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Spatial heterogeneity of element and litter turnover in a Bornean rain forest

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ABSTRACT. The spatial heterogeneity of element fluxes was quantified by measuring litterfall, throughfall and litter decomposition for 1 y in 30 randomly located sampling areas in a lowland dipterocarp rain forest. The idea tested was that turnover of elements is more variable than turnover of dry matter in a forest with extremely high tree species diversity. In spite of the low fertility of the soil (an ultisol), total litter production (leaves, trash, and wood <2 cm in diameter) was high (1105 g m^{-2} y^{-1}) with inputs to the forest floor of carbon, nitrogen, phosphorus, calcium, magnesium, potassium, manganese and iron of 550, 15.3, 0.47, 6.26, 2.49, 4.75, 0.95 and 0.14 g m^{-2} y^{-1} respectively. Throughfall was 81% of the annual rainfall and transferred 22.2, 1.37, 0.14, 1.07, 0.67, 0.39, 7.92, <0.06, and <0.06 g m^{-2} y^{-1} of organic carbon, nitrogen (all forms), phosphorus, sulphur, calcium, magnesium, potassium, manganese and iron, respectively. Average turnover rates of nutrients in litter were highest for potassium and decreased in the sequence calcium, magnesium, carbon, nitrogen and phosphorus. Concentrations of phosphorus, nitrogen and potassium in litterfall, litter mass and topsoil were closely correlated with each other. Concentrations of calcium and manganese were positively correlated with each other and with elevation. Variations in leaf chemistry and total litterfall caused the spatial heterogeneity of element input to the forest floor to have a coefficient of variation of 30 – 70%, depending on the element. Due to the strong positive correlation between element fluxes and pools, the spatial variability of turnover rates (CV *c.* 20%) was lower than that of element input. Turnover rates for K varied by a factor of 4, and for Ca by a factor of 2.8 when the different sites were compared. The results strongly suggest that the most important factor determining spatial heterogeneity of organic matter and element dynamics on the forest floor is the site-specific amount of leaf fall, rather than spatially variable decomposition rates.

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KEY WORDS: calcium, decomposition, litterfall, litter turnover, nitrogen, nutrient cycling, phosphorus, rain forest, spatial heterogeneity, throughfall

INTRODUCTION

A major aspect of ecosystem research concerns the factors that determine the rate of nutrient fluxes and turnover in the system. Nutrient cycling rates in forests are usually inferred from a comparison of nutrient concentrations and amounts in litterfall, forest floor litter, and crown drip (Proctor 1987, Vitousek & Sanford 1986), however, due to variations in canopy architecture and tree species, amounts and rates of litterfall, throughfall and decomposition show considerable spatial variation. This spatial heterogeneity allows coexistence of species (Tilman 1982) and contributes to niche differentiation for seedlings (Molofsky & Augspurger 1992) and forest floor organisms (Swift & Anderson 1989). Spatial heterogeneity is expected to be particularly prominent in lowland tropical rain forests because of the variable canopy structure and the extremely high species diversity found in these forests (Richards 1996). In spite of its importance to the mosaic-like growth cycle of rain forests (Whitmore 1990), this spatial heterogeneity has received little attention in the context of element cycling (Swift & Anderson 1989, Vitousek & Sanford 1986).

For a long time, the forest floor of lowland tropical rain forests was thought of as a uniform, thin layer of leaf litter covering plain mineral soil (Whitmore 1984). Ashton (1964), however, observed a marked patchy accumulation of litter under the crowns of two dipterocarp species in Borneo. Similarly, the 'sclerophyllous' character of the leaves of various tree species in a Nigerian rain forest only received attention after the observation that partly decomposed litter accumulated under those trees (Madge 1965). Differences in chemical composition between leaves of different tree species in a variety of rain forests have been shown to be associated to some extent with different decomposition rates (Anderson *et al.* 1983, Spain & LeFeuvre 1987, Tanner 1981). These observations suggest that the forest floor in species-rich forests consists of a mosaic of leaf litter of variable nutrient content resulting in spatially variable decomposition rates.

In our previous studies of leaf fall and leaf-litter decomposition in a lowland dipterocarp forest setting in the Ulu Segama Forest Reserve (Sabah, Malaysia), amounts of leaf litter on the forest floor were found to be strongly correlated with local amounts of total leaf fall (Burghouts *et al.* 1992). This suggests that spatial variation in litter turnover may be smaller than expected from variation in litter fall alone. This hypothesis needs to be tested more thoroughly, however, by comparing total element fluxes, rather than decomposition rates only. It may be expected that the variable chemical composition of leaves will cause turnover of elements to be more variable than turnover of dry matter. The objective of the present paper is therefore to provide an insight into the spatial variability of element turnover, through an analysis of nutrient contents in

throughfall, litterfall and litter layer mass. By comparison of turnovers measured at a number of replicated sites within a single forest plot, an attempt is made to identify factors associated with heterogeneity.

STUDY AREA

Location

The study was carried out during the period March 1988 – January 1990 in the Danum Valley Conservation Area in the Upper Segama area in Sabah, Malaysia, in the northeastern part of Borneo (4° 58′ N, 117° 48′ E). The lowland rain forest of the study area is dominated in its upper and emergent canopy by Dipterocarpaceae. This family reaches its highest diversity in Borneo with 10 genera and 270 species described to date (Whitmore 1984). Dipterocarps make up 88% of the total volume of large trees in the Danum Valley Concession Area (Marsh & Greer 1992).

The 4-ha (100-m × 400-m) research plot used in this study was located near the Danum Valley Field Centre (DVFC); trees of the plot ('plot 1') were enumerated by Newbery *et al*. (1992). The plot lies at 210–240 m a.s.l., with slopes varying between 10–40° (25° on average) and is underlain by sandstones of the Kuamut formation in which an ultisol has developed (Leong 1974, Newbery *et al.* 1992). The soil had a typical particle size distribution at 30 cm depth of *c*. 38% clay, 36% silt, and 26% sand, i.e. of sandy-loam texture (Van der Plas & Bruijnzeel 1993).

Climate

Rainfall data over a period of 5 y (1986–1990) suggest a slightly bimodal annual distribution with a mean annual value of *c*. 2800 mm. This pattern is influenced by edge effects of two monsoons: the wetter northeast monsoon from November to March and the drier but more consistent southwestern monsoon in June and July. Although the onset of both monsoons is quite variable there is a general trend for drier spells during the transition months of April and September (Marsh & Greer 1992). Showers usually fall as short, intensive events in the afternoon or evening. Daily average temperatures vary little throughout the year, with a mean of 26.7 °C recorded at the DVFC climate station over the 5-y period, but there is considerable diurnal variation (typically ranging from 22.5 °C in the early morning to *c*. 31 °C shortly after noon). The average relative humidity in the open at the DVFC is close to 100% from 18h00 to 08h00 whereas it fluctuates between 60 and 100% during daytime, with annual means of 95% at 08h00 and 72% at 14h00 (Burghouts *et al.* 1992, Marsh & Greer 1992). Characteristics of the forest micro-climate have been given by Brown (1990) and Brown & Whitmore (1992). Mean minimum and maximum temperatures within the forest were 21.2 and 28.4 °C (1987–1988), whereas the minimum and maximum relative humidity fluctuated between 90 and 100%. The stagnant atmospheric conditions prevailing close to the forest

floor, below a largely closed canopy, effectively limit rates of evaporation from the litter layer during the rainy season to values as low as 0.1 mm d^{-1} (L.A. Bruijnzeel, unpubl. data).

METHODS

Sampling points and sampling areas

Thirty sampling points were randomly selected within the research plot. Around each of these points a sampling area of 10-m radius was defined which in a few cases overlapped with an adjacent sampling area when the corresponding centres were less than 20 m apart. Litterfall and throughfall were measured from 1 April 1988 until 1 January 1990 at each of the 30 sampling points. The botanical composition of vegetation and litterfall within the 30 sampling areas has been presented in Burghouts *et al.* (1994), whereas results on spatial and temporal variations in leaf litterfall, leaf-litter mass, leaf-litter disappearance and abundance of forest floor invertebrates were reported in Burghouts *et al.*(1992).

Litterfall

Each litter trap consisted of 0.1-mm nylon mesh with an area of 0.7 m^2 suspended on four PVC poles placed 0.5 m above ground level. Litterfall was collected weekly, dried to constant weight for 1 wk in a solar drying house (generally at 65 °C but at variable temperatures during cloudy days), bulked to monthly amounts for each trap and then sorted into the following fractions which were subsequently weighed to the nearest 0.1 g: (1) leaves or leaf fragments (>10.0 mm, designated as LLF); (2) coarse trash (5.1–10.0 mm, including leaf fragments and reproductive parts); (3) fine trash (0.1–5.0 mm, including leaf fragments, insect frass and fine reproductive parts); and (4) twigs (<2 cm diameter) and small woody litterfall (<2 cm along the longest axis).

Dried leaf samples for each sampling point were bulked to 3-mo samples (50–300 g) which were dried for another 3 d to enable pulverization by hand into fragments <1 cm. Representative samples of 50 g from this mixture were stored in sealed plastic bags for transport to Amsterdam and subsequent chemical analysis. Monthly samples of trash (both coarse and fine) were bulked to yearly samples for each sampling point whereas monthly amounts of woody litterfall were bulked to 3-mo samples for the entire plot. The material was chopped in small fragments after which representative samples were taken for chemical analysis.

Non-woody litterfall (LF) was calculated for each sampling area as the sum of leaf fall (LLF) and coarse and fine trash (FLF) but excluding woody litterfall of any kind. An overview of the symbols used and their units is provided in Table 1.

Forest floor litter mass and topsoil

The mass of litter (including fine roots) on the forest floor was determined five times at 3-mo intervals between December 1988 and December 1989. On

Table 1. Overview of nomenclature used in this paper for litter and element fluxes, pools and turnovers.

Variable	Symbol
Fluxes (g m^{-2} y^{-1})	
Leaf fall	LLF
Coarse and fine trash fall	FLF
Non-woody litterfall	LF = LLF + FLF
Woody litterfall	WLF
Rainfall	RF
Throughfall	TF
Net throughfall	TF – RF
Pools (g m^{-2})	
Leaf litter mass	LLM
Fine litter mass	FLM
Litter mass	LM = LLM + FLM
Turnovers (y^{-1})	
Leaf litter turnover	k_{LLF} = LLF/LLM
Non-woody litter turnover	k_{LF} = LF/LM
Element turnover including throughfall	k_{LF+TF} = (LF + TF – RF)/LM

each occasion, two random samples were taken in each sampling area using a 25-cm diameter steel corer. Although the litter layer was easily distinguished from the mineral soil by its loose structure and brown colour which contrasted with the compact, yellow-red soil material, it was not always possible to separate the two in practice. After sampling, the spots were marked to avoid resampling.

Litter-layer material was separated into four fractions at the DVFC laboratory (*cf.* Table 1): (1) leaf-litter mass: leaves and recognizable leaf parts (>10 mm, designated LLM); (2) fine, or fragmented litter mass (≤10 mm, designated FLM); (3) twigs (<2 cm diameter) or small woody litter (<2 cm along the longest axis); and (4) fine root mass (<3 mm diameter). The total litter mass (LM) was defined as the sum of leaf-litter mass (LLM) and fine litter mass (FLM) but without any material that was recognizable as fine roots or woody litter.

Litter-mass samples were treated in a manner similar to litterfall samples, except that every 3 mo for each sampling point 40 and 100 g of coarse and fine litter mass, respectively, were kept separate for chemical analysis.

After removal of the litter layer, ten topsoil (0–8 cm) samples were taken randomly in each sampling area with a 2-cm diameter corer within a distance of 5 m from the litter collector. Soil samples were bulked to one sample per sampling area, dried to constant weight during one week in the solar drying house at the field station, and stored in sealed plastic bags for transport to Amsterdam.

Throughfall

Throughfall was measured every 2 wk using locally constructed gauges placed within 3 m from each litter trap in each of the 30 sampling areas between 1 January 1989 and 30 January 1990. The gauges consisted of plastic containers (5-l capacity) equipped with sharp-rimmed funnels (21-cm diameter). Each funnel was mounted on a 30-cm-long PVC pipe extending

from the container to prevent soil particles and organic matter from the forest floor splashing into the funnel. To minimize contamination by fine organic debris falling into the funnels pieces of nylon wire mesh (2-mm mesh width) were fitted at their outlets. Any coarse material that had fallen into the funnels was regularly removed by hand. The containers were wrapped in black plastic to retard the growth of algae. No chemicals were added to prevent bacterial growth. The gauges were attached to a PVC pole stuck in the soil for stability. Volumes of throughfall were determined using a 500-ml measuring cylinder. On each sampling occasion, a well-mixed sample (250 ml) was taken from each gauge to the DVFC laboratory. Gauges were randomly relocated within a radius of 3 m around the litter collector after emptying (*cf.* Lloyd & Marques 1988).

The self-made gauges were calibrated against standard gauges at the DVFC meteorological station using data for 48 rain events. Correlation between the two types of gauges was excellent ($r_s = 0.995$, df = 47, $P < 0.001$). Stemflow was not measured in this study. Concurrent work by Sinun *et al.* (1992) in an adjacent stand indicated that stemflow was only *c.* 2% of incident rainfall.

Chemical analysis

The soil samples were lightly crushed with a mortar to pass through a 0.1 mm sieve. Litter samples (30 g) were ground and homogenized in a centrifugal ballmill (Retsch, model S2) for 5–15 min until a fine homogeneous powder was obtained.

The organic matter contents of duplicate litter and soil samples were estimated from their loss-on-ignition following burning in a muffle furnace for 9 h, carried out in three successive steps of 1 h at 200 °C, 3 h at 350 °C and 6 h at 600 °C. Total carbon and nitrogen concentrations were measured by burning 1 to 5 mg duplicate samples in a stream of pure oxygen in combination with column chromatography and an elemental analyzer (Carlo Erba Strumentazione, Milan, Model 1106), using atropine (Merck, Darmstadt) for calibration. Concentrations of calcium, iron, magnesium, manganese, phosphorus and potassium were measured in 100 mg sub-samples (litter) and 1 g samples (soil) after hot acid digestion in teflon cups in a micro-wave oven using a concentrated nitric acid: hydrochloric acid: water (4 : 1 : 1) mixture. Digests were divided over two 10-ml plastic test tubes per sample and stored at 5 °C. One of the samples was analyzed for cations within 2 d, the other sample was analyzed for phosphorus within 3 mo (see below).

Acidity and electrical conductivity were measured in a mixture of litter and deionized water (1 : 10) or soil and deionized water (1 : 2). Concentrations of exchangeable nutrients in soil were measured by atomic absorption spectrophotometry (AAS, Perkin-Elmer 4000) using an air-acetylene flame, after extraction with 1 M ammonium acetate (pH 7) for calcium, magnesium, manganese, and potassium, and 12.5% calcium lactate (pH 7) for iron. Calcium and magnesium were measured in the presence of lanthane nitrate to minimize interference of the matrix. Samples showing suspect matrix effects and very low

concentrations of calcium (<0.05 mg g^{-1}) were also measured by inductively coupled plasma-atomic emission spectrometry (ICP-AES). The results obtained by ICP-AES were within 5% from those obtained by AAS, and so only the latter are presented here. Phosphate was measured colorimetrically with an auto-analyzer (Skalar SA 400) at 880 nm, using an ascorbic acid-molybdate complex after extraction with 12.5% calcium lactate (pH 7) (Chen *et al.* 1956). The composition of rinsing medium, calibration samples and reagents were adjusted to those of the digest solutions.

Differences between replicates (AAS) rarely exceeded 10%. BCR (Community Bureau of Reference, Brussels) reference materials (CRM 062, 101, 129) were used to control the quality of the analyses. Results for all elements deviated less than 5%, and for phosphorus less than 10%, from the certified values.

The throughfall samples were analyzed for pH (Consort P907 pH meter, glass electrode) and electrical conductivity (EC, precalibrated conductivity meter manufactured at Vrije Universiteit Amsterdam) immediately after collection in the DVFC laboratory. The EC values ($\mu S\ cm^{-1}$) were automatically normalized to a standard temperature of 25 °C and the accuracy was typically 2 $\mu S\ cm^{-1}$ in the range of 0–100 $\mu S\ cm^{-1}$. The 30 throughfall samples were bulked to one sample per sampling occasion (weighted by volume), filtered through acid-washed Whatman G/F glass microfibre filters and stored in a refrigerator (4 °C). At the end of each month, the 2-wk samples were bulked to 1-mo sample (again weighted by volume), and filtered through a 0.45 μm Millipore filter. Monthly samples were divided over two clean 100 ml polyethylene bottles. One of the aliquots was acidified with 0.7 ml of 65% concentrated nitric acid (suprapur) for conservation purposes, resulting in a final sample pH value of *c.* 2. Concentrations of sodium and potassium were determined by flame photometry using Eppendorf equipment. Concentrations of aluminium, calcium, total iron, magnesium, manganese and silicium were determined on a Perkin-Elmer (Model 6500) ICP emission spectrophotometer (Appelo 1988). Concentrations of chloride, sulphate, nitrate, phosphate and ammonia were determined by spectrophotometry on Technicon and Skalar Auto-analyzers according to the following automated methods. Chloride was determined with the ferricyanide method of Zall *et al.* (1956), sulphate by the methylthymol-blue method of Greenberg *et al.* (1985), nitrate by cadmium reduction (Hendrikson & Selmer-Olsen 1970), phosphate by ascorbic acid reduction (Black *et al.* 1965) and ammonia with the modified Berthelot reaction using salicylate and dichloroisocyanurate (Krom 1980). The analytical accuracy was within 2% of the concentrations in the highest standard solutions (T. Bäer, *pers. comm.*).

Data processing and statistical analysis

Fluxes and pools of organic matter and elements were calculated by multiplying the respective concentrations times the pertinent above-ground inputs

and forest-floor pools. Turnover rates (k_L, y^{-1})(Swift *et al.* 1979) were calculated by dividing annual above-ground inputs by average forest floor pools, see Table 1. Turnover rates of litter were calculated for two fractions, *viz.* leaf litter (excluding fine litter) and total non-woody litter (including fine litter), indicated as k_{LLF} and k_{LF}, respectively. The former relates to the initial fragmentation and leaching whereas the latter represents the full spectrum of decomposition stages.

In the fine litter mass, organic matter is intimately mixed with mineral soil and this tends to increase the weight of the litter mass. This obviously results in underestimation of k_{LF} and of the associated turnover rates for those elements that occur in relatively high concentrations in the mineral soil (iron, magnesium and potassium). Estimates for the amounts of these elements in the litter layer were adjusted for contributions by mineral soil using the ash content of the litter and the element concentrations in mineral topsoil.

So-called relative element turnover rates were calculated for all sampling areas by dividing element turnover rates by carbon turnover rates. Carbon turnover is assumed to be indicative of amounts of energy needed by decomposer organisms for element mineralization (Swift *et al.* 1979), whereas relative turnover rates indicate enrichment and release of elements (in organic and inorganic form) relative to that of carbon in the decomposing litter.

Spatial heterogeneity was analyzed using Spearman's rank correlation test for the various variables (Spearman's rank correlation coefficient indicated as r_s). This analysis answered the question as to what extent a sampling area ranking high with respect to one variable also ranked high with respect to another. Spatial heterogeneity of litter turnover was also displayed graphically by frequency distributions of k_{LF} values for litter dry weight and for seven nutrients. The relationship between fluxes (litterfall) and pools (forest floor litter mass) was descibed by a linear regression; because both variables in this relationship are subject to error, slope estimates were derived using the geometric mean regression method (Sokal & Rohlf 1981). Differences between the means for element concentrations in different pools or fluxes were tested for significance using a *t*-test for paired comparisons. Homogeneity of variances was assessed using Bartlett's chi-squared logarithmic test. When data were not normally distributed and variances not homogeneous, logarithmic transformation of the data was applied and geometric averages were calculated. The statistical package SYSTAT (Wilkinson 1990) was used throughout.

RESULTS

Element concentrations in soil and litter

The average pH of the topsoil (0 – 8 cm) in the study plot was 4.6, with a standard error of 0.13. The average concentrations of major elements,

Table 2. Average bulk densities and chemical composition of the topsoil (0–8 cm) in the study plot, together with coefficients of variation (standard deviation as a percentage of the mean, CV), calculated over 30 replicate sampling areas. All concentrations are expressed per dry weight of soil. Exchangeable concentrations were derived from extractions with 1 M NH_4Ac (Ca, Mg, Mn and K), or 12.5% calcium lactate (P, Fe).

	Mean	CV (%)
Bulk density (g cm^{-3})	0.98	16.8
Organic matter (%)	11.36	23.6
Total C (%)	5.21	28.4
Total N (%)	0.388	24.0
P total (μg/g)	210	20.9
exchangeable (μg/g)	4.22	48.0
K total (μg/g)	1760	31.7
exchangeable (μg/g)	92.9	25.1
Ca total (μg/g)	62	35.3
exchangeable (μg/g)	2.43	78.9
Mg total (μg/g)	1,230	42.7
exchangeable (μg/g)	4.95	43.2
Mn total (μg/g)	35	46.9
exchangeable (μg/g)	7.40	71.1
Fe total (μg/g)	1625	26.6
exchangeable (μg/g)	1494	13.0

given in Table 2, show that the topsoil was very poor in calcium, but rich in organic matter. The total amount of organic matter in the top 8 cm may be estimated at 35 kg m^{-2}, with a carbon:nitrogen ratio of *c.* 13. Variability among sampling areas, assessed by the coefficient of variation, was not the same for all elements. Spatial variability was particularly high for manganese, magnesium and calcium, and relatively low for bulk density and organic matter (Table 2).

Concentrations of organic matter, carbon and potassium were greater in leaf fall than in fine trash whereas the reverse was found for nitrogen, phosphorus and iron (Table 3). Consequently, carbon: element ratios were higher in fine trash than in leaf fall for nitrogen (36 *vs* 24), phosphorus (1350 *vs* 610), calcium (90 *vs* 76), magnesium (205 *vs* 194) and iron (6200 *vs* 1210). Concentrations of iron in leaf fall were very low compared to those in leaf litter mass, fine litter mass and soil and even lower in small woody litterfall (see Table 3). Similarly, concentrations of nitrogen, phosphorus and manganese were also lower in leaf fall than in leaf-litter mass. On the other hand, concentrations of organic matter, carbon, potassium, calcium and magnesium were all significantly higher in leaf fall than in leaf litter mass, although the differences were small for the latter two elements. Despite these differences, the relative abundances of elements in leaf fall and in leaf layer mass were similar (significant correlation between the ranks: $r_s = 0.950$, $df = 28$, $P < 0.001$).

Within the litter layer, all element concentrations were lower in the fine litter mass than in the leaf-litter mass, except for iron. The large difference in element composition between fine litter and leaf litter was further illustrated by the non-significant correlation between the concentrations of elements in the two litter types ($r_s = 0.171$, $df = 28$, $P > 0.05$). Concentrations of organic matter and various elements in the fine litter mass were significantly greater

than those in topsoil ($t > 4.0$, $df = 28$, $P < 0.01$), except for magnesium ($t = 0.854$, $df = 28$, $P > 0.05$) and potassium ($t = 0.734$, $df = 28$, $P > 0.05$). Although element concentrations in the fine litter mass and topsoil differed, the rankings of the elements were similar ($r_s = 0.933$, $df = 28$, $P < 0.001$). Total concentrations of organic matter and carbon in leaf litter and fine litter layer were lower than in litterfall, due to mineral soil present in the litter. Mineral soil was calculated to contribute 8 and 54% to the dry weight of the leaf litter mass and fine litter mass, respectively. After correcting for this (see Methods section), the fine litter mass showed an organic matter content similar to that of leaf fall (*c.* 95%).

As in the soil, concentrations of elements in leaf fall varied considerably between the sites, especially for manganese and calcium (see coefficients of variation in Table 3). Organic matter, carbon and nitrogen had the lowest coefficient of variation in leaf fall, while those for magnesium, phosphorus and potassium were intermediate. For most of the elements, spatial variability was higher in the fine litter mass compared to leaf fall and trash fall, however, for potasium spatial variability in litter mass was significantly lower than in leaf and trash fall (Table 3). It seems that small differences in leaf fall chemistry between sites are amplified in the litter layer due to a process of accumulation, except for elements that are quickly removed from the litter, such as potassium.

To illustrate the fate of elements during litter decomposition, concentrations in leaf litter mass, fine litter mass and topsoil were expressed as a percentage of the corresponding concentrations in leaf fall and non-woody litterfall in Table 4. On a dry weight basis, concentrations of nearly all elements decreased rapidly when going from leaf litter via fine litter to soil, except for magnesium, potassium and iron. Nitrogen, phosphorus and manganese concentrations initially increased in the leaf litter layer before gradually decreasing in fine litter mass and soil. Concentrations of organic matter, carbon and calcium immediately decreased to low levels upon reaching the topsoil, indicating rapid mineralization. Because concentrations of nitrogen, phosphorus, calcium and manganese in the mineral soil were low compared to those in leaf fall (Tables 2 and 3), they have also been expressed as a percentage of the organic matter content (Table 4). Concentrations of nitrogen and phosphorus computed in this way increased when passing from leaf litter to soil, indicating their accumulation in organic matter. As expected, concentrations of carbon were relatively constant when expressed per unit of organic matter.

Element concentrations in rainfall and throughfall

Volume-weighted mean concentrations of elements in bulk rainfall and throughfall decreased in the sequence: chloride, sulphate, nitrate, sodium, potassium, calcium, ammonium, magnesium and phosphate (Table 5). Total nutrient concentrations in throughfall, as indicated by electrical conductivity, were

Table 3. Average concentrations (and coefficients of variation) of organic matter and major elements in annual litterfall and litter mass collected in 30 sampling areas between December 1988 and December 1989. All concentrations are expressed on a dry weight basis. Comparisons between leaf fall and trash litterfall, between leaf fall and leaf-layer mass, and between leaf-layer mass and fine litter mass were made using a t-test for paired comparisons; means with different superscripts differ significantly ($P < 0.05$). Woody litterfall and mass were not included in the comparisons. na = not applicable.

	OM %	C %	N %	P $\mu g\ g^{-1}$	K $\mu g\ g^{-1}$	Ca $\mu g\ g^{-1}$	Mg $\mu g\ g^{-1}$	Mn $\mu g\ g^{-1}$	Fe $\mu g\ g^{-1}$
Leaf fall (LLF)	94.54[a]	49.93[a]	1.38[a]	0.37[a]	4.78[a]	5.54[a]	2.44[a]	0.96[a]	0.08[a]
(>10.0 mm)	(1.2)	(2.0)	(7.9)	(14.8)	(25.2)	(32.6)	(18.0)	(34.2)	(34.2)
Coarse trash litterfall	95.39[a]	49.91[a]	1.72[b]	0.66[b]	4.63[a]	5.79[a]	2.41[a]	0.82[a]	0.15[b]
(5.1–10.0 mm)	(1.3)	(2.0)	(9.6)	(16.6)	(24.8)	(33.1)	(18.2)	(33.4)	(18.3)
Fine trash litterfall	93.56[c]	48.54[c]	2.01[c]	0.80[c]	3.33[c]	6.36[a]	2.50[a]	1.03[a]	0.40[c]
(0.1–5.0 mm)	(1.2)	(2.0)	(8.2)	(13.7)	(24.7)	(32.7)	(19.7)	(37.2)	(13.7)
Small woody litterfall (WLF)*	97.05	50.84	0.83	0.20	3.18	5.02	1.32	0.57	0.04
(diameter < 2.0 cm)	na	na	na	na	na	na	na	na	na
Leaf litter mass (LLM)	87.03[d]	45.67[d]	1.54[d]	0.44[d]	2.24[d]	5.14[d]	2.23[d]	1.03[d]	1.47[d]
(>10.0 mm)	(3.1)	(3.5)	(7.1)	(12.4)	(17.1)	(28.8)	(2.5)	(31.9)	(26.1)
Fine litter mass (FLM)	41.70[e]	21.63[e]	1.06[e]	0.36[e]	1.78[e]	1.03[e]	1.32[e]	0.32[e]	9.82[e]
(<10.0 mm)	(20.8)	(21.5)	(20.7)	(12.2)	(12.2)	(53.2)	(29.0)	(51.3)	(20.1)
Small woody litter mass*	93.88	48.73	0.88	0.21	1.79	4.10	1.22	0.47	0.80
(diameter <2.0 cm)	na	na	na	na	na	na	na	na	na

* single value for annual bulk sample

Table 4. Concentrations of elements in the leaf-litter mass (LLM) expressed as a percentage of the corresponding mean concentrations in leaf fall (LLF); concentrations in fine litter mass (FLM) and soil expressed as percentages of the corresponding mean concentrations in total non-woody litterfall (LF), both on the basis of dry weight (dw) and organic matter content (OM).

	OM		C		N		P		K	Ca		Mg	Mn		Fe
	dw	OM	dw	OM	dw	OM	dw	OM	dw	dw	OM	dw	dw	OM	dw
Leaf litter mass (LLM)	92	100	91	99	111	121	119	129	47	93	101	91	107	117	1755
Fine litter mass (FLM)	44	100	44	98	69	160	76	183	39	18	41	54	33	79	6620
Soil (0–8 cm)	12	100	10	87	26	212	44	369	39	1	9	50	4	30	10 959

Table 5. Volume-weighted electrical conductivity (EC, μS cm^{-1}) and nutrient concentrations (mg l^{-1}) in rainfall and throughfall in the study plot. Rainfall was sampled at the meteorological station of the Danum Valley Field Station between October 1989 and January 1990. Throughfall was sampled in the 30 sampling areas between January 1989 and January 1990. na = not applicable.

	EC	NH_4	NO_3	PO_4	SO_4	Cl	Na	K	Ca	Mg	Mn	Fe
Rainfall (RF)	5.3	0.085	0.307	0.031	0.342	0.427	0.246	0.160	0.093	0.033	<0.050	<0.050
Throughfall (TF)	17.7	0.263	1.461	0.168	2.097	1.306	0.300	3.093	0.262	0.153	<0.050	<0.050
TF/RF ratio	3.3	3.09	4.75	5.41	6.13	3.06	1.22	19.33	2.82	4.64	na	na

about three times higher than in rainfall (Table 5). Concentrations in throughfall decreased in the sequence: potassium, sulphate, nitrate, chloride, sodium, ammonium and calcium. As in rainfall, iron and manganese were not detectable in throughfall. Nutrient enrichment of rainfall after passing the canopy was most pronounced for potassium and decreased in the sequence: sulphate, phosphate, nitrate, magnesium, ammonium, chloride and calcium, and sodium.

Element inputs to the forest floor

Mean annual leaf fall, in terms of dry mass input to the forest floor, constituted *c.* 60% of total litter fall (1105 g m^{-2} y^{-1}, being the sum of leaves, coarse trash, fine trash, and small wood, see Table 6). Amounts of iron, phosphorus and nitrogen in trash fall approximated the corresponding inputs via leaf fall because of the high concentrations for these elements in trash litterfall (Table 3). About 70% of the fine trash dry weight was <2 mm, and *c.* 40% consisted of insect frass (Burghouts 1993).

The importance of nutrient input from litterfall to nutrient availability in the topsoil was particularly evident in the case of calcium and phosphorus. Annual inputs of phosphorus, calcium, magnesium and manganese in litterfall exceeded the respective exchangeable stocks in the top 8 cm of soil. For the other elements, annual inputs via litterfall were smaller than corresponding quantities of exchangeable elements in the mineral soil.

Spatial variability among the 30 sampling areas, as indicated by coefficients of variation in Table 6, suggests that heterogeneity is lowest for total leaf fall (26%) and carbon, nitrogen and phosphorus. Spatial heterogeneity for K, Ca, Mg, Mn and Fe in leaf fall was higher; this implies that leaf chemistry provides additional variation to the basic variability in total leaf fall. It is also interesting to note that spatial variability in trash and woody litterfall was higher than for leaf fall, while for leaf-litter mass it was generally lower (Table 6).

In addition to litterfall, throughfall constitutes another important pathway for nutrients to reach the forest floor. As could be expected, biweekly amounts of throughfall were strongly correlated with rainfall ($r_s = 0.972$, $df = 25$, $P < 0.01$), and 81% ± 1.3 (SE) of the 3257 mm of rainfall were converted to throughfall. Inputs of elements via throughfall and total litterfall (including woody litterfall) are given in Table 7. From these data, total nutrient returns were estimated by adding net throughfall (throughfall minus rainfall) to total leaf fall. The percentage contribution of litterfall to total nutrient returns was above 90% for most of the elements, however, leaf fall contributed only 39% to the flux of potassium and 81% to the flux of phosphorus (Table 7).

Litter and element turnover rates

Figure 1 illustrates the relationship between element inputs to the forest floor via litterfall and the corresponding pools in litter layer mass for the 30

Table 6. Mean annual values and coefficients of variation (%, in brackets) for leaf and trash litterfall (g m^{-2} y^{-1}), leaf and fine litter layer mass (g m^{-2}) for dry weight, organic matter and quantities of elements in 30 sampling areas for the period December 1988–December 1989. Magnesium and potassium masses in litter layer were corrected for contributions by soil material. na = not applicable.

	DW	OM	C	N	P	K	Ca	Mg	Mn	Fe
Leaf fall (LLF)	653	618	326	9.05	0.25	3.18	3.66	1.62	0.62	0.054
(>10.0 mm)	(26.0)	(26.6)	(26.9)	(29.1)	(21.9)	(37.9)	(44.9)	(37.2)	(44.2)	(30.4)
Coarse trash litterfall*	62.4	59.4	31.3	1.08	0.04	0.30	0.38	0.16	0.05	0.009
(5.1–10.0 mm)	(38.6)	(38.7)	(38.5)	(40.6)	(68.5)	(54.8)	(57.7)	(68.5)	(54.8)	(60.9)
Fine trash litterfall*	162	151	78.2	3.27	0.13	0.56	1.08	0.42	0.16	0.066
(0.1–5.0 mm)	(37.2)	(39.9)	(38.5)	(41.9)	(42.1)	(58.7)	(60.9)	(52.2)	(68.5)	(41.5)
Small woody litterfall (WLF)*	228	221	114	1.89	0.05	0.71	1.13	0.30	0.13	0.010
(diameter <2.0 cm)	(50.4)	na	na	na	na	na	na	na	na	na
Leaf litter mass (LLM)	251	218	115	3.87	0.11	0.53	1.30	0.53	0.26	0.385
(>10.0 mm)	(26.2)	(27.6)	(28.6)	(28.3)	(49.8)	(31.0)	(46.3)	(41.3)	(42.1)	(44.1)
Fine litter mass (FLM)	1781	707	367	17.95	0.62	1.36	1.72	1.17	0.49	17.79
(<10.0 mm)	(46.1)	(69.7)	(71.6)	(61.9)	(53.0)	(52.4)	(112)	(84.3)	(55.9)	(44.0)

* single value for annual bulk sample.

Table 7. Nutrient inputs via rainfall (RF), throughfall (TF) and total litterfall (LF) in 30 sampling areas in the study plot (g m^{-2} y^{-1}) from 1 January 1989 until 31 January 1990. na: not applicable.

	C	N	P	S	K	Ca	Mg	Mn	Fe
Rainfall (RF)	<1.0[a]	0.42[b]	0.03[c]	0.21[d]	0.50	0.29	0.10	<0.05	<0.05
Throughfall (TF)	22.2[a]	1.37[b]	0.14[c]	1.07[d]	7.92	0.67	0.39	<0.06	<0.06
Total litterfall (LF + WLF)	549.5	15.30	0.47	na	4.75	6.26	2.49	0.95	0.09
Total nutrient returns (LF+WLF+TF-RF)	570.7	16.25	0.58	–	12.17	6.64	2.78	0.96	0.10
Percentage contribution of litterfall to total nutrient returns	96	94	81	–	39	94	90	99	90

[a] DOC; [b] $N\text{-}NO_3$ + $N\text{-}NH_4$; [c] $P\text{–}PO_4$; [d] $S\text{–}SO_4$

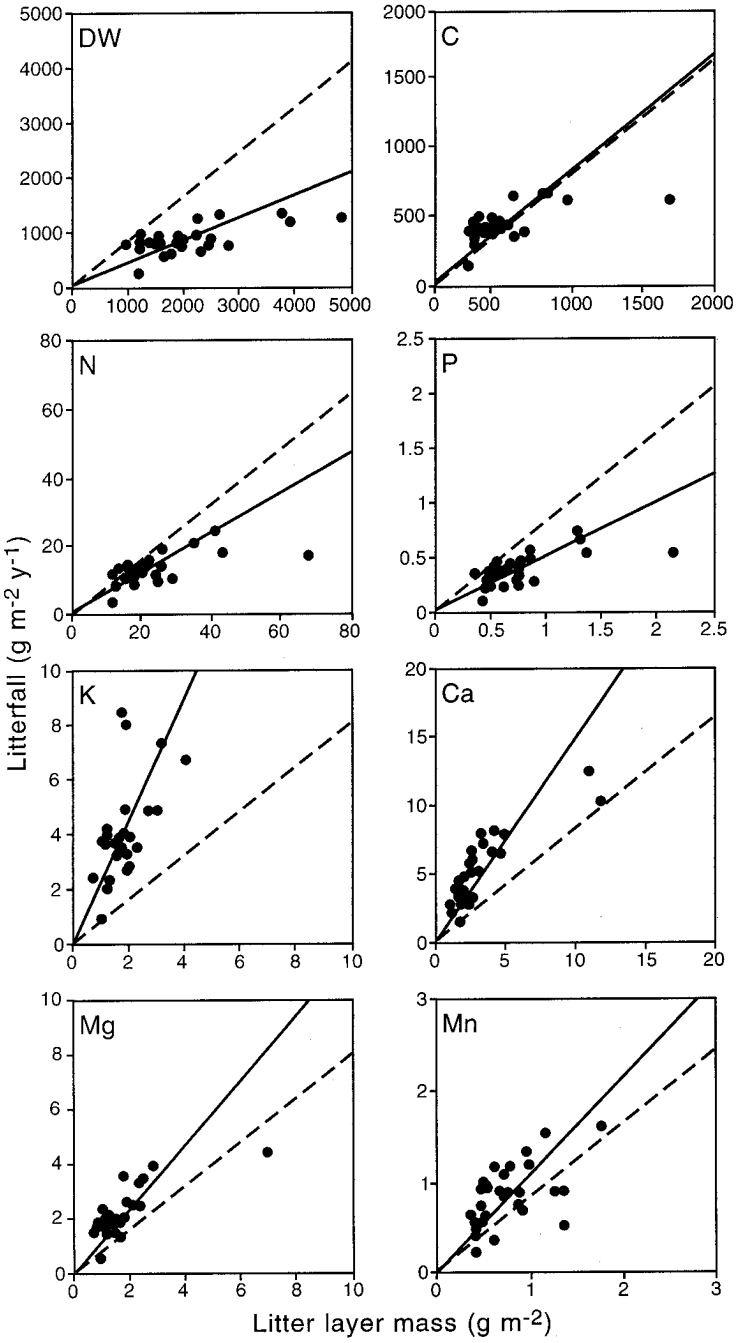

Figure 1. Relationships between litterfall (g m^{-2} y^{-1}) and litter mass (g m^{-2}) for dry weight and seven elements in 30 sampling areas of a dipterocarp forest plot in the Danum Valley Conservation Area. The solid line is a linear regression (forced through the origin) of the data. The broken line in each case represents the regression line for organic matter (original data not shown). The slope of each line can be interpreted as the average turnover (flux relative to pool, y^{-1}).

sampling areas. The regression lines illustrate that there are major differences in turnover rates of different groups of elements. The slopes are below unity for litter dry weight, phosphorus, nitrogen and organic matter, above unity for potassium, calcium, magnesium and manganese, and approximately equal to 1 for carbon. Turnover rates for dry weight, organic matter and eight different elements in leaf litter (k_{LLF}) and total litter (k_{LF}), were calculated for each sampling area from the annual litter fall and the time-averaged litter layer mass. The mean of these 30 turnovers is given with its coefficient of variation for each element in Table 8. Carbon and calcium showed turnover rates that were similar to those for organic matter in leaf litter. Potassium and magnesium showed higher turnover rates than organic matter (indicating leaching) but those of manganese, nitrogen and phosphorus were lower (indicating relative enrichment). The turnover of magnesium was faster than that of calcium. Correction for content of mineral soil in the leaf litter mass did not significantly alter element turnover rates in leaf litter (k_{LLF}) but it did for turnover rates in total litter (k_{LF}), particularly for magnesium and potassium. The turnover of magnesium increased from 0.80 to 1.46 y^{-1} while that of potassium increased from 1.15 to 2.38 y^{-1}. Estimates for turnover rates of iron were not feasible due to the insignificant contribution of organic matter to the iron concentration in the litter mass which is dominated by iron originating from mineral soil particles. Concentrations in mineral soil for the other elements were too small to alter turnover rates significantly.

The highest corrected turnover rates in total litter were found for potassium (2.38 y^{-1}), followed by, in decreasing order, calcium, magnesium, manganese, carbon, organic matter, nitrogen and phosphorus. Significances of the differences are shown in Table 8. Interestingly, the element turnover rates differed more from each other in total litter than in leaf litter. Calcium showed higher turnover rates than organic matter in total litter, whereas no difference was found between Ca and organic matter in leaf litter. Similarly, manganese showed a higher turnover rate than organic matter in total litter, but the opposite was true in leaf litter (Table 8).

Element turnover was also calculated with inclusion of net throughfall, using the ratio (LF + TF − RF)/LM (Table 8). The contribution of throughfall had the largest influence on turnover rate in the case of potassium, followed by, in decreasing order, phosphorus, magnesium, calcium, nitrogen and manganese. When the contribution in net throughfall was added to the input via litterfall, the turnover of phosphorus became higher than that of nitrogen. Spatial heterogeneity of element turnover appeared to be lower than spatial heterogeneity of element input through leaf fall (*cf.* coefficients of variation in Tables 8 and 6). This is a reflection of the strong positive correlations between fluxes and pools shown in Figure 1. It seems that locally high amounts of leaf fall are associated with relatively high amounts of litter on the forest floor, while turnovers are also variable, but to a lesser extent.

Table 8. Mean annual turnover rates of litter dry weight, organic matter and seven elements, expressed as (i) the ratio of leaf litterfall (LLF) to leaf-litter mass, (ii) as total non-woody litterfall (LF) relative to total non-woody litter layer mass, and (iii) on the basis of total element inputs via litterfall (LF) and net throughfall (TF–RF), in the 30 sampling areas (*cf.* Table 1). The coefficient of variation (%) is given within brackets for each mean. Comparisons were made for k_{LLF} (letters a to f) and k_{LF} (letters g to p) between dry weight, organic matter and seven elements using dependent t-tests; means with different superscripts differ significantly ($P < 0.05$). Variation coefficients for k_{LF+TF} are not available because rainfall was not collected per site. na: not applicable, nd: not determined.

Turnover	DW	OM	C	N	P	K	Ca	Mg	Mn
(i) k_{LLF}	2.62^{a}	2.86^{b}	2.88^{b}	2.36^{c}	2.23^{d}	6.08^{f}	2.86^{b}	3.07^{e}	2.46^{c}
	(18.8)	(17.2)	(17.1)	(18.6)	(19.6)	(24.3)	(21.1)	(17.8)	(22.3)
(ii) k_{LF}	0.47^{g}	1.00^{h}	1.02^{j}	0.68^{k}	0.62^{l}	2.38^{o}	1.92^{m}	1.46^{n}	1.22^{p}
	(35.0)	(27.4)	(26.8)	(32.2)	(26.5)	(36.8)	(28.5)	(20.0)	(25.9)
(iii) k_{LF+TF}	na	nd	1.18	0.74	0.79	6.43	2.20	1.64	1.28

Table 9. Spearman's rank correlation coefficients (r_s) for the concentrations of organic matter and eight elements between leaf fall (LLF), leaf litter mass (LLM), fine litter mass (FLM) and topsoil in the 30 sampling areas (**$P < 0.005$; ***$P < 0.001$). na = not applicable.

Correlations	OM	C	N	P	K	Ca	Mg	Mn	Fe
Between LLF and LLM	0.524**	0.482**	0.824***	0.814***	0.663***	0.923***	0.780***	0.9145***	0.102
Between LLM and FLM	0.590**	0.594**	0.242	0.703***	0.228	0.876***	0.353	0.493**	0.502**
Between FLM and topsoil	0.641***	0.597***	0.699***	0.779***	0.660***	0.539**	0.781***	0.620***	0.758***
Between total and available amounts in topsoil	na	na	na	0.569***	0.481**	0.532**	0.204	0.767***	–0.165

The variability in turnover rates among the 30 sampling areas is illustrated graphically in Figure 2. The maximum difference between sites is indicated by the ratio, d, between the turnover of the highest and the lowest class. Spatial heterogeneity of turnovers amounted to a factor 2.8 (for Ca) to 4.0 (for Mn and K). The variation showed a normal distribution for most elements, but the distribution for potassium and calcium was somewhat skewed. The irregular distribution found for litter dry weight possibly reflects the inaccurate estimation of litter layer mass because of the presence of mineral soil. The skewed distribution obtained for potassium is probably caused by the high potassium inputs via throughfall in some of the sampling areas, which was not included in the calculation of k_{LF}.

Further insight into the relationship between element concentrations in litterfall and element mineralization in the litter layer can obtained by expressing the turnover rates of nutrients per unit of mineralized carbon. This factor indicates the extent to which nutrients are conserved in the litter, relative to carbon. For each sampling area k_L for a nutrient was divided by the k_L for carbon to obtain a relative turnover rate for that nutrient. Relationships between relative turnover and element concentrations in litter fall and litter mass were investigated by means of correlation analysis. Two groups of elements could be distinguished: (i) nitrogen, phosphorus and potassium; these exhibited relative turnover rates that were positively correlated with their total input via litterfall as well as with their respective concentrations in litterfall (smallest $r_s = 0.556$, $df = 28$, $P < 0.001$), and (ii) calcium and manganese; these had relative turnover rates that were negatively correlated with their concentrations in the litter layer (smallest $r_s = -0.564$, $df = 28$, $P < 0.001$). The data for relative nitrogen turnover are displayed in Figures 3a and 3b. These results illustrate the fact that nitrogen turnover is slower than carbon turnover (relative turnover is smaller than unity), hence nitrogen is conserved in the litter compared to carbon; this effect is, however, less strong at sites with high nitrogen in litterfall (relative turnover increases in Figure 3a). Similarly, sites with a low quality of litterfall (measured by the C : N ratio) show a lower relative turnover of nitrogen, so a higher rate of conservation (Figure 3b).

Correlations between variables

Concentrations of nitrogen and phosphorus in litterfall were positively correlated with each other ($r_s = 0.791$, $P < 0.001$; $df = 28$ here and for all other tests in this section), and so were carbon and organic matter ($r_s = 0.830$, $P < 0.001$), potassium and magnesium ($r_s = 0.588$, $P < 0.001$), and calcium and phosphorus ($r_s = 0.415$, $0.05 < P < 0.01$). Concentrations of carbon were negatively correlated with magnesium ($r_s = -0.679$, $P < 0.001$) and with potassium ($r_s = -0.660$, $P < 0.001$). In the topsoil, total organic matter, carbon and nitrogen concentrations were positively correlated with

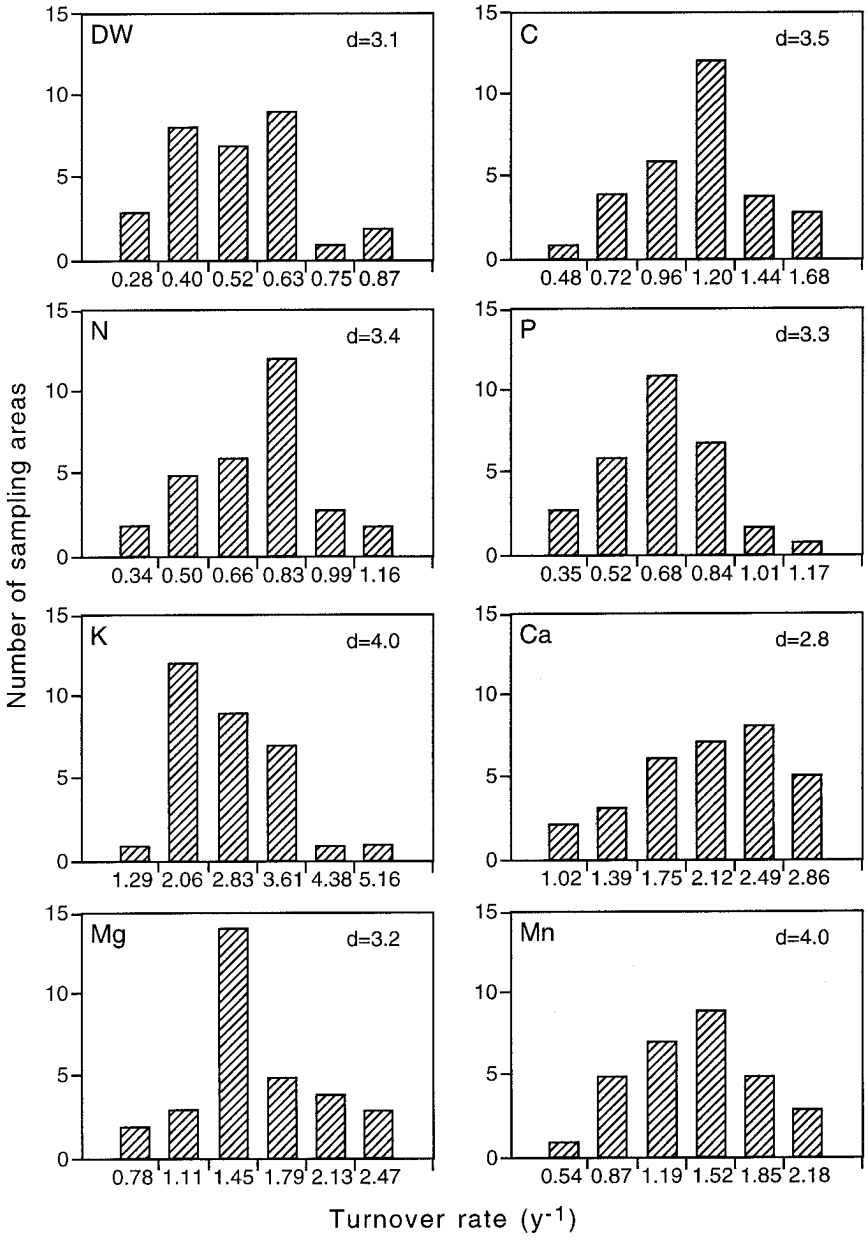

Figure 2. Frequency distributions of turnovers, expressed as k_{LF} values (y^{-1}) for litter dry mass and seven elements over the 30 sampling areas at Danum. To allow a comparison among the distributions, an equal number of classes has been made for each element. The median value of the class is given below each bar. Spatial heterogeneity is indicated by the quantity d, which is the ratio of the highest to the lowest class. In this way it can be seen that Ca turnover varies by a factor of 2.8, while K turnover varies by a factor of 4.

each other ($r_s > 0.700$, $P < 0.001$). Exchangeable calcium and manganese increased with their respective total concentrations but were not correlated with organic matter content ($r_s < 0.205$, $P > 0.05$). Exchangeable phosphorus was low (<10 mg kg^{-1}) but was positively correlated with total phosphorus, as well as with organic matter content ($r_s = 0.551$, $P < 0.001$) and exchangeable potassium ($r_s = 0.683$, $P < 0.001$). Total amounts (g m^{-2}) of potassium, magnesium, phosphorus and iron were positively correlated with each other ($r_s > 0.576$, $P < 0.001$).

Spatial variations in the chemical composition of litterfall reflected the chemical composition of both litter layer and topsoil, as well as element availability in the top 8 cm of soil (Table 9). Element concentrations were generally strongly correlated (i) between leaf fall and leaf layer mass, (ii) between leaf-litter mass and fine litter mass, and (iii) between fine litter mass and topsoil (Table 9), more so than between litterfall and topsoil ($r_s < 0.450$, $P > 0.05$, not shown in Table 9). Elevation of sampling area was negatively correlated with calcium concentrations in litterfall ($r_s = -0.849$, $P < 0.001$) and litter mass ($r_s = -0.800$, $P < 0.001$), as well as with those of total ($r_s = -0.664$, $df = 28$, $P < 0.001$) and available ($r_s = -0.460$, $0.01 < P < 0.05$) calcium in topsoil, suggesting lower concentrations towards ridge positions.

The mean fine root mass (± SE) in the litter layer was 137 (± 16.4) g m^{-2} and was positively correlated with inputs via litterfall of all elements among the 30 sampling areas ($r_s > 0.489$, $0.01 < P < 0.001$), except for calcium and manganese. Also, fine root mass was positively correlated with concentrations of magnesium ($r_s = 0.454$, $0.01 < P < 0.05$) and potassium ($r_s = 0.463$, $0.01 < P < 0.05$) in litterfall, as well as with masses of organic matter, carbon, nitrogen, phosphorus, potassium and magnesium in the litter layer ($r_s > 0.452$, $0.01 < P < 0.05$).

The heterogeneity of the forest canopy resulted in high spatial variation of inputs of organic matter and elements in litterfall. Woody litterfall among the 30 sampling areas was also strongly correlated with non-woody litterfall ($r_s = 0.647$, $df = 28$, $P < 0.001$). The effect was amplified by the effect of the overhead canopy on nutrient inputs via throughfall. Figure 4 shows that throughfall, expressed as a percentage of annual rainfall, was negatively correlated with litterfall ($r_s = -0.699$, $df = 28$, $P < 0.001$) for the 30 sampling areas. This suggests that throughfall is higher in sampling areas with lower canopy biomass, assuming that amounts of litterfall are indicative of canopy biomass. Nutrient concentrations in throughfall, on the other hand, increased with canopy biomass as suggested by the positive correlations between total litterfall, trash litterfall and the volume weighted EC ($r_s > 0.816$, $0.01 < P < 0.001$) and pH ($r_s > 0.645$, $P < 0.001$) of throughfall (Figure 5).

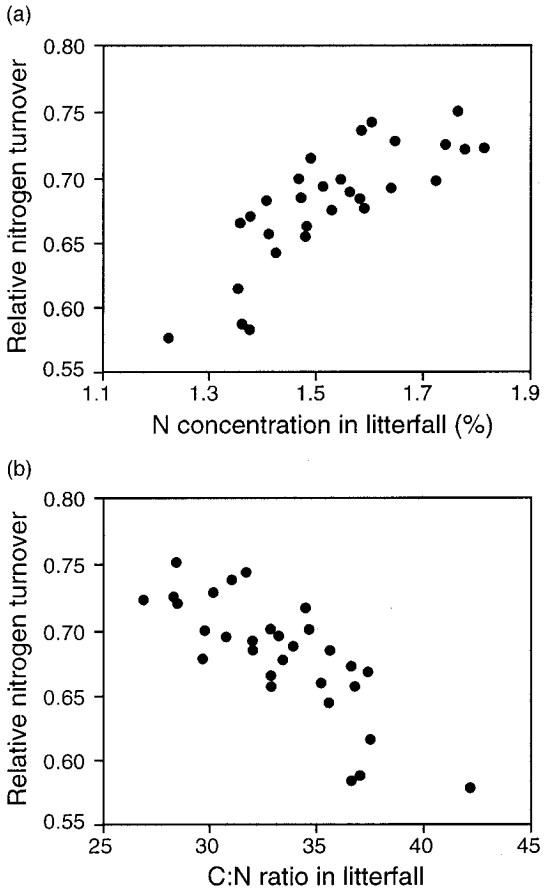

Figure 3. Relationship between relative nitrogen turnover (k_L of N relative to k_L of C) and (a) nitrogen concentration in leaf fall, and (b) C : N ratio of leaf fall in 30 sampling areas in dipterocarp forest at Danum.

DISCUSSION

Litterfall and associated element inputs

Total small litterfall in our study was 1105 g m^{-2} y^{-1} (= 11.1 t ha^{-1} y^{-1}) for the period 1 December 1988 to 1 January 1990. Despite the low fertility of the soil in our plot, the litterfall we found is among the highest in the range reported by 18 other studies in moist tropical forest on oxisols and ultisols (Anderson *et al.* 1983, Gong & Ong 1983, Pendry & Proctor 1996, Proctor 1984, Scott *et al.* 1992, Vitousek & Sanford 1986: 5.5–12.0 t ha^{-1} y^{-1}).

Annual inputs of nitrogen, phosphorus, calcium, magnesium and potassium in litterfall were higher than corresponding inputs reported for other studies dealing with forests growing on moderately to highly infertile soils (Vitousek & Sanford 1986). In fact, our values were within the range reported for the moderately fertile soils group of Vitousek & Sanford (1986). Element inputs and

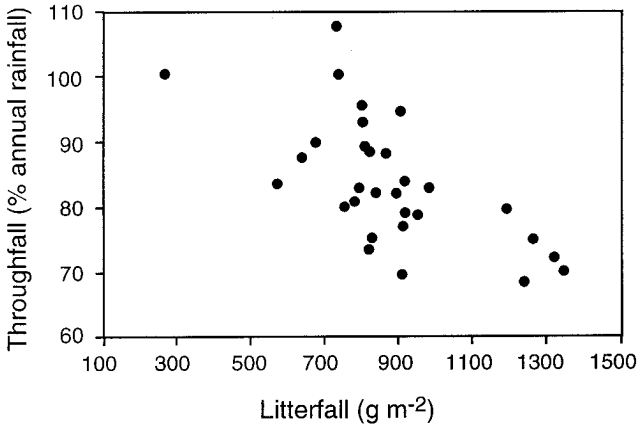

Figure 4. Relationship between throughfall (as a percentage of annual rainfall) and litterfall in 30 sampling areas in dipterocarp forest at Danum.

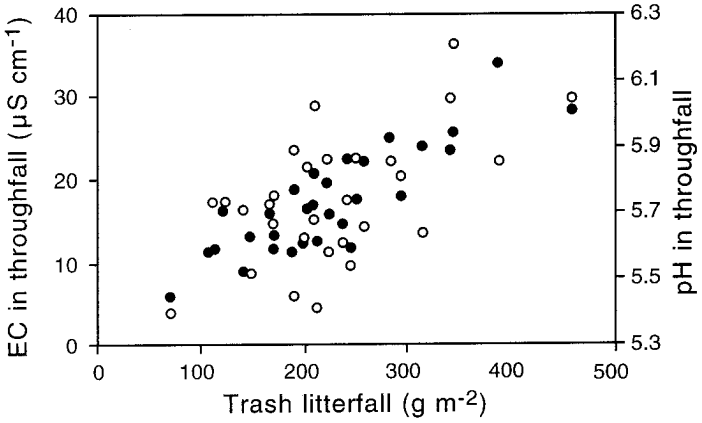

Figure 5. Relationship between electrical conductivity of throughfall (EC, weighted means: ●), pH in throughfall (○) and trash litterfall in 30 sampling areas in dipterocarp forest at Danum.

concentrations in litterfall in the Danum Valley were at least twice those obtained in lowland dipterocarp forest in the Gunung Mulu area in Sarawak, except for potassium, for which concentrations were similar (Anderson *et al.* 1983). Our data regarding element concentrations in litterfall showed striking similarities to values reported by Scott *et al.* (1992) for evergreen rain forest on an infertile sandy soil at Maracá, North Brasil. Except for phosphorus concentrations in all litterfall fractions, which were 1.5 times higher in the Brazilian study, all other element concentrations deviated by less than 10% from our values. The similarity is surprising because the Maracá climate, soil, forest composition, tree size-class distribution and forest floor composition (Thompson *et al.* 1992, Scott *et al.* 1992, T. B. A. Burghouts *pers. obs.*) are all markedly different from our study plot.

Our high estimates of litter input may be explained partly by the inclusion

of a litterfall fraction smaller than 2 mm. The 0.1–2.0 mm trash fraction, which is often excluded in other studies (Proctor 1984), contributed 6–10% of total litterfall dry weight and up to, respectively, 10–15% and 15–20% of the total inputs of nitrogen and phosphorus (Tables 6 and 7). Element concentrations in fine trash were all high in comparison to those in leaf fall, particularly for iron (*c*. 500% higher), phosphorus (*c*. 215%) and nitrogen (*c*. 145%) In comparison to leaf fall, however, potassium concentrations were lower by 70%. Similar differences between element concentrations in leaf fall and trash were found in the Maracá study (Scott *et al.* 1992), for a tall montane forest on fertile soil in Papua New Guinea (Edwards 1982), and for various forest types in Sarawak and Brunei (Proctor *et al.* 1983, Pendry & Proctor 1996). However, potassium concentrations in the Maracá study were higher in trash than in leaf fall, while the reverse was found in our study and in Pendry & Proctor (1996). Edwards (1982), Proctor *et al.* (1983) and Pendry & Proctor (1996) also found relatively higher phosphorus (300 to 257%) and nitrogen (182 to 158%) concentrations in trash compared to leaf fall.

Throughfall and associated element inputs

Throughfall is generally considered to be an important source of directly available elements for roots and forest floor organisms (Parker 1983). Nutrient inputs in throughfall are thought to be particularly important for the availability of nitrogen and phosphorus in the present case, because these elements accumulated immediately in the surface leaf-litter (*cf.* Tables 3 and 4). Enrichment of nutrients in throughfall was most pronounced for potassium and phosphorus. This phenomenon is well-documented for potassium but has been observed much more rarely in the case of phosphorus (Parker 1983). Inputs of nutrients via precipitation were comparable to values presented by Edwards (1982) for a montane forest in Papua New Guinea receiving a similar amount of precipitation. Inputs of calcium, magnesium and potassium were also similar to values for two rain forest sites in northern Australia (Brasell & Sinclair 1983) and, as could be expected, even more similar to values reported by Sinun *et al.* (1992) for a location close to our plot. Nutrient inputs in precipitation and in throughfall at Ulu Segama are generally low in comparison to other lowland forest sites reviewed by Proctor (1987) and Forti & Neal (1992). The observation of Bruijnzeel (1989) that average elemental concentrations of nutrients in bulk precipitation in the humid tropics seem to reflect the rigidity of sampling procedures rather than environmental factors may be pertinent here because amounts of rainfall and throughfall were not particularly low.

Our throughfall estimate of 81% ± 1.8 (SE) of rainfall is in the lower part of the range reported for lowland rain forests: 78–88% (Bruijnzeel 1990). It is very similar to the estimates (81–83%) given by Sinun *et al.* (1992) for a forest in the vicinity of our plot and by Dykes (1997) for a lowland forest in Brunei.

These relatively low values reflect the high rainfall interception rates prevailing in lowland tropical sites subject to maritime influences (Bruijnzeel & Wiersum 1987, Dykes 1997, Scatena 1990).

Litterfall and element turnover

Turnover rates for leaf litter, in this study denoted by k_{LLF}, describe the fragmentation and disappearance of leaf litter into the fine litter layer. Both organic matter and elements were transferred at high rates from the surface leaf layer to the underlying fine litter mass, except for potassium. The latter element had a higher turnover rate than organic matter, indicating quick leaching from the litter. Phosphorus and nitrogen exhibited rapid immobilization, while magnesium had a higher turnover rate than calcium (Table 8), suggesting that magnesium is more susceptible to leaching than calcium. Turnover rates of organic matter were higher for leaf litter (k_{LLF} = 2.9 y^{-1}) than for total litter (k_{LF} = 1.0 y^{-1}). Changes in the chemical composition of decomposing material were illustrated more clearly by k_{LF} than by k_{LLF} because the former showed larger differences between organic matter and element turnover rates. Immobilization in the litter layer was clearly shown for phosphorus, nitrogen and manganese, whereas release rates higher than those for organic matter were obtained for potassium, calcium, magnesium and manganese (Table 4).

Studies in lowland tropical rain forests reviewed by Anderson & Swift (1983) and Proctor (1987), have shown variable turnover rates for litter dry mass (1.0–3.3 y^{-1}), with the litter mass being more variable (1.7–11.2 t ha^{-1}) than litterfall (5.8–12.0 t ha^{-1} y^{-1}). Regional variations in climate, soil type and vegetation composition obviously contributed to these markedly different rates of organic matter turnover, mineralization, and soil organic matter accumulation (Swift *et al.* 1979) although methodological aspects may have played a role as well (see below). Turnover rates for litter dry mass (1.3 y^{-1}) and elements in the mixed dipterocarp forest at Gunung Mulu (Anderson *et al.* 1983) were in between our estimates for turnover rates of coarse and total litter, although site characteristics differed considerably from our site. A climate such as that at Gunung Mulu with high annual rainfall (5000 mm y^{-1}), and lower inputs via litterfall of organic matter and elements, probably results in a more pronounced accumulation of organic matter. In comparison to our study, turnover rates of nitrogen and phosphorus at Gunung Mulu were relatively high, that of calcium was lower, and those of potassium and magnesium were similar. Our estimates for turnover rates of nitrogen, phosphorus, potassium, calcium and magnesium (k_{LLF}) are all higher than those in the lowland rain forest in Brunei studied by Pendry & Proctor (1996).

Studies in temperate forests, such as those by Nihlgård (1972) and others cited in Swift *et al.* (1979) and Duchaufour (1982), showed a similar ranking of turnover rates of element and organic matter as found in our study. Nitrogen

and phosphorus exhibited lower turnover rates than organic matter or carbon which, in turn, had lower turnover rates than calcium and magnesium. Potassium is usually the most mobile element (Duchaufour 1982). Although organic matter exhibits variable turnover rates among various studies, the values reported by Nihlgård (1972) for temperate forests were surprisingly similar to ours.

Methodological problems in litter turnover studies

Major problems in interpreting k_L values for organic matter and elements from other studies concern the heterogeneity of forest floor profiles among different forest types, definitions of the litterfall size fractions, and the consequently often arbitrary descriptions and approaches to sampling of the litter layer mass (Anderson & Swift 1983; Proctor 1984, 1987).

The problem of heterogeneity of forest floor profiles within and among forest types is difficult to overcome. Gradual transitions from litter to soil organic matter are an important ecosystem characteristic in montane forests, podzolic soils and heath forests (Anderson *et al.* 1983, Edwards 1977). Estimates of litter turnover depend very much on the distinction made between forest floor litter and soil organic matter (Coleman *et al.* 1989), and require accurate profile descriptions to estimate temporal and spatial changes in organic matter standing crops (Young 1989). Both Anderson *et al.* (1983) and Scott *et al.* (1992) defined litter particles exceeding 2 mm in diameter as litter and below 2 mm as soil organic matter, although these size fractions were difficult to separate in practice. In their studies, litter turnover was estimated using litterfall and litter mass fractions >2 mm. In the present study, litterfall particles with a minimum size of 0.1 mm were collected, whereas no minimum size was used for litter-layer material. The litter layer was defined as the loose and platy layer of leaves, leaf fragments and humus, covering the compact top layer of mineral soil. From this layer the majority of the macro-invertebrates and fine root mass was collected (Burghouts *et al.* 1992).

Mineral soil particles contributed significantly to the gross dry mass of the samples of leaf litter and of fine litter in particular. Corrections for this were made in the present study by determining the organic matter content of all fractions. By doing so, we were able to demonstrate that the dry mass of fine litter was a two- to three-fold overestimation of the amount of organic matter in the litter layer. Turnover rates, calculated on the basis of gross litter dry weight, therefore, would underestimate the turnover rates of litter and elements. For the estimates of litter mass on organic profiles in montane forests (Edwards 1977) and podzolic mixed dipterocarp and heath forests (Anderson *et al.* 1983), the litter mass was not adjusted for the inclusion of mineral soil particles.

Other problems in interpretation of k_L-values concern the direct underestimation of input and/or mass of litter and elements. The underestimation of

inputs resulting from exclusion of the litterfall fraction <2 mm has already been mentioned. The use of litter traps with a fine mesh width (0.1 mm) increased our estimates of organic matter and element inputs in litterfall. As shown in Table 6, excluding the fraction <5 mm would have resulted in a marked underestimation of organic matter and element inputs and associated turnover rates, in particular of phosphorus and nitrogen. In other studies on litter decomposition, such as those reviewed by Anderson & Swift (1983), total litterfall (>2 mm) was related to the leaf-litter standing crop. The latter was not further defined, but obviously the fine litter mass was excluded. This underestimation of the litter layer mass may well have resulted in overestimations of turnover rates of dry mass, organic matter and elements. In our case, this would have resulted in an organic matter turnover ratio of *c*. 3.4 y^{-1} instead of the present value of *c*. 1.0 y^{-1}.

Spatial heterogeneity of litter turnover

Litterfall and litter mass as well as the corresponding element inputs and element pools were highly variable among the 30 sampling areas in our plot, however, they showed surprisingly strong correlations with each other (Figure 2). The variability among sampling areas is mainly due to heterogeneity in the total amount of litterfall. Generally speaking, the periodicity and synchronization of leaf fall between trees or taxonomic groups determine the heterogeneity of litter on the forest floor. Although there were 305 species of trees in the study plot, quantitatively, leaf fall was dominated by a relatively small number of large, and by implication old, emergent and upper canopy trees (Burghouts *et al.* 1994). A major part of the annual leaf fall occurred during generally large or intense peaks that were either synchronized or alternated among individual trees, and that exhibited a regular periodicity which differed between tree species.

It was expected that variable litter chemistry would cause additional heterogeneity on top of the heterogeneity in total leaf fall, such that element turnovers would be more variable than dry matter and C turnover. This proved indeed to be the case, but the effect was evident only for K and Mn. Most of the other elements (Mg, N, P, Ca) seemed to add little extra variation to the already considerably large variation in total leaf fall. Similarly, Burghouts (1993) did not observe large seasonal changes in the chemical composition of litter although the species composition of litterfall varied greatly from one month to another (*cf.* Burghouts *et al.* 1994). In the present study, element turnover was less variable between sampling sites, due to the positive correlations between litterfall and litter mass (Figure 2).

Concentrations of nitrogen, phosphorus and potassium in leaf fall were strongly correlated with each other among the 30 sampling areas. Relative nitrogen turnover was also correlated with nitrogen in litterfall, suggesting a higher degree of nitrogen conservation in litter at sites with low nitrogen in litterfall (Figure 3). A different pattern was found for calcium and

manganese. The turnover and availability of these two elements were correlated with each other and with elevation, more than with turnover of organic matter, while relative turnover of calcium was negatively correlated with calcium in litterfall. This contrast in element behaviour illustrates the importance of biological processes in the turnover of nitrogen, phosphorus and potassium as opposed to the perhaps more pedological character of processes governing the turnover and availability of calcium and manganese.

The strong interactions between nutrient inputs, nutrient availability and nutrient uptake in the studied ecosystem are indicative of the strong interrelationships that exist between above-ground nutrient cycling and forest productivity on infertile tropical soils (Swift *et al.* 1979). This illustrates how the vegetation depends on the rapid recycling of nutrients to maintain or even increase its foliar nutrient levels on soils as poor in nutrients as in the present study. The increasing demand for nutrient release from the decomposing forest floor during biomass accumulation should become an important consideration with respect to the sustainability of productivity in tropical forestry.

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