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Fine litter input to terrestrial humus forms in Colombian Amazonia

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Abstract A comparative litter fall study was made in five rain forest stands along a gradient of humus form development and soils in the Amazon lowlands of eastern Colombia. The total fine litter fall was highest in a plot on a well drained soil of the flood plain of the Caquetá River ($1.07 \text{ kg} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$), lower in three plots on well drained upland soils (0.86 , 0.69 , and $0.68 \text{ kg} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$), and lowest in a plot on a poorly drained, upland podzolised soil ($0.62 \text{ kg} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$). In the four upland plots, leaf litter fall patterns were highly associated, which points at climatic regulation. Litter resource quality, as represented by nutrient concentrations and area/weight ratio of the leaf litter fall, was comparatively high in the flood plain plot. In the upland plots, concentrations and fluxes of Ca, Mg, K, and P were as low as in oligotrophic central Amazonian upland forests. This questions generalisations that the western peripheral region of the Amazon basin should be less oligotrophic than central Amazonia. The upland plot on the podzolised soil showed the lowest concentrations and fluxes of N. Mean residence times of organic matter and nutrients in the L horizons hardly differed between the five plots, suggesting that edaphic properties and litter resource quality are of little importance in the first step of decomposition. Mean residence time of organic matter in all ectorganic horizons combined (estimated on the basis of litter input and necromass on the forest floor, and uncorrected for dead fine root input) varied from 1.0 y in the flood plain forest, 1.1–3.3 y in the well drained up-

land forests, and 10.2 y in the forest on the podzolised soil.

Key words Decomposition · Fine roots · Forest floor · Nutrient cycling · Tropical forest

Introduction

A recent survey of forest soils along the middle stretch of the Caquetá River in the Amazon lowlands of eastern Colombia has revealed a general trend of increasing thickness, necromass, and fine root content of terrestrial humus forms along a gradient of decreasing soil nutrient status (Duivenvoorden and Lips 1993, 1995). With the aim of providing more insight into factors of humus form development in this area, a comparative analysis of litter fall and nutrient fluxes was made for 1 year in five forest plots, selected to represent the regional range of humus form variation.

The study represents the first quantitative record of litter fall in the northwestern fringe of the Amazon basin. Fine litter fall represents a major input of organic matter and nutrients to ectorganic horizons in forest ecosystems (Vogt et al. 1986; Vitousek and Sanford 1986), in combination with throughfall (Gosz et al. 1976; Burghouts 1993) and dead fine root input (Vogt et al. 1983, 1986). Decomposition rate or residence time of organic matter as well as nutrient mobility can be estimated on the basis of input and standing stock, by means of a mass balance model (Olsen 1963). Usually only input from above-ground fine litter fall is taken into account, even though this may lead to overestimation of residence times on nutrient-poor soils with well rooted ectorganic horizons (Vogt et al. 1983, 1986).

This study may also contribute to a characterisation of northwestern Amazonia in terms of nutrient economies. Because information on wood and root production is scarce, inverse nutrient concentrations (dry mass/nutrient ratios) in litter fall are widely used as an index of mineral cycling and nutrient availability in forest stands (Cha-

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Fig. 1 Location of the middle Caquetá area in Colombia and northwest Amazonia. The grey-toned area in South America represents Amazonia according to Fittkau (1974). The detailed map shows the approximate position of the litter fall measurement plots

pin 1980; Vitousek 1982, 1984; Silver 1994). This kind of study has shown that tropical lowland rain forests on nutrient-poor substrata, particularly in central Amazonia, make highly efficient use of phosphorus, and possibly also of calcium and magnesium. Nitrogen does not appear to cycle efficiently in tropical rain forests, apart from forests on podzolised soils (Vitousek 1982, 1984; Cuevas and Medina 1986; Silver 1994).

Materials and methods

Site descriptions

Climate, geology, land forms, mineral soils, humus forms, and vegetation of the middle Caquetá area ($0^{\circ}25'-1^{\circ}30'S$, $72^{\circ}30'-70^{\circ}40'W$; Fig. 1) are described and mapped in recent studies, carried out within the framework of the Tropenbos programme in Colombia (Duivenvoorden and Lips 1993, 1995; Duivenvoorden 1994, 1995, 1996; Hoorn 1994; Van der Hammen et al. 1992a,b). At Araracuara (Fig. 1) mean yearly rainfall is 3060 mm and mean yearly temperature is $25.7^{\circ}C$. Mean monthly rainfall of all months exceeds 100 mm. Current climate of the area classifies as Af (Köppen 1936) and the area belongs to the life zone of Humid Tropical Forest (bH-T) of the Holdridge life zone system (Holdridge et al. 1971). The five litter fall measurement plots are located in the vicinity of Araracuara and some 25–30 km downstream (Fig. 1). Plot altitudes were about 155 m (plot 1) to 280 m (plot 5) above sea level. Selected plot data on soils and forests are given in Table 1. All plots have closed canopy forests.

As best shown by the total nutrient analyses, the soils in the five plots are arranged along a gradient of decreasing soil nutrient richness. Plot 1 is situated in the rarely inundated flood plain of the Caquetá River, which is a "white water" river originating in the Andes. The soil in this plot is fine textured and imperfectly to

moderately well drained, and belongs to the so-called moderately poor flood plain soils of the middle Caquetá area (Duivenvoorden and Lips 1993, 1995). The soil is covered by a thin humus form characterised by a leafy F horizon. Plot 2 is situated on a Pleistocene low terrace (non-flooded) of the Caquetá River, while plot 3 is located on the summit of a low hill of a Tertiary sedimentary plain, here built up of clayey sediments of Miocene age. Mineral soils in both these plots are characterised by fine-textured, reddish B horizons within 100 cm depth, and belong to the so-called Ali-Acrisol group (Lips and Duivenvoorden 1996). The humus form in plot 2 is thin, and is characterised by the presence of a leafy F horizon. In plot 3, the humus form is somewhat thicker, and contains a fibrous F and a discontinuous granular H horizon. Plot 4 is situated on a convex upper slope (6°) of a low hill in the Tertiary sedimentary plain, built up of medium to coarse textured Miocene fluvial sediments. The soil in this plot has a medium textured, yellowish B horizon within 100 cm depth, and belongs to the so-called Acri-Ferralsol group (Lips and Duivenvoorden 1996). It is covered by a thick humus form characterised by a well-developed fibrous F and a discontinuous granular H horizon. Finally, plot 5 is located on top of a sandstone plateau, consisting of Paleozoic sandstone of the Araracuara Formation (Bogotá 1983), near Araracuara. The podzolised ("white sand") soil in this plot is shallow (about 50 cm over sandstone) saturated with stagnant water during a large part of the year. The humus form here is very thick and consists mostly of a well rooted, massive H horizon.

Litter fall measurements and laboratory analyses

Fine litter fall, defined as leaves, reproductive parts (flowers and fruits), and twig fractions (pieces of bark and twigs with diameters ≤ 2.5 cm), was measured in 15 traps in each of the five measurement plots of 0.1 ha. Traps were randomly placed at 20 cm above ground level. They consisted of wooden frames of 0.25 m² surface and 10 cm depth, and were floored with a 5 mm wire mesh. They were emptied approximately every 3 weeks. Synchronous emptying in all five plots was impossible for logistic reasons.

