Nutrient dynamics within amazonian forests

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II. Fine root growth, nutrient availability and leaf litter decomposition

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Summary. Relationships between fine root growth, rates of litter decomposition and nutrient release were analysed in a mixed forest on Tierra Firme, a Tall Amazon Caatinga and a Low Bana on podsolized sands near San Carlos de Rio Negro. Fine root growth in the upper soil layers (root mat + 10 cm upper soil) was considerably higher in the Tierra Firme forest ($1117 \ g \ m^{-2} \ yr^{-1}$) than in tall Cattinga (120) and Bana (235). Fine root growth on top of the root mat was stimulated significantly by added N in Tall Caatinga and Low Bana forests, by P in Tierra Firme and Bana forests, and by Ca only in the Tierra Firme forest. Rate of fine root growth in Tierra Firme forest on fresh litter is strongly correlated with the Mg and Ca content of litter. Rate of litter decomposition was inversely related to % lignin and the lignin/N ratio of litter. Litter contact with the dense root mat of the Tierra Firme increased rates of disappearance for biomass, Ca and Mg as compared with litter permanently separated or lifted weekly from the root mat to avoid root attachment. Nitrogen concentration of decomposing litter increased in all forests, net N released being observed only in *Caryocar glabrum* and *Aspidosperma megalocarpum* of the Tierra Firme forest after one year of exposure. Results emphasize the differences in limiting nutrients in amazonian forest ecosystems on contrasting soil types: Tierra Firme forests are particularly limited by Ca and Mg, while Caatinga and Bana forests are limited mainly by N availability.

Key words: Amazonian forests – Root growth – Nutrient release – Organic matter decomposition

Conservation of nutrients in amazonian forest ecosystems growing on poor, heavily leached soils is considered of utmost importance for their sustained productivity (Herrera et al. 1978, 1981). Most of the mechanisms that enhance nutrient conservation are related to the development of a dense superficial root mat which filters out nutrients released from decomposing organic matter (Medina et al. 1977; Herrera et al. 1978). The efficiency of the root mat to capture or to extract nutrients from decomposing litter or throughfall appears to be associated with strong development of vesicular-arbuscular mycorrhizal symbiosis (Stark and Spratt 1977; Stark and Jordan 1978; Herrera et al.

1978) which allegedly maintains a very tight nutrient cycle allowing for little leaching (Went and Stark 1968; Fittkau et al. 1975).

The diversity of amazonian ecosystems in the San Carlos area allows the study of rain forests under similar climate but contrasting soil environments. Examples of this diversity of systems include Tall Amazon Caatinga and Low Bana forests on sandy soils of varying flooding regimes and Tierra Firme forests on oxisols and ultisols which are never flooded. These ecosystems produce litters of contrasting nutritional quality (Cuevas and Medina 1986). Tierra Firme litter fall is rich in N but very low in K, Ca and Mg; Tall Amazon Caatinga is low in N, K, Ca and Mg, but relatively high in P; Low Bana is low in N and P, but relatively high in K, Ca and Mg. Thus, nutrient use efficiency (*sensu* Vitousek 1982) of N, P and K, and litter concentration of Ca and Mg may be used to differentiate the three forest types. Low Ca and Mg content in biotic and abiotic compartments has been shown to occur in amazonian forests on oxisols elsewhere (Furch and Klinge 1978). Furthermore, low concentrations of N and P in soils and vegetation of Tall Amazon Caatinga and Low Bana forests appear to select for highly sclerophyllous tree species (Klinge and Medina 1979; Sobrado and Medina 1980).

The present investigation deals with fine root growth in mixed Tierra Firme, Tall Amazon Caatlinga and Low Bana forests, and its role on processes of nutrient release from decomposing litter. Experiments were conducted to test the following hypotheses:

a) Fine root production is regulated by the nutrient availability in forest litter. Annual supply of nutrients in litterfall suggests strongly that N probably limits root growth in the Caatinga-Bana forest complex, while Ca may play a similar role in the Tierra Firme forest.

b) Rate of nutrient release from litterfall is regulated by decomposition processes, but at least in the Tierra Firme forest, root mat growth and adherence to litter in the upper litter layer promote nutrient release, in particular of K, Ca and Mg.

c) Decomposition processes and root mat growth in the litter layer are influenced by original leaf structure and chemical composition.

Study area

The working area is located along the San Carlos – Solano road, Federal Amazon Territory of Venezuela (1° 54' N,

67° 03′ W) in the experimental area of IVIC Amazon Project (Medina et al. 1977), at approximately 100 m elevation. Average annual rainfall is 3565 mm, and average annual temperature is 26° C. 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 Klinge and Herrera (1983), and c) Low Bana woodlands described by Bongers et al. (1985).

The mixed forest on Tierra Firme is characterized by the presence of a well developed superficial root mat, 5–50 cm thick, that constitutes up to 36% of total root biomass (Stark and Spratt 1977). A few days after leaves fall, absorbing fine roots from the root mat adhere to them, and after a few months only a net of roots is left where the leaves were originally located (Herrera et al. 1978). Fallen logs and branches are also actively invaded. Almost all roots from this superficial root mat are mycorrhizal (Stark and Spratt 1977; St John and Uhl 1983).

Tall Caatinga and Low Bana also produce a root mat that constitutes a substantial fraction of total root biomass (Klinge and Herrera 1983; Bongers et al. 1985). It is embedded in a humus matrix and fine roots do not grow freely upwards, as in Tierra Firme forest, unless new organic matter is deposited. This is easily observed in earthworm mounds (Nemeth and Herrera 1982). In both the tall Caatinga (St John and Uhl 1983) and the Low Bana (V. Garcia, personal communication) the majority of roots have well developed vesicular-arbuscular mycorrhiza.

Edaphic conditions

The mixed forest on Tierra Firme is generally found growing on hills consisting of oxisols covered by a sandy layer, while Tall Caatinga and Low Bana grow on sandy spodosols (phreatic podsol or tropaquod) (Herrera 1977, 1979; Dubroeck and Sánchez 1981; Breimer 1985). Both soil types contain a high proportion of sand (more than 60% down to 80 cm depth), and consequently, have low water retention capacity, especially in the spodosol A_2 horizon. Soil nutrient analyses of the different forests published elsewhere (Herrera 1977; Stark and Spratt 1977; Jordan 1982; Cuevas and Medina 1986) show that the oxisols are notably impoverished in available cations compared to the spodosol. The superficial horizons of the spodosols are richer in organic matter but impoverished in N, while in the oxisols the superficial horizons are richer in total P, although it is not readily available to plants due to its immobilization by Al and Fe (Jordan 1982).

Methods

The experimental approach was designed to measure fine root growth both in ingrowth cylinders with artificial substrate, and on fresh litter confined in decomposition bags. The purpose was to establish potential nutritional limitations for fine root growth, and to analyse the relationships between litter physical and nutritional characteristics and the vigor of fine root growth on them. Besides, the rates of fresh litter disappearance and nutrient release were measured in the three forest ecosystems described above and the influence of the root mat contact on these processes was assesed.

Fine root production

High density polyethylene, plastic cylinders, 4 mm² mesh, 10 cm tall, 7.5 cm diameter, were used to measure fine root production. Medium-sized vermiculite, imbibed for 48 h in 0.1 M solutions of either NH_4Cl, K_2PO_4, or $CaCl_2$ was used as the medium for root growth. Vermiculite imbibed in river water was used as control. The cylinders were filled with vermiculite saturated with the salt solutions and placed in the field.

