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Nutrient dynamics within amazonian forest ecosystems

I. Nutrient flux in fine litter fall and efficiency of nutrient utilization

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Summary. A comparative analysis on the rate of fine litterfall and its associated nutrient fluxes was carried out in a mixed forest on Tierra Firme, a tall Amazon Caatinga and a Bana on podsolized sands near San Carlos de Rio Negro. There was seasonality in leaf fall and total litterfall in mixed forest and tall Amazon Caatinga forest but no definite trend in the Bana. Litterfall curves were significantly correlated among sites indicating common regulating factors in the three forests. Leaf litter from mixed forest on Tierra Firme was richer in N with extremely low Ca and Mg concentrations; tall Amazon Caatinga litter had higher P and Mg concentration, while Bana litter was low in N but K concentration was twice as high as in the other two forests. Annual fine litterfall in Tierra Firme mixed forest was nearly 4 times higher than in Bana, but N flux was 10 times higher, while Ca and Mg fluxes were similar. Tall Amazon Caatinga had Ca and Mg fluxes in litterfall 2–3 times higher than the other two forests. Within-stand efficiency of nitrogen, calcium and magnesium use, as measured by biomass/nutrient ratios, differentiates Tierra Firme from Caatinga and Bana forest: Tierra Firme has the lowest N, but the highest Ca and Mg use efficiencies. Higher P use efficiency was measured in Bana followed by Tierra Firme and Caatinga; while Tierra Firme and Caatinga showed similar higher K use efficiencies than Bana. N/P ratios indicates that Tierra Firme forest is limited by P availability, while low N availability predominates in Caatinga. Bana appears limited by both N and P. These differences probably relate to variations in degree of sclerophylly and leaf duration which determine leaf nutrient concentrations in the ecosystems studied.

Forest ecosystems found in the northern portion of the Amazon basin, mainly the Rio Negro watershed, are characterized by highly leached soils with very low nutrient availability (Fittkau et al. 1975). As in many other tropical forests, a major proportion of nutrients in these ecosystems are tied up in organic matter (Richards 1952; Walter 1973; Klinge 1976; Jordan 1982; Klinge and Herrera 1983), so that decomposition constitutes a critical path for maintenance of ecosystem production. Decomposition rates are not only determined by the environment but also by characteristics of the decomposing material (Singh and Gupta 1977; Swift et al. 1979; Schlesinger and Hasey 1981; Melillo et al. 1982). Leaves of dominant species in many Amazon forests are characterized by a high degree of sclerophylly, as defined by low values of Specific Leaf Area, $cm^2\ g^{-1}$ dry weight, and low foliar nitrogen and phosphorus content (Sobrado and Medina 1980), which can result in low decomposition rates (Klinge 1977) and, in turn, slow nutrient release. This situation can be critical in the case of those plant nutrients cycled externally due to their slow or lack of mobility via the phloem.

Amazon forests growing on soils of low fertility have been described as oligotrophic due to their low N, P, and Ca availability (Herrera et al. 1978, 1981; Jordan and Herrera 1981). An identical concept was applied to heathlands ecosystems in mediterranean, subtropical and tropical climates (Specht 1979; Cooper 1979; Klinge and Medina 1979). In oligotrophic forests nutrients accumulate in the upper layers of mineral soil and litter, thus possibly contributing to the development of a mat of absorbing fine roots near the soil surface and even within the non-decomposed litter layer (Lawson et al. 1970; Cornforth 1970; Klinge 1976; St. John 1983; Cuevas and Medina 1983; Proctor et al. 1983a).

The area of San Carlos de Rio Negro, Federal Amazon Territory of Venezuela, belongs to the upper Rio Negro basin which constitutes the northern frontier of the great Amazon basin. In this region various forest types can be found: 1) Tierra Firme forests (non-flooded) on oxisols (Jordan and Uhl 1978; Uhl and Murphy 1981; Jordan 1982) and legume-dominated forests growing on ultisols (Yévaro forest dominated by *Eperua purpurea*, and Guaco forest dominated by *Monopterix uacu*); 2) the Amazon Caatinga forest complex growing on white sands (flooded by raising of the water table for periods of variable duration) where tall Amazon Caatinga is located in lower geomorphological positions, and low Amazon Caatinga or Bana in relatively higher ones (Klinge and Herrera 1983). These forests constitute an intricate mosaic around San Carlos de Rio Negro; however it is possible to differentiate each unit and subunit according to their geomorphological position, soil characteristics and floristic composition (Brünig et al. 1977; Herrera 1977; Klinge et al. 1977; Dubroeck and Sánchez 1981; Breimer 1982; Sanford et al. 1985).