At the four upland plots, measurements took place during a continuous period of 50–51 weeks (plots 2 and 3 from 3 March 1989 to 22 February 1990, plot 5 from 3 March 1989 to 21 February 1990, and plot 4 from 7 March 1989 to 19 February 1990; Fig. 2). Initial measurements at the flood plain site (plot 1, from 7 March 1989 to 20 May 1989) were interrupted by flooding of the Caquetá River. After the flooding, traps were replaced and measurements resumed for a continuous period of 51 weeks (from 25 August 1989 to 15 August 1990; Fig. 2). Calculations of the yearly fine litter fall and all chemical analyses of the litter fall in this flood plain plot were based on this second period of measurements.

Litter fall samples were air-dried after collection, and afterwards dried at $60^{\circ}C$ to constant weight. After lumping the leaf litter fall from each of the four periods of leaf fall intensity (see Results), a sample of approximately 200 g was taken for chemical analyses. The twig fraction and the reproductive parts were lumped together into one (yearly) sample for each plot. Before the analyses, the material was coarsely ground (1 cm mesh). Samples of this material were finely ground (0.5 mm mesh).

After digestion with HNO_3 (65%) and H_2O_2 (Westerman 1990), total Ca, Mg, K, and Na were determined by atomic absorption/emission spectrometry, and total P was analysed colorimetrically with a continuous flow auto analyser, using the molybdate blue method (Murphy and Riley 1962). Total N was determined by the Kjeldahl method, with addition of salicylic acid (Bremner and Mulvaney 1982). The organic matter content was estimated by loss on ignition (LOI; 16 h at $500^{\circ}C$). The C percentage was calculated as $LOI/2$. In order to determine area weight ratios, approximately 50 g of leaf litter from each litter fall period was carefully spread out on a perspex plate, photocopied, scanned, and weighted after being dried at $60^{\circ}C$ to constant weight. The surface of the leaves was measured using image-processing computer software (Adobe Photoshop). Methods of sampling and ana-

Table 1 Selected soil and forest data from the five litter fall measurement plots. Total soil nutrient concentrations in parentheses represent ranges from *n* samples in similar physiographic units,

elsewhere in the middle Caquetá area. Original plot numbers are: plot 1=126, plot 2=54, plot 3=112, plot 4=125, plot 5=113. See Duivenvoorden and Lips (1993) for general methods

Plot	Physiographic unit	Soil classification (SSS, 1992)	Depth cm	Sand %	Silt %	Clay %	pH water	CEC ^a	P BrayII mg · kg ⁻¹	Al+H (in KCl) cmol _c · kg ⁻¹	Sum bases ^a soil
1	Flood plain Caquetá River	oxyaquic Dystropept	0–20 50–100	17 25	44 38	39 37	3.9 4.7	15 15	1 1	4.2 6.0	1.4 1.0
2	Low terrace Caquetá River	typic Paleudult	0–20 50–100	36 18	33 34	31 48	4.4 4.5	13 10	3 1	3.8 4.2	<0.6 <0.5
3	Tertiary sedi- mentary plain	typic Paleudult	0–20 50–100	30 21	40 26	30 53	4.2 4.8	15 16	1 2	5.2 7.7	<0.7 <0.6
4	Tertiary sedi- mentary plain	typic Kandiudult	0–20 50–100	56 42	12 9	31 49	4.0 4.7	11 5	1 1	1.8 1.0	<0.7 <0.6
5	Sandstone plateau	typic Psammaquent	0–20 20–50	72 82	24 16	4 2	4.3 –	4 2	1 1	0.6 0.1	<0.8 <0.5

Depth		Total concentrations ^b mineral soil profile (g · kg ⁻¹)						
cm		Ca	Mg	K	Na	P	N	
1	0–20	(0.29–2.28)	(1.78–6.07)	(7.18–12.19)	(0.64–2.89)	(0.20–0.48)	(1.38–3.26)	(n=2)
	50–100	(0.17–0.80)	(2.47–4.76)	(8.83–12.49)	(0.71–1.96)	(0.21–0.37)	(0.60–1.13)	
2	0–20	(0.09–0.17)	(1.23–2.74)	(2.78–7.71)	(0.36–0.56)	(0.23–0.40)	(1.62–4.03)	(n=3)
	50–100	(0.09–0.12)	(1.74–3.24)	(4.29–9.01)	(0.46–0.63)	(0.19–0.34)	(0.72–1.28)	
3	0–20	0.08	1.25	3.84	0.43	0.17	2.00	(n=5)
	50–100	0.08	2.40	9.18	0.79	0.28	0.82	
4	0–20	(0.03–0.08)	(0.06–0.32)	(0.19–0.40)	(0.03–0.11)	(0.06–0.16)	(0.47–1.78)	(n=5)
	50–100	(0.04–0.07)	(0.6–0.41)	(0.24–0.77)	(0.05–0.27)	(0.10–0.20)	(0.26–0.49)	
5	0–20	0.04	0.03	0.11	0.06	0.04	0.64	(n=5)
	20–50	0.045	0.018	0.092	0.056	0.016	0.03	

Humus form type		Necromass (Ø <2.5 cm) (ash-free)			Fine root (Ø ≤5 mm) mass		Sample frames (n)
		L	F	H	F	H	
		mean ± standard error (g · m ⁻²)			mean ± standard error (g · m ⁻²)		
1	1-LF _{leafA}	310 ± 47	650 ± 81	0 ± 0	63 ± 11	0 ± 0	20
2	3-LF _{leafC} Ah	101 ± 18	600 ± 55	0 ± 0	94 ± 14	0 ± 0	15
3	4-LF _{rootA} H _{granularA} Ah	207 ± 22	1000 ± 188	200 ± 218	112 ± 28	60 ± 57	5
4	5-LF _{rootB} H _{granularA}	199 ± 12	1440 ± 147	540 ± 132	690 ± 65	250 ± 73	20
5	8-LF _{rootB} H _{massiveB}	200 ± 52	1460 ± 158	4600 ± 570	380 ± 47	1020 ± 154	5

Floristic forest community		Height canopy m	Density treelets ^c no · (0.1 ha) ⁻¹	Density trees ^d no · (0.1 ha) ⁻¹	Basal area trees ^d m ² · (0.1 ha) ⁻¹	Crown volume trees ^d m ³ · (0.1 ha) ⁻¹
1	<i>Brownea grandiceps</i> – <i>Iriartea deltoidea</i>	19	340	68	2.2	5800
2	<i>Goupia glabra</i> – <i>Clathrotropis macrocarpa</i>	21	1040	72	2.4	5500
3	<i>Goupia glabra</i> – <i>Clathrotropis macrocarpa</i>	30	770	103	4.5	12400
4	<i>Swartzia schomburgkii</i> – <i>Clathrotropis macrocarpa</i>	30	730	100	3.0	12100
5	<i>Mauritia carana</i> – <i>Rhodognaphalopsis brevipes</i>	22	780	82	3.4	7600

^a pH=7, NH₄OAc method^c 1 ≤ DBH < 10 cm, ≥ 2 m height^b Ca, Mg, K, Na, and P in HF/H₂SO₄ extract after combustion at 500 °C, N according to Kjeldahl method^d DBH ≥ 10 cm

Table 2 Yearly above-ground fine litter fall at five mature forest plots in the middle Caquetá area. Based on 15 traps in each plot; SE=standard error; results of Tukey-Kramer HSD pairwise mean comparison tests are shown in parentheses

