaceae (dbh 35 cm, over 22 m in height) was blown off by a storm and added 7.4 kg leaves, 102.5 kg branches, and 18.5 kg twigs (fresh matter) to the litter layer. At night one could hear occasionally when a large tree collapsed in the far distance.

Table 1 shows the percentage composition of the fine litter fall and fine litter with respect to leaves, wood, and flowers and fruits. The percentage of leaves in litter fall is much higher than in the litter layer which contains correspondingly more wood.

Table 2 shows the standing crop of fine litter in June and November, together with the amounts added by fine litter fall, and the amounts of decomposed litter. An average of 2.4 t/ha leaves and 2.9 t/ha other fine litter was found on the soil in June 1970. As a result of fine litter fall from July to November the following amounts (in t/ha) were added to the soil: 3.6 leaves and 0.8 other fine litter. In November there were 3.6 t/ha leaves (equal to 150% of the amount in June), and 2.5 t/ha other fine litter (88% of the June amount) in the litter layer. 2.5 t leaves and 1.1 t other fine litter per ha therefore decomposed in 4.5 months. This means that during the dry season less leaves disappeared than were added, but the reverse is true for other fine litter. In terms of weight about twice as much leaf litter as

Table 1: Percentage composition of fine litter fall and fine litter in the seasonal evergreen rain forest near Manaus.

Litter fraction	Year	% Leaves	% Wood	% Flowers and fruits	Remarks
Fine litter fall	1963	81.0	16.5	2.5	Whole year[1)]
	1964	71.6	20.9	7.5	" "
	1970	93.4	0.7	5.9	July[2)]
		82.6	17.4	0	November[2)]
		80.6	17.6	1.6	July-November
Fine litter	1970	46.8	49.0	4.1	June[3)]
		60.2	36.8	3.0	November[4)]

1) Average of ten litter traps (KLINGE & RODRIGUES 1968)
2) Average of 4 samples
3) Average of 9 samples
4) Average of 6 samples

Table 2: Variation of standing crop of fine litter, and fine litter fall (oven-dry matter) in the seasonal evergreen rain forest near Manaus during the 1970 dry season.

Fine litter fraction	Standing crop of fine litter (t / ha) June Mean	June s	November Mean	November s	Fine litter fall July-November Mean	s	Litter decomposition June-November Mean
Leaves	2.37	0.80	3.55	1.25	3.64	0.68	2.46
Other fine litter	2.85	1.39	2.50	1.24	0.77	0.70	1.12
Total	5.22	1.54	6.05	1.83	4.41	0.72	3.58

other fine litter decomposed. The amount of leaf litter at the end of the dry season is about 50% greater than it was at its onset, while the other fine litter fraction was reduced by 12%. As leaves make up the larger proportion of fine litter fall, however, there is a net gain in fine litter at the end of the dry season, due to an accumulation of leaves.

If the forest under study is in a steady state situation, this litter accumulation should be reduced in the wet season, by accelerated decomposition and a lower fine litter fall (KLINGE & RODRIGUES 1968), so that litter decomposition may catch up on litter fall.

b) Nutrient release from decomposing litter

According to Table 1 leaves are the prominent fraction both of the fine litter and fine litter fall. The following discussion takes into account the leaf fraction only, whilst data for other fine litter will be neglected.

An impressive constancy of N, K, Mg, and Na in leaf fall of different years is evident from the data in Table 3. Differences are generally larger for leaf litter. The 1967 dry season leaf fall (acc. to STARK 1971 a) is fairly lower in N, but much richer in P than leaf fall in other years. Leaf fall has a higher nutrient concentration than leaf litter. The lower nutrient content in leaf litter may be interpreted as the result of leaching to which the leaf litter was exposed for a longer or a shorter time. Leaf litter sampled in June includes the low leaf fall occured in the preceding rainy season during which it was heavily leached, and shows a lower nutrient concentration than leaf litter sampled in November including the heavy dry season leaf fall. The latter was less intensively leached in the preceding dry season. Some leaching however goes on also in the dry season. This is demonstrated by a lower nutrient concentration in leaf litter in November 1970 when compared to the dry season leaf fall of that year.

Table 3: Nutrient concentration in leaf fall and leaf litter in seasonal evergreen rain forests of Amazonia.