The numerous studies carried out in mixed forest, tall Amazon Caatinga and Bana in relation to biomass distribution (Jordan and Uhl 1978; Stark and Spratt 1977; Klinge

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and Herrera 1978, 1983; Bongers and Engelen 1982), recovery mechanisms after forest disturbance (Uhl et al. 1981), and nutrient retention capacity of the root mat (Jordan and Stark 1978), point clearly to the important role of the rootmat-litter layer as the place where highly efficient nutrient conservation mechanisms operate in these oligotrophic forests.

This paper presents a comparative analysis on the rate of fine litterfall and associated nutrient fluxes carried out in three contrasting forest units: mixed forest on oxysol, Tall Amazon Caatinga, and Bana (Low Amazon Caatinga) on white sands. The objective is to seek patterns of litterfall and within stand nutrient cycling efficiency (sensu Vitousek 1982, 1984) among forests growing under similar climate but contrasting soil characteristics.

Study area

San Carlos de Rio Negro has a tropical rain forest climate, monthly rainfall being always higher than Tank A evaporation, with an average annual temperature of 26° C and an average annual rainfall of 3565 mm. Mean annual relative humidity reaches 85%, and daily insolation reaches an annual average of 5.2 h, for an average annual radiation of 1465 J cm^{-2} per day. Average daily Tank A evaporation is 5.4 mm, so evaporation demands about 90% of available radiant energy (Heuveldop 1979).

The forests studied are located in the San Carlos – Solano road, Federal Amazon Territory of Venezuela (1° 54′N, 67° 03′ W), in the experimental area of the IVIC Amazon Project (Medina et al. 1977), at approximately 100 m elevation. All collections and measurements were carried out within the control areas of a) mixed forest on Tierra Firme described by Uhl and Murphy (1981); b) Tall Amazon Caatinga described by Brünig et al. (1978), and c) Bana described by Medina et al. (1978), Sobrado and Medina (1980) and Bongers and Engelen (1982).

Tierra Firme mixed forests are found on hills of concretional oxisols covered by a sandy layer, while Tall Amazon Caatinga and Bana grow on sandy podsolized soils (phreatic podsol or tropaquod). Both concretional oxisol and phreatic podsols are characterized by high sand content and low water retention capacity.

There is marked contrast between soils of Tierra Firme and Tall Amazon Caatinga regarding nutrient availability. Concretional oxisols appear impoverished in available cations in comparison to podsols (Herrera 1979), while podsol superficial horizons are richer in organic matter but relatively impoverished in nitrogen. Oxisol superficial horizons are richer in total phosphorus, as compared to podsols, although this phosphorus is not easily available for plants due to its association with aluminum and iron (Jordan 1982).

Methods

Litterfall

Ten 0.5 m^2 wire mesh baskets, placed 15 cm above the forest floor were distributed in an area of approximately 400 m^2 in each of the forest plots studied. Accumulated litter was collected weekly for a period of 57 weeks. Frequent collections were carried out in order to reduce nutrient losses due to leaching and decomposition in the basket. Litter collected was oven-dried at 60° C for a minimum of 5 days and later separated into leaves, flowers + fruits, and small wood fractions. The leaf fraction was stored for chemical analysis.

Chemical analysis

The 10 replicates per collection were pooled and ground through a 0.2 mm sieve with a high speed Cyclotec mill. Samples of 500 mg were dry digested at 400° C for 4 h and later dissolved in Plasma Tissue Solution (20% HNO_3 + 10 ppm Mo) (Blood et al. 1981) for P, Ca, Mg, and K analyses carried out in an induced coupling plasma emission spectrometer at the Institute of Ecology, University of Georgia (USA).

Nitrogen was measured by the micro-Kjeldahl method using a semi-automatic Kjeltec Analyzer.

Meteorological measurements

Evaporation from Tank A and rainfall values were obtained from a standard meteorological station run by the Venezuelan Ministry of the Environment, located within 5 km of the Tierra Firme and Amazon Caatinga plots and 11 km from the Bana plot.

Results

Rainfall and evaporation during the observation period

Although the general climatic pattern of San Carlos shows high rainfall throughout the year, there is seasonality in rainfall distribution which can be expressed as frequency of dry days, defined as those days in which rainfall is lower than Tank A evaporation (Medina et al. 1978), or as frequency of rainless days (Heuveldop 1979). The seasonal pattern in rainfall distribution becomes very clear when the number of dry days are plotted on a 4 weeks basis (Fig. 1). Due to the general low water retention capacity of these soils, during a series of few dry days substantial water stress may develop (Cuevas and Medina 1983).