Plot	Total fine litter		Leaves		Twigs		Reproductive parts	
	mean±SE g · m ⁻² · y ⁻¹	SE/mean %	mean±SE g · m ⁻² · y ⁻¹	SE/mean %	mean±SE g · m ⁻² · y ⁻¹	SE/mean %	mean±SE g · m ⁻² · y ⁻¹	SE/mean %
1	1070±132 (a)	12	710±42 (a)	6	340±112 (a)	33	15±5.3 (a)	36
2	690±57 (bc)	8	610±45 (ab)	7	72±15 (b)	21	5±1.6 (b)	33
3	860±52 (ab)	6	677±23 (a)	3	130±40 (ab)	30	47±17.9 (a)	38
4	680±54 (bc)	8	540±36 (b)	7	113±29 (ab)	26	33±10.9 (a)	32
5	623±21 (c)	3	536±20 (b)	4	68±8 (b)	12	19±4.2 (a)	22

lyses of mineral soil, ectorganic horizons, forest composition, and forest structure are described in Duivenvoorden and Lips (1993, 1995) and Duivenvoorden 1996 and Duivenvoorden (1995, 1996).

Data analyses and statistics

Between-plot differences of litter fall (Table 2) were tested with ANOVA and Tukey-Kramer HSD pairwise mean comparison tests with a significance level of 0.05 (SYSTAT 1992). Prior to these analyses, data were log-transformed in order to homogenise variances, and to increase additivity and normality. Linear spatial autocorrelation of litter fall was analysed by comparing matrices of Euclidean distances between yearly trap data of above-ground total and leaf litter fall in each plot with the matrix of trap distances, by means of Mantel tests applying 250 permutations (R package; Legendre and Vaudor 1991). Pearson correlation coefficients of log-transformed leaf litter fall data between plots (Table 3) were determined, after calculating weighted litter fall sums of uniform intervals of three weeks, assuming constant fall in these intervals. Likewise, cross-correlograms (Davis 1986) were made between log-transformed rainfall and leaf litter fall (Fig. 2), applying successive forward shifts of weekly rainfall periods which were calculated on the basis of daily records from Araracuara. Yearly average elemental concentrations in the total fine litter fall (Table 4) were based on weighted mean concentrations of the litter fall fractions. With respect to leaf litter fall (Table 4), these yearly averages were weighted according to the leaf litter fall in the four litter fall periods. Assuming steady state conditions (Anderson and Swift 1983), decomposition rates are calculated according to the following formula (Olsen 1963):

$$K_1 = L \cdot X^{-1}$$

where K_1 represents the decomposition rate factor of fine litter; L represents the yearly amount of fine litter fall; and X represents the standing stock of fine litter necromass in the ectorganic horizons. Mean residence times represent the reciprocal values of K_1 (Frissel 1981).

Results

Quantity and composition of fine litter fall

Total above-ground fine litter fall varied from 623 g · m⁻² · y⁻¹ on the sandstone plateau to 1070 g · m⁻² · y⁻¹ in the flood plain of the Caquetá River (Table 2). Standard errors of this total fall were 3–12% of the yearly averages. Leaf litter fall was less variable, with standard errors fluctuating around 3–7% (Table 2), which is near the recommended level of 5% (Proctor 1983; Anderson and Ingram 1989). Again, the highest leaf litter fall was recorded in the flood plain (710 g · m⁻² · y⁻¹) and the lowest on

Table 3 Pearson correlation coefficients between leaf litter fall in five mature forest plots in the middle Caquetá area. Based on 13 three weekly sums of overlapping measurement periods

Plot	1	2	3	4	5
1	–				
2	0.48	–			
3	0.54	0.96**	–		
4	0.49	0.94**	0.91**	–	
5	0.29	0.78*	0.80*	0.81*	–

* 0.05 ≤ P < 0.01; ** P < 0.0005 (probabilities Bonferroni adjusted)

the sandstone plateau (536 g · m⁻² · y⁻¹). The Mantel tests did not reveal any significant patterns of linear spatial relationships (Legendre and Fortin 1989) of above-ground total fine and leaf litter fall in the plots (P > 0.05), apart from the total fall in plot 5 (P < 0.04 for both untransformed and log-transformed total fall data). The litter fall of twigs and reproductive parts was relatively low, and varied between 68 and 340, and 5 and 47 g · m⁻² · y⁻¹, respectively (Table 2).

Fine litter fall seasonality

Four periods of leaf fall intensity were arbitrarily distinguished at each plot, by examination of graphs of the leaf fall distribution (Fig. 2). These four periods largely coincided for the four upland plots. A correspondingly high correlation was found between leaf litter fall in upland plots (Table 3). The leaf litter fall in the flood plain plot was less correlated with that from the upland plots. Precipitation at Araracuara did not show any correlation with the leaf litter fall (nor with total litter fall, or the fall of any of the other fractions) in any of the plots. However, the correspondence improved when leaf litter fall was shifted back. Greatest cross-correlations occurred at lags of about 12–13 weeks (Fig. 2). The leaf litter fall seasonality, expressed as the ratio maximum/minimum fall (Morellato 1992), was low in the flood plain and low terrace plots (3.2 and 3.3, respectively), and higher in the three remaining upland plots (7.7, 5.2, and 7.0 in plots 3, 4, and 5, respectively). Seasonality of the total fine litter fall varied from 2.9 to 6.4, which is in the range of 1.6–6.3 encountered in other Amazonian forests (Morellato 1992).

Fig. 2 *Left:* leaf litter fall distribution in the five measurement plots and rainfall recorded at Araracuara. Different shades depict arbitrarily distinguished periods of leaf litter fall intensity. Note that the first measurement period in the flood plain plot was not assigned to any leaf fall intensity period. *Right:* cross-correlograms showing Pearson correlation coefficients between leaf litter fall and rainfall at Araracuara, applying successive lags of 1 week.

Leaf litter area/weight ratio

The specific leaf area/weight ratio (SLA) is inversely related to sclerophylly and is usually applied to living leaves of individual species (Sobrado and Medina 1980;

Medina et al. 1990). Here this ratio is applied to dead leaves originating from various species, as collected in the litter fall traps. Leaf area/weight ratio of samples from each of the four leaf litter fall intensity periods (Fig. 3) yielded highest ratios ($82\text{--}92 \text{ cm}^2 \cdot \text{g}^{-1}$) in the

Fig. 3 Area/weight ratio of leaf litter fall samples from each of the four periods of leaf fall intensity in five rain forest plots in the middle Caquetá area

Fig. 4 Elemental concentrations of leaf litter fall samples from each of the four periods of leaf litter fall intensity in the five measurement plots

flood plain plot. Ratios in the remaining four upland plots were lower (55–69 cm²·g⁻¹).

Nutrient concentrations and fluxes in fine litter fall

Leaf litter fall concentrations of Ca, Mg, P, and N in the four periods of leaf litter fall intensity hardly varied (Fig. 4). Also the ash contents were practically constant in these four periods (not shown). Apart from plot 4, K

concentrations showed an increasing trend, while concentrations of Na decreased, particularly in plots 2 and 5 from period I to II.

Highest concentrations of Ca, Mg, K, P, and N in total fine and leaf litter fall were found in the flood plain plot (Table 4; Fig. 4). Of the four upland plots, the plot on the soil of the Acriferralsol group yielded the lowest Ca, Mg, K, and Na concentrations, while those of P were lowest in plot 3 on a soil of the Ali-Acrisol group. The plot on the sandstone plateau showed the lowest N concentrations and highest C/N ratios.