The experiments were conducted twice in Tierra Firme and Tall Caatinga and once in the Low Bana. The first experiment was carried out in the three sites from September 1980 until January 1981, and the second was carried out in Tierra Firme from May until August 1981, and in Tall Caatinga from May until November 1981. A total of 128 cylinders per site were used in the first experiment, 32 per nutrient treatment plus control. Half the cylinders were placed within the root mat in Tierra Firme or on top of the soil in Tall Caatinga and Low Bana. The other half was inserted in the top 10 cm of soil. Eight cylinders were collected per treatment (4 from above and 4 from within the soil) approximately every 30 days. During collection, roots that had penetrated the cylinders were carefully cut before lifting. Within two days after collection the cylinders were transported to the laboratory in Caracas and frozen until further analysis. For root separation cylinders were thawed, and the vermiculite plus roots taken out for processing under a 10 × magnifying lens. The roots were dried in a ventilated oven at 60° C for a minimum of 72 h, weighed, and stored for chemical analyses. The second experiment was carried out in a similar manner except that the replicate number increased from 4 to 6.

To calculate root production rates, root biomass accumulated inside the cylinders was divided by the basal area of the cylinder. This production values correspond only to the root mat and the top 10 cm of soil (measured by cylinder height), so it is only a fraction of fine root production in the whole profile. Estimations are based on the two experiments conducted in Tierra Firme and Tall Caatinga, and one experiment in Low Bana.

Leaf litter decomposition

From each vegetation type three species were selected: *Caryocar glabrum*, *Aspidosperma megalocarpum* and *Licania heteromorpha* from Tierra Firme forest; *Micrandra sprucei*, *Manilkara* sp. and *Eperua leucantha* from Tall Caatinga forest; *Rodognaphalopsis discolor*, *Remijia involucrata* and *Macairea rufescens* from Low Bana forest. These species are representative of the dominants in each of the three ecosystems in terms of litter input to the forest floor (Cuevas and Medina 1986). Adult fresh leaves were used for the experiments because not enough litter per species could be collected at any one time. Storage of collected fresh litter over several days was rejected because of the potential heterogeneous nutrient content and the problem of storage under high humidity conditions in the field station. The collected leaves, without petioles, were dried at the field station in a ventilated oven at 60° C during 3–4 days. Around 10 g of leaves of each species, weighed to 0.01 g precision, were placed in 20 × 20 cm plastic bags of the same mesh as the root cylinders, and individually tagged. The mesh size was chosen to allow fine roots characteristic of

the root mat and the upper soil layer to enter the bags. Initial chemical composition was measured on all species. Additional characterization of the leaf material included the measurement of specific leaf area (SLA, $cm^2\ g^{-1}$).

Groups of bags for each of the species were exposed to one of three treatments: 1) left undisturbed on top of the intact soil (root mat + litter) to allow root penetration and attachment, 2) placed on top of the intact soil and lifted weekly in order to prevent root penetration, and 3) put on a $1\ m^2$, $1\ cm^2$ mesh wire baskets, elevated 15 cm from the soil surface. The bags placed in the wire baskets were not at any time in contact with either soil or roots, so any colonization by microorganisms was airborne. Humidity conditions were similar for all treatments because evaporation from the forest floor is low (Jordan and Heuveldop 1981). Within a few weeks of placement fresh litter fall covered all the bags.

There were three replicates per species, per treatment, and per collection. The bags were randomly placed in areas approximately 30×30 m; in Low Bana bags were placed only in vegetation covered mounds (Bongers et al. 1985). Replicates were collected at 14, 32, 71, 132, 242, and 482 days. During collections roots that had penetrated bags were cut carefully. Bags and their contents were oven-dried at 60° C at the field station and later sent to Caracas. There they were oven-dried again for a minimum of 72 h, outside roots cut close to bag surface, and the remaining leaves and roots separated, weighed, and stored for chemical analysis.

Decomposition was analysed following and exponential model (Olson 1963). In each case a regression analysis was carried out with the natural logarithms of per cent weight remaining of biomass and nutrients in relation to exposure time. The regression coefficient thus calculated is the decomposition constant of biomass or release constant of nutrients (when nutrient and biomass are compared simultaneously the term disappearance rates will be used). For all ecosystems, a maximum time of 242 days was selected, period during which the original K concentration of the leaf material has been reduced to or less than 20% of the original (see Fig. 1). Variations in nutrient mass, and frequently of biomass, were less marked after 242 days, because remaining material was harder to decompose. Comparisons between species are made on the basis of constants of mass loss rates for biomass and nutrients, for which a confidence interval of 95% was calculated.

The unique development of a root mat above the mineral soil in the Tierra Firme forest (Stark and Spratt 1977; Cuevas and Medina 1983; Sanford 1987) provided the opportunity to conduct a second experiment to evaluate fine root growth on fresh litter and its influence on organic matter decomposition and nutrient release. In this experiment all species selected from the three ecosystems were placed on top of the root mat in the Tierra Firme forest.

Chemical analysis

Root and leaf samples were ground to pass a 0.2 mm sieve. In some cases, when the sample was not enough, replicates were pooled and ground together. 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). Concentrations of P, Ca, Mg, and K were determined with an indu-
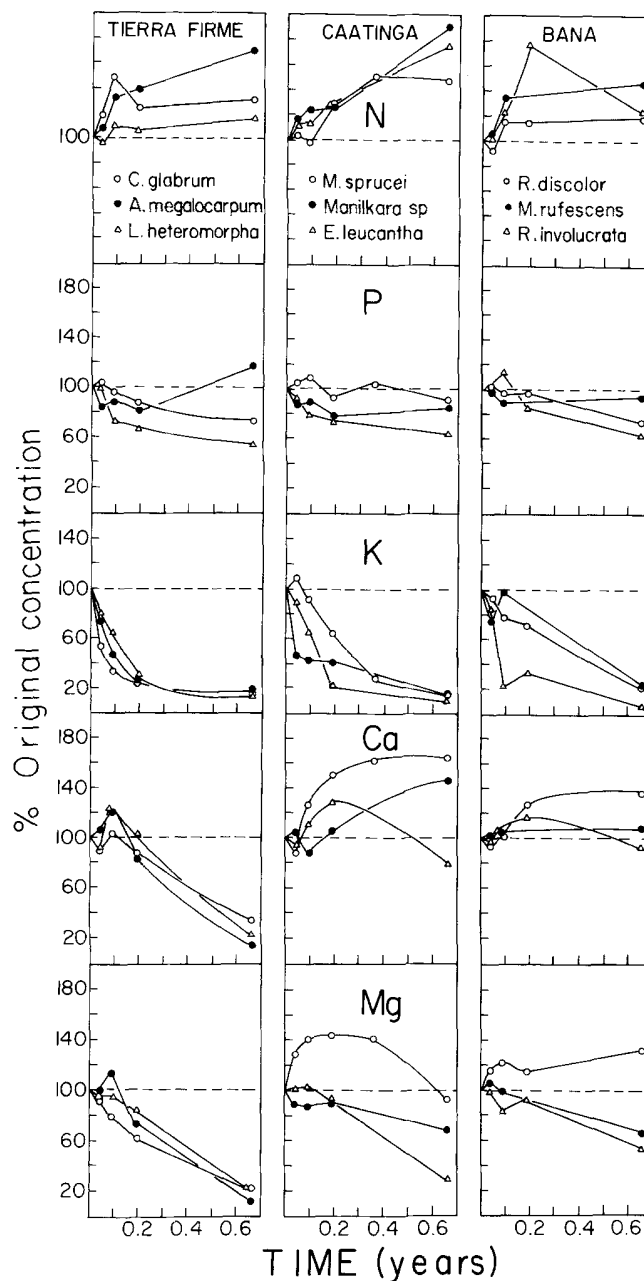

Fig. 1. Temporal variation of percent original nutrient concentration in remaining leaf litter contained in litter bags

ced coupling plasma emission spectrometer (Blood et al. 1981).

Nitrogen was analyzed by the micro-Kjeldahl method. Analysis of soil samples (10 cm depth) from the three forests were done with conventional analytical techniques (Jackson 1964). Tissue content of acid detergent fiber (ADF), cellulose, and lignin of leaves were measured by the van Soest method (1963). Leaf carbon content was measured with the Walkley Black's method (Jackson 1964) using sucrose and starch as standards.

Number of replicates given in the Tables for the different nutrients may vary depending on the amount of plant material available for analysis. When samples were too small replicates were pooled together.

Table 1. Fine root production on an area basis (10 cm thick layer) calculated from the amounts of roots grown into the cylinders, divided by the cylinder basal area and the number of days of exposure (g m^{-2} day^{-1}). Values given are averages $\pm$ standard error of the mean

	n	Control	+NH$_4$Cl	+KH$_2$PO$_4$	+CaCl$_2$
Root Mat					
Tierra Firme	9	0.852 (0.222)	2.581 (1.132)	3.148 (0.934)*	3.874 (0.921)*
Tall Caatinga	14	0.068 (0.027)	0.408 (0.110)*	0.118 (0.049)	0.173 (0.041)
Low Bana	4	0.058 (0.022)	0.255 (0.052)*	0.551 (0.164)*	0.167 (0.055)
Top Soil					
Tierra Firme	9	2.208 (0.942)	2.200 (0.748)	3.282 (1.151)	2.871 (1.178)
Tall Caatinga	14	0.260 (0.068)	0.266 (0.074)	0.334 (0.047)	0.304 (0.068)
Low Bana	4	0.586 (0.068)	0.959 (0.373)	0.715 (0.186)	0.677 (0.074)

* Differences with respect to the control significant at $P=0.1$ (Kruskal-Wallis non parametric analysis of variance, Siegel 1956)

Results

Root growth and productivity in vermiculite-filled cylinders

All cylinders placed on top of the mineral soil of the Tierra Firme forest, and surrounded by root mat, were penetrated at 32 days. Within the same interval, 7 out of 16 cylinders placed in the mineral soil had been invaded. After 70 days, all cylinders, independent of placement, had been invaded. Cylinders placed in the soil of the Tall Caatinga were invaded first, while those placed on top of the soil were irregularly invaded until 71 days. In the Low Bana, all cylinders, within and on top of the soil, had been invaded after 71 days. After 180 days of exposure, all cylinders were saturated with roots. Root production calculations are based on exposure periods when maximum root density was reached: after 90 days in Tierra Firme, and 135 days in Tall Caatinga and Low Bana.

Fine root production in the first 10 cm of soil (top soil) was higher in Tierra Firme followed by Low Bana and Tall Caatinga for all treatments (Table 1). Fine root production was higher in Low Bana than in Tall Caatinga, probably as a result of flooding in the Tall Caatinga area that may impair root production. Although no systematic measurements were performed, fine superficial roots harvested in Tall Caatinga appeared to be thicker, with less weight per unit length than roots from the other two systems.

Fine root production in the cylinders placed on the root mat was also higher in Tierra Firme than in the other two sites (Table 1) but no differences between Tall Caatinga and Low Bana were detected. Fine root production measured in the control cylinders in the upper 10 cm of soil was higher than that measured in the cylinders on the root mat in the three forest types.

Addition of P and Ca resulted in higher fine root production in the root mat of Tierra Firme. In Tall Caatinga only N had a significant effect while P and N increased root productivity in the Low Bana (Table 1). In the upper 10 cm of mineral soil no significant differences between treatments were detected, probably as a result of the greater variability caused by extensive leaching of the vermiculite. This is surely an important factor in Tall Caatinga where flooding is common after heavy rains. These results point to differences in limiting nutritional factors in the ecosystems studied. The pronounced effect of added Ca on root mat growth emphasizes the low availability of this element in Tierra Firme.

Nutrient concentration of roots inside the cylinders

Addition of NH$_4$Cl increased the N concentration of fine roots by only 2% in the Tierra Firme, by 13% in the Tall Caatinga and by 36% in the Low Bana. Addition of K$_2$HPO$_4$ increased P concentration in the fine roots by 17% in the Tierra Firme, 48% in the Tall Caatinga and 68% in the Low Bana. Effects of increased K in this treatment were less noticeable. Addition of CaCl$_2$ had a noticeable effect only in the Low Bana roots. A one way analysis of variance (Anova) showed no significant effect of treatments on root nutrient concentration.

For the purpose of comparisons among ecosystems an Anova was performed on the data of nutrient concentration of fine roots pooled by forest type (Table 2). Tierra Firme fine roots had higher concentrations of N and P but lower concentrations of K, Ca and Mg than those of the other two forests. It is of particular interest that the Low Bana roots had significantly higher K and Mg, but lower N and P concentrations than the Tierra Firme roots, characteristics that have been also observed in the Low Bana leaf litter (Cuevas and Medina 1986).

Root growth in decomposition bags

Average fine root biomass accumulation measured in all bags filled with leaves from the three forest types was 0.220 ± 0.109 g m^{-2} day^{-1} (Table 3). Higher root growth rate values were recorded on leaf litter of non-Tierra Firme species. A regression analysis of root biomass accumulation and nutrient content of leaves was carried out to explain differences in root growth rates. Root biomass was weakly and negatively correlated with N content, but positively and strongly correlated with Ca and Mg (Table 4). Mg effect on root growth appeared to be particularly strong. This alkali-earth metal is found also in comparatively low concentrations in litter fall of Tierra Firme forests (Cuevas and Medina 1986), but its effect could not be independently assessed in the ingrowth cylinders experiment because vermiculite can be a source of Mg (Russell 1973).

A comparison of average nutrient concentrations of bag roots (Table 5) with those corresponding to control cylinder roots of Tierra Firme (Table 2), shows that all concentra-

Table 2. Nutrient concentration of fine roots grown in the cylinders. Values in mg g^{-1} dry weight (standard error of the mean). Numbers in a column followed by the same letter are not statistically different at $P=0.95$. * indicates significant F values in a one way Anova

	N	P	K	Ca	Mg
Tierra Firme	23.0 (0.8)a	1.13 (0.10)a	6.7 (0.6)a	2.1 (0.2)a	2.6 (0.1)a
Tall Caatinga	10.4 (0.4)b	0.95 (0.10)a	8.3 (0.8)ab	3.0 (0.5)a	3.9 (0.2)b
Bana	8.4 (0.6)b	0.51 (0.04)b	12.2 (1.7)b	3.5 (0.5)a	3.7 (0.2)b
F value	174*	28*	8*	4	19*

Number of samples: Tierra Firme 37–39; Tall Caatinga 24–34; Bana 17–23

Table 3. Mean fine root biomass accumulation inside decomposition bags of each of the nine species placed on the root mat in Tierra Firme forest. Values in g m^{-2} day^{-1} (standard error of the mean). n = number of bags measured for fine root accumulation

Species	n	Fine root accumulation
Tierra Firme		
Caryocar glabrum	7	0.151 (0.092)
Aspidosperma megalocarpum	20	0.121 (0.038)
Licania heteromorpha	20	0.059 (0.018)
Tall Caatinga		
Micrandra sprucei	17	0.321 (0.081)
Manilkara sp.	13	0.232 (0.106)
Eperua leucantha	20	0.132 (0.048)
Low Bana		
Rodognaphalopsis discolor	9	0.351 (0.107)
Remijia involucrata	19	0.266 (0.078)
Macairea rufescens	9	0.349 (0.131)

Table 4. Regression analysis of the relation between fine root biomass and leaf nutrient concentration in decomposition bags

	n	Slope	Interc.	r^2	F
Biomass vs Nitrogen	9	−20.0	0.5	0.48	6.4
Biomass vs Phosphorus	9	−105.0	290.0	0.05	n.s.
Biomass vs Potassium	9	5.5	185.6	0.01	n.s.
Biomass vs Calcium	9	34.6	48.0	0.67	14.5
Biomass vs Magnesium	9	99.4	0.3	0.90	66.6

Table 5. Mean nutrient concentration of roots harvested inside decomposition bags containing leaves of the selected species. Values in mg g^{-1} dry weight (standard error of the mean)

Element	n	Concentration
Nitrogen	88	15.9 (0.24)
Phosphorus	67	0.85 (0.02)
Potassium	67	4.30 (0.15)
Calcium	67	0.87 (0.04)
Magnesium	67	0.97 (0.03)

decomposition bags containing leaves from dominant trees from Tierra Firme were calculated on an annual areal basis and compared with the production of roots per unit of cylinder surface area. Average root production in decomposition bags containing leaves from *C. glabrum, A. megalocarpum* and *L. heteromorpha* averaged $0.106 + 0.067$ g m^{-2} bag surface day^{-1} ($n = 23$), equivalent to 39 g m^{-2} year^{-1}. The average root production in the control cylinders in Tierra Firme after 90 days was 0.120 g m^{-2} cylinder surface day^{-1}, corresponding to 44 g m^{-2} per year. The difference in root accumulation per unit of bag or cylinder surface per year is negligible considering the variation among cylinders. The conclusion is that root production in the vermiculite filled cylinders is comparable with the rates measured in natural substrate in spite of the potential higher Mg availability.

Variations of litter nutrient content during the decomposition process

The species selected for the decomposition study varied markedly in physical and chemical properties of their adult leaves (Table 6). All the species, except *E. leucantha* had low SLAs. Tierra Firme species had higher N concentrations, while Ca and Mg concentrations were considerably lower. The Low Bana species are characterized by low N and P concentrations, as expected from their low SLAs (Sobrado and Medina 1980).

Nitrogen concentration of decomposing litter increased rapidly during the first two months of exposure, thereafter it continued to increase, although at a slower rate, until 242 days in all species and systems with the exceptions of *M. sprucei* in the Tall Caatinga and *R. involucrata* in the Low Bana (Fig. 1). In most species N concentration continued to increase until 482 days (values not shown in Fig. 1). Species behaved differently within each system. In Tierra

tions were lower in the decomposition bags, and varied according to the element considered. Higher concentration differences were found for Ca and Mg. Concentration of Mg in the cylinder roots may have been artificially high because of potential Mg release by the vermiculite. The reason for lower concentration of the other elements in the roots grown in the bags is unclear. A possible explanation is that cylinder grown roots had a lower fiber content per unit dry weight.

Because of the potential availability of Mg from the vermiculite in the cylinders, root productivity data calculated from them may be suspect, at least in Tierra Firme, where alkaline-earth metals appear to limit root growth. To resolve this question root production measured in the

Table 6. Specific leaf area and chemical composition of mature leaves of the species studied. Bulk sample of 20 leaves per species, differences between homogenized replicates = 10%. SLA = specific leaf area; ADF = acid detergent fiber

Species	SLA $cm^2 \, g^{-1}$	ADF	Cellulose %	Lignin	C	N	P $mg \cdot g^{-1}$ dry weight	K	Ca	Mg
Tierra Firme										
Caryocar glabrum	77	32.5	17.3	14.2	490	17.1	0.87	5.8	3.2	1.5
Aspidosperma megalocarpum	64	45.6	22.9	21.3	570	11.8	0.53	3.9	1.8	1.2
Licania heteromorpha	62	68.3	39.4	26.3	500	11.2	0.48	3.4	1.7	1.0
Tall Caatinga										
Eperua leucantha	110	57.4	35.0	21.4	530	11.5	1.37	7.5	5.8	2.2
Micrandra sprucei	55	55.9	30.0	24.9	490	8.5	0.62	7.8	2.3	2.0
Manilkara sp	61	53.6	30.1	22.1	510	7.6	0.73	7.3	4.2	2.8
Low Bana										
Rodognaphalopsis discolor	32	59.9	38.5	18.5	460	7.7	0.49	8.0	7.4	2.5
Macairea rufescens	55	59.4	23.9	34.1	490	8.1	0.46	2.5	5.9	3.0
Remijia involucrata	35	61.4	27.8	32.9	580	5.5	0.35	5.1	2.7	1.8

Firme, there was a higher increase in N concentration in leaves of *A. megalocarpum* than in *C. glabrum*. The smallest increase in N concentration was observed in *L. heteromorpha*. The Tall Caatinga species were similar in relative N increase; at 482 days (not shown in Fig. 1) initial concentration had increased between 165 and 200%. In the Low Bana species relative increase was more pronounced in *M. rufescens* (up to 210%) and less marked in *R. involucrata* (up to 140%).

Phosphorus concentration in the decomposing litter changed very little during the course of the experiment (Fig. 1). The absence of increase in P concentration during the decomposition process is noteworthy because the difference between the C/P ratios of the decomposing material (400–1600, calculated from Table 6) and the one frequently found in decomposer fungi (50–150, calculated from Swift et al. 1979) was much more marked than the differences observed between the respectives C/N ratios.

As expected, concentration of K decreased rapidly in all species, reaching 10–20% of the initial concentration by 242 days (Fig. 1). Species in Tall Caatinga and Low Bana tended to lose K at a slower rate than species in Tierra Firme. The slower rates in the Low Bana are probably associated with the frequent wet-dry cycles which occur in this open vegetation (Medina et al. 1978).

Change in Ca concentration during decomposition exhibited quite different temporal patterns in the forests studied (Fig. 1). In Tierra Firme, after a slight initial increase in concentration, Ca declined uniformly in the three species until reaching 10–20% of the original concentration after 242 days. In Tall Caatinga Ca concentration increased until 72 days in *E. leucantha* and until 242 days in *M. sprucei* and *Manilkara* sp. In these last two species Ca concentration was still higher than initial at 482 days. In Low Bana Ca concentration either increased (*R. discolor*) or exhibited no significant change (*R. involucrata* and *M. rufescens*).

Concentration of Mg followed a pattern similar to that for Ca in Tierra Firme species. In Tall Caatinga and Low Bana, Mg concentration increased in *M. sprucei* and *R. discolor*, the same species that showed a clear Ca concentration increase. In the other species concentration of Mg showed a clear reduction, although not as marked as in Tierra Firme's species.

Organic matter decomposition and nutrient release

Tierra Firme species are clearly differentiated by their rates of mass loss (Fig. 2). *Caryocar glabrum* disappeared very fast, after 132 days there was a 95% initial weight reduction. *L. heteromorpha* was the most resistant species with only 38% biomass reduction at 482 days. Initial mass loss rate appeared to be inversely correlated to fiber and lignin content of the decomposing leaves (Table 6).

Rates of mass loss of leaf litter for species in Tall Caatinga and Low Bana were slower and more uniform. Average rates of mass loss in Tierra Firme leaf litter were higher, although more variable, than in Tall Caatinga and Low Bana. After 242 days 28.6 ± 9.8% of the original litter mass remained in Tierra Firme, while 49.1 ± 2.3% remained in Tall Caatinga and 77.7 ± 1.3% remained in Low Bana. Differences between means were tested with an *a posteriori* test (Gabriel's test, Sokal and Rohlf 1969) and resulted significant at $p = 0.1$ to $p = 0.05$. In Low Bana the sparsity of the vegetation, allowing for more frequent desiccation periods, and also the marked toughness of the leaves, determined slower mass loss rates.

As previously shown (Fig. 1), N concentration increased markedly during decomposition in all species, therefore, net N accumulation occurred for intervals of different duration. In Tierra Firme, after an initial very short period in which % N content decreased, there was a tendency toward N net accumulation that lasted from 2 to 4 months (Fig. 2). After this period a net release of N was observed. Percentages of N remaining in each of the collection dates were higher than the corresponding percentage of remaining biomass, indicating N immobilisation by decomposer organisms.

In Tall Caatinga, the same tendencies as in Tierra Firme are observed. There was an initial period of accumulation (absent in *M. sprucei*), followed by slow, approximately linear, reduction of N content (Fig. 2).

In Low Bana, total N accumulation was very marked due essentially to the slow mass loss rates (Fig. 2). Nitrogen accumulation is observed up to 2 months in *R. discolor*, 4 months in *R. involucrata* and throughout the whole observation period in *M. rufescens*. No net release of N was detected during the observation period.
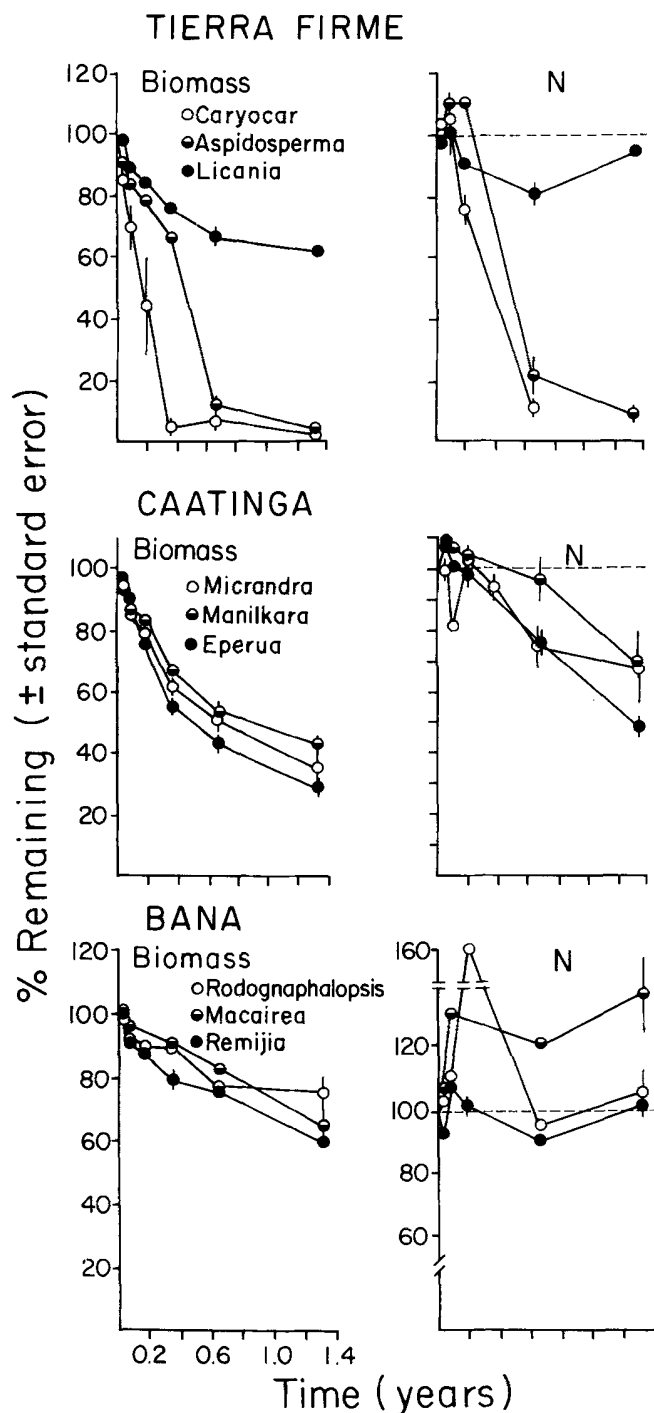
Fig. 2. Temporal variation in percent original mass remaining of organic matter and nitrogen of leaf material contained in litter bags

In Fig. 3 average constants of mass and nutrients loss have been plotted together for easy comparison. Phosphorus tended to disappear at a similar or slightly faster rate than mass, while K disappeared faster than mass in all species and ecosystems studied, except in *C. glabrum* (Fig. 3). Calcium and Mg showed contrasting behaviour within ecosystems. In Tierra Firme these two elements disappeared at a similar rate as K, and faster than mass in *A. megalocarpum* and *L. heteromorpha*. In Tall Caatinga

and Low Bana these two elements had always slower disappearance rates than K (except for Mg in *E. leucantha*), and Ca disappeared at similar or slower rates than mass. *Eperua leucantha* from Tall Caatinga and *R. involucrata* from Low Bana are peculiar in so far as their Ca and Mg disappear faster than mass, indicating that probably a significant portion of these elements is in soluble form.

Effect of root and soil contact on litter mass loss and nutrient release

Separating decomposition bags from the soil substrate, either permanently in baskets 15 cm above the soil, or intermittently, by lifting them weekly to prevent root penetration and attachment, resulted in substantial lowering of mass loss constant only in two Tierra Firme species, *C. glabrum* and *A. megalocarpum* (Fig. 4). In the Tall Caatinga *E. leucantha* and *Manilkara* sp showed a slight reduction in biomass disappearance constant when the bags were placed in baskets, while in Low Bana no significant differences were detected between treatments during the 482 days observation period.

Rates of nutrient release for all treatments, were similar to mass loss rates in Tall Caatinga and Low Bana, the general pattern being P and Ca disappearing at the same or slower, Mg disappearing at equal or higher rate than mass, and K disappearing up to 4 times faster than mass (Fig. 4). In Tierra Firme, however, permanent or intermittent separation of the decomposition bags from the soil substrate produced a significant reduction in the rate of release of P, Ca and Mg in all species. In *C. glabrum* and *A. megalocarpum* these reductions might have been associated with reduction in mass loss rates, but this was not the case of *L. heteromorpha*, in which mass loss was not affected by the treatments (Fig. 4). Release of K tended to remain high in all treatments across species and ecosystems.

Biomass and nutrient disappearance constants of species from each forest exposed in Tierra Firme forest

In all species, absolute concentration of N increased significantly, varying between 8% in *L. heteromorpha* to 109% in *A. megalocarpum* (Table 7). Phosphorus concentration decreased between 23–54% of the original amount in all species, except *A. megalocarpum* in Tierra Firme and *M. rufescens* in Low Bana. Losses of K during the measured time interval were very high with the original concentration being reduced between 86–93% for most species. *Macairea rufescens* with lower original K concentration was the exception.

Concentrations of Ca and Mg showed a reduction in concentration varying between 56–95% for Ca and 62–96% for Mg, a pattern similar to the previous experiment.

We calculated mass loss rate constants for biomass and nutrients (except N) assuming that after a 182 days exposure period, the data can be fitted into an exponential model. Results clearly suggest a common pattern in all species (Fig. 5). Mass loss rate constants of Tierra Firme and Tall Caatinga species are not significantly different from those observed in the control experiment previously discussed. For the Low Bana species, however, there was a significant increase in the rate of biomass disappearance (compare Figs. 3 and 5). This confirms the argument that environ-
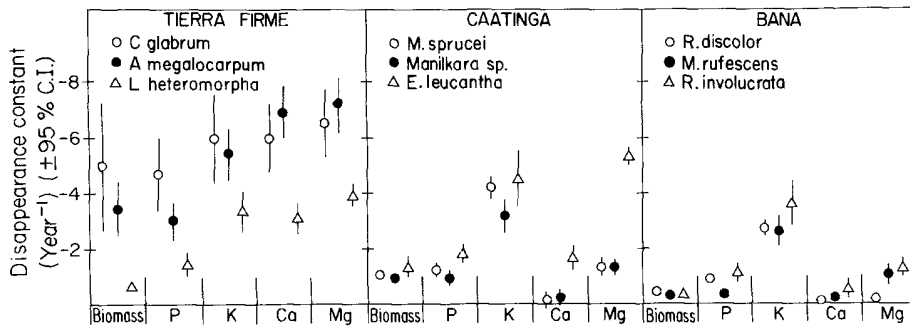
Fig. 3. Mass loss rate constants calculated from logarithmic regressions between percent of leaf or nutrient mass remaining and elapsed time. Bars correspond to 95% confidence intervals
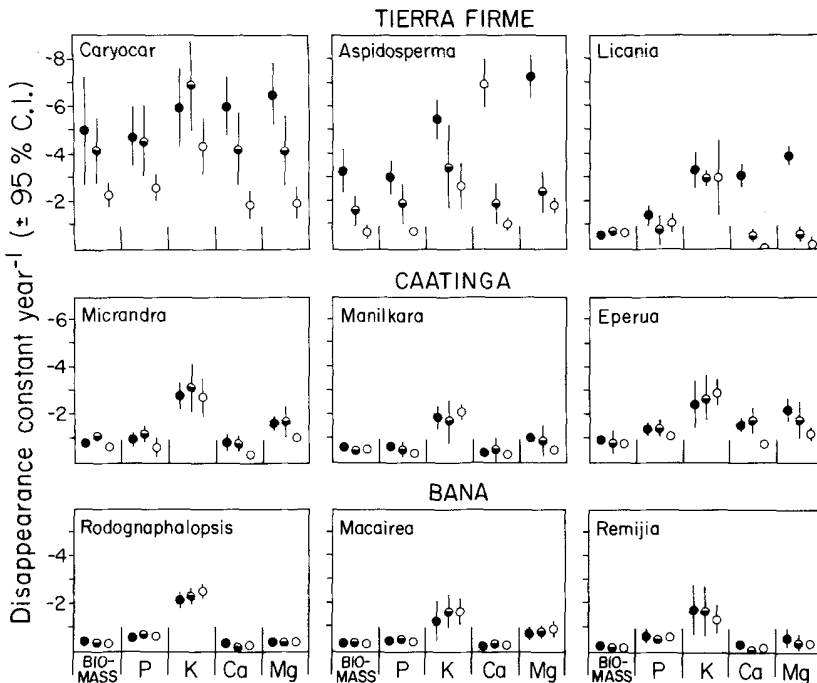

Fig. 4. Effect of root mat contact on the rate of disappearance of biomass and nutrients. ● Litter bags in permanent contact with root mat; ◐ litter bags lifted weekly and returned to the original position on top of the root mat; o Litter bags 15 cm above the root mat

mental conditions are less favourable for decomposition in the Low Bana due to factors related to the sparsity of the vegetation cover.

In all species, P was lost at similar or slightly higher rates than biomass, while K, Ca and Mg disappeared at rates several times faster than biomass, confirming previous observations in the control treatment in Tierra Firme. Only in *L. heteromorpha* were Ca and Mg released at a slower rate than K.

Turnover times of the different species, when exposed to similar conditions in Tierra Firme forest, show that Low Bana species still decomposed at a slower rate than the other species studied (Table 8), although the rates for Low Bana species were higher than those observed in their natural environment. Turnover times were linearly and positively correlated with %lignin ($r^2 = 0.66$) and the %lignin/%Nitrogen ratio ($r^2 = 0.60$).

Phosphorus has a shorter turnover time than biomass in all species except the Tierra Firme species *A. megalocarpum* and the Low Bana species *R. discolor*. Turnover times for K, Ca and Mg were generally shorter than a year, they thus disappear much faster than biomass and P.

Discussion

Fine root production in different forests

Fine root production is of considerable importance in evaluating productive capacity of terrestrial ecosystems. In conifer ecosystems in Sweden, a sizable fraction of annual photosynthesis, more than 50%, was used for production and maintenance of the root system (Persson 1980). Measurement of fine root production in natural ecosystems is extremely difficult, certainly the cause for the scarcity of published data, and those so far available show a wide range of variation (Table 9). Rates of root production reported here represent an average of six months (2 experiments) for Tierra Firme and Tall Caatinga forests, and only 3 months for Low Bana. Expressed on a year basis our results show a wide range of variation in fine root production (upper 10 cm of soil + root mat), ranging from 1117 g m^{-2} yr^{-1} in Tierra Firme to 120 g m^{-2} yr^{-1} in Tall Caatinga. High values of fine root production both within the litter layer and in the upper soil layers are not unusual even in temperate forests, but the low values of Tall Caat-

Table 7. Mean initial and final nutrient concentration of leaf litter from the three forest types placed on the root mat in Tierra Firme (values mg g^{-1} dry weight are averages with respective 95% confidence interval). (Duration of the experiment: 182 days)

	N	P	K	Ca	Mg
Tierra Firme					
Caryocar glabrum					
initial	16.8	0.85	6.1	4.5	1.8
final	21.2 (1.4)	0.59 (0.09)	0.8 (0.3)	0.5 (0.1)	0.2 (0.1)
Aspidosperma megalocarpum					
initial	10.2	0.72	7.1	1.3	1.2
final	21.4 (0.4)	0.72 (0.05)	0.9 (0.1)	0.1 (0.1)	0.1 (0.03)
Licania heteromorpha					
initial	12.3	0.54	4.4	1.8	0.9
final	13.3 (0.4)	0.25 (0.03)	0.4 (0.0)	0.8 (0.2)	0.3 (60.1)
Tall Caatinga					
Eperua leucantha					
initial	15.4	0.96	5.9	5.3	1.6
final	18.9 (0.5)	0.74 (0.05)	0.6 (0.1)	0.9 (0.5)	0.2 (0.1)
Micrandra sprucei					
initial	9.7	1.03	9.1	6.3	3.0
final	12.9 (0.4)	0.48 (0.02)	0.7 60.1)	0.8 (0.3)	0.2 (0.1)
Manilkara sp.					
initial	7.8	0.49	8.6	4.9	1.7
final	11.7 (0.8)	0.36 (0.06)	0.7 (0.2)	1.4 (1.0)	0.4 (0.3)
Low Bana					
Rodognaphalopsis discolor					
initial	7.9	0.60	7.7	9.9	3.6
final	10.6 (0.7)	0.43 (0.06)	0.7 (0.1)	3.7 (1.7)	0.5 (0.3)
Macairea rufescens					
initial	6.9	0.36	2.5	6.4	3.8
final	9.3 (0.7)	0.37 (0.25)	1.0 (0.5)	0.5 (0.3)	0.2 (60.1)
Remijia involucrata					
initial	6.3	0.43	4.8	4.4	2.3
final	8.6 (0.6)	0.30 60.03)	0.6 (0.1)	0.2 (0.1)	0.1 (0.0)
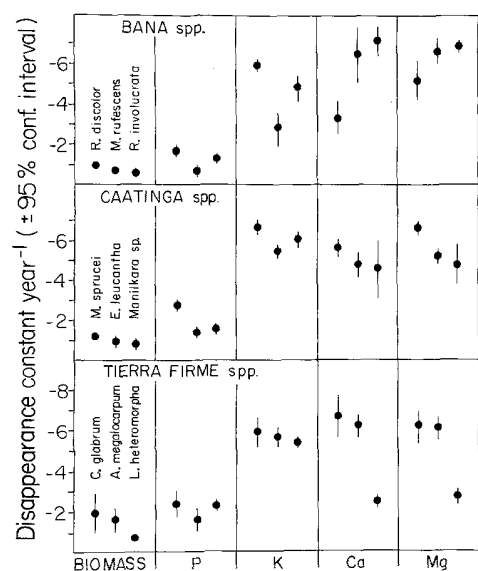
Fig. 5. Mass loss rate constants for leaf litter of tree species from different ecosystems put in litter bags to decompose in the Tierra Firme forest

inga and Low Bana are noteworthy, because they reflect their lower productivity. In these forests, organic matter production is restricted not only by nutrient availability, but also by frequent flooding (Caatinga) or the alternation of flooding and drought (Bana) (Medina et al. 1978; Herrera 1979; Bongers et al. 1985). In Low Bana fine root production near the soil surface is higher than in Caatinga, while its litter production is about one half of the litter production in Tall Caatinga (Cuevas and Medina 1986). This may reflect the increased above ground/below ground biomass ratio shown in the Caatinga-Bana catena complex (Klinge and Herrera 1983; Bongers et al. 1985).

Values reported here for Tierra Firme forest are highly variable, but appear to be considerably higher than those previously published by Jordan and Escalante (1980), particularly in the upper layers of the mineral soil where the differences are about one order of magnitude. Our method of ingrowth cylinders may stimulate root production because of the availability of "free spaces" for roots to invade. However, some of the methods used by Jordan and Escalante (1980) are comparable to ours, because living roots free spaces were created in the soil and root ingrowth was measured after several months. A possible explanation may be found in the intrinsic variability in depth, and per-

Table 8. Time required for 95% (3/k) of the initial biomass and nutrient content of litter from the three forest types to disappear when in contact with the root mat in Tierra Firme forest

	Biomass	P	K	Ca	Mg
Tierra Firme					
Caryocar glabrum	1.63	1.27	0.51	0.45	0.48
Aspidosperma megalocarpum	1.95	1.92	0.53	0.48	0.49
Licania heteromorpha	4.55	1.33	0.56	1.25	1.09
Tall Caatinga					
Eperua leucantha	3.49	2.17	0.56	0.63	0.58
Micrandra sprucei	3.95	1.97	0.50	0.66	0.63
Manilkara sp	2.61	1.12	0.46	0.54	0.45
Low Bana					
Rodognaphalopsis discolor	4.55	4.69	1.09	0.47	0.46
Macairea rufescens	5.88	2.40	0.63	0.43	0.44
Remijia involucrata	3.06	1.79	0.51	0.92	0.58

Table 9. Fine root production in litter and superficial soil layers in different forests. Values in $g\,m^{-2}\,year^{-1}$

Type of forest	Litter layer	Superficial soil layer	Source
Pinus sylvestris-Calluna vulgaris, 15–20 years old, Sweden[a]	108	93	Persson 1980
80-year broad-leaved forest, Massachusetts, USA[b]	270	170	McLaugherty and Aber 1982
53-year Pinus resinosa plantation, Massachusetts, USA[b]	130	190	McLaugherty and Aber 1982
Broad leaved and needle temperate forests[c]	–	160–591	Nadelhoffer et al. 1985
Coffee plantation, IVIC, Venezuela[d]	10	661	Cuenca 1981
Tierra Firme forest, San Carlos de Rio Negro, Venezuela[e]	123	87	Jordan and Escalante 1980
Tierra Firme forest, San Carlos de Rio Negro[f]	311	806	Present study
Tall Caatinga, Eperua leucantha area, San Carlos de Rio Negro	25	95	Present study
Low Bana, San Carlos de Rio Negro	21	214	Present study

[a] Production calculated on biomass increment. Superficial layer down to 30 cm depth
[b] Superficial layer down to 15 cm depth
[c] Superficial soil layer down to 20 cm
[d] Superficial layer down to 7 cm depth
[e] Superficial layer down to 40 cm depth
[f] Superficial layer down to 10 cm depth

haps vigor of the root mat, depending on the density of trees surrounding the experimental areas. It has been recently reported that root mat in Tierra Firme forest is thicker near tree stems (Sanford 1987).

Fine root growth and nutrient availability

Production of roots on top of the mineral soil in amazonian forests of the upper Rio Negro has been explained as a consequence of the low nutrient availability in those forests (Herrera et al. 1978; Cuevas and Medina 1983; Sanford 1987). Our experiments showed increased fine root production caused by added nutrients only in the cylinders placed on top of the root mat (Table 2). It seems clear however, that root growth is not limited by the same set of nutrients in the three forests. Fine root growth in Tierra Firme forest increased by added P and Ca; in Low Bana significant effects were observed by added N and P, while in Tall Caatinga fine root respond only to added N. The role of Ca on fine root growth in Tierra Firme was confirmed by mea-

suring root growth inside of decomposition bags, experiments by which the previously unsuspected strong effect of Mg was unveiled (Table 4).

Biomass decomposition rates in tropical forests

Biomass and nutrient (except N) loss rates measured in this study fitted satisfactorily the exponential model as discussed by Olson (1963) for confined litter. In other tropical forests, with leaves markedly different regarding thickness and hardness, it has been found that the course of biomass loss is linear because there is no accelerated initial loss of material (Bernhard-Reversat 1972; Edwards 1977). There is no adequate explanation for the occurrence of either linear or logarithmic decomposition kinetics, but differences may be caused by variations in soluble material content of the decomposing substrate (Gosz et al. 1973).

It has been frequently reported in the literature that litter of tropical forests has high decomposition rates due to prevalence of favourable conditions for microbial activity
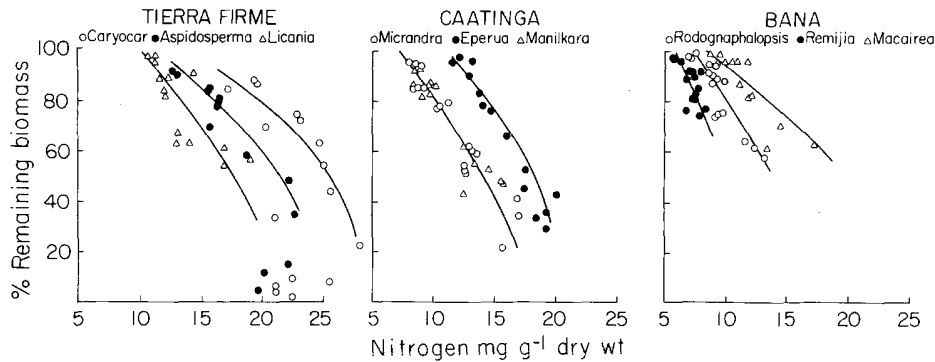
Fig. 6. Relationship between nitrogen concentration in leaf litter and percent of original biomass remaining within the litter bags. Leaf litter of each species decomposing in their original forest. Included are all values included in experiment of Fig. 4

Table 10. Selected values of decomposition constants estimated for humid tropical forests. $3/k$ = time required for 95% loss of initial litter biomass

Locality	k year^{-1}	$3/k$ years	Source
Summary for tropical forests	1–4	0.7–3.0	Olson 1963
Humid forest on latosol, Colombia	0.4	7.5	Foelster and de las Salas 1976
Leaves of Eperua falcata French Guiana	0.5	6.0	Kiffer et al. 1981
Banco forest			Bernhard-Reversat 1972
Ivory Coast			
Isolated species	3.2–7.5	0.4–0.9	
Forest			
Plateau	3.3	0.9	
Talweg	4.2	0.7	
Sarawak forests			Anderson et al. 1983
Alluvial	1.7		
Dipterocarp	1.7		
Heath	1.4		
Flooded forests, Manaos			Irmler and Furch 1980
Eschweilera coriacea	2.2	1.4	
Buchenavia ochrosperma	2.9	1.0	
Fresh litter Igapó	0.48	6.2	
Varzea	1.08	2.8	
Tierra Firme, Manaos	1.3	2.3	Klinge 1977
San Carlos de Rio Negro, Tall Amazon Caatinga	0.87	3.4	Herrera 1979
San Carlos de Rio Negro, Venezuela			Present study
Tierra Firme	0.58–5.00	0.6–5.2	
Tall Amazon Caatinga	0.80–1.33	2.3–3.8	
Bana	0.22–0.44	6.8–13.6	

throughout the year (Jenny et al. 1949; Singh and Gupta 1977). An examination of published values from humid tropical forests, however, reveals a high degree of variability (Table 10). Olson (1963) gives k values (yr^{-1}) for tropical forests that vary between 1 and 4, meaning that 95% of initial biomass would disappear in 0.7–3 years. Bernhard-Reversat (1972) obtained decomposition rates which are among the highest found in tropical forests.

Others have obtained very low decomposition rates (0.4–0.5) (Fölster and de las Salas 1976; Irmler and Furch 1980). Our values for San Carlos are also very low. With the exception of *C. glabrum*, turnover time for the species were always longer than a year. These low decomposition

rates are most probably associated with the low nutritional value of the decomposing litter as has been proposed by Klinge (1977) for the Amazon and Edwards (1977) for montane forests in New Guinea. Flooding after heavy rains occurs frequently in Caatinga, producing anoxic conditions in the soil, thus notably reducing decomposition rates (Day 1982). In Bana, on the other hand, due to sparse vegetation cover, there can be superficial soil dessication after a few days without rain, which also delays decomposition processes.

Faster decomposition rates when litter is in contact with the root mat contrasts with Gadgil and Gadgil's (1975) results, who found that disappearance rates from *Pinus ra-*

diata litter were inhibited by presence of ectomycorrhiza, probably due to competition with free living decomposer microorganisms.

Nitrogen accumulation and release during decomposition

Nitrogen increases in concentration during the decomposition process as a result of colonization by decomposer microorganisms (Gosz et al. 1973; Aber and Melillo 1980; Lousier and Parkinson 1978). The actual source for this increase in absolute quantity in decomposition bags has several explanations, such as fixation by N_2 fixing organisms (Wood 1974), contamination from the environment (Bocock 1964), or transport via decomposer fungal hyphae (Gosz et al. 1973; Wood 1974). Nitrogen accumulation during litter decomposition seems to be a general occurrence, although in some tropical forests N disappears at the same rate as biomass (Bernhard-Reversat 1972) or accumulation is of very short duration (Irmler and Furch 1980; Cuenca 1981; Aranguren et al. 1982a, b). Aber and Melillo (1980) and Melillo et al. (1982) found that per cent remaining biomass in decomposition bags was inversely related to N concentration of the decomposing material. This linearity is maintained as long as there are no transport processes after fragmentation such as ingestion by detritivore insects, and that N be available in the environment surrounding the decomposing material (Aber and Melillo 1980). Deviation from linearity could be interpreted as the start of net N release. Figure 6 shows that the relationship between per cent biomass remaining and N concentration in the litter for all three exposure treatments in each of the three ecosystems in San Carlos is almost linear, N concentration increasing rapidly as remaining biomass diminishes. This fact is of great importance because it indicates that decomposition processes operated in a similar manner in the three treatments, and the differences observed in rates of mass and nutrient loss may be attributed to root contact effect or to hyphal invasion. Interestingly, each species seems to have a particular linear relationship. The reason why N concentration should be so different among different species at similar stages of decomposition is not clear at the moment. These differences appear to be related to SLA and lignin content but not to initial C/N ratios.

Net N release was observed only in the Tierra Firme species *A. megalocarpum* and *C. glabrum*. Therefore, net N losses suggested for Caatinga and Bana species by the curves of % remaining mass of N in Fig. 2 correspond to organic matter transport from the decomposition bags and not to true mineralization of N.

Berg and Staaf (1981) analysed the published values of net N accumulation in decomposition bags. They distinguish three types of kinetics: a) sequential phases of leaching, accumulation and release; b) sequential phases of accumulation and release, and c) simultaneous phases of leaching and release. Data from our study essentially fits within the first model, where initial leaching is of very short duration. The accumulation phase depends on the initial N concentration. Bana species, with their lower initial N contents, accumulate more N during longer periods. Caatinga species have intermediate magnitudes and periods of accumulation, while accumulation phase is very short in Tierra Firme species (Fig. 2). In the Bana species, the net release phase was never reached during the study (482 days), indicating the marked N deficiency in this forest.

Rates of nutrient loss from decomposing litter

The relative nutrient release rates from litter vary in different ecosystems, but in general the most mobile nutrient is K, while Ca and Mg tend to be retained in biomass. Nitrogen and P are two elements which vary in their mobility according to their initial concentration and availability in the soil (Attiwill 1968; Bernhard-Reversat 1972; Gosz et al. 1973; Wood 1974; Lousier and Parkinson 1978; Irmler and Furch 1980; Day 1982).

The relationships between nutrient and biomass disappearance rates are interpreted as follows: an element whose disappearance rate is equal to or lower than that of biomass is released through decomposition, while nutrient loss rates above that of biomass are a result of leaching (Gosz et al. 1973; Swift et al. 1979). Our results show that the ratio of nutrient to biomass loss rates may change with conditions during decomposition. In fact, we showed a clearcut effect of the fine roots from the root mat in the Tierra Firme on decomposition rates and also nutrient release rates. The presence and adherence of fine roots in Tierra Firme results in very similar disappearance rates of K, Ca, and Mg, whereas, when the bags were either intermittently or permanently separated from the root mat, K was released at the same high rate, while Mg and especially Ca tend to be retained and accumulated in decomposing biomass. Faster Ca and Mg release rates when litter was in contact with fine roots from Tierra Firme root mat can not be explained simply by leaching. There must be a nutrient release mechanism mediated by these roots and/or its associated microorganisms. Neither in Caatinga nor in Bana is this effect observed because fine roots are not associated with freshly fallen litter, as is the case in Tierra Firme, but are found in decomposing detritus.

Explanations for this Ca and Mg extraction from decomposing litter may be found in the study of the chemical nature of the Ca and Mg compounds in the leaves of different species, and perhaps the acidity of root exudates.

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