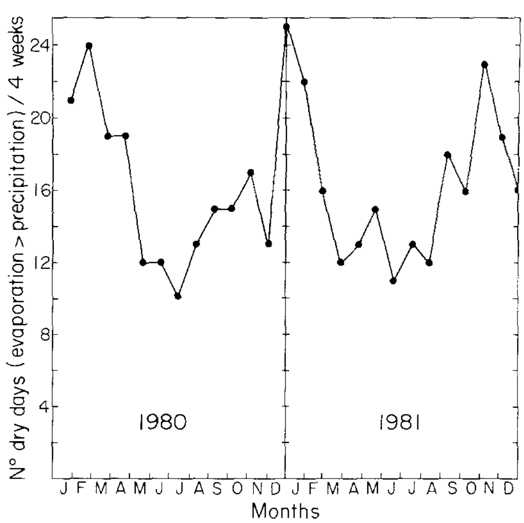

Fig. 1. Rainfall distribution in San Carlos de Rio Negro, Federal Amazon Territory, Venezuela. Number of dry days (rainfall < evaporation) on a 4 weeks basis for 1980–1981

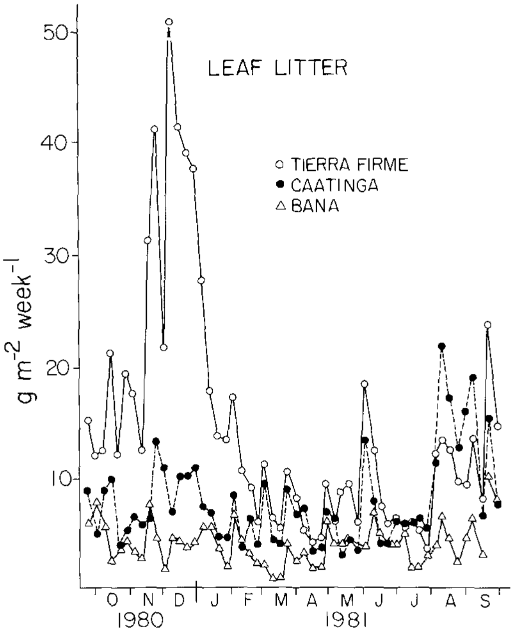

Fig. 2. Weekly rates of litter production in mixed forest on Tierra Firme, Tall Amazon Caatinga, and Bana from September 1980 – September 1981. Each point is the average of 10 0.5 m^2 baskets per collection per forest

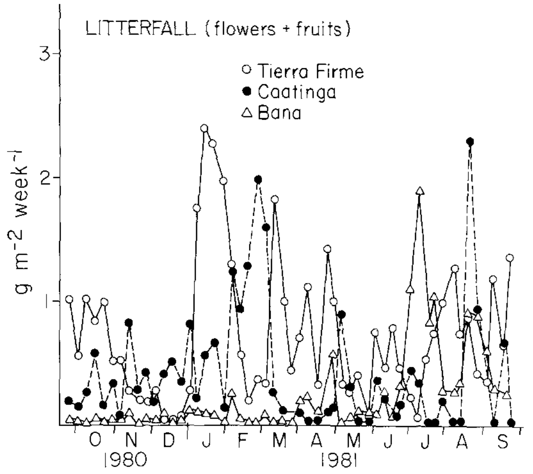

Fig. 3. Weekly rates of the flowers + fruits fraction of litterfall from mixed forest on Tierra Firme, Amazon Caatinga, and Bana from September 1980 – September 1981. Each point is the average of 10 0.5 m^2 baskets per collection per forest

Litter production

From September 1980 – September 1981 seasonality in leaf fall and total litterfall was observed in the Tierra Firme and Amazon Caatinga forests, but it was less apparent in the Bana, probably due to a smaller litterfall flux (Fig. 2). Weekly rates of litter production were almost always higher in the Tierra Firme plot. Tierra Firme and Amazon Caatinga differed also in timing of litterfall peaks. In Tierra Firme a well defined litterfall peak occurred between November and January, while in Amazon Caatinga litterfall was higher between August and September, with a lower peak during December. Litterfall curves, however, were significantly correlated among sites suggesting that common regulating factors were operating in the 3 systems (at $p=0.05$, 52 d.f.: Tierra Firme vs Amazon Caatinga $r=0.289$; Tierra Firme vs Bana $r=0.29$; Amazon Caatinga vs Bana $r=0.354$).

Annual course of flower + fruit fraction was more irregular (Fig. 3). There was a higher production rate in Tierra Firme between January and February, which diminished slowly during the following months. Between August and September 1981 there was again a slight increase. A similar pattern was observed in the Amazon Caatinga, with a peak in February, decreasing rapidly in the following months, and again increasing slightly between August and September. The Bana had a well defined peak of flower and fruit fall between July and September.

Litter production, total or its fractions, was always higher in the Tierra Firme forest (Table 1). Leaf litter constituted nearly 70% of total litter in Tierra Firme and Amazon Caatinga, and more than 80% of total in Bana.