Table 4 Average yearly elemental concentrations of total above-ground fine litter and leaf litter fall in five mature rain forest plots in the middle Caquetá area

	Plot	Ca	Mg	K	Na	P	N	C	C/N
Elemental concentrations ($\text{g} \cdot \text{kg}^{-1}$)									
Total fine litter fall	1	11.6	2.5	3.4	0.04	0.37	16.7	470	28
	2	2.1	1.2	2.2	0.04	0.17	15.5	485	31
	3	1.7	1.2	3.0	0.03	0.13	12.1	488	40
	4	0.9	0.7	1.4	0.02	0.17	14.9	492	33
	5	1.9	1.5	3.1	0.05	0.17	10.9	491	45
Leaf litter fall	1	10.4	2.7	3.8	0.05	0.41	18.8	467	25
	2	2.0	1.2	2.2	0.04	0.17	16.0	486	30
	3	1.6	1.3	2.9	0.03	0.12	12.9	487	38
	4	1.0	0.8	1.4	0.02	0.15	15.5	492	32
	5	2.0	1.6	3.0	0.05	0.16	11.1	492	44
Litter fall twigs+ reproductive parts	1	14.1	2.1	2.4	0.04	0.27	12.4	467	38
	2	2.5	1.1	1.9	0.03	0.15	12.0	459	39
	3	1.7	0.9	3.1	0.02	0.15	8.9	477	55
	4	0.8	0.6	1.7	0.02	0.23	12.6	475	39
	5	1.7	1.2	3.5	0.02	0.24	9.8	487	50

Table 5 Yearly elemental fluxes of total above-ground fine litter and leaf litter fall in five mature rain forest plots in the middle Caquetá area

	Plot	Ca	Mg	K	Na	P	N	C
Elemental fluxes ($\text{g} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$)								
Total fine litter fall	1	12.4	2.7	3.6	0.05	0.39	17.8	500
	2	1.4	0.8	1.5	0.03	0.11	10.6	332
	3	1.4	1.0	2.6	0.03	0.11	10.4	419
	4	0.6	0.5	1.0	0.02	0.11	10.1	335
	5	1.2	1.0	1.9	0.03	0.11	6.8	306
Leaf litter fall	1	7.4	1.9	2.7	0.03	0.29	13.4	334
	2	1.2	0.7	1.3	0.02	0.10	9.7	296
	3	1.1	0.9	2.0	0.02	0.08	8.7	330
	4	0.5	0.4	0.8	0.01	0.08	8.4	268
	5	1.1	0.8	1.6	0.03	0.09	5.9	264

The flood plain plot showed the highest yearly fluxes of all elements in total fine and in leaf litter fall (Table 5). N had lowest fluxes in the plot on the sandstone plateau. The plot on the soil of the Acri-Ferralsol group showed the lowest yearly fluxes of Ca, Mg, K, and Na. Fluxes of P were remarkably constant in all upland plots.

Fine litter decomposition

Mean residence times for nutrients and organic matter in the L horizon were short, 1.5–4.5 months (Table 6). K shows the shortest mean residence time in the L horizon, and disappears faster than organic matter (Table 7). Ca, Mg, N, and P disappear at more or less the same rate as that of organic matter in all plots.

When F and H horizons are included, residence times (uncorrected for fine root input, see Discussion) of N, P, and organic matter become longer from plot 1 to 5 (Table 6). The order of residence time shifts from $K < Mg < Ca < \text{organic matter} < N \approx P$ in plots 1 and 2, to $K \approx Mg \approx Ca < \text{organic matter} < N < P$ in plot 3, and to $Ca \approx Mg < K < \text{organic matter} < N \approx P$ in plots 4 and 5. Correspondingly, the release of Ca, Mg and, to a lesser degree, of K relative to organic matter (relative turnover

rate, Burghouts 1993), becomes faster from plot 1 to 5 (Table 7). The relative turnover rate of N and P remains more or less constant between the plots.

Discussion

Quantity of total fine and leaf litter fall

In Table 8 the total fine and leaf litter fall data from the five plots in the middle Caquetá area are compared with those from lowland tropical evergreen forests on comparable substrata (i.e. excluding poorly drained, swamp forests and tropical deciduous forests). The flood plain plot from the middle Caquetá area shows a somewhat higher fine litter fall than the average flood plain litter fall in this overview, which is partly related to the low litter fall data from a poor soil, black water "Igapo" flood plain forest near Manaus. The fine litter fall of the three upland plots from the middle Caquetá area is near or below the average fine litter fall from the upland forests on Ulti/Oxisols. The low fine litter fall of the plot on the sandstone plateau near Araracuara corresponds to the low average values found in other humid tropical forests on podzolised soils. The data from the middle Caquetá

Table 6 Mean residence time of major elements and organic matter in the ectorganic horizons of five mature forest plots in the middle Caquetá area. Based on total above-ground fine litter input. Values in parentheses are corrected for dead fine root input (see text)

	Plot	Ca	Mg	K	P	N	OM ^a	OM ^a corrected
Mean residence time (y)								
L horizons	1	0.3	0.4	0.2	0.4	0.4	0.3	
	2	0.2	0.1	0.1	0.1	0.1	0.2	
	3	0.2	0.2	0.1	0.3	0.2	0.2	
	4	0.3	0.2	0.2	0.3	0.3	0.3	
	5	0.2	0.3	0.2	0.4	0.3	0.3	
L+F horizons	1	0.9	0.6	0.5	1.5	1.3	1.0	(0.9)
	2	0.6	0.6	0.4	1.4	1.3	1.1	(0.9)
	3	0.6	0.7	0.6	3.1	1.9	1.4	(1.3)
	4	0.7	0.7	1.0	3.4	3.5	2.5	(1.3)
	5	0.5	0.7	0.9	5.4	3.8	2.7	(1.8)
L+F+H horizons	1	0.9	0.6	0.5	1.5	1.3	1.0	(0.9)
	2	0.6	0.6	0.4	1.4	1.3	1.1	(0.9)
	3	0.6	0.7	0.7	4.1	2.4	1.7	(1.5)
	4	0.7	0.8	1.2	4.7	4.8	3.3	(1.5)
	5	1.0	1.5	2.2	23.5	19.4	10.2	(3.5)

^a OM organic matter

Table 7 Turnover relative to organic matter (relative turnover rate) in five mature forest plots in the middle Caquetá area. Based on above-ground fine litter fall

	Plot	Ca	Mg	K	P	N
L horizons	1	1.0	0.9	1.3	0.8	0.9
	2	1.0	1.2	1.4	1.1	1.1
	3	1.3	1.5	2.3	0.8	1.1
	4	1.0	1.2	1.7	1.2	0.9
	5	1.3	1.2	2.0	0.9	1.2
L+F horizons	1	1.1	1.5	2.1	0.6	0.7
	2	1.7	1.8	2.9	0.8	0.8
	3	2.3	2.0	2.4	0.5	0.8
	4	3.6	3.5	2.4	0.7	0.7
	5	5.0	3.8	3.0	0.5	0.7
L+F+H horizons	1	1.1	1.5	2.1	0.6	0.7
	2	1.7	1.8	2.9	0.8	0.8
	3	2.6	2.3	2.4	0.4	0.7
	4	4.4	4.2	2.7	0.7	0.7
	5	10.0	7.0	4.7	0.4	0.5

area confirm the trend of a decreasing above-ground fine litter production on more nutrient poor soils in humid tropical forests, detected by Vitousek and Sanford (1986).