Litter fraction and period	Number of samples analyzed individually	%					
		N	P	K	Ca	Mg	Na
Leaf fall							
1963 whole year[1]	10	1.50	0.029	0.18	0.21	0.18	0.08
1964 dry season[2]	17	1.57	0.027	0.16	0.24	0.17	0.08
1970 dry season[2]	4	1.55	0.037	0.17	0.40	0.20	0.07
1967 dry season[3]	20	1.48	0.060	0.16	0.22	0.17	0.11
Leaf litter							
1970 June[2]	6	1.29	0.016	0.037	0.14	0.06	0.016
November[2]	4	1.45	0.016	0.061	0.36	0.17	0.023
1967 dry season[3]	15	1.54	0.038	0.114	0.34	0.17	0.056

1) acc. to KLINGE & RODRIGUES 1968
2) this study
3) acc. to STARK 1971 a

Using the nutrient concentration in the 1970 leaf fall and the average decomposition rate of 82% for leaves in the dry season (KLINGE 1973 a), the amount of nutrients was calculated which theoretically could be released from decomposing leaf litter during the dry season (table 4). Nutrient input by rain fall during the dry season is given for comparison (ANON. 1972 a). The values show that nutrient transfer to the soil via leaf fall and nutrient release from decomposing leaf litter are processes of much more relevance to the nutrient dynamics in the ecosystem than is nutrient input via rainfall (CORNFORTH 1970, HOWARD-WILLIAMS 1974).

Since the nutrient concentration in rain fall over Amazonia is equal to the nutrient concentration observed in some of its natural waters (ANON. 1972 a, 1972 b, FITTKAU (1976) refers to those waters as 'rain water rivers') this similarity of natural waters and rainfall with regard to their nutrient concentrations may be taken as an indication of a steady state situation of the respective Amazonian ecosystems.

Table 4: Nutrients in the fall of leaves and rain, and theoretical release of nutrients by leaf decomposition in the seasonal evergreen rain forest near Manaus, during the dry season.

Fraction	N	P	K	Ca	Mg	Na
	kg / ha / dry season					
Leaf fall in 1970	55.8	1.3	6.1	14.4	7.2	2.5
Rain fall[1)]	0.74-0.98	0.02-0.03	n.d.	0.43-0.57	0.29-0.38	n.d.
Theoretical release from decomposing leaves	45.8	1.1	5.0	11.8	5.9	2.1

1) Means for dry seasons of 1966 and 1967 (ANON. 1972 a)

The loss of nutrients by leaching in tropical forests is considered severe, by FASSBENDER (1972) who referred to data for a wet lowland forest in northeastern Costa Rica (McCOLL 1970), and for a tropical moist forest in Panama (McGINNIS et al. 1969). Available limnochemical data for the oligotrophic Amazon region, however, seem to indicate only a small nutrient loss by leaching from terrestrial ecosystems (ANON. 1972 b, FITTKAU 1971, FURCH 1976, GIBBS 1967, KLINGE & OHLE 1964, SCHMIDT 1972). The oligotrophic status of fine litter produced by a rain forest in the Manaus region has already been stated by KLINGE & RODRIGUES (1968). Soils are also strikingly poor in nutrients (ANON. 1969 b, IRION 1976, KLINGE 1976 a, STARK 1970 a, STARK & HOLLEY 1975). But no data for directly measured leaching effects in Amazon rain forests exist.

The nutrient content in the standing crop of leaf litter in June and November, and in leaf fall during July-November 1970 are given in Table 5. The amounts of nutrients released from decomposing leaves in the dry season are also given. The actually released amounts of nutrients agree well with the predicted amounts, except for calcium and magnesium.

Table 5: Average nutrient content of leaf litter and leaf fall (oven-dry matter) in the dry season of 1970, and amounts of nutrients released from decomposing leaves during this period, in the seasonal evergreen rain forest near Manaus.

Leaf fraction	N	P	K	Ca	Mg	Na
	kg / ha					
Leaf litter in June (2,4 t/ha)	31.0	0.4	0.9	3.4	1.4	0.4
Leaf fall from July to November (3.6 t/ha)	55.8	1.3	6.1	14.4	7.2	2.5
Leaf litter in November (3.6 t/ha)	52.2	0.6	2.2	13.0	6.1	0.8
Leaf decomposition (2.5 t/ha)	34.6	1.1	4.8	4.8	2.5	2.1
Leaf decomposition in % of leaf fall	62.0	84.6	78.7	33.3	34.7	84.0

Relative to the nutrient content in June leaf litter, the addition of nutrients via leaf fall was higher for mobile elements (K,Na) than for the more stable elements Mg, Ca, and P, or N. The increase in the nutrient content from June to November however is, relative to both increase in leaf litter and June leaf litter, lowest for P and highest for Mg. Therefore, an accumulation of Ca, K, and Mg took place in the leaf litter. By leaf decomposition, much larger amounts of the mobile elements K and Na and of P than of Ca or Mg became available to the vegetation, relative to the amount of organic matter decomposed.