To evaluate the significance of differences among baskets within each site a one way analysis of variance was carried out (54 observations per basket at each site). Baskets in Tierra Firme were homogeneous ($P<0.05$) for leaf and wood fractions, but not for the flower + fruit fraction (annual rates of fall between 12–85 g m^{-2}yr^{-1}). Differences between baskets in the Amazon Caatinga were significant for leaf fall (annual rates of fall between 312–534 g m^{-2}yr^{-1}) and for flower + fruit fraction but not so for small wood fraction and total litter production. Differences between baskets for the Bana were significant for all fractions except small wood. These differences may indicate that sample size was too small in some cases, or that litter production is patchy. However, they do not affect the purpose of the analysis which was to detect relationships between litter and nutrient fluxes within contrasting forest types.

Table 1. Annual fine litter production. Values in g m$^{-2}\cdot$yr^{-1} (standard error of the mean)

Forest	Leaves	Small wood	Flowers + fruits	Total
Tierra Firme	757 (24)	228 (24)	40 (7)	1,025 (47)
Tall Amazon Caatinga	399 (19)	136 (16)	21 (4)	561 (24)
Bana	207 (18)	26 (9)	12 (5)	243 (25)

Annual course of nutrient content in litterfall

The nutrient content in the leaf fraction of litterfall during the observation period revealed fundamental differences between the three forests studied (Fig. 4). Nitrogen concentration showed little variation throughout the year being significantly higher in Tierra Firme than in Amazon Caatinga and Bana. The latter two forests had similar nitrogen concentrations in leaf litterfall.

Phosphorus concentration was more variable, with no seasonal tendency in Amazon Caatinga and Bana. Leaf fall in Tierra Firme had a smaller P content between November-January, than in February-July (Fig. 4).

The annual course of potassium (data not shown) concentration was similar to that phosphorus in Tierra Firme. There was greater variability in the Bana but values tended to be higher between September and February than in the rest of the period. Litterfall in the Amazon Caatinga had lower potassium concentrations without a definite annual variation, although there was also a tendency toward higher values between September-February.

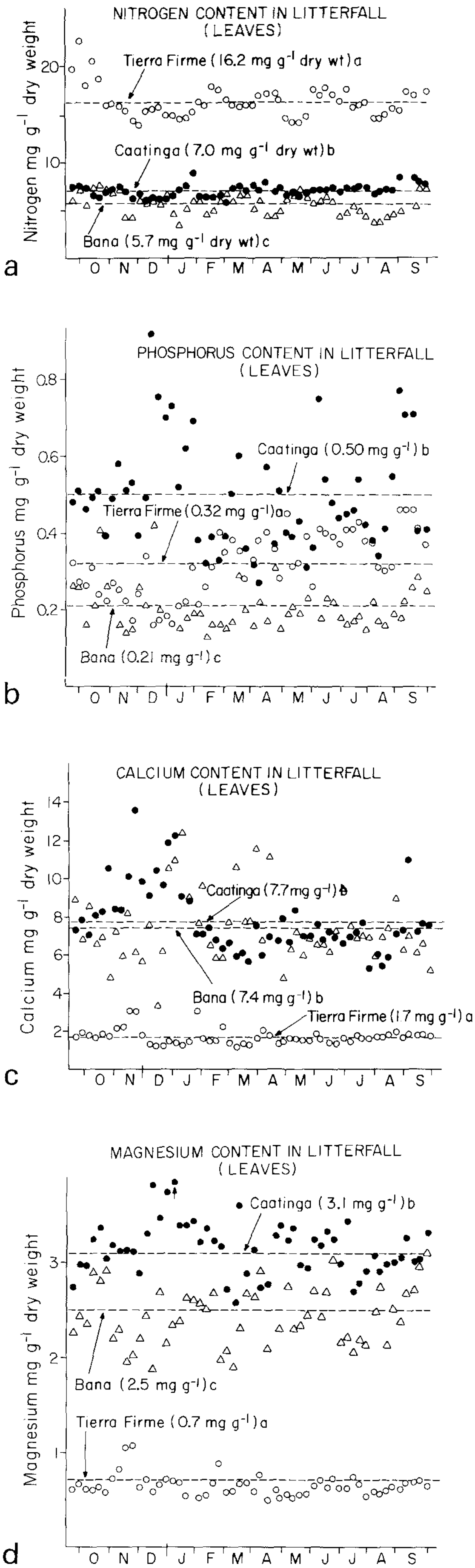

Table 2. Leaf litter and nutrient fluxes in the three forests studied

Forest	leaves g m^{-2}·yr^{-1} (s.e.)	N g m^{-2}·yr^{-1}	P	K	Ca	Mg
Tierra Firme						
this study[a]	757 (24)	12.11	0.212	1.54	1.30	0.52
1975–1977[b]	611	6.13	0.079	0.59	0.84	0.45
Tall Amazon Caatinga						
this study	399 (19)	2.79	0.203	0.80	3.14	1.25
1975–1977[c]	565	4.21	0.260	2.73	3.10	0.88
Bana						
this study	207 (18)	1.21	0.043	0.99	1.52	0.51

[a] Fluxes calculated as the sum of litter mass multiplied by nutrient concentration at each harvest

[b] Jordan and Uhl 1980: given by the authors as fine litter fall but using leaf litter nutrient concentration

[c] Herrera 1979: fluxes calculated by multiplying 70% of fine litter fall by nutrient concentration given in Herrera's table A1

There was no definite annual variation in the concentration of calcium and magnesium (Fig. 4) in any of the forests studied. Concentrations in the leaf fraction of Tierra Firme were always lower than for Amazon Caatinga and Bana.