Seasonality

The highly correlated patterns of leaf litter fall in the upland plots (Fig. 2; Table 3) suggest that leaf litter fall is somehow regulated by regionally operating climatic factors. In other studies from humid tropical lowland forests, peaks in leaf litter fall have been associated with periods of low rainfall, high insolation, or with large number of dry days (Klinge and Rodrigues 1968a; Franken et al. 1979; Adis et al. 1979; Luizão 1989; Cuevas and Medina 1986; Dantas and Phillipson 1989; Scott et al. 1992), but also with periods of high rainfall (Cornforth

1970; Proctor et al. 1983). Lim (1978) reported a negative association between leaf litter fall and rainfall after a lag of 1 month. On the other hand, Puig and Delobelle (1988) found a positive association with a lag of 2–3 months, just as in the present study. Understanding of this delayed response of leaf shedding to rainfall or associated climatic factors requires insight in complex eco-physiological processes, including, for example, leaf growth, longevity, senescence, and nutrient retranslocation before abscission. Less variable soil moisture conditions may be responsible for the low seasonality in the flood plain and the low terrace plots, as both plots occur in non-dissected and topographically low terrain, in contrast to the plots 3 and 4. The high seasonality of plot 5 on the sandstone plateau may be induced by alternating conditions of water saturation and shortage in the “white sand” soil. Seasonality effects might also be responsible for the increasing K and decreasing Na concentrations (Fig. 4). Edwards (1982) and Scott et al. (1992) reported higher K concentrations in litter fall at times of reduced rainfall.

Litter resource quality, nutrient concentrations, and nutrient fluxes

Nutrient concentrations in the litter fall and area/weight ratio of the leaf litter are relatively high in the flood plain plot, compared to the well drained upland plots (plots 2–4). In view of the comparatively rich soil in the flood plain plot, these results are in conformity with trends of declining leaf litter nutrient concentration and increased sclerophylly on more nutrient poor substrata (Chapin 1980; Vitousek and Sanford 1986; Medina et al. 1990). A parallel trend is also found in concentrations of L horizons in humus forms from the Middle Caquetá area (Duivenvoorden and Lips 1995).

In the three upland plots on Ulti/Oxisols, concentrations and fluxes of Ca, Mg, and P are remarkably low

compared to most records from other tropical rain forests on similar substrata. Concentrations are best compared to those of the Central Amazonian forests from San Carlos and Manaus and the Dipterocarp forest of Mulu, Sarawak. The concentrations and fluxes of the metal cations Ca, Mg, K and Na in the litter fall of plot 4 are among the lowest measured in well drained humid tropical evergreen lowland forests around the world. The inferred low mineral cycling in the upland forest stands (Chapin 1980; Vitousek 1982, 1984; Silver 1994) might be related to the occurrence of intensively leached soils and the high rainfall. It is perhaps also due to low levels of atmospheric deposition as a consequence of the prevailing northeast and southeast trade winds passing forested areas, and the substantial water vapour recycling within the Amazon basin (Salati 1985). The belief that the western peripheral region of the Amazon basin would be less oligotrophic than central Amazonia, which is largely based on limnological studies and the presence of less pre-weathered parent materials (Fittkau et al. 1975; Irion 1976; Sombroek 1984; Moura and Kroonenberg 1988; Richter and Babbar 1991), seems not to accord with the tight nutrient cycling observed in the upland forest plots.

Litter fall concentrations may depend on possible leaching during the measurement intervals. Cuevas and Medina (1986) used this line of reasoning to explain the differences in nutrient fluxes in a 1-week interval litter fall study in San Carlos, Venezuela, compared to results from a 4-week interval study of Herrera (1979) and Jordan and Uhl (1980) in the same area. As shown in Table 8, more frequent sampling indeed yielded higher K concentrations ($1.0\text{--}2.4\text{ g} \cdot \text{kg}^{-1}$), but the increase in Ca concentration was much smaller, Mg remained equally low, and P concentration even dropped. In initial phases of litter bag experiments in San Carlos, P, Ca, and Mg concentrations showed hardly any decreases (Cuevas and Medina 1988). Moreover, the permanent separation of the decomposition bags from the soil substratum in these experiments, as in the litter traps in this study, produced a significant reduction of the rate of release of these elements. It seems unlikely, therefore, that initial leaching was responsible for the low Ca, Mg, and P concentrations in this study. However, initial leaching of K cannot be ruled out, especially in view of rapid leaching of K from living and dead leaves found in several other studies (Gosz et al. 1973, 1976; Anderson et al. 1983; Medina 1984).

The plot of the sandstone plateau has a outlying position because Ca and Mg concentrations in the litter fall were higher as would be expected on the basis of the extremely low nutrient concentrations in the mineral horizons of the white sand soil. Again, similar patterns of litter resource quality on white sand soils have been observed elsewhere in the tropics (see Table 8; Whitmore 1989) and were also found in L horizons over podzolised soils in the middle Caquetá area (Duivenvoorden and Lips 1995). They are perhaps related to aspects of leaf longevity, residuary accumulation, or other ecophysiological processes (Chapin 1980). It is also remarkable

that the area/weight ratio of the leaf litter in the plot on the sandstone did not deviate substantially from those of the well drained upland plots (Fig. 3). In the San Carlos area, Venezuela, dominant tree species from upland forests on Ulti/Oxisols and tall Caatinga forests on podzolised soils showed comparable mean specific leaf area (from living leaves) as well (Medina et al. 1990). SLA and area/weight ratio of litter provide only a broad measure of sclerophylly, because, for instance, lignin content and crude fibre to protein ratios may vary as well (Medina et al. 1990). The low N concentration in the plot on the sandstone plateau corresponds to a high N efficiency and assumed N limitation of tropical forests on podzolised soils (Vitousek 1984; Cuevas and Medina 1986).

Decomposition

The small differences in residence times of organic matter and nutrients in the L horizons between the five plots indicate that edaphic properties and litter resource quality are of little importance in the first step of decomposition (i.e. the fragmentation of the litter by soil fauna and the invasion of fungi and roots). Residence times of organic matter and macro nutrients in L horizons of all five plots are equal to or lower than those reported by Burghouts (1993) for leaves in a rain forest of Borneo. Because leaves were defined as fragments $>10\text{ mm}$ by Burghouts (1993), part of the F material may have been included. This may explain the longer residence times in this study.

The mean residence time of the organic matter in all ectorganic horizons combined (uncorrected for fine root input) varied from 1.0 to 3.3 y in the well drained flood plain and upland forests. This is in the range of 0.4–7.7 y recorded for forest floors of 14 tropical evergreen lowland forests (overview in Vogt et al. 1986). The residence time in the plot on the sandstone plateau (10.2 y) is well outside this range. It should be realised that comparisons between decomposition studies are seriously hampered by the high variation in methods applied (Proctor 1983; Burghouts 1993).

