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Litterflow chemistry and nutrient uptake from the forest floor in northwest Amazonian forest ecosystems

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Abstract. Samples of the fraction of net rainfall passing through the forest floor collected at monthly intervals in four pristine forests in Colombian Amazonia, during the period between 1995–1997 were analysed for solute concentrations to estimate the element fluxes from the forest floor into the mineral soil and root nutrient uptake from these forest floors. Results were compared with inputs by throughfall, stemflow, litterfall and fine root decay. Element concentrations were tested for their relationship with litterflow amounts, rainfall intensity and length of the antecedent dry period and differences in element fluxes between ecosystems were assessed. Concentrations of elements in litterflow followed a similar pattern as those in throughfall, which indicates that element outputs from the forest floor are strongly related to those inputs in throughfall. In the forests studied, the average concentrations of elements as K, Mg, orthoP and the pH of the litterflow decreased relative to that in throughfall in most events, while the concentration of elements such as dissolved organic carbon, H, SO_4 and Si increased in litterflow from these forests. Element concentrations in litterflow showed a poor correlation with variables such as litterflow amounts, rainfall intensity and antecedent dry period, except for K which showed a significant correlation ($p>0.95$) with analysed variables in all forests. Outputs were significantly different between forests ($p>0.95$); these fluxes, which particularly concerned cations, being the largest in the flood plain, while for anions outputs increased from the flood plain to the sedimentary plain. After adding the nutrient contributed by litter decomposition and fine root decay, the net outputs of main elements from the forest floors were still smaller than inputs by net precipitation (throughfall + stemflow) indicating that the litter layers clearly acted as a sink for most nutrients. Accordingly, the element balances confirm that the forest floors acted as a sink for nutrients coming in by throughfall, stemflow, litterfall and fine root decomposition. P, Mg and N appeared to be the most limiting nutrients and the forests studied efficiently recycled these nutrients.

Introduction

Most Amazonian soils are highly weathered and leached, their mineral fraction being composed of quartz, kaolinite, gibbsite and hematite. Furthermore, soil organic matter contents are very low and these soils therefore have a very low cation exchange capacity. However, with rainforest vegetation, they often have a thick litter layer, hereafter referred to as 'forest floor', of which the capacity to retain nutrients seems to be much higher. It results from the accumulation of slowly

decomposing aboveground litter and root litter, and contains a dense root mat. The development of the forest floor and root mat has been linked to the availability of nutrients from decomposing litter and to the inputs of solutes in throughfall and stemflow, relative to their low availability in the mineral soil (Fittkau et al. 1975; Jordan and Escalante 1980; Golley 1983; Jordan 1985; Cuevas and Medina 1988) and the high competition for available nutrients (Klinge 1977; Jordan and Escalante 1980; Vogt et al. 1983).

Nutrient availability on the soil substrata in this part of the Amazonia is very low and the contributions by rock weathering are negligible (Proradam 1979), although relatively higher than in other sites within the Amazon basin (Sanchez 1976). Moreover, leaching losses can be substantial, particularly under conditions of high rainfall and soils with a low nutrient retention capacity, high porosity and low root mat, as it the case here. Under these conditions the importance of the forest floor with a large root mat and associated mycorrhiza would increase, being capable of capturing released nutrients and even extracting these directly from the litter (Went and Stark 1968; Stark and Jordan 1978; Arunachalam et al. 1996). The forest floor thus plays an important role in nutrient cycling (Jordan 1985; Burnham 1989; Green et al. 1993), particularly in nutrient-poor forest ecosystems (Salati et al. 1979; Tiessen et al. 1994). Moreover, in such systems the nutrients in litter and in throughfall and stemflow seem to be recycled with great efficiency (Longman and Jeník 1990), resulting in a very tight nutrient cycle in which the mineral soil compartment plays a minor role (Jordan and Herrera 1981; Burnham 1989). This was demonstrated by Stark and Jordan (1978) who found that after spraying radioactive phosphate and calcium on the forest floor of an Amazonian rain forest in Venezuela, less than 0.1% of these elements reached the underlying mineral soil compartment.

Several authors thus recognised that the forest floor is important for the supply of water and nutrients to trees in tropical rain forests. However, most studies concentrate on the input of nutrients by litterfall and their release with litter decomposition (Franken 1979; Jordan 1982; Medina and Cuevas 1989; Duivenvoorden and Lips 1995). Other studies concern solute inputs in throughfall and stemflow (Stark and Jordan 1978; Cuevas and Medina 1986; Tiessen et al. 1994; Brouwer 1996), while studies which specifically deal with the role of the forest floor and its fine roots in the nutrient cycling, nutrient uptake and solute fluxes to the mineral soil for nearby forest ecosystems having similar atmospheric inputs (dealt with preceding paper by Tellez et al., submitted), but with differences on their structure, litter inputs, fine root content and on soil nutrient status, are very scarce. This holds for most of Amazonia, particularly for the Northwest part of the basin.

Within a framework of an entire research project focus on the hydrology and nutrient fluxes in these forest ecosystems, the amounts of water flowing to (throughfall and stemflow) and through the forest floor to the mineral soil (litterflow) and the water uptake by roots from the forest floor were investigated (Tobón 1999; Tobón et al. 2000). These forest floors were found to play a key role in the water storage, root water uptake and overall water balance of the forests concerned and differences between forest ecosystems were found. Moreover, the available

water in the forest floor was found to contribute significantly to forest transpiration, which appeared to differ among the systems studied and to be related to the amount of litter and abundance of fine roots (Tobón et al. 2000).

Earlier study on the biotic part of these forests also showed that there are clear differences between ecosystems in composition and structure of the vegetation, in size and composition of the litterfall, in soil properties, in soil nutrient status and on standing litter amounts in the forest floor (Duivenvoorden and Lips 1993, 1995). Moreover, within the hydrological study of these forests, it was found that canopy water storage, throughfall amounts, leaf area index differ between these ecosystems (Tobón 1999; Tobón et al. 2000). According to Wassenaar (1995) and de Vente (1999) the root biomass and root distribution in the forest floor also differ between studied forests. Base on these results Tobón (1999) concluded that these differences very likely lead to differences in nutrient dynamics of the forest floors, as chemical composition of the litterflow and nutrient uptake by roots.

This paper deals with the litterflow chemistry and solute fluxes from the forest floor to the mineral soil in four nearby pristine forest ecosystems in Colombian Amazonia. It focuses on the changes in the chemistry of throughfall and stemflow when passing the forest floor and the temporal and spatial dynamics (comparisons between ecosystems) of the forest floor solute fluxes. Furthermore, element inputs by throughfall and stemflow in each forest ecosystem are compared with the inputs by litterfall and fine root decay and balanced with the forest floor outputs. Results are translated into uptake by roots, outputs to the mineral soil and differences between sites. In earlier papers, attention has been paid to the solute fluxes in gross rainfall (Tellez et al., in press) and solute inputs to the forest floor in throughfall and stemflow (Tobón et al. (in press)). Data from these papers on total solute inputs in throughfall and stemflow and data on the input by litterfall and root decomposition are used in this paper to derive the element budget at the forest floor level.

Research sites

The area of study is in an indigenous territory (Nonuya Indian community) near Araracuara, Middle Caquetá, Colombia (0°37′ and 1°24′S, 72°23′ and 70°43′W). The landscape in this part of the Amazon basin comprises a large dissected Tertiary sedimentary plain (about 250 a.s.l.) and the alluvial system of the River Caquetá, which includes high and low terraces and a recent floodplain. The research was carried out in four forest ecosystems, located in respective landscape units, covering the sequence from the flood plain of the River Caquetá to the Tertiary sedimentary plain. Since 1992, detailed climatic and hydrological data have been collected by an automatic weather station (AWS) in an open area of approximately 20 ha, close to the plots.

In all plots, the vegetation is mature pristine rain forest (ombrophillous tropical rain forest). The canopy reaches an altitude of 25–30 m above the forest floor with some emergent trees reaching up to 45 m in the rarely inundated flood plain. Differences in total standing biomass, species diversity, tree density, soil nutrient

status and litter standing stocks between the forests in the four landscape units were found and explained by Duivenvoorden and Lips (1995). The floodplain forest is less sclerophyllic, has more abundant epiphytes and growths in a more fertile soils, a trend gradually reversing towards the forest of the sedimentary plain (Duivenvoorden and Lips 1995). Other important differences between plots pertain to the structure of the forest canopy, such as canopy cover and LAI, both being largest in the flood plain (Tobón 1999) mainly due to the abundance of epiphytes, climbers and aerial roots. Differences between these forests on root distribution, growth and decomposition in the forest floor and in the mineral soil were also found and explained by Wassenaar (1995) and de Vente (1999).

In these research sites, Duivenvoorden and Lips (1995) described eight types of terrestrial humus forms with associated differences in amounts and distribution of fine roots and in structure. They observed that with decreasing nutrient status upland (Tertiary sedimentary plain and high terrace) soils have a thicker forest floor with higher root content and root density, while in the floodplain the forest floor is absent or very thin (<5 cm). All forest floors consisted of dead leaves, fine roots and debris (twigs, bark, wood, flowers, fruits and seeds) in various stages of decomposition, in which layers were difficult to separate. Their average dry mass, inclusive of living fine roots, ranged from 3.6 to 12 kg m^{-2}. Where the forest floor was well developed, a prominent root mat occurred consisting of a dense network of mostly medium and fine roots in a matrix of decomposing organic matter. The average percentage of fine roots in the forest floor, relative to the total amount of roots over a depth of 1 m, was 34% in the sedimentary plain, 19% in the high and low terraces and 12% in the flood plain of the River Caquetá (Wassenaar 1995; de Vente 1999).

Duivenvoorden and Lips (1995) and Proradam (1979) extensively studied the soils in the middle Caquetá area. Except for the very recent soils of the floodplain, the soils generally have a clay loam to sandy clay loam topsoil over clayey subsoil. The floodplain soils that regularly received fresh sediments from the River Caquetá, which originates from the Andes, were relatively nutrient rich and contained significant amounts of weatherable minerals. While the soils of the low terrace held an intermediate position, the strongly weathered and leached soils of the high terrace and sedimentary plain had a very low base saturation and contained very low amounts of weatherable minerals. This was reflected in their very low stocks of phosphorus, potassium, calcium and magnesium and the dominance of quartz and kaolinite in the mineral fraction. The physical properties of the soils were quite optimal: they were well structured, had a high porosity in the first 50 cm, a high water infiltration capacity and observe high values of hydraulic conductivity (Tobón 1999). However, external drainage differed from rather poor with shallow groundwater on the floodplain and low terrace to overall well drained soils on the high terrace and sedimentary plain.

Based on data collected during the period between 1992 and 1997, mean annual rainfall was about 3400 mm. The period December–February was relatively dry, mean monthly rainfall still exceeding 100 mm. The relative humidity was generally above 75% and close to saturation ($>95\%$) during the nights. The mean daily

temperature was around 24 °C. During the day, inside the forest the temperature was slightly lower than outside, but the humidity was always higher and the radiation was low and patchy. Forest floor and soil temperature in these undisturbed forests followed the 'in-forest' temperature, which during the day on average was 2–4° lower than the 'above-forest' temperature and during the night 2–5° higher.

Methodology

The hydrology of the forest floors, notably the amounts of water passing through the forest floor, their water storage capacity and the volumetric water content dynamics were investigated in the four forest ecosystems, during the period between January 1995 and August 1997 (Tobón et al. 2000). To measure the amounts of water percolating through the forest floors, in each forest ecosystem, three subplots were selected where 15 randomly located commercial drainage plates were installed horizontally in the contact zone between the forest floor and mineral soil and connected to plastic collectors of 20 l (painted black to prevent inside algae growth) installed in a soil pit dug at a distance of approximately 0.2 m from the plate. Collectors were manually measured on daily basis. These subplots were also used to measure other hydrological variables, as gross rainfall, throughfall and stemflow (Tobón 1999).

To avoid any solid material to enter the plates and funnels, a fine plastic mesh (240 μm) was attached to the upper part of each plate and between the funnel and the collector. Each collector was washed with a solution of HCl (10%) and rinsed with abundant distilled water before installation for sampling. For a full description of the methodology used to study the forest floor water dynamics readers are referred to Tobón et al. (2000) and Tobón (1999).

For the purpose of this chemistry study, water samples of 100 ml were collected from each collector, during the daily measurements (on event basis). The criterion for this sampling was the temporal distribution of gross rainfall in the area, in such a way that samples were collected at monthly intervals and contiguous with the sampling of gross rainfall, throughfall and stemflow. Sampling dates covered all wet and dry periods during the 2-year period, following rainfall patterns in the area. In total 35 samplings were carried out for each forest ecosystem, 11 during dry periods and 24 during wet periods. The hydrological study in these forests found that there were not significant differences on the amounts of water passing as throughfall and litterflow within subplots in each forest ecosystem (Tobón 1999), which agreed with that found by Duivenvoorden and Lips (1995), who concluded that forest structure, the amounts and chemical composition of litterfall and soil nutrient status did not vary significantly ($p>0.95$) within sites in the same landscape unit.

As there were not differences on the analysed variables within same forest ecosystem, we expect a low variability on the chemical composition of separate samples from the subplots. Therefore, during each sampling, the total water sampled in subplots was bulked per plot and from these bulk samples, three

sub-samples of 250 ml were taken in a polyethylene bottles, after rinsed with a 10% HNO_3 solution and washed with distilled water: two samples were filtered (0.45 μm Millipore filter) and used for chemical analysis. Sub-samples for the determination of cations and dissolved organic carbon (DOC) were acidified with concentrated HNO_3 to pH 2.0. Sub-samples were kept in the dark at approximately 5 °C until their transport to the Netherlands where they were immediately analysed. The third non-filtered sub-sample was used for the field estimation of the electrical conductivity and pH immediately after sampling.

Ec and pH from water samples were determined in the field through WTW conductimeter and a pH meter calibrated against buffer solutions (Baker Chemical Co.) with pHs of 4.0 and 7.0 at 25 °C. Concentrations of metals (K, Na, Ca, Mg, total Fe, Mn and Si) were determined with a flame Pekin-Elmer AA/AES inductively coupled plasma emission (ICP) spectrophotometer, after acidification till pH 1.0 with concentrated HNO_3. The concentrations of non-metals Cl, NO_3, NO_2, SO_4, orthoP, NH_4 and DOC, were determined by spectrophotometry on Technicon and skalar continuous flow auto-analyzer according to the standard automated methods. Total N was determined as NH_4 on the ICP after destruction (Kjeldahl digest). Accuracy of the analysis was assumed to be within the 2% of the concentrations, while maximum errors for each constituent were between 0.02 and 0.04. Detection limits for metals were as follows in $mg\,l^{-1}$: K = 0.02, Na = 0.03, Ca = 0.05, Mg = 0.01, Fe = 0.02, Mn = 0.01 and Si = 0.5. As for non-metals the detection limits were: $NH_4 = 0.2$, $NO_3 = 0.2$, $NO_2 = 0.02$, $SO_4 = 2.0$, Cl = 0.4, orthoP = 0.01, DOC = 2.0.

As described under methodology, litterflow at plot level was sampled by taking 100 ml per individual collector, provided that collectors contained a minimum quantity of 100 ml which was not always the case, and bulking these samples into one bulk sample per plot. This methodology had to be chosen because of the very difficult terrain conditions and variability in litterflow size, which seriously hampered a reliable volume based sampling. This implies that the chemical composition of the bulk litterflow is not corrected for any volume-related differences in chemical composition of individual samples by sampling a fixed proportion of the litterflow in each collector and bulking these. If the chemical composition of the litterflow would indeed depend on its volume, this would lead to bias in the results, for example, higher bulk values if concentrations would increase when litterflow decreases. However, as will be discussed in more detail later on, we found no systematic relation between solute concentrations in and the magnitude of the litterflow, as is also evidenced by the low CV for element concentrations in litterflow. The implication is that such bias due to the sampling strategy, if occurring at all, must be of very minor importance.

Changes in net solute concentrations (CC) in litterflow in each ecosystem were calculated for each sampled event, using the data on the bulk concentration of solutes in litterflow and those in net precipitation (throughfall + stemflow). Solute fluxes in litterflow were calculated for individual rainfall events by multiplying the bulk concentration of each solute by the measured volume of litterflow. Daily solute fluxes during the entire period or the Volume Weighted Mean Concentration of the

i-solute ($VWMC_i$) in litterflow were estimated from the paired measurements of solute concentration and litterflow amounts in each plot.

$$VWMC_i = \frac{\sum_{j=1}^{n} C_{ij} \cdot Lf_j}{\sum_{j=1}^{n} Lf_j} \quad (1)$$

Where C_{ij} is the *i*-solute concentration in litterflow during the *j*-event, Lf is the total water passing the forest floor and *n* is the total number of events sampled. The annual fluxes of solutes in litterflow into the mineral soil were calculated as the product of the VWMC of each solute and the cumulative yearly measured litterflow. Although the concentrations of most elements were expected to be very low, when compared with other forest ecosystems or sites, the concentration of most elements were within the detection limits; except for orthoP in the sedimentary plain forest (in 3 out of the 35 sampled events) whose concentration felt below the detection limit. In these cases, respective fluxes and the weighted mean concentration were calculated only from available data, leading to unavoidable overestimation of its concentration and fluxes. However, in terms of its impact on the total flux, such values will be of minor importance since very low concentrations will lead to minor fluxes as compared to periods with relatively high concentrations.

The ratios of litterflow enrichment/depletion of elements (*E*/*D*) or nutrient recycling rates were calculated for each element as the net fluxes in litterflow minus total inputs in net precipitation, and adding element inputs from decomposed litterfall and fine root decay, divided by those in net precipitation, litterfall decomposition and fine root decay. To that purpose, results from previous studies carried out in these forest ecosystems, as part of our research project, which included litterfall and its chemistry (Overman 1994) as well as results from fine root studies and their chemistry (Wassenaar 1995; de Vente 1999) were used for the element balance in the forest floor compartment.

The nutrient balance for the forest floor compartment was based on comparison of inputs of major elements associated with litterfall and fine root decay plus those in throughfall and stemflow with outputs through litterflow. The Student's t-test (by paired forests at the time) was applied to determine whether the means of the set of values found for each forest are distinct, in order to know the spatial variability of litterflow element fluxes between forests. To test relationships between element concentration in litterflow and litterflow amounts, rainfall intensity and the antecedent dry period, the product-moment Pearson correlation and regression analysis were applied.

Results and discussion

Solute concentrations in litterflow

The average values of solute concentrations in litterflow, their coefficient of variation (CV) and the VWMC in the four forests are presented in Table 1. For several

Table 1. Mean solute concentrations in litterflow (μmol l^{-1}, * in μmol l^{-1}), their coefficient of variation (CV in %), the volume weighted mean concentration (VWMC) and solute concentration changes (CC) relative to that in net precipitation (litterflow minus throughfall and stemflow concentrations) during the period 1995–1997 in four pristine forests in Colombian Amazonia.

Element	Sedimentary plain				High terrace				Low terrace				Flood plain			
	Mean	CV	VWMC	CC	Mean	CV	VWMC	CC	Mean	CV	VWMC	CC	Mean	CV	VWMC	CC
H	112.4	1.1	126.9	103.5	79.0	1.3	79.1	72.5	84.0	1.8	92.6	73.5	62.1	2.0	59.1	57.2
K	17.6	1.4	17.2	−7.7	19.9	2.1	21.1	−13.3	17.8	2.4	17.0	−15.7	22.5	2.8	22.4	−12.5
Na	22.6	2.7	22.8	2.4	21.8	2.7	22.9	−2.7	22.2	2.6	21.2	−1.9	24.7	3.1	24.8	1.5
NH_4	2.3	1.4	24.7	4.4	16.5	1.9	16.6	−6.8	19.6	1.7	19.6	−4.0	16.2	2.2	17.0	−7.3
Ca	9.0	2.7	9.1	0.9	12.4	1.7	13.2	3.7	9.0	3.5	8.6	−0.04	14.9	3.4	14.1	2.4
Mg	5.0	2.4	4.7	−1.7	8.3	1.9	8.6	1.3	6.2	2.0	5.8	−0.9	9.9	1.8	9.4	−1.9
Fe	4.5	1.1	4.2	3.5	5.5	1.2	6.1	4.2	3.8	1.8	4.0	2.6	4.1	1.4	3.6	3.1
Mn	0.2	2.2	0.2	−0.1	0.5	0.9	0.6	0.4	0.3	1.5	0.3	0.1	0.4	2.6	0.4	0.2
Si	17.6	1.9	16.2	13.0	15.5	1.7	14.0	9.1	19.6	2.2	18.2	13.8	31.6	1.7	29.9	23.5
Cl	28.8	2.2	28.4	4.6	33.5	1.9	32.8	7.4	28.3	1.7	26.1	−5.6	26.7	2.0	25.9	−0.2
NO_3	16.2	1.6	17.3	1.3	14.7	1.3	14.6	3.9	12.8	1.4	12.4	−8.1	13.1	1.3	13.8	−7.1
OrthoP	0.3	1.4	0.3	−0.4	0.4	1.1	0.4	−0.2	0.3	1.4	0.3	−0.6	0.3	1.7	0.3	−0.6
SO_4	74.9	2.3	73.1	20.6	67.5	2.2	67.5	11.0	56.4	3.0	56.4	−2.6	54.5	2.2	49.0	7.1
Cations	194.5	1.8	209.7	105.1	163.8	1.6	168.0	59.5	162.9	4.0	169.0	53.6	154.5	4.5	150.7	42.8
Anions	120.1	2.9	119.0	26.1	115.6	2.0	115.3	22.1	97.8	3.4	95.2	−16.9	94.6	2.9	88.9	−0.8
*DOC	973.3	3.2	971.5	548.8	1098.0	3.1	1085.7	554.8	1002.0	2.8	882.8	344.4	672.7	3.4	657.2	213.7

elements, average concentrations in litterflow decreased relative to those in the corresponding net precipitation: K, Mg, and orthoP decreased in all forests, while Na, NH_4, Cl and NO_3 concentrations decreased in the high and low terraces and in the flood plain forests. After DOC and hydrogen, SO_4, Cl, NH_4, Si, Na, NO_3 and K were the most abundant elements flushed from the litter layer in the forests studied, fluxes being larger in the sedimentary plain and the high terrace ecosystems. The dynamics of solute concentrations in litterflow in studied forests followed the same pattern as those in throughfall (Figure 1, for the sedimentary plain as an example). Thus, on the sedimentary plain the correlation between concentrations of K, Mg, Cl, Na, SO_4 and NH_4 in litterflow and that in net precipitation were significant at the 0.01 level. On the high terrace, a high correlation was found for NH_4, Cl, K, Na and orthoP, while on the low terrace such correlation was only observed for SO_4, Ca and Mg, and on the flood plain for SO_4, NH_4, Cl and K. Such correlations imply that in these forests solute inputs to the forest floor, mainly those highlighted above, largely originate from the throughfall, as will be discussed further on. For some elements, concentrations in the litterflow were also significantly correlated ($p > 0.99$) with those in the corresponding rainfall.

It is not surprising that in the litterflow the concentration of most solutes often clearly decreased relative to the throughfall, particularly in forest growing in soil poor nutrient conditions. However, the pattern in forest studied was rather complex through the time, site and element dependent: in the sedimentary plain forest, decreases in solute concentrations ranged from 83% of the measured events for Mg, 80% for K, 77% for Mn and orthoP, and 43% for Na. Litterflow concentrations of other elements also decreased in some events relative to throughfall, except for H, Si, Fe and DOC. In the high terrace forest, these decreases ranged from 77% for orthoP, 62% for K, 41% for Na and 35% for Mn, while most other elements on average decreased in 28% of the sampled events, except for H, Si and Mn, which did not decrease in any event. In the low terrace forest, values ranged from 87% for K, 81% for orthoP, 68% for Cl, 64% for Mg and 45% for NO_3, while in the flood plain forest similar values were found: orthoP decreased in 88% of the events, K in 80%, Mg in 72%, Cl in 68% and NO_3 in 52%.

Though concentrations of elements decreased in a number of events, after net precipitation passed the forest floors, as described above, Table 1 demonstrates that for most elements overall concentrations slightly increased respective to those in throughfall plus stemflow, which is mainly due to the larger increases in concentration during some larger events relative to the decreases in other relatively small events. On average, on the sedimentary plain and the high terrace the water passing through the litter layer was enriched to a greater degree than on the low terrace and flood plain, being the least in the low terrace forest. Solutes whose concentration increased the most were DOC, H, SO_4 and Si (see Table 1).

Solute concentrations in litterflow are not only affected by their uptake or release, but also by the decreases in amounts of water passing through the forest floor as a result of water uptake by roots and evaporation of intercepted water. According to Tobón et al. (2000), these forest floors intercepted large amounts of water with values ranging from 7 to 75% of net rainfall depending on the amounts and

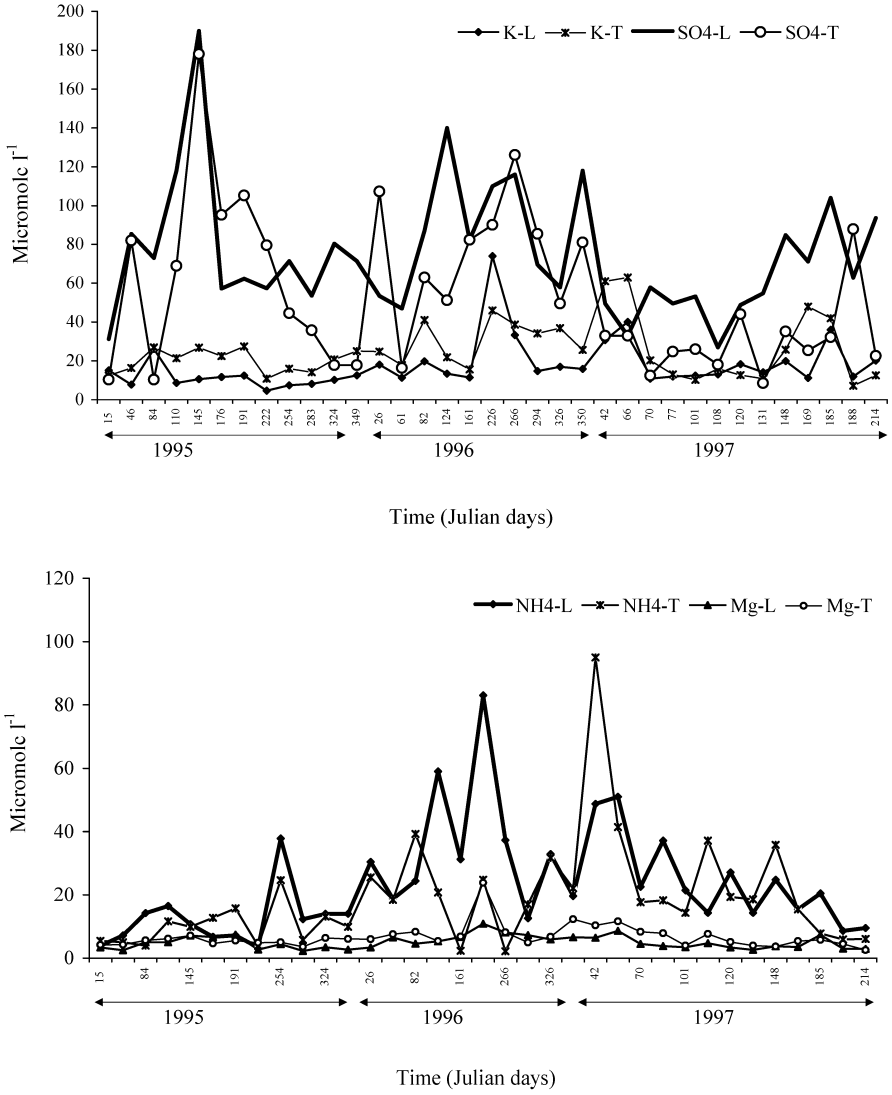
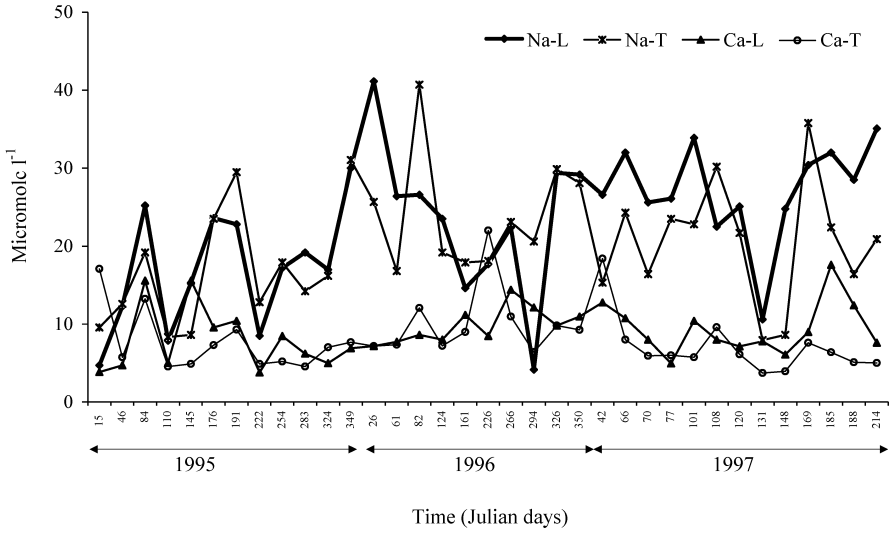


Figure 1. Concentrations of main elements (μmol l^{-1}) in forest floor (L) water samples ($n = 35$) and the corresponding concentrations in throughfall (T) in the sedimentary plain forest ecosystem (as an example for the four forests).

characteristics of rainfalls and on litter amounts in the forest floor. This water interception by the forest floor causes a proportional increase of solute concentrations in the litter layer and affects the fluxes of these solutes in the same way. However, in several small rainfalls the increases of solute concentrations in litterflow were not observed, which were probably masked by a high nutrient uptake by roots during such events and mycorrhiza immobilisation.



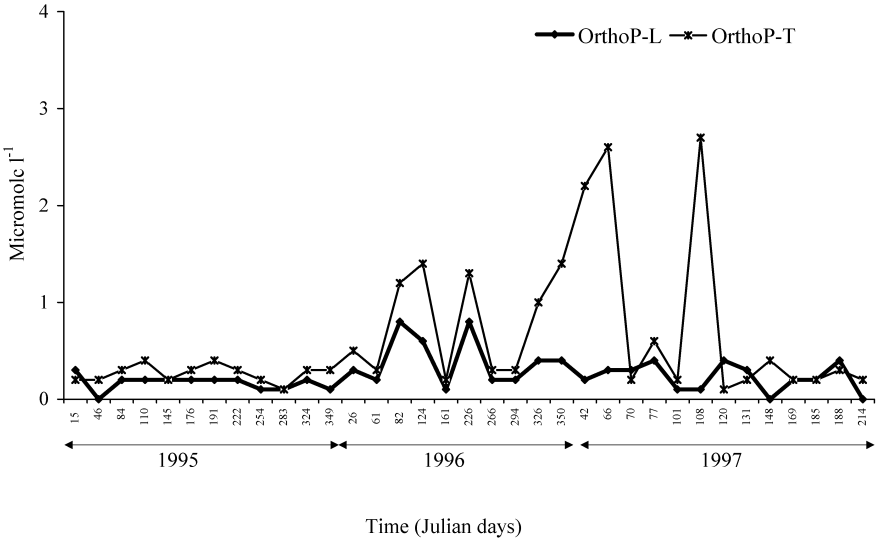


Figure 1. (continued).

Considerable differences on the concentration dynamics existed between the various elements as is described and discussed below. Inputs of orthoP by throughfall and stemflow were very small (Tobón et al., in press) and its availability in the soils was very low as well (Tobón 1999). In litter, phosphorus had one of the longest residence times of all plant nutrients and, probably related to its strong retranslocation before leaf abscission, in both plant tissues and litter the

P-concentration appeared to be very low (Duivenvoorden and Lips 1995). The calculated negative values for the changes of P concentration in litterflow in these forests (see Table 1) clearly indicated that the vegetation was capable of recapturing most phosphorus, although some immobilisation may occur. This is fully in line with the observations by Vitousek (1984), who found that nitrogen is a limiting factor in temperate forests while phosphorus acts as such in tropical forests. The negative values for inputs–outputs of P to the forest floor, does not compare well with the balanced budgets reported for other forests within the Amazonia (Bruijnzeel 1991), with similar soil nutrient status (Sanchez 1976).

It should be stressed that in the net precipitation (throughfall and stemflow) and in the litterflow orthoP concentrations were estimated, while organicP (DOP) will also have been present as solute. Inputs and outputs therefore will have been larger than estimated on the basis of the orthoP values only, reducing the reliability of estimates of the efficiency of the forest to recycle P. However, the contribution of organicP can be roughly estimated on the basis of the DOC-values and reported values for C/P ratios (in g/g) of DOP, which are between 400 and 600 (Gressel and McColl 1997). This leads to values for organic P similar to those of orthoP.

Potassium appeared to have the shortest residence time in the litter (Duivenvoorden and Lips 1995), which can be explained by its well known high leachability from living and dead plant tissues. In spite of this very high mobility, its concentration in litterflow decreased considerably relative to throughfall in all ecosystems. This implies that K was rapidly and efficiently taken up by the vegetation and soil micro-organisms. Magnesium concentrations exhibited a similar trend as that of orthoP and K, indicating that the demand by these forests for these three nutrients was also high.

Net increases in concentrations of NH_4 and NO_3 relative to net precipitation were only observed in the sedimentary plain forest, which correspond well to the high N use efficiency by three out of the four forest ecosystems. These results partly confirm the assumption of N limitation of tropical forests growing on podzolised soils (Vitousek 1984; Cuevas and Medina 1986). The low increase of N in the sedimentary plain forest will have been due to the large amounts of N released by litter decomposition (Duivenvoorden and Lips 1995), in line with the abundance of litter in this ecosystem as compared to the others forests studied.

The uptake of Ca and Mg from the forest floor was relatively high considering the changes in their concentrations and fluxes. These elements are not strongly retranslocated before leaf abscission (Gauch 1972) and therefore losses from the vegetation through leaf shedding will be relatively important as compared to N and orthoP. However, their concentration in litter from these forests was rather low as shown by Duivenvoorden and Lips (1995) and amounts released during litter decomposition were also relatively low, which is in line with their lesser mobility as compared to K. Moreover, in the forest floor roots and micro-organisms compete for Ca and Mg, which are taken up by decomposers to be immobilised in microbial mass (Golley et al. 1975). These conditions and the competition between roots and micro-organisms will explain their low concentration in the litterflow.

The values for sodium clearly demonstrated that this element is basically not required by the forest studied or by micro-organisms (see e.g., Gauch 1972), its concentration in net precipitation even increasing when passing the forest floor. This increase may be partly attributed to the uptake of water by roots and evaporation from the forest floor leading to a higher solute concentration in the litterflow, but some Na will also have been released from the litter.

The concentrations of DOC in litterflow doubled relative to throughfall and stemflow, values for the sedimentary plain and high terrace forests being significantly higher ($p > 0.95$) than for the low terrace and floodplain forests. The large increase in DOC will have been due to leaching of organic acids from the forest floor, which indeed was thickest in the sedimentary plain and high terrace forests. According to Keene et al. (1983) the anion deficits, which were in the order of 2 as can be seen in Table 1, can be attributed to the concentration of organic acids as derived from the DOC-values.

Contrary to most elements, SO_4 increased considerably in litterflow, which implies that it must have been released from the litter in the forest floor. Sulphate is one of the elements which has a long residence time in plant tissues and is an important plant nutrient. The quite considerable losses of SO_4 from the forest floor therefore clearly indicated that the combined atmospheric input of sulphate and sulphate uptake by roots from deeper soil horizons exceeded the vegetation requirements. Such situation can be expected, since in the Tertiary sediments pyrite-containing strata abound (Hoorn 1993) and drainage water from these sediments tends to be high in sulphate, formed upon oxidation of the pyrite and related sulphides. This also holds for the Caquetá terraces, which at some depth are underlain by this pyrite containing Tertiary sediments. In other words, in deeper layers sulphate concentrations will be considerable, preventing S limitations to the vegetation.

In all forests, the litterflow pH decreased relative to net precipitation with a value of about 1.2, the largest decreases occurring in the high terrace system. These observations imply that a considerable amount of hydrogen is released or produced by the decomposing litter and fine roots, being the largest in the high terrace system. However, hydrogen concentrations did not exhibit any specific seasonality or distinct relationship with variables such as rainfall amounts, rainfall intensity or antecedent dry period. These findings are in line with those of Duivenvoorden and Lips (1995) who found that there was no clear seasonality in fine litter decomposition in the forests studied, the decay rate being about constant throughout the year, most probably due to the absence of a truly dry period and the relatively constant temperatures throughout the year.

Temporal variability in solute concentrations

The temporal variability in element outputs from the forest floor was low and rather similar in all forests. This variability is reflected in the CV (Table 1) with the highest temporal variability for DOC, Na, Ca, Mg, SO_4, Mn and Cl. Most of this

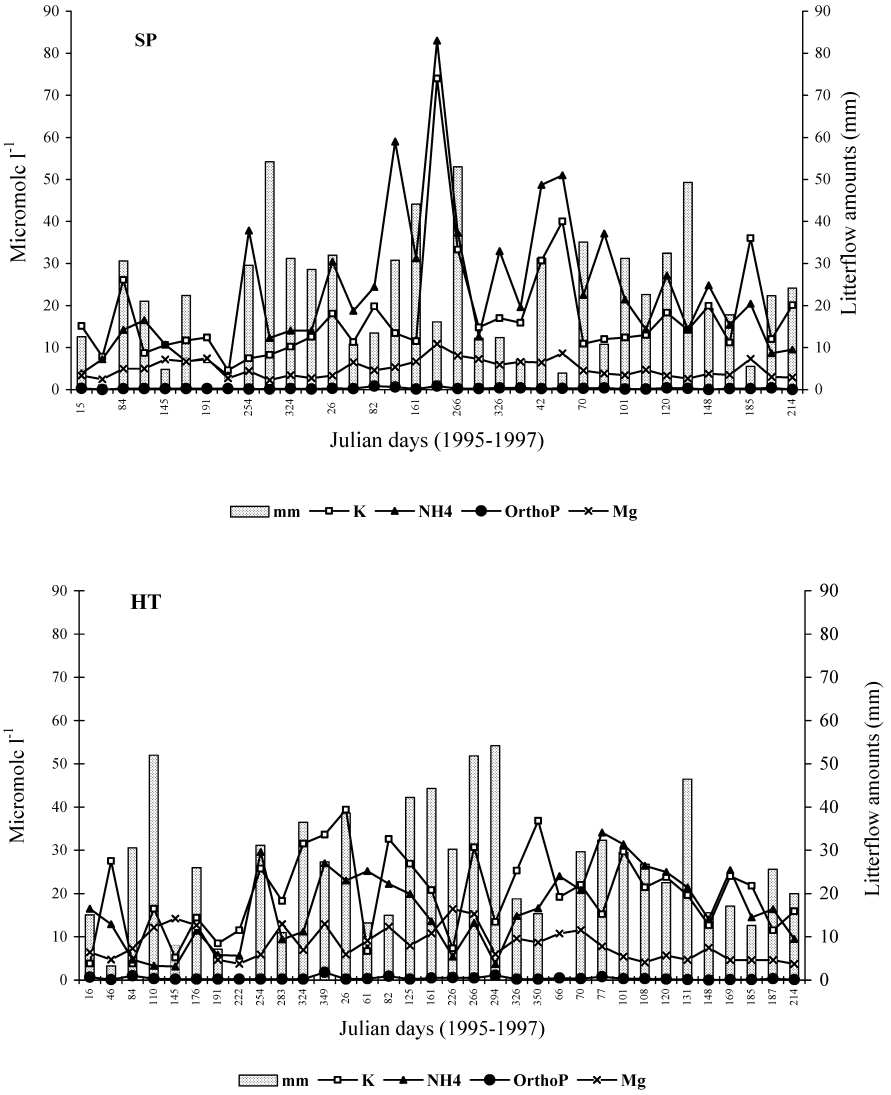


Figure 2. Dynamics of main ion concentration in litterflow and their relationship with litterflow amounts in four pristine forests in Colombian Amazonia (shown some of the major elements only as the examples for each forest ecosystem).

variability was comparable to that in net precipitation, except for ions such as Si, Fe, SO_4 and DOC, of which the variability was limited. For most elements, the solute concentration correlated poorly with litterflow amounts even at the 0.05 significance level (Figure 2). K formed an exception in the sedimentary plain and SO_4 in the flood plain, their concentrations being significantly correlated with litterflow amounts ($p > 0.99$). Element concentrations in the litterflow were also