The forests appear to be clearly differentiated: Tierra Firme produced leaf litter richer in nitrogen and with extremely low levels of calcium and magnesium. Leaf litter in the Amazon Caatinga had higher P and Mg concentrations, while Bana litter had twice the K concentration measured in the other two forests (average values are included in Table 3).

Nutrient flux via litterfall

Nutrient flux values were calculated multiplying each nutrient concentration by the corresponding leaf litter mass at each harvest (Table 2). Ratios of leaf litter and nutrients fluxes among ecosystems were not constant due to marked differences in nutrient concentrations. Leaf litter mass flux in Tierra Firme was 2 times higher than in Caatinga and nearly 4 times higher than in Bana, but its N flux was up to 4 and 10 times higher respectively. However, Ca and Mg fluxes were similar in Tierra Firme and Bana, and 2–3 times lower than in Amazon Caatinga.

Discussion and conclusions

Litterfall seasonality recorded in this study agrees with observations previously reported (Jordan and Golley 1977; Herrera 1979). It appears that there is a consistent phenological pattern in dominant trees, probably related with distribution of dry days throughout the year.

The highest incidence of dry days occurred between October and February, which could explain the maximum in Tierra Firme forest. The correlation in the case of Tall

Fig. 4a–d. Concentration of Nitrogen, Phosphorus, Calcium and Magnesium in leaf fall from mixed forest on Tierra Firme, Amazon Caatinga, and Bana from September 1980 – September 1981. Average values followed by the same letter are not statistically different at $P = 0.01$

Table 3. Leaf litter production and nutrient concentration in different humid tropical forests

Place	Production ton $ha^{-1} \cdot yr^{-1}$	N mg·g^1 dry weight	P	K	Ca	Mg	Author
Africa							
Ivory Coast							
Banco I	8.2	15.4	0.69	2.2	5.6	4.6	
II	7.4	18.0	1.58	9.1	9.5	4.1	[a]
Yapo I	7.1	14.0	0.50	2.8	13.2	2.9	
II	6.2	13.9	0.53	4.9	13.6	3.2	
Asia							
Pasoh forest	6.4	11.6	0.3	3.7	7.0	2.2	[b]
Mulu, Sarawak							
Alluvial forest	6.6	9.0	0.27	2.6	24.4	2.0	
Keranga	5.6	5.7	0.14	2.3	8.8	1.6	
Dipterocarpus	5.4	9.5	0.11	4.5	1.5	1.1	[c]
Calcareous	7.3	11.7	0.38	1.6	31.8	3.3	
America							
Humid tropical forest, Colombia (BPa + BPb)	6.6	12.8	0.38	2.3	10.8	1.6	[d]
Mora excelsa forest, Trinidad	6.9	9.5	0.40	1.6	9.1	2.2	[e]
Tierra Firme forest, Manaus	6.0	15.5	0.3	2.0	2.0	2.0	[f,g]
Averages	6.6	12.2	0.47	3.3	11.4	2.6	
Variation coeff. %	12	28	83	63	77	42	
San Carlos de Rio Negro, this study							
Tierra Firme	7.6	16.3	0.3	2.4	1.7	0.7	
Tall Caatinga	4.0	7.0	0.5	2.1	7.7	3.1	
Bana	2.1	5.8	0.2	4.7	7.4	2.5	

[a] Bernhard-Reversat 1972
[b] Lim 1978
[c] Proctor et al. 1983b
[d] Fölster and de las Salas 1976
[e] Cornforth 1970
[f,g] Klinge and Rodrigues 1968a, b

Amazon Caatinga is not as clear, because this forest is found in lower geomorphological levels in comparison to Tierra Firme and Bana, and as a result, receives drainage water from those units (Herrera 1977). Therefore, a delay in drought stress brought about by a sequence of dry days is to be expected.