The different behaviour of individual elements may be explained by the (unknown) proportion of excess bases in the litter (BROADFOOT & PIERRE 1939), and by interference of nutrient input of the leaf litter via rain fall and canopy leaching. The ratios of carbon and phosphorus to individual elements, immobilization of nutrients by microorganisms as well as general leaching may also be effective. Comparable data for the nutrient release from decomposing litter in tropical forests are scarce. BERNHARD-REVERSAT (1972) observed a decreasing mobility for K > P, Mg > Ca, in a rain forest at Ivory Coast. McCOLL (1970) found the litter solution much richer in Mg and Ca than in Na and K. McGINNIS et al. (1969) measured a transfer of 12 stable metallic elements, and P from the litter compartment to the detritivores, which equaled to 60.09 kg/ha/month. Quantitative data for the nutrient release from decomposing litter in other tropical and temperate forests are shown in Table 6.

Table 6: Nutrient release from decomposing litter in tropical and temperate forests.

Forest	kg / ha / month						References
	N	P	K	Ca	Mg	Na	
Tropical rain forest, Zaire	6.3	0.26	3.2	3.9	1.8	-	LAUDELOUT & MEYER 1955
Tropical rain forest, Malaysia	-	-	3.7	0.8	0.6	-	KENWORTHY 1971
Tropical rain forest, Manaus	8.0	0.2	1.1	1.1	0.6	0.5	This study, leaf litter only
Tropical rain forest, Manaus	25.3	1.1	2.7	3.8	2.8	1.8	STARK 1971 b
Temperate forest, Solling	54.3	3.2	22.7	13.2	1.2	1.6	MAYER 1971, 1972
Temperate forest, Hubbard Brook	-	0.23	-	0.75	0.08	-	GOSZ et al. 1973

Estimates of the nutrient concentration in both other fine litter and coarse litter in the Amazon forest suggest a nutrient accumulation in these litter forms, which accounts for approximately the double of the nutrient concentration in leaf litter. Even if coarse litter decay is slow (KLINGE 1973 a, 1974, FITTAU & KLINGE 1973), the estimates point on the importance of nutrient release by decomposition of woody litter, for the maintenance of the forest ecosystem. It should be noted that the method used for the estimation of nutrient release from decomposing leaves includes the microbial and fungal biomass of the litter, but does not consider their nutrient content and nutrient immobilization. In relation to this and to the direct nutrient cycling theory put foward by WENT and STARK (1968 a,b, 1968 b, STARK 1969, 1970 b, 1971 b), it is noteworthy that STARK (1972) showed that the nutrient content of fungal rhizomorph tissue from tropical soils including specimens from the Manaus area, decreased in the order N, Ca> K>Mg>Na, P, while fruiting bodies were higher in P and lower in Ca. In an experimental assay, Ca and Mg were rapidly captured from a modified Hoagland solution by rhizomorph tissue, while P assimilation was small. Na was lost from the tissue, and K behaved indifferently.

Summary

The release of nutrients (N, P, K, Ca, Mg, Na) from decomposing leaves during the dry season in a neotropical seasonal evergreen rain forest near Manaus, State of Amazonas, Brasil was measured estimating the nutrient amounts in leaf litter in June and November 1970, and of leaf fall in between. The following amounts in kg/ha/dry season were released: 162.2 N, 4.7 P, 18.9 K, 41.5 Ca, 11.9 Mg, and 9.4 Na. The results cannot be used for extrapolation of the nutrient release over the whole year, as no estimates were made in the rainy season.

Resumo

La liberación de nutrientes (N, P, K, Ca, Mg, Na) por descomposición de hojas durante la estación seca en la pluviselva neotropical alrededor de Manaus, Estado de Amazonas, Brasil ha sido estimado por determinación de cantidades de nutrientes en la fracción hoja de la hojarasca, en junio y noviembre de 1970 como tambien en las hojas caídas entre ambas fechas. La siguientes cantidades en kg/ha por estacíon seca han sido liberado: 162.2 N, 4.7 P, 18.9 K, 41.5 Ca, 11.9 Mg y 9.4 Na.

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