Rainfall input, throughfall and stemflow of nutrients in a central African rain forest dominated by ectomycorrhizal trees

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Abstract. Incident rainfall is a major source of nutrient input to a forest ecosystem and the consequent throughfall and stemflow contribute to nutrient cycling. These rain-based fluxes were measured over 12 mo in two forest types in Korup National Park, Cameroon, one with low (LEM) and one with high (HEM) ectomycorrhizal abundances of trees. Throughfall was 96.6 and 92.4% of the incident annual rainfall (5370 mm) in LEM and HEM forests respectively; stemflow was correspondingly 1.5 and 2.2%. Architectural analysis showed that ln(funneling ratio) declined linearly with increasing ln(basal area) of trees. Mean annual inputs of N, P, K, Mg and Ca in incident rainfall were 1.50, 1.07, 7.77, 5.25 and 9.27 kg ha^{-1}, and total rain-based inputs to the forest floor were 5.0, 3.2, 123.4, 14.4 and 37.7 kg ha^{-1} respectively. The value for K is high for tropical forests and that for N is low. Nitrogen showed a significantly lower loading of throughfall and stemflow in HEM than in LEM forest, this being associated in the HEM forest with a greater abundance of epiphytic bryophytes which may absorb more N. Incident rainfall provided *c*. 35% of the gross input of P to the forest floor (i.e., rain-based plus small litter inputs), a surprisingly high contribution given the sandy P-poor soils. At the start of the wet season leaching of K from the canopy was particularly high. Calcium in the rain was also highest at this time, most likely due to washing off of dry-deposited Harmattan dusts. It is proposed that throughfall has an important 'priming' function in the rapid decomposition of litter and mineralization of P at the start of the wet season. The contribution of P inputted from the atmosphere appears to be significant when compared to the rates of P mineralization from leaf litter.

Introduction

In tropical forest ecosystems, important interactions occur between hydrological and nutrient cycles (Bruijnzeel 1989, 1991). Independent of the amounts of nutrients in the incident rainfall, significant amounts are added and transferred from above-ground plant parts to the forest floor as the rainwater passes through the canopy. The two routes are by throughfall and by stemflow. Throughfall is that part of the incident rainfall which passes through the forest canopy, this either directly in gaps or interacting with the vegetation (Bruijnzeel 1989; Lloyd and Marques

1988). Stemflow is the part which is funnelled down the trunks of the trees (Herwitz 1986; Jordan 1978). The difference between the sum of these two fluxes and the incident rainfall gives the canopy interception. Compared to the rate of mineralization from decomposing litter, fluxes of nutrients as throughfall and stemflow are much more rapid. The elements are largely in dissolved inorganic forms which can be taken up immediately by trees. Throughfall data for tropical forests have been reported to be highly variable within sites (Clarke 1987; Forti and Neal 1992). Sampling designs which did not take full account of the high spatial, and sometimes high temporal, heterogeneity of the forest canopy were the main reason (Lloyd and Marques 1988). Stemflow studies have received far less attention in this respect.

At edaphically extreme sites, mechanisms are expected to minimize the potential rapid loss of dissolved nutrients mainly by leaching. This is an important principle in forest ecosystem thinking (DeAngelis 1992; Likens et al. 1977) and is especially important in the tropics where high rainfall occurs at sites with well-draining soils. Selection should favour species that maximally retain potentially limiting nutrients. There are different ways in which this can be achieved but in old primary forest particularly advanced long-evolved forms of optimal cycling are to be found (Chuyong et al. 2000; Jordan and Herrera 1981). The formation of a surface soil root mat which captures and retains leachable nutrients is one such adaptation (Newbery et al. 1997; Stark and Jordan 1978).

Newman (1995) has shown that phosphorus (P) inputs from the atmosphere and lithosphere (deposition and weathering respectively) can be very critical to the long-term stability of many ecosystems. Inputs from both sources are typically in the order of 0.1–1.0 kg ha^{-1} yr^{-1}, and these are in a similar range to estimated losses of 0.01–0.7 kg ha^{-1} yr^{-1} (Bruijnzeel 1990, 1991). There are good grounds for suggesting that P input is an essential determinant of long-term tropical forest dynamics on highly-weather substrates.

In Korup National Park, Cameroon, groves of large ectomycorrhizal legumes of high stature are found growing on sandy, acidic and characteristically low-P soils (Gartlan et al. 1986; Newbery et al. 1988). Nutrient studies within and outside of these groves have shown a characteristic cycle for P enhanced by ectomycorrhizal symbiosis (Chuyong et al. 2000; Newbery et al. 1997). With a high rainfall of typically > 5200 mm yr^{-1} and a long rainy season of 9 mo (Newbery et al. 1998), rain water constitutes an important pathway for nutrient transfer to the forest floor. In the first weeks of the wet season much of the annual litter decomposition occurs and this is also a time, after the 3-mo dry season, when rainfall and nutrient cycles might strongly interact (Chuyong 1994). Lodge et al. (1994) have discussed the pulsed nature of mineralization in tropical forests in terms mainly of water and carbon availability to the soil microflora.

This paper aims to quantify the inputs of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg) and calcium (Ca) from rainfall, and the throughfall and stemflow of these elements to the forest floor within and outside of the ectomycorrhizal groves, to highlight the role that these nutrients may play in facilitating litter decomposition and mineralization. The thesis presented here is that rain-based

input of P may ameliorate a P-limitation to early decomposition in the P-poor soils of Korup. The paper is the third and final part of a set of nutrient studies. Parts 1 and 2 were Chuyong et al. (2000, 2002).

Materials and methods

Sample plot selection and layout

Two blocks of 50 m × 50 m (0.25 ha) were demarcated along the southern edge of transect 'P', close to the subplots used for the already-reported studies of nutrient cycling through litterfall (Chuyong et al. 2000; Newbery et al. 1997) and litter decomposition (Chuyong et al. 2002). Block 1 was within the eastern half of the transect characterized by low abundance of ectomycorrhizal species (LEM forest), 60 m south of plot '3A'; and block 2 was within the central half (i.e., the grove) which had a high abundance of ectomycorrhizal trees (HEM forest), 10 m south of plot '15A'. A detailed map of the plots is shown in Newbery et al. (1997).

The square shape and size of the blocks allowed the inclusion of whole crowns of several emergent and dominant species, some of which reached 25 m in diameter. A total of 303 and 331 stems (with dbh, diameter at breast height, $\geqslant$ 5 cm) were enumerated in blocks 1 and 2 respectively and these were classifiable into twenty-two 5-cm-interval dbh classes. The floristic composition of both blocks was similar to that described for transect P in Gartlan et al. (1986) and Newbery et al. (1997): block 1 was close to their plot P1 and block 2 close to plot P15.

Branching angles were classified on a nominal scale as follows: 1 – obtuse (> 90°), 2 – perpendicular (75–90°), 3 – oblique (45–75°), 4 – very oblique (< 45°). The crown positions of the trees in relation to the upper canopy level were also scaled as: 1 – understorey, 2 – lower canopy, 3 – upper canopy, and 4 – emergents.

Water flow

Rainfall
Incident rainfall sampled for chemical analysis was collected in a steep-angle polyethylene funnel (20 cm in diameter) mounted on a 3-m wooden pole and fixed at the top of a crownless 32-m-tall tree. The funnel was connected to a covered 20-l plastic collecting bucket on the forest floor by a long 20-mm-diameter rubber hose. The collector was positioned between the two blocks, in the centre of a gap 2000 m^2 in area. The surrounding trees were 35–40 m tall with an average crown depth of 8 m. This meant that the collector was not within the projection of the tallest trees and there was little chance of contamination from rain drops splashing neighbouring foliage.

Incident rainfall, for the purposes of comparison with throughfall and stemflow, was taken from the records for a conventional rain-gauge (0.0127-m^2 collecting

area) at the Bulu meteorological station (PAMOL Ndian) located *c*. 10 km SE of the two blocks.

Stemflow

To measure stemflow volumes, samples of 18 and 20 stems were selected from blocks 1 and 2 respectively. These sample sizes were based on the equation of Freese (1962) using 95% confidence limits from preliminary sampling. Trees that were to be fitted with stemflow collars were selected randomly and, as far as was possible, in numbers proportional to the total number of trees in each diameter class in the blocks. The frequency distribution, the numbers of collared trees for each dbh class and morphological descriptions (species type, dbh, crown position, branching habit) are to be found in Chuyong (1994). Stemflow collars consisted of a 25-mm-diameter high-quality rubber hose slit longitudinally and sealed to the trunk in an upward spiral with U-shaped steel clips and an inert silicon sealant (SILASTIC[R]). The lower complete portions of hosing directed the stemflow into black 50-l plastic jerrycans. The collars were mounted at the breast height (1.3 m above the forest floor). For stems with buttresses or malformations at breast height, collars were mounted 0.3 m above these irregularities. The spirals were steep enough to allow a rapid emptying of the rain water from the collars. Collars were checked regularly for leakages.

Throughfall

Ten collectors were laid-out in each block in a systematic pattern to sample throughfall. Each block was subdivided into five E-W strips (5 m × 50 m) and two collectors were located within each. They were randomly relocated within the same strip after each collection. The throughfall collectors consisted of steep-angle polyethylene funnels (20 cm in diameter) mounted on 16-l plastic buckets standing on the forest floor. Each funnel was held upright by a stopper of solidified silicon sealant at the centre of the bucket lid. The rims of the funnels were 0.7 m above the ground to prevent water droplets and soil particles splashing in from the forest floor. The steep angle of the collecting funnels also minimized splash-out during rain storms. The neck of each funnel had a piece of 2-mm nylon gauze to prevent litter and debris entering the collectors. Gauzes were cleaned regularly to avoid blockages.

Nutrients

Collection, preservation and storage of samples

Incident rainfall, throughfall and stemflow were measured and sampled over a period of 12 months from February 1992 to January 1993. From March 1992 to June 1992, volumetric measurements were taken fortnightly (mid and end of each month) as rainfall intensity was then low. Between July and November 1992 the frequency of measurement was increased to 4–7 times per month to prevent the collectors from overflowing. In December 1992 and January 1993, the rainfall was so low that it generated neither throughfall nor stemflow in either forest block. Samples were measured in the field using a 10-l graduated bucket (with 0.5-l graduations)

for stemflow and throughfall, and a 500-ml measuring cylinder (with 5-ml graduations) for incident rainfall. Subsamples of 30 ml were collected from each collector at each sampling occasion and returned to laboratory at the Forest Research Station, Kumba. These samples were stored in high quality polyethylene bottles at < 3 °C with the addition of five drops of chloroform (1% pro volume) to minimize microbial degradation.

In the laboratory, the samples collected for a particular month and collector were bulked and a final subsample of 30 ml was stored for chemical analysis. The bottles had very tight caps which prevented volatilization and diffusion of gases. Photochemical reactions were minimized by storing them in black polythene bags. In March 1993 all of the stored water samples were air-freighted to the University of Stirling, and stored in a cold room (< 3 °C) until analysis.

Chemical analysis

Subsamples of incident rainfall and throughfall were pooled for each month and block to give composite samples. Stemflow samples of the individual trees were also pooled as composite samples the months of March/April, June/July, September/October and May/August/November. Of each composite sample, 25 ml was digested in 1.0 ml of digestion mixture (H_2SO_4:Se:$LiSO_4$) for 3 h. After cooling, each digested sample was filtered through a Whatman filter paper (N° 44) and made up to 20 ml with deionised water used in rinsing the digestion tube and paper. Total N and P were determined colorimetrically on a flow-injection autoanalyzer, Ca and Mg by atomic absorption spectrophotometry, and K by flame emission spectrophotometry. The analytical methods are described in Chuyong (1994) and Chuyong et al. (2000). The detection range was 0–1.0 mg l^{-1} for N and P as their concentrations were low in the samples.

Confirmatory checks on cation and anion concentrations were made on 30-ml composite samples of throughfall and incident rainfall by the Institute of Hydrology, Wallingford, UK (courtesy of Dr C. Neal). The data are not used in this paper.

To check for nutrient adsorption to walls of collectors and storage bottles, standard stock solutions of N (10 and 50 mg l^{-1}) and P (5 and 10 mg l^{-1}) were left in collectors for 2 wk in the field and then stored in plastic bottles for 6 mo at < 3 °C. Samples were analyzed with the same procedures as the composites ones above.

Data analysis

Rainfall (mm, Bulu) was converted to litres of rain on an entire block (0.25-ha) basis: the units of measurement for throughfall and stemflow were already in litres (31.83 l of rainwater is equivalent to 1 mm).

Throughfall was also estimated for the entire block in each forest type and corrected for the basal area of stems (i.e., the area over which throughfall was collected was the total plot area minus the area of the stems). The total stem basal areas sampled were 8.2 and 8.9 m^2, representing 0.33 and 0.36% of the total area of blocks 1 and 2 in LEM and HEM forests respectively. The sampled trees were grouped into size classes (5–<10, 10–<15, 15–<25, 25–<40, 40–<65 and ⩾65

cm dbh). Mean stemflow volumes were calculated for each of these classes, and then multiplied by the number of trees in those size classes, for each block. These values were then summed to provide estimates of the total stemflow for both blocks. Finally, proportions of throughfall and stemflow to incident rainfall and the interception loss in both forests were calculated.

Throughfall variability in each forest type was examined by expressing the throughfall catch of the individual collectors at each sample point and duration as a percentage of incident rainfall recorded for that same duration.

Stemflow from each sample tree was summed over the entire period and the total volume used to compute the funneling ratio from the equation of Herwitz (1986):

$$FR = V/BG$$

where FR = funneling ratio, V = stemflow volume (l), B = basal area (m^2) and G = the depth equivalent of rainfall (mm). Funneling ratio relates stemflow volume to the expected volume from a rain-gauge with a collecting area equivalent to the stem's basal area. Trees with ratios exceeding unity indicate that funneling of rain water had occurred. These ratios were used to compare the magnitude of stemflow for the different trees and individuals of the same species. Dbh, canopy position and branching angle were correlated with stemflow and FR using the Spearman non-parametric coefficient.

Volumetric weighted means were found by multiplying individual nutrient concentrations by their sample volumes, summing and then dividing by the total volume collected.

The annual inputs per block of N, P, K, Mg and Ca in incident rainfall, throughfall and stemflow for both forests were found by multiplying their respective weighted mean concentrations by the estimated volumes. These were then expressed per unit area of forest. Net nutrient transfer from plant parts were obtained by subtracting the inputs in incident rain from the sum of throughfall and stemflow. Stemflow inputs of the each sample tree were also summed over the entire period and expressed per unit forest area. These were then used to compare the nutrient inputs of the different species, and different individuals of those species.

Results

Water flow

Incident rainfall
The incident rainfall recorded within the study area from February 1992 to January 1993 was 5370 mm (Table 1), a value slightly higher than the annual mean rainfall of 5011 mm (range 4023–6146) for the period 1984–2000. Rainfall was recorded during each month of the study period though less frequently in the dry season. Rainfall was low in February 1992 (dry season) and increased sharply from April to a peak in July 1992. This was followed by a gradual drop in rainfall until the

Table 1. Monthly records (mm) of incident rainfall, throughfall and stemflow from February 1992 to January 1993 in forest plots with low (LEM) and high (HEM) abundances of ectomycorrhizal trees in Korup National Park, Cameroon. Throughfall and stemflow estimates are expressed in depth equivalence of incident rainfall.

Months	Incident rainfall (mm)		Throughfall (mm)		Stemflow (mm)	
	Amount	No of rainy days	LEM	HEM	LEM	HEM
February 1992	2	1	0	0	0	0
March	169	15	154	114	1.9	1.6
April	227	19	230	176	2.8	2.7
May	340	20	266	215	3.7	3.4
June	831	25	680	653	8.9	14.2
July	1197	26	1091	1166	15.0	26.5
August	1048	29	986	919	17.8	28.2
September	751	22	795	754	14.9	23.2
October	509	24	727	720	10.7	15.6
November	255	19	258	245	3.7	4.9
December	35	3	0	0	0	0
January 1993	6	1	0	0	0	0
TOTAL	5370	204	5187	4962	79.5	120.3

next dry season in December 1992. A total of 204 rainy days were recorded, with the highest number of rainy days in August 1992 (Table 1).

Throughfall
The total amounts of throughfall recorded from February 1992 to January 1993 were 5187 and 4962 mm in the LEM and HEM forests respectively. These values corresponded to 96.6 and 92.4% of incident rainfall in the two forests (Table 1). The estimated interception loss was 1.6 and 5.4% in the LEM and HEM forests respectively. Rainfall was low in the months of February 1992, December 1992 and January 1993, being just enough to wet the forest canopy but not generating any throughfall (Table 1). Total annual throughfall was only 4% lower in HEM than LEM forest. Nevertheless, there were considerable spatial and temporal variations in the amounts of throughfall recorded in both forests. The relocation of the throughfall collectors led to 410 and 400 individual sampling points being used in LEM and HEM forests respectively.

Individual throughfall at each point, expressed as a percentage of incident rainfall, ranged from 0% (in the dry season with little or no rain) to 810%, with medians of 94.2 and 105.3% in the LEM and HEM forests respectively. Forty-one (49%) of these individual points recorded greater throughfall than incident rainfall, and nine (12%) of them had more than twice the rainfall in the LEM and HEM forests (Figure 1). Comparisons of percentage point records with the Mann-Whitney U-test showed significantly lower throughfall in the HEM than LEM forest as a result of higher canopy interception loss in the former ($P < 0.05$). Monthly
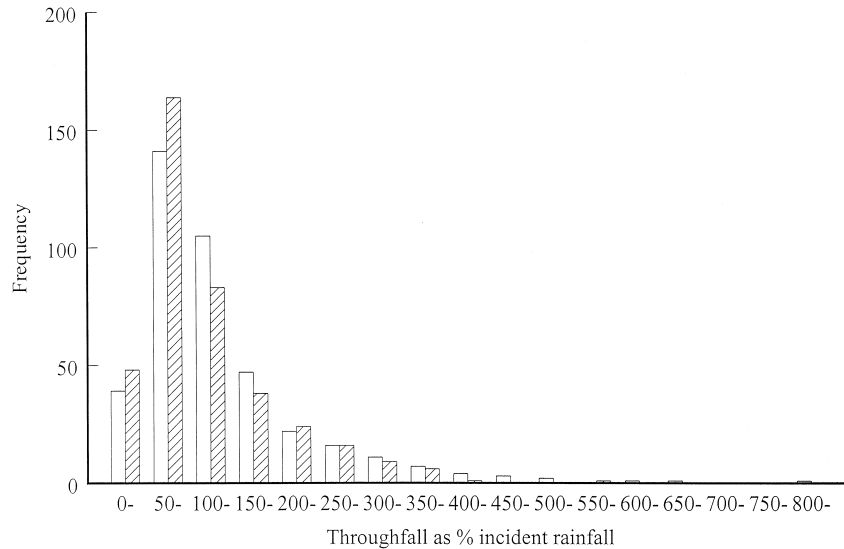
Figure 1. Frequency distribution of throughfall catch expressed as percentage of incident rainfall from 410 and 400 sample points respectively in one 50-m × 50-m block in each of forest with low (LEM, open bars) and forest with high (HEM, hatched bars) abundances of ectomycorrhizal trees in Korup National Park, Cameroon.

throughfall was strongly correlated with incident rainfall (r = 0.91 and 0.90 for LEM and HEM forests respectively, n = 12, P < 0.001).

Stemflow

Total stemflow estimates (expressed in mm of incident rainfall) for the period February 1992 to January 1993 were 80 and 120 mm (Table 1), constituting 1.5 and 2.2% of the annual incident rainfall in LEM and HEM forests respectively. Monthly stemflow was significantly and positively correlated with incident rainfall (r = 0.91 and 0.94 for LEM and HEM forests respectively, n = 12, P < 0.001). Rainfall in the months of February 1992 and January 1993 was below the threshold (10 mm) expected to generate any stemflow, whilst the highest value of stemflow for both forests was in August 1992. Total annual stemflow was 51% higher in the HEM than in the LEM forest (Table 1).

Stemflow estimates were very variable and high values were recorded for lower canopy and even understorey species. This variability among different trees (also within the same species) was reflected in their funneling ratios (FR). These ratios ranged from 0.1 to 54.1, with 75% of the sampled trees having FR > 1.0, 56% with > 5.0 and 21% with > 20.0.

Stemflow was not significantly correlated with dbh or basal area (r_s = 0.074, df = 36, P = 0.659), and not with canopy position (r_s = 0.195, P = 0.240); it did show a significant positive correlation with branching angle (r_s = 0.481, P = 0.002), however. Funnelling ratio was strongly negatively correlated with dbh and basal area
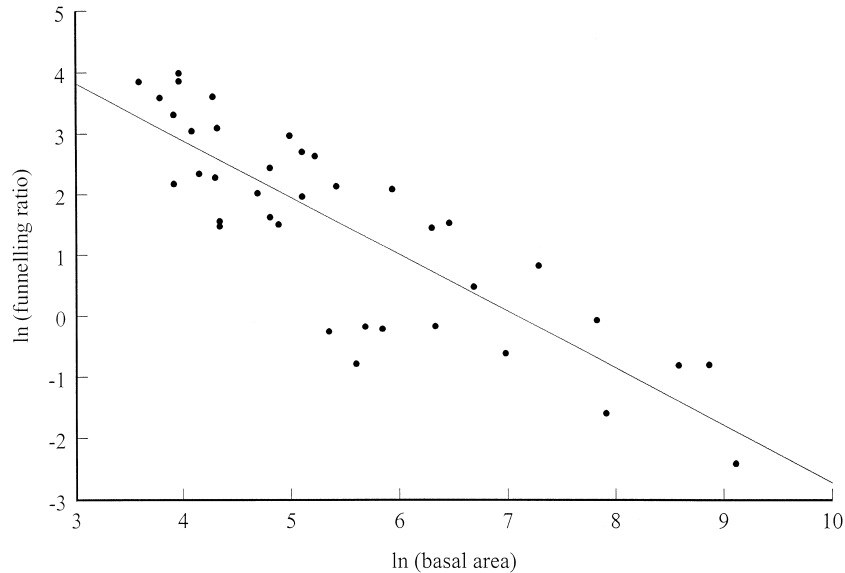
Figure 2. Relationship between funneling ratio and basal area for 38 individual trees measured for stem flow, combined for the two blocks, one in forest with low and one in forest with high abundances of ectomycorrhizal trees in Korup National Park, Cameroon. (ln (FR) = 6.63–0.935 ln(BA), df = 36, r^2 = 0.709, P < 0.001)

(r_s = −0.846, P < 0.001; Figure 2) and canopy position (r_s = −0.635, P < 0.001) but not with branching angle (r_s = 0.177, P = 0.287).

Nutrients

Nutrient concentrations and fluxes

The concentrations of the various elements in incident rainfall, throughfall and stemflow fluctuated throughout the year because there was a strong interaction with the amount of incident rainfall (Table 2). The volumetric weighted mean concentration of the different nutrient elements in incident rainfall were in the following order: Ca > K > Mg > N > P. The weighted concentration of K in throughfall-plus-stemflow was 12.4–14.4 fold (i.e., 'LEM-HEM') that of incident rainfall, a value much higher than those of 2.7–2.3 for N, 3.3–3.7 for P, 2.9–3.5 for Mg and 2.21 (both forests) for Ca. The fluxes of these nutrient elements showed little or no differences in throughfall and stemflow between forest blocks, except for N which had a mean throughfall concentration in the LEM forest almost 2-fold (maximum > 3-fold) that in HEM forest (Table 3).

Two further variables can be defined:

$$\text{Total input} = \text{throughfall} + \text{stemflow}$$

$$\text{Rainfall loading} = (\text{throughfall} + \text{stemflow}) - \text{incident rainfall}.$$

Table 2. Mean and ranges of concentrations (mg l^{-1}) of N, P, K, Mg and Ca in composite samples of incident rainfall, throughfall and stemflow collected from February 1992 to January 1993 in LEM and HEM plots in Korup National Park. The values in parenthesis are weighted volumetric means.

Element		Incident rainfall	Throughfall		Stemflow	
			LEM	HEM	LEM	HEM
N	means	0.04 (0.03)	0.11 (0.13)	0.07 (0.06)	0.09 (0.07)	0.11 (0.06)
	range	0.001–0.07	0.04–0.44	0.04–0.13	0.01–0.86	0.001–1.26
P	means	0.03 (0.02)	0.10 (0.06)	0.11 (0.07)	0.11 (0.06)	0.11 (0.05)
	range	0.001–0.08	0.22–0.45	0.03–0.33	0.001–1.35	0.001–0.78
K	mean	0.29 (0.15)	3.73 (2.37)	4.14 (2.41)	3.98 (2.88)	5.07 (2.78)
	range	0.01–0.79	1.10–12.5	1.23–13.5	0.13–14.2	0.06–61.6
Mg	mean	0.13 (0.10)	0.37 (0.34)	0.45 (0.32)	0.50 (0.34)	0.42 (0.29)
	range	0.03–0.34	0.13–1.16	0.18–1.18	0.01–3.21	0.01–1.70
Ca	mean	0.52 (0.17)	1.14 (0.70)	1.14 (0.75)	1.58 (1.20)	1.51 (0.93)
	range	0.01–2.50	0.20–3.54	0.43–3.66	0.19–9.10	0.20–10.40

Table 3. Nutrient fluxes in incident rainfall, throughfall and stemflow in LEM and HEM forests in Korup National Park, and a comparison with small litterfall fluxes.

Source	Forest type	Nutrient fluxes (kg ha^{-1} yr^{-1})				
		N	P	K	Mg	Ca
Incident rainfall		1.50	1.07	7.77	5.25	9.27
Throughfall	LEM	6.93	2.95	122.4	12.3	36.1
	HEM	2.87	3.31	118.9	15.8	37.2
Stemflow	LEM	0.06	0.04	2.22	0.27	0.92
	HEM	0.07	0.06	3.27	0.34	1.09
Rainfall loading	LEM	5.49	1.92	116.9	7.27	27.8
	HEM	1.44	2.32	114.4	10.9	29.1
Total (rain-based) input	LEM	6.99	2.99	124.6	12.5	37.1
	HEM	2.94	3.39	122.2	16.2	38.3
Total small litterfall input	LEM	150	6.13	39.5	19.7	111
(from Chuyong (1994))	HEM	136	5.89	34.7	19.7	96.0
Total rain-based and small	LEM	157	9.12	164	32.2	148
litter input (gross input)	HEM	139	9.28	157	35.9	134
% incident rainfall of mean		1.0	11.6	4.8	15.4	6.6
gross input (LEM + HEM)						
% total (rain-based) input of	LEM	4.5	32.8	76.0	38.8	25.1
gross input	HEM	2.1	36.5	77.8	45.1	28.6

The amounts of nutrients reaching the forest floor as rain-based input annually, averaging over the two forest types, were 5.0, 3.2, 123.4, 14.4 and 37.7 kg ha^{-1} for N, P, K, Mg and Ca respectively. Of the total N inputs to the forest floor, 21% was from incident rainfall and 79% from rainfall loading in the LEM block but 51%

was from incident rainfall and 49% from rainfall loading in the HEM block (Table 3). Average rainfall loadings were 94% for K, 65% for P, 60% for Mg and 75% for Ca.

Variation in concentrations with time

Concentrations of K, Ca and Mg declined throughout the wet season (March to November) but increased again with the last rains before the dry season (in December; Figure 3). Nitrogen and P showed little seasonal variation. Calcium decreased the most and the fastest in incident rainfall, followed by K and then Mg (Figure 3a), but K decreased the most in throughfall followed by smaller changes in Ca and then Mg (Figure 3b). This reflects, for the three cations, a combining of the different relative nutrient concentrations in the early wet season rainfall with their relative susceptibilities to early canopy leaching.

Storage checks

Standard solutions showed that less than 2% of N and P was lost due to storage in plastic containers at low concentrations, and between 10 and 18% at high concentrations. With the low to very low concentrations of the samples it is safe to conclude that the storage effect was indeed negligible.

Discussion

Throughfall and stemflow

Throughfall and stemflow results at Korup, expressed as proportions of incident rainfall, were similar to those found in other studies. For example, in lowland rain forest in Sabah and in central Kalimantan throughfall was 81 and 87% and stemflow 2 and 1% respectively (Asdak et al. 1998; Sinun et al. 1992), whilst in central and western Amazonian lowland forest the values were correspondingly 91 and 85% and 1 and 2% (Lloyd and Marques 1988; Marin et al. 2000). Sites will largely vary depending on amount of rainfall per annum and the proportion of rain falling in the day and night which determines the degree of canopy evaporation (Parker 1983).

Tree architecture is an important factor in stemflow and funneling. Trees with more oblique branch angles (plagiotrophic) spread their canopies wider than those with more perpendicular branches (orthotropic): they present greater areas of catchment. Whilst stemflow was not correlated, funneling ratio declined strongly with tree size and canopy position. Smaller (understorey) trees funnelled proportionally more water down their stems than larger (canopy) ones. Presumably smaller trees caught much of the water that dripped from larger trees especially during stronger rains, whilst in light showers the taller trees absorbed more water and evaporated much of it before it fell through or ran down the stems. The double logarithmic
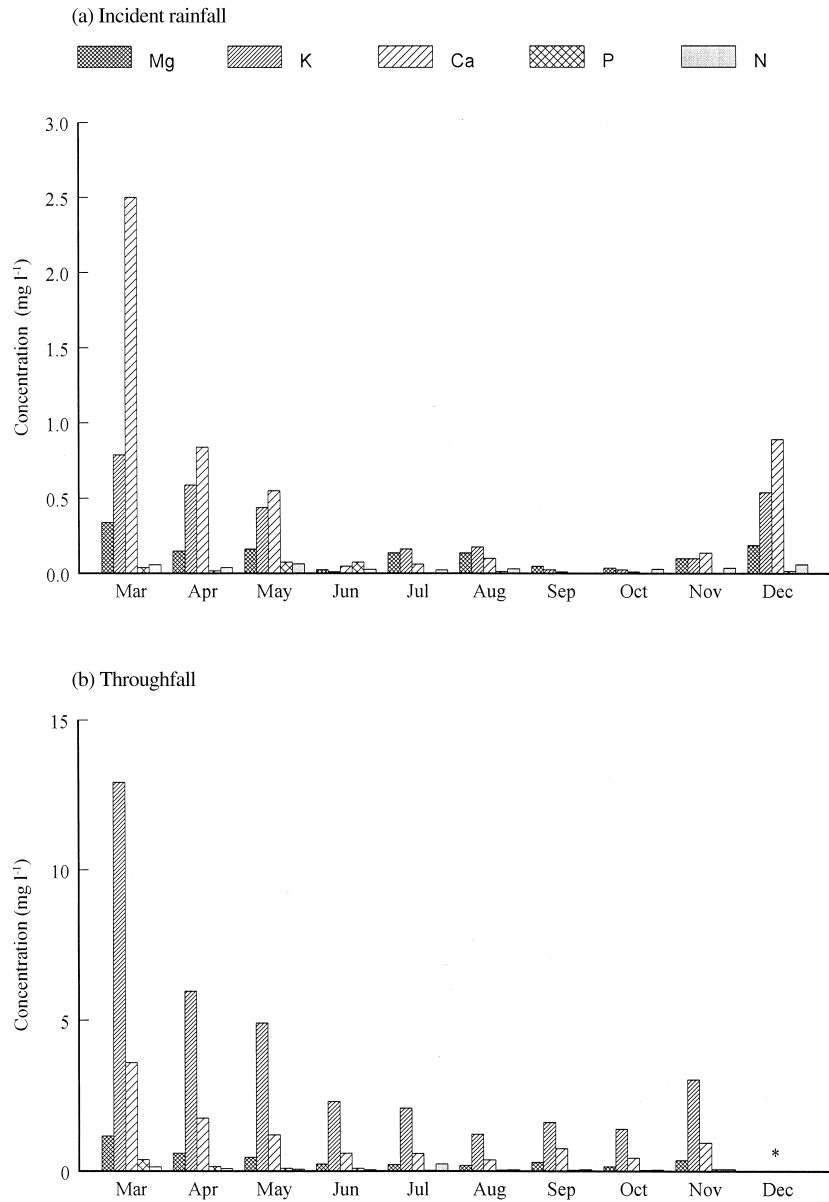
(a) Incident rainfall

Mg   K   Ca   P   N

(b) Throughfall

Figure 3. Change in the concentrations of five nutrients (N, P, K, Mg and Ca) in (a) incident rainfall, and (b) throughfall, in Korup National Park, averaged for the two blocks (LEM and HEM). March and December are the starting months of the wet and dry seasons respectively. The '*' indicates no data since for this month there was no throughfall (see Table 1).

relationship in Figure 2 suggests that at least two exponential processes are involved.

The high rainfall at Korup favours considerable growth of the epiphytic bryophytes on leaves, branches, trunks and other plant parts. Chuyong et al. (2000) showed a 4-fold higher fall (implying production) of mosses and lichens in the HEM compared to LEM forest, with much of that in the HEM forest being associated with the large limbs of trees of the dominant ectomycorrhizal species, *Microberlinia bisulcata* A. Chev. This led to an increased canopy interception (retention of rainwater and lower throughfall in HEM). Epiphytic bryophytes have been shown, at least for montane sites, to retain a considerable proportion of the inorganic N in incident rainfall (Clark et al. 1998a, 1998b) so this would probably account for the lower throughfall N concentrations in HEM than LEM forest.

Inputs via rainfall

Incident rainfall is not only an important source of nutrient input to the forest ecosystem but it is also an important means of nutrient transfer from the canopy to the forest floor. Total small litterfall inputs (Chuyong 1994; Chuyong et al. 2000) allow the gross inputs (litter plus rain-based) to be found (Table 3). Phosphorus and Mg in incident rainfall contributed 12 and 15% respectively of the gross input to the forest floor whilst for N, K and Ca the values were only 1–7% (Table 3). Total rain-based inputs (incident plus loaded) accounted for 39–45 and 25–29% (i.e., 'LEM-HEM') of the gross inputs of Mg and Ca, with a substantial 76–78% for K. It is nevertheless remarkable that as much as 33–37% of the gross input of P was rain-based. Nitrogen by contrast contributed very little by way of incident rain or total rain-based inputs (2–5%).

There are relatively few data with which to compare the Korup site. In a review, Proctor (1987) showed that nutrient input in total rainfall (kg ha^{-1} yr^{-1}) in tropical lowland forests (five sites) ranged between 5–21 for N, 0.4–2.3 for P, 4–18 for K, 0.2–20 for Mg, and 3–30 for Ca. The minimum and maximum for P (0.4, 2.3) are for the only two known African sites to date in Ghana and in Côte d'Ivoire, these being the works of Nye (1961) and Bernhard-Reversat (1975) respectively. The values for Korup (Table 3) were therefore lower for N, but lying within the ranges reported for P, K, Mg and Ca.

Additionally for P, the nutrient of focal interest here, Lewis (1981) reported 1.68 kg ha^{-1} yr^{-1} atmospheric input to rain forest in Venezuela, and Wilcke et al. (2001) 0.6 kg ha^{-1} yr^{-1} in montane Ecuador, but by contrast Campo et al. (2001) recorded 0.16 kg ha^{-1} yr^{-1} for Mexican dry forest, Hendry et al. (1984) 0.2 kg ha^{-1} yr^{-1} for dry forest in Costa Rica, and Filoso et al. (1999) 0.1 kg ha^{-1} yr^{-1} for the Negro River area in NE Brazil. Some of the other studies of nutrients incident in rainfall either did not include P, or did not measure it over a whole year. Overall, however, P input in rainfall shows a 10-fold range in the tropics, with an indication that wetter sites tend to have greater P inputs than drier ones: Korup with 1.07 kg ha^{-1} yr^{-1} P lies accordingly towards the upper end of the range since it has a 9-mo wet season. Newman (1995), in his valuable review of P inputs worldwide, used just the most reliable and technically sound data available (20 studies), and concluded that atmospheric P inputs ranged from 0.07 to 1.7 kg ha^{-1} yr^{-1}.

The nutrients in incident rainfall are largely either in the form of dissolved elements or particles. Their concentrations are determined by many natural and anthropogenic factors (such as wind movements, incidence of fires and dusts, distance from the sea). In the present context, it is worth noting that N was low at Korup but P and Ca were relatively high (especially in the early wet season) which suggest that inputs from fire might have been small in 1992–93 (see Robertson and Rosswall (1986) for a review of N). Calcium is generally associated with airborne soil dust (Lovett and Lindberg 1984; Møberg et al. 1991) and this most likely accounts for the high input of Ca at the end of the dry season and early wet season in Korup (Figure 3a). Analyses of Harmattan dusts show that fine silt fractions are carried the furthest from their source in the Chad basin and that they are relatively rich in Ca. Tiessen et al. (1991) recorded ratios of Mg: K: Ca of 0.37: 0.82: 1 in northern Ghana, whilst Stoorvogel et al. (1997) found ratios of 0.11: 0.71: 1 in trapped dust in the Taï region of Côte d'Ivoire. For comparison, incident rain in March at Korup (Figure 3a) had ratios of 0.14: 0.32: 1.

Concentrations of Mg (besides Na) in incident rainfall have been associated with maritime air masses. The Korup site is 50 km directly north of the Bay of Biafra and therefore probably experiences some maritime effect on the air masses causing rainfall, and more especially in the main wet season. The Ca/Mg ratio in rainfall over the whole year for the present study was 1.77, a value higher than the ratio of 1.0 found for two sites close to the sea (Brasell and Sinclair 1983; Waterloo et al. 1997), suggesting that the maritime influence was weaker than the Saharan one.

The measurements in Korup using funnel collectors did not distinguish completely between dry and wet deposition. It is likely, however, that dry impaction of fine dust and other particles on the funnels was less than that on vegetation surfaces, when expressed per unit ground area (see Newman (1995)). This means that throughfall probably contained further dry-deposited P; and throughfall-minus-incident-rainfall estimates (Table 3) were part atmospheric inputs and part canopy leachates. Only further more sophisticated recording will separate these components properly.

Link with decomposition and nutrient cycling

The first rains of the wet season leach the canopy of nutrients, especially of K, and the throughfall wets the litter on forest floor (Table 1, Figure 3). At this time the leaf litter mass is at its greatest after a build-up over the dry season (Chuyong et al. 2000; Newbery et al. 1997). Litter-bag studies revealed a mean turn-over time (i.e., when litter dry mass has been reduced by *c.* 99%) of 3.6 mo for leaves in the LEM and HEM forests (Chuyong et al. 2002). This agrees closely with estimates of earlier studies where the half-life of decomposing leaf litter was found to be 53 days (Newbery et al. 1997). Furthermore, the rate of leaf litter disappearance on the forest floor (based on the balance of litter fall and litter mass over time) was highest in April, 1 mo into the wet season (Chuyong et al. 2000). Thus despite the soil being poor in nutrients (especially P and K; Gartlan et al. (1986) and Newbery et

al. (1988, 1997)), leaf litter decomposition was found to be rapid. Could the nutrients – particularly P or K – in throughfall and stemflow facilitate decomposition?

The litter bag studies of Chuyong et al. (2002) also showed that *c.* 80% of the K in freshly fallen leaf litter was released in the first month and thereafter (until month 6) there was little change. This was not different in LEM and HEM forests and species differed very little in their rates of K mineralization. Phosphorus, Mg and Ca were mineralized much more gradually over time and, for six of the seven species tested, N was immobilized. Species differed though in their rates of loss in dry mass and in P concentration, with ectomycorrhizal species (which dominate HEM forest) losing less dry mass yet having a net mineralization of P over 6 mo, compared with non-ectomycorrhizal species losing more dry mass and tending to immobilize P. But decomposition did not differ significantly between forest types, and forest × species and forest × time interactions were very weak. Since throughfall and stemflow inputs of P and K were very similar (Table 3) in both forest types, it seems that the overall differences in decomposition rates between species was largely due to physical and chemical properties of those species, primarily their litter P concentrations (Chuyong et al. 2002).

The organic layer of fine roots and ectomycorrhizas above the sandy soil is more developed in the HEM than LEM forest (Moyersoen et al. 1998; Newbery et al. 1988, 1997) and hence, the retention is likely to be better in HEM than in LEM surface soils. It is therefore likely that more rain-based P is held in the organic layer of HEM than LEM forest and this could facilitate further the decomposition of leaf litter (mostly of ectomycorrhizal species) in HEM forest.

Whilst P mineralization and immobilization were quite closely balanced over a 6-mo period of decomposition (Chuyong et al. 2002), the amount of P inputted from rain and via throughfall and stemflow might be a critical factor determining the rate of mineralization. *Microberlinia bisulcata*, the dominant species in HEM forest for example (contributing 39% of the leaf litter mass; Chuyong et al. (2000)) had a 20% decrease in the concentration of litter P at the end of month 1, this remaining as such up to month 4, and then gradually immobilizing again by month 6 to the same concentration as at the start. These four months were the time when nearly all of the annual P was inputted in rainfall and subsequently as throughfall and stemflow (Figure 3). This P would have been added to the inorganic pool in the surface soil and could perhaps have released a potential limitation of P on decomposition. This would be an example of an input to an ecosystem which increased its internal rate of cycling.

Whilst Table 3 shows the litter input of P when fully decomposed over a year, a more precise calculation is afforded for the early wet season from several related studies of the HEM forest at Korup. Litter mass on the forest floor was recorded as 0.33 kg m^{-2} in early March by Newbery et al. (1997). Chuyong et al. (2000) found that freshly fallen litter had a P concentration of 0.68 mg g^{-1}, which means an amount of P in the litter of 2.244 kg ha^{-1}. By mid-May litter mass had fallen to 0.08 kg m^{-2} with an estimated concentration of 0.544 mg g^{-1}, or P amounting to 0.435 kg ha^{-1}. The difference in amounts, 1.809 kg ha^{-1}, is what presumably was mostly mineralized. Table 3 shows a total rain-based input to the HEM forest floor

of 3.39 kg ha^{-1} yr^{-1}, this mostlyl coming in March-June. Close to a third of this input was of external origin via the rainfall (Table 3). The input to the litter layer and soil was thus 1.9-fold the amount mineralized to the soil in the early wet season. In this context it can be hypothesized, by association, that throughfall and stemflow is probably an important 'primer' of litter decomposition and mineralization.

The thin layer of organic matter, fine roots and ectomycorrhizas, developed especially in the HEM forest (Newbery et al. 1988, 1997) is very important for the recycling of nutrients such as P, but also probably for the efficient capture of more mobile ones such as K and Mg. The importance of the root mat with such a function was first proposed for Amazonian forests by Stark and Jordan (1978). The early weeks of decomposition in Korup at the start of the wet season are likely to involve some synchrony between the leaching and mineralization of not only P, but also other nutrients. It might be speculated that the strong rain-based input of K and Mg stimulates fine root and ectomycorrhizal activity which in turn facilitates and maximizes the mineralization and uptake of P. This leads to new ideas about the interactions between parts of connected cycles of different nutrients.

Conclusion

This paper completes a set of three (the former two being Chuyong et al. (2000, 2002)) which have compared in detail the nutrient cycling in LEM and HEM forests. The relatively high concentrations of P in falling leaf litter of ectomycorrhizal species (Chuyong et al. 2000) leads to their rapid decomposition and P mineralization on the surface of the P-poor soil (Chuyong et al. 2002). It is here shown that this is probably facilitated by the rain input and throughfall of P to the litter layer. That this seemingly 'non-conservative' type of nutrient cycle can work at all, without presumably too much loss by leaching, depends on the fine-root and ectomycorrhizal mat just below the litter layer which, it is proposed, catches and retains P and other elements efficiently. A fast rate of return of P to the tree (mineralization plus 'directly' associated mycorrhizal activity; see Newbery et al. (1997)) allows for adequate tree growth rates, especially of the dominant ectomycorrhizal species. It also largely explains how such a high-biomass forest is indeed possible on such an infertile site (Gartlan et al. 1986; Newbery and Gartlan 1996). Nevertheless, this ecosystem is probably highly unstable and if the essential thin surface organic layer of the soil were destroyed the forest would likely be unsustainable and possibly irrecoverable for maybe several centuries.

Elucidating this advanced cycle with its highly adapted ectomycorrhizal tree species, has been possible because of the considerable evolutionary age of the Guinea-Congolean rain forest refugium in which Korup lies (see Gartlan (1992)). Forest dynamic cycles have presumably established a long-term equilibrium in terms of the utilization of nutrient resources by the trees. The nutrient cycle of P now allows a more refined hypothesis of how this tropical ecosystem functions.

Acknowledgements

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