Nutrient contents reported by Jordan and Uhl (1980) and Herrera (1979) are not directly comparable with data reported here because their longer intervals between collections can lead to nutrient leaching and decomposition of litter in the collection baskets. Leaf litterfall for Tierra Firme in the present study was higher than that reported for 1975–1977. Associated N, P, K and Ca fluxes however, increased in a higher proportion than that expected from litter mass. In Amazon Caatinga, leaf litter and associated fluxes of N and Mg in the present study were similar to, while those of P, K and Ca were higher than values calculated from Herrera (1979; leaf litter calculated as 70% of total fine litter; nutrient fluxes were obtained multiplying estimated leaf biomass flux by nutrient concentrations given in Herrera's Table A1). These differences are due to the generally higher nutrient concentrations in leaf litter of the present study.

Interannual variations in litter production in tropical forests have been documented in numerous reports and for that reason these studies should be carried out through several years. On the other hand, an important fraction of the observed variability could be a result of the dimension differences of collectors (which could affect efficiency of litter collection), and to collection intervals (which would affect not only litter quantity by in situ destruction but also nutrient concentration through leaching). In the present study the collectors had 0.5 m^2 surface, while in Jordan and Herrera's they were 0.12 m^2. Jordan's and Herrera's collection intervals were once a month, while our collection was carried out on a weekly basis.

Pertinent literature on litter production and nutrient fluxes in tropical ecosystems has been recently reviewed (Brown and Lugo 1982; Proctor et al. 1983b; Steinhardt 1979; Vitousek 1984). As a matter of comparison tropical humid forests with reduced seasonality were selected for which biomass and nutrient content of the leaf litter fraction had been measured (Table 3). Leaf litter production is homogeneous and reaches an average of 6.6 ton/ha per year with a variation coefficient of 12%. This value is similar to the one measured in Tierra Firme and only slightly higher

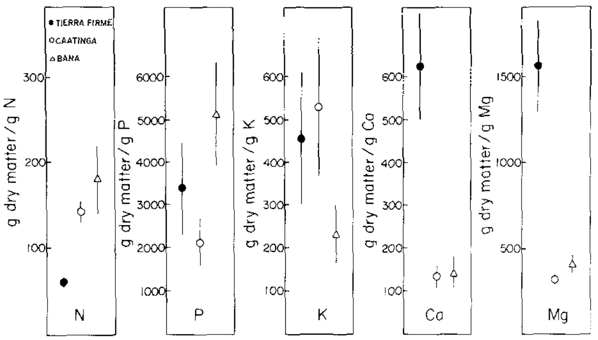

Fig. 5. Nutrient use efficiency (biomass/nutrient ratio in leaf fall) in the forests studied

than that of Amazon Caatinga. The Keranga forest, similar to Amazon Caatinga in structure and soil characteristics (Brünig 1970; Proctor et al. 1983b), has a litter production value within the measured range for Amazon Caatinga.

Nutrient content values are more variable, especially for P and Ca, which present variation coefficients of 83 and 77% respectively. Again Keranga presents similar leaf litter nutrient composition as measured for Amazon Caatinga and Bana, most likely a consequence of dominant foliar structural characteristics in these systems (Sobrado and Medina 1980; Peace and MacDonald 1981). The Dipterocarpus forest studied by Proctor et al. (1983b) produce leaf litter with similar concentrations of P, Ca and Mg but lower N concentration than those found in Amazon Tierra Firme forests.

The mixed Tierra Firme forest of San Carlos is very similar in litter production and nutrient content to the Tierra Firme forests studied by Klinge and Rodrigues (1968a, b; see also Adis et al. 1979) near Manaos. Most striking characteristics are relative N abundance and low levels of Ca.

Application of biomass/nutrient ratios as indicators of within-stand nutrient use efficiency (Vitousek 1982) in the forests studied shows that efficiency is higher the lower the corresponding nutrient circulation via litter. Tall Amazon Caatinga and Bana conform a unit with higher N but considerably lower Ca and Mg use efficiency than Tierra Firme (Fig. 5). Bana however, has higher P use efficiency and lower K use efficiency than the other two forest types. Nutritional differences among the forests studied could be then stated as follows: Tierra Firme is limited by Ca, Mg, K and P; Caatinga is limited by N and K; while the Bana is limited by N and P. Limitations of N and P in tropical forests have been frequently reported (Vitousek 1984), while Ca and Mg limitations seem to be less common (Klinge 1976; Vitousek 1984).

Differences in requirements of N and P for leaf construction among tree species might be indicated by leaf litter N/P ratios (Medina 1984). These ratios are very high in Tierra Firme litter throughout the year (55 ± 17), intermediate in Bana (29 ± 6) and low in Caatinga (15 ± 4). They indicate again higher P availability in Caatinga, high N availability in Tierra Firme and low vailability of both N and P in Bana.

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References

Adis K, Furch J, Irmler U (1979) Litter production of a Central-Amazonian black water inundation forest. Trop Ecol 20:236–245

Bernhard-Reversat F (1972) Decomposition de la litiere de feuilles en foret ombrophile de basse Cote-d'Ivoire. Oecol Plant 7:279–300

Blood R, Tate C, Nicora M (1981) Factors affecting the analysis of environmental samples using inductively coupled plasma. Annual Report to National Science Foundation Okefenokee Swamp Project. Inst of Ecol Univ Georgia. Athens, Georgia

Bongers F, Engelen D (1982) Some aspects of the structure and ecology of an Amazon Caatinga forest in Southern Venezuela. M Sc thesis, Nijmegen University, Holland

Breimer R (1982) Some observations on soils in relation to forest type in San Carlos de Rio Negro. UNESCO Report, Montevideo

Brown S, Lugo A (1982) The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14:161–187

Brünig EF (1970) Stand structure, physiognomy and environmental factors in some lowland forests in Sarawak. Trop Ecol 11:243–264

Brünig EF, Herrera R, Heuveldop J, Jordan CF, Klinge H, Medina E (1977) The International Amazon Project coordinated by Centro de Ecologia, Instituto Venezolano de Investigaciones Cientificas: organization and recent advances. Trans Int MAB-IUFRO Tropical Forest Ecosystem Research. Hamburg-Reinbeck. pp 104–131

Brünig EF, Heuveldop J, Smith J, Alder D (1978) Structure and functions of a rainforest in the International Amazon Project: floristic stratification and variation of some features of stand structure and precipitation. In: Glimpses of Ecology (Singh JS, Gopal B (eds), Int Scient Publ. Jaipur, Indi. pp 125–144

Cooper A (1979) Muri and white sand savannah in Guyana, Surinam and French Guiana. In: Specht RL (ed) Heathlands and Related Shrublands. Ecosystems of the World 9A. Elsevier Scient Publ Co. Amsterdam. pp 471–481

Cornforth IS (1970) Leaf-fall in a tropical rain forest. J Appl Ecol 7:603–608

Cuevas E, Medina E (1983) Root production and organic matter decomposition in a Tierra Firme forest of the Upper Rio Negro Basin. In: Wurzelökologie und ihre Nutzanwendung/Root Ecology and its Practical Applications. Int Symp Gumpenstein, 1982. pp 653–666

Dubroeck D, Sánchez V (1981) Características ambientales y y edáficas del área muestra San Carlos de Rio Negro-Solano, MARN, Dirección General de Información e Investigación del Ambiente, Dirección de Suelos, Vegetación y Fauna. Caracas, Venezuela

Fittkau EJ, Junk W, Klinge H, Sioli H (1975) Substrate and vegetation in the Amazon. In: Tuxen R (ed) Vegetation and Substrat. Berichte der Internationalen Vereinigung für Vegetationskunde. J Cramer Vaduz. Liechtenstein. pp 73–90

Fölster H, de las Salas G (1976) Litter fall and mineralization in three tropical evergreen forest stands, Colombia. Acta Cient Ven 21:196–202

Herrera R (1977) Soil and terrain conditions in the San Carlos project (Venezuela MAB-1) study site correlation with vegetation types. Trans Int MAB-IUFRO Workshop Trop Rain For Ecosystem Res. Hamburg-Reinbeck. pp 132–188

Herrera R (1979) Nutrient Distribution and Cycling in an Amazon

Caatinga Forest on Spodosols in Southern Venezuela. Ph.D. dissertation. University of Reading. England
Herrera R, Jordan CF, Klinge H, Medina E (1978) Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients. Interciencia 3:223–232
Herrera R, Jordan CF, Medina E, Klinge H (1981) How human activities disturb the nutrient cycles of a tropical rain forest in Amazonia. Ambio 10:109–114
Heuveldop J (1979) The International Amazon MAB rain forest ecosystem pilot project at San Carlos de Rio Negro: micrometeorological studies. Trans 2nd Int MAB-IUFRO Workshop Trop Rain For Ecosystem Res. Jakarta, Indonesia. pp 106–123
Jordan CF (1982) The nutrient balance of an amazonian rain forest. Ecology 61:14–18
Jordan CF, Herrera R (1981) Tropical rain forests: are nutrients really critical? Amer Nat 117:167–180
Jordan CF, Stark N (1978) Retención de nutrientes en la estera de raíces de un bosque pluvial amazónico. Acta Cient Ven 29:263–267
Jordan CF, Uhl C (1978) Biomass of a "tierra firme" forest of the Amazon basin. Oecol Plant 13:387–400
Jordan CF, Uhl C (1980) Sixth Year Report for the National Science Foundation Sponsored Project: Nutrient dynamics of a tropical rain forest ecosystem and changes in the nutrient cycle due to cutting and burning. Institute of Ecology, University of Georgia, Athens
Klinge H (1976) Bilanzierung von Hauptnährstoffen im Ökosystem tropischer Regenwald. Biogeographica 7:59–76
Klinge H (1977) Preliminary data on nutrient release from decomposing leaf litter in a neotropical rain forest. Amazoniana 6:193–202
Klinge H, Herrera R (1978) Biomass studies in Amazon Caatinga forest in Southern Venezuela. 1. Standing crop of composite root mass in selected stands. Trop Ecol 19:93–110
Klinge H, Herrera R (1983) Phytomass structure of the Amazon Caatinga ecosystem in Southern Venezuela 1. Tall Amazon Caatinga. Vegetatio 53:65–84
Klinge H, Medina E (1979) Rio Negro caatingas and campinas, Amazonas states of Venezuela and Brazil. In: Specht RL (ed) Heathland and Related Shrublands. Ecosystems of the World 9A. Elsevier Scient Publ Co. Amsterdam. pp 483–487
Klinge H, Rodrigues WA (1968a) Litter production in an area of Amazonian Terra Firme forest. I. Litterfall, organic carbon and total nitrogen contents of litter. Amazoniana 1:287–302
Klinge H, Rodrigues WA (1968b) Litter production in an area of Amazonian Terra Firme forest. II. Mineral nutrient content of the litter. Amazoniana 1:303–310
Klinge H, Medina E, Herrera R (1977) Studies on the ecology of Amazon Caatinga forest in Southern Venezuela. I. General features. Acta Cient Ven 28:270–276
Lawson GW, Armstrong-Mensah KO, Hall JB (1970) A catena in tropical moist semi-deciduous forest near Kade, Ghana. J Ecol 58:371–398
Lim MT (1978) Litterfall and mineral nutrient content in litter in Pasoh forest reserve. Malay Nat J Bot 30(2):375–380
Medina E (1984) Nutrient balance and physiological processes at the leaf level. In: Physiological Ecology of Plants of the Wet Tropics. (Medina E, Mooney HA and Vázquez-Yánes eds.) Tasks in Vegetation Science 12, Dr W Junk, Publ. Amsterdam. pp 139–154
Medina E, Herrera R, Jordan CF, Klinge H (1977) The Amazon project of the Venezuelan Institute for Scientific Research. Nature and Resources UNESCO 13(3):4–6
Medina E, Sobrado M, Herrera R (1978) Significance of leaf orientation for leaf temperature in an Amazon sclerophyll vegetation. J Rad Environ Biophys 15:131–140
Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626
Peace WH, MacDonald FD (1981) An investigation of the leaf anatomy, foliar mineral levels, and water relation of trees of a Sarawak forest. Biotropica 13:100–109
Proctor J, Anderson JM, Chai P, Vallack WH (1983a) Ecological studies in four contrasting lowland rain forests in Gulung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. J Ecol 71:237–260
Proctor J, Anderson JM, Fodgen SC, Vallack HW (1983b) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litterfall, standing crop and preliminary observations on herbivory. J Ecol 71:261–283
Richards PW (1952) The Tropical Rain Forest. Cambridge Univ Press. New York. pp 561–692
Sanford Jr R, Saldarriaga J, Clark K, Uhl C, Herrera R (1985) Amazon rain-forest fires. Science 227:53–55
Schlesinger WH, Hasey MM (1981) Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. Ecology 62:762–764
Singh JS, Gupta SR (1977) Plant decomposition and soil respiration in terrestrial ecosystems. The Bot Rev 43:449–528
Sobrado M, Medina E (1980) General morphology, anatomical structure and nutrient content of sclerophyllous leaves of the "Bana" vegetation of Amazonas. Oecologia (Berlin) 45:341–345
Specht RL (1979) Heathland and related shrublands of the world. In: Specht RL (ed) Heathlands and Related Shrublands. Ecosystems of the World 9A. Elsevier Scient Publ Co. Amsterdam. pp 1–17
Stark N, Spratt M (1977) Root bioamass and nutrient storage in rain forest oxisols near San Carlos de Rio Negro. Trop Ecol 18:1–9
Steinhardt U (1979) Untersuchungen über den Wasser- und Nährstoffhaushalt eines andinen Wolkenwaldes in Venezuela. Göttinger Bodenkundliche Berichte 56:1–185
Swift MJ, Heal OW, Anderson JM (1979) Decomposition in Terrestrial Ecosystems. Univ of California Press. Berkeley
Uhl C, Murphy PG (1981) Composition, structure, and regeneration of a Tierra Firme forest in the Amazon basin of Venezuela. Trop Ecol 22:219–237
Uhl C, Clark K, Clark H, Murphy P (1981) Early plant succession after cutting and burning in the Upper Rio Negro region of the Amazon basin. J Ecol 69:631–649
Vitousek P (1982) Nutrient cycling and nutrient use efficiency. Amer Nat 119:553–572
Vitousek P (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65(1):285–298
Walter H (1973) Die Vegetation der Erde. Bd I. III. Auflage. VEB Fischer

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