Despite the uniform method applied here, the comparison of the decomposition between the five plots remains difficult due to the lack of information concerning input from dead fine roots. A crude correction for fine root input was applied to illustrate the possible effect of fine root mortality upon decay rates of organic matter in the ectorganic horizons (Table 6). Fine root mortality rates from the humid tropics are as yet hardly known, and moreover highly divergent (Sanford 1985; Jordan and Escalante 1980). The correction was, therefore, arbitrarily based on the average fine root mortality rate of 84% derived from 27 records of fine root production and total fine root mass in temperate and boreal forests (Vogt et al. 1986). When corrected for fine root input, the reduction of mean residence times of organic matter was small in the plots with the least amount of fine roots in the ectorganic horizons (7–18% in the plots 1–3). In the plots

Table 8 Overview of above-ground fine litter production, elemental concentrations in leaf litter fall, and elemental fluxes in total above-ground fine litter fall in lowland evergreen tropical rain forests on moderately to well drained flood plain and upland soils (i.e. excluding poorly drained, swamp forests), as well as on podzolised (white sand) soils

	Litter fall		Elemental concentration in leaf litter					Fluxes in total fine litter fall						
	Total fine kg · m ⁻² · y ⁻¹	Leaf kg · m ⁻² · y ⁻¹	Ca g · kg ⁻¹	Mg	K	Na	P	N	Ca g · m ⁻² · y ⁻¹	Mg	K	Na	P	N
Flood plains														
Guamá, Pará, Brazil (11)	0.88	0.70	8.7	3.0	2.6	0.7	0.36	12.4	6.2	—	—	—	0.34	9.6
Guamá, Pará, Brazil (11)	0.77	0.69	8.0	3.8	3.2	0.7	0.36	12.5	7.6	—	—	—	0.34	11.0
Manaus, Brazil (1)	—	—	15.4	3.2	4.9	0.09	0.78	21.0	—	—	—	—	—	—
Manaus, Brazil (1)	0.68	0.53	5.3	1.3	2.9	0.07	0.24	15.0	3.4	0.8	2.0	0.04	0.14	9.5
Mulu, Malaysia (2)	1.15	0.66	24.4	2.0	2.6	0.06	0.27	9.0	28.6	2.0	2.6	0.07	0.41	11.1
<i>Average (excluding present study)</i>	0.87	0.65	12.4	2.7	3.2	0.32	0.43	15.0	11.5	1.4	2.3	0.06	0.31	10.3
Araracuara, Colombia (19)	1.07	0.71	10.4	2.7	3.4	0.05	0.41	18.8	10.4	2.7	3.6	0.05	0.39	17.8
Upland on Ulti/Oxisols														
Guamá, Pará, Brazil (11)	0.93	0.73	3.1	2.8	1.7	0.7	0.41	16.8	3.3	2.7	1.7	0.7	0.41	15.7
Tucuruí, Pará, Brazil (17)	0.67	0.48	7.4	2.3	3.7	0.5	0.5	19.9	4.9	1.4	2.6	0.33	0.30	12.6
Capitao, Pará, Brazil (6)	0.80	—	13.2	1.8	3.3	—	0.41	13.3	11.4	1.6	2.9	—	0.36	11.5
Manaus, Brazil (12)	0.73	0.56	2	2	2	0.8	0.3	15	1.8	1.3	1.3	0.50	0.21	10.5
Manaus, Brazil (7)	0.79	0.64	4.8	1.8	2.1	0.5	0.26	15	—	—	—	—	—	—
Central Amazonia, Brazil (14)	0.83	0.54	3.8	1.8	1.5	—	0.2	18	3.7	1.4	1.5	—	0.31	15.1
San Carlos, Venezuela (13)	—	0.70	1.8	0.9	1.3	—	0.26	12.2	—	—	—	—	—	—
San Carlos, Venezuela (9)	—	0.61	1.4	0.7	1.0	—	0.5	10.0	—	—	—	—	—	—
San Carlos, Venezuela (5)	1.03	0.76	1.7	0.7	2.4	—	0.32	16.3	—	—	—	—	—	—
Maracá, Roraima, Brazil (10)	0.93	0.63	7.4	2.7	4.7	—	0.58	13	6.4	2.4	4.9	—	0.67	11.8
St-Elite, French Guyana (16)	0.77	0.55	3.3	0.5	0.9	1.2	—	14.7	2.5	0.3	3.0	0.60	—	11.5
Maturá, Trinidad (4)	0.70	—	8.2	2.1	1.5	—	0.3	8.0	5.7	1.5	1.1	—	0.24	5.6
Mulu, Malaysia (2)	0.88	0.54	1.5	1.1	4.5	0.09	0.11	9.5	1.3	0.9	3.3	0.08	0.12	8.1
Pasoh, Malaysia (15)	0.89	0.64	7.0	2.2	3.8	—	0.3	11.7	7.0	1.8	3.1	—	0.28	10.0
Banco I, Ivory Coast (3)	1.24	0.82	5.6	4.6	2.2	—	0.69	15.4	6.1	5.1	2.8	—	0.80	17.0
Yapo I, Ivory Coast (3)	0.96	0.71	13.2	2.9	2.8	—	0.50	14.0	10.5	2.3	2.6	—	0.42	11.3
Sabah, Malaysia (18)	1.11	0.65	5.5	2.4	4.8	—	0.37	13.8	6.3	2.5	4.8	—	0.47	15.3
<i>Average (excluding present study)</i>	0.88	0.64	5.3	2.0	2.6	0.63	0.37	13.9	5.4	1.9	2.7	0.44	0.38	12.0
Araracuara, Colombia (20)	0.69	0.61	2.0	1.2	2.2	0.04	0.17	16.0	1.4	0.8	1.5	0.03	0.11	10.6
Araracuara, Colombia (21)	0.86	0.68	1.6	1.3	2.9	0.03	0.12	12.9	1.4	1.0	2.6	0.03	0.11	10.4
Araracuara, Colombia (22)	0.68	0.54	1.0	0.8	1.4	0.02	0.15	15.5	0.6	0.5	1.0	0.02	0.11	10.1
Upland on podzolised soils														
Central Amazonia, Brazil (14)	0.74	0.47	7.7	2.1	3.0	—	0.3	14	5.8	1.4	2.2	—	0.37	10.9
San Carlos, Venezuela (8)	0.81	0.57	5.5	1.6	4.8	—	0.50	7.5	—	—	—	—	—	—
San Carlos, Venezuela (5)	0.56	0.40	7.7	3.1	2.1	—	0.50	7.0	—	—	—	—	—	—
Mulu, Malaysia (2)	0.92	0.56	8.8	1.6	2.3	0.05	0.14	5.7	8.3	1.22	1.8	0.05	0.16	5.5
<i>Average (excluding present study)</i>	0.76	0.50	7.4	2.1	3.1	0.05	0.35	8.5	7.1	1.3	2.0	0.06	0.27	8.2
Araracuara, Colombia (23)	0.62	0.54	2.0	1.6	3.0	0.05	0.16	11.1	1.2	1.0	1.9	0.03	0.11	6.8

(References, see page 148)

with well rooted ectorganic horizons, the reduction was much larger (55 and 66% in the plots 4 and 5, respectively; Table 6). Interestingly, the decomposition rates in plot 3 and 4 approach each other after the correction. This suggests that the much higher necromass of the ectorganic horizons in plot 4 compared to that in plot 3 (Table 1) is possibly not related to lower decomposition rates of above-ground fine litter, but to the larger input of dead fine roots.

Corrections for nutrient residence times in all ectorganic horizons, based on nutrient input by dead fine roots were not attempted, because too little information is available on nutrient concentrations in fine roots, in comparison to those in fine litter (Bloomfield et al. 1993). The mobility sequence and relative turnover rates in the plots 1 and 2, where effects of fine root input are small, stem with results obtained by Burghouts (1993) in a rain forest of Borneo. They also correspond to conclusions based on changing concentrations in ectorganic horizons in the area (Duivenvoorden and Lips 1995). The same sequence is also commonly observed in temperate forests (Gosz et al. 1976; Swift et al. 1979). With respect to the plots 3, 4, and 5, the unknown input of nutrients by fine roots obliterates conclusions on residence times and relative turnover rates. Nevertheless, the change from K as most mobile element to Ca and Mg, as well as the substantial increase in relative turnover rate of Ca and Mg in these plots is remarkable. It coincides with the positive correlation between fine root concentration and proportional decrease in Ca and Mg concentrations in F horizons in the middle Caquetá area, suggesting a highly efficient uptake of these nutrients by fine roots

References to Table 8:

- 1 Adis et al. (1979)
- 2 Anderson et al. (1983); Proctor et al. (1983)
- 3 Bernhard (1970)
- 4 Cornforth (1970); site 2, unclear if litter fall data represent total fine or leaf litter
- 5 Cuevas and Medina (1986)
- 6 Dantas and Phillipson (1989); elemental concentrations of total fine litter fall
- 7 Franken et al. (1979); Klinge, in Adis et al. (1979)
- 8 Herrera (1979) in Cuevas and Medina (1986)
- 9 Jordan and Uhl (1980) in Cuevas and Medina (1986); Jordan et al. (1982)
- 10 Scott et al. (1992)
- 11 Klinge (1977) in Vitousek (1984), Klinge (1976), and Scott et al. (1992); Silva and Lobo (1982)
- 12 Klinge and Rodrigues (1968a, 1968b)
- 13 Medina and Cuevas (1989)
- 14 Luizão and Schubart (1987); Luizão (1989) in Scott et al. (1992)
- 15 Lim (1978)
- 16 Puig and Delobelle (1988); site D; unclear if elemental concentrations are from total fine or leaf litter; data of N represent averages from 4 sites, including a poorly drained site
- 17 Silva (1984)
- 18 Burghouts (1993)
- 19 This study, plot 1
- 20 This study, plot 2
- 21 This study, plot 3
- 22 This study, plot 4
- 23 This study, plot 5

(Duivenvoorden and Lips 1995). Experiments in tropical rain forests in the Río Negro area (Cuevas and Medina 1988) and Singapore (Burslem et al. 1994) also point at nutrient limitations by Ca and Mg. Further research directed to understand the role of Ca and Mg in the nutrient supply and uptake by fine roots, as well as the effects of dead fine root input on humus form development and decomposition in humid tropical rain forests, is needed.

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References

- Adis J, Furch K, Irmeler U (1979) Litter production of a central-Amazonian black water inundation forest. *Trop Ecol* 20: 236–245
- Anderson JM, Ingram JSI (eds) (1989) Tropical soil biology and fertility: a handbook of methods. CAB International, Wallingford
- Anderson JM, Swift MJ (1983) Decomposition in tropical forests. In: Sutton SL, Withmore TC, Chadwick AC (eds) Tropical rain forest: ecology and management. Blackwell, Oxford, pp 287–309
- Anderson JM, Proctor J, Vallack HW (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu national Park, Sarawak. III Decomposition processes and nutrient losses from leaf litter. *J Ecol* 71: 503–527
- Bernhard F (1970) Etude de la litière et de sa contribution au cycle des éléments minéraux en forêt ombrophile de Côte-D'Ivoire. *Oecol Plant* 5: 247–266
- Bloomfield J, Vogt KA, Vogt DJ (1993) Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental forest, Puerto Rico. *Plant Soil* 150: 233–245
- Bogotá J (1983) Estratigrafía del paleozóico inferior en el área Amazónica de Colombia. *Geol Norandina* 6: 29–38
- Bremner JM, Mulvaney CS (1982) Nitrogen – total. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis. Part 2. Chemical and microbiological properties. Soil Science Society of America, Madison, pp 595–624
- Burslem DFRP, Turner IM, Grubb PJ (1994) Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: bioassays of nutrient limitation. *J Trop Ecol* 10: 579–599
- Burghouts TBA (1993) Spatial heterogeneity of nutrient cycling in Bornean rain forest. PhD thesis, Vrije Universiteit, Amsterdam
- Chapin FS III (1980) The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11: 233–260
- Cornforth IS (1970) Leaf-fall in a tropical rain forest. *J Appl Ecol* 7: 603–608
- Cuevas E, Medina E (1986) Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia* 68: 466–472
- Cuevas E, Medina E (1988) Nutrient dynamics within Amazonian forest ecosystems. II. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia* 76: 222–235

- Dantas M, Phillipson J (1989) Litter fall and litter nutrient content in primary and secondary Amazonian 'terra firme' rain forest. *J Trop Ecol* 5: 27–36
- Davis JC (1986) Statistics and data analysis in geology. Wiley, New York
- Duivenvoorden JF (1994) Vascular plant species counts in the rain forests of the middle Caquetá area, Colombian Amazonia. *Biodiversity Conserv* 3: 685–715
- Duivenvoorden JF (1995) Tree species composition and rain forest-environment relationships in the middle Caquetá area, Colombia, NW Amazonia. *Vegetatio* 120: 91–113
- Duivenvoorden JF (1996) Patterns of tree species richness in rain forests of the middle Caquetá area, Colombia, NW Amazonia. *Biotropica* 28, in press
- Duivenvoorden JF, Lips JM (1993) La ecología del paisaje del Medio Caquetá. Estudios en la Amazonia Colombiana, vol 3. Programa Tropenbos-Colombia, Santafé de Bogotá
- Duivenvoorden JF, Lips JM (1995) A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia. Tropenbos Foundation, Wageningen
- Edwards PJ (1982) Studies of mineral cycling in a montane rain forest in New Guinea. V. Rates of cycling in throughfall and litter fall. *J Ecol* 70: 807–827
- Fittkau EJ (1974) Zur ökologischen Gliederung Amazoniens I. Die erdgeschichtliche Entwicklung Amazoniens. *Amazoniana* 5: 77–134
- Fittkau EJ, Irmiler U, WJ, Reiss F, Schmidt GW (1975) Productivity, biomass, and population dynamics in Amazonian water bodies. In: Golley FB, Medina E (eds) Tropical ecological systems. Springer, Berlin Heidelberg New York, pp 289–311
- Franken M, Irmiler U, Klinge H (1979) Litter fall in inundation, riverine and terra firme forests of central Amazonia. *Trop Ecol* 20: 225–235
- Frissel MJ (1981) The definition of residence times in ecological models. *Ecol Bull* 33: 117–122
- Gosz JR, Likens GE, Bormann FH (1973) Nutrient release from decomposing leaf and branch litter in the Hubbard Brook forest, New Hampshire. *Ecol Monogr* 43: 171–191
- Gosz JR, Likens GE, Bormann FH (1976) Organic matter and nutrient dynamics of the forest floor in the Hubbard Brook Forest. *Oecologia* 22: 305–320
- Herrera RA (1979) Nutrient distribution and cycling in an Amazon caatinga forest on Spodosols in southern Venezuela. PhD dissertation, University of Reading, England
- Holdridge LR, Grenke WC, Hathway WH, Liang T, Tosi JA (1971) Forest environments in tropical life zones, a pilot study. Pergamon, Oxford
- Hoorn C (1994) Miocene palynostratigraphy and paleoenvironments of northwestern Amazonia. PhD thesis, University of Amsterdam
- Irion G (1976) Mineralogisch-geochemische Untersuchungen an der pelitischen Fraktion amazonischer Oberböden und Sedimente. *Biogeographica* 7: 7–25
- Jordan CF, Escalante G (1980) Root productivity in an Amazonian rain forest. *Ecology* 61: 14–18
- 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
- Jordan C, Caskey W, Escalante G, Herrera R, Montagnini F, Todd R, Uhl C (1982) The nitrogen cycle in a 'Terra Firme' rainforest on oxisol in the Amazon territory of Venezuela. *Plant Soil* 67: 325–332
- Klinge H, Rodrigues WA (1968a) Litter production in an area of Amazonian terra firme forest. Part I. Litter-fall, 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. Part II. Mineral nutrient content of the litter. *Amazoniana* 1: 303–310
- Klinge H (1976) Bilanzierung von Hauptnährstoffen im Ökosystem tropischer Regenwald (Manaus)-vorläufige Daten. *Biogeographica* 7: 59–77
- Klinge H (1977) Fine litter production and nutrient return to the soil in three natural forest stands of eastern Amazonia. *Geo-Eco-Trop* 1: 159–167
- Köppen W (1936) Das geographische System der Klimate. In: Köppen W, Geiger R (eds) Handbuch der Klimatologie, Bd I, teil C. Gebr. Bornträger, Berlin
- Legendre P, Fortin M (1989) Spatial pattern and ecological analysis. *Vegetatio* 80: 107–138
- Legendre P, Vaudor A (1991) The R package: multidimensional analysis, spatial analysis. Département de sciences biologiques, Université de Montréal
- Lim MT (1978) Litter fall and mineral nutrient content of litter in Pasoh Forest Reserve. *Malaysian Nat J* 30: 375–380
- Lips JM, Duivenvoorden JF (1996) Regional patterns of well drained upland soil differentiation in the middle Caquetá basin of Colombian Amazonia. *Geoderma* 1098 (in press)
- Luizão FJ (1989) Litter production and mineral element input to the forest floor in central Amazonian forest. *Geo J* 19: 407–417
- Luizão FJ, Schubart HOR (1987) Litter production and decomposition in a terra-firme forest of Central Amazonia. *Experientia* 43: 259–265
- Medina E (1984) Nutrient balance and physiological processes at the leaf level. In: Medina E, Mooney HA, Vazquez-Yanes C (eds) Physiological ecology of plants in the wet tropics. Junk, The Hague, pp 139–154
- Medina E, Cuevas E (1989) Patterns of nutrient accumulation and release in Amazonian forests of the upper Rio Negro basin. In: Proctor J (ed) Mineral nutrients in tropical forest and savanna ecosystems. Blackwell, Oxford, pp 217–240
- Medina E, García V, Cuevas E (1990) Sclerophylly and oligotrophic environments: Relationships between leaf structure, mineral nutrient content and drought resistance in tropical rain forests of the upper Río Negro region. *Biotropica* 22: 51–64
- Morellato LPC (1992) Nutrient cycling in two south-east Brazilian forests. I. Litter fall and litter standing crop. *J Trop Ecol* 8: 205–215
- Moura ML, Kroonenberg SB (1988) Major and minor elements geochemistry and mineralogy of four soil profiles from Aracua, Colombian Amazonas. *Catena* 15: 81–97
- Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Anal Chim Acta* 27: 31–36
- Olsen JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322–331
- Proctor J (1983) Tropical forest litter fall. I. Problems of data comparison. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rain forest: ecology and management. Blackwell, Oxford, pp 267–273
- Proctor J, Anderson JM, Fogden SCL, Vallack HW (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litter fall, litter standing crop and preliminary observations on herbivory. *J Ecol* 71: 261–283
- Puig H, Delobelle J (1988) Production de litière, nécromasse, apports minéraux au sol par la litière en forêt guyanaise. *Rev Ecol Terre Vie* 43: 3–22
- Richter DD, Babbar LI (1991) Soil diversity in the tropics. *Adv Ecol Res* 21: 315–389
- Salati E (1985) The climatology and hydrology of Amazonia. In: Prance GT, Lovejoy TE (eds) Key environments: Amazonia. Pergamon, Oxford, pp 18–48
- Sanford RL (1985) Root ecology of mature and successional Amazon forests. PhD thesis, University of California, Berkeley
- Scott DA, Proctor J, Thompson J (1992) Ecological studies on a lowland evergreen rain forest on Maracá Island Roraima, Brazil. II. Litter and nutrient cycling. *J Ecol* 80: 705–717
- Silva MFF da, Lobo MA (1982) Nota sobre deposição de matéria orgânica em floresta de terra firme, várzea e igapó. *Bol Mus Paraense Emílio Goeldi N S Botânica* 56: 1–13
- Silva MFF da (1984) Produção anual de serrapilheira e seu conteúdo mineralógico em mata tropical de terra firme. *Tucuruí-Pa. Bol Mus Paraense Emílio Goeldi Botânica* 1: 111–158

- Silver WL (1994) Is nutrient availability related to plant nutrient use in humid tropical forests? *Oecologia* 98: 336–343
- Sobrado MA, Medina E (1980) General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the 'Bana' vegetation of Amazonas. *Oecologia* 45: 341–345
- Sombroek WG (1984) Soils of the Amazon region. In: Sioli H (ed) *The Amazon: limnology and landscape ecology of a mighty tropical river and its basin*. Junk, Dordrecht, pp 521–535
- SSS (Soil Survey Staff) (1992) *Keys to soil taxonomy*, 5th edn (SMSS technical monograph 19). Blacksburg, Virginia
- Swift MJ, Heal OW, Anderson JM (1979) *Decomposition in terrestrial ecosystems*. Blackwell, Oxford
- SYSTAT (1992) SYSTAT: Statistics, version 5.2 edn. SYSTAT, Evanston
- Van der Hammen T, Duivenvoorden JF, Lips JM, Urrego LE, Espejo N (1992a) Late Quaternary of the middle Caquetá River area (Colombian Amazonia). *J Quat Sci* 7: 45–55
- Van der Hammen T, Urrego LE, Espejo N, Duivenvoorden JF, Lips JM (1992b) Late-glacial and Holocene sedimentation and fluctuations of river water level in the Caquetá River area (Colombian Amazonia). *J Quat Sci* 7: 57–67
- Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forest. *Annu Rev Ecol Syst* 17: 137–167
- Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. *Am Nat* 119: 553–572
- Vitousek PM (1984) Litter fall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285–298
- Vogt KA, Grier CC, Meier CE, Keyes MR (1983) Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root input. *Ecol Monogr* 53: 139–157
- Vogt KA, Grier CC, Vogt DJ (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Adv Ecol Res* 15: 303–377
- Westerman RL (1990) *Soil testing and plant analysis*, 3rd edn (Soil Science Society of America Book Series 3). SSSA, Madison
- Whitmore TC (1989) Tropical forest nutrients, where do we stand? A tour de horizon. In: Proctor J (ed) *Mineral nutrients in tropical forest and savanna ecosystems*. Blackwell, Oxford, pp 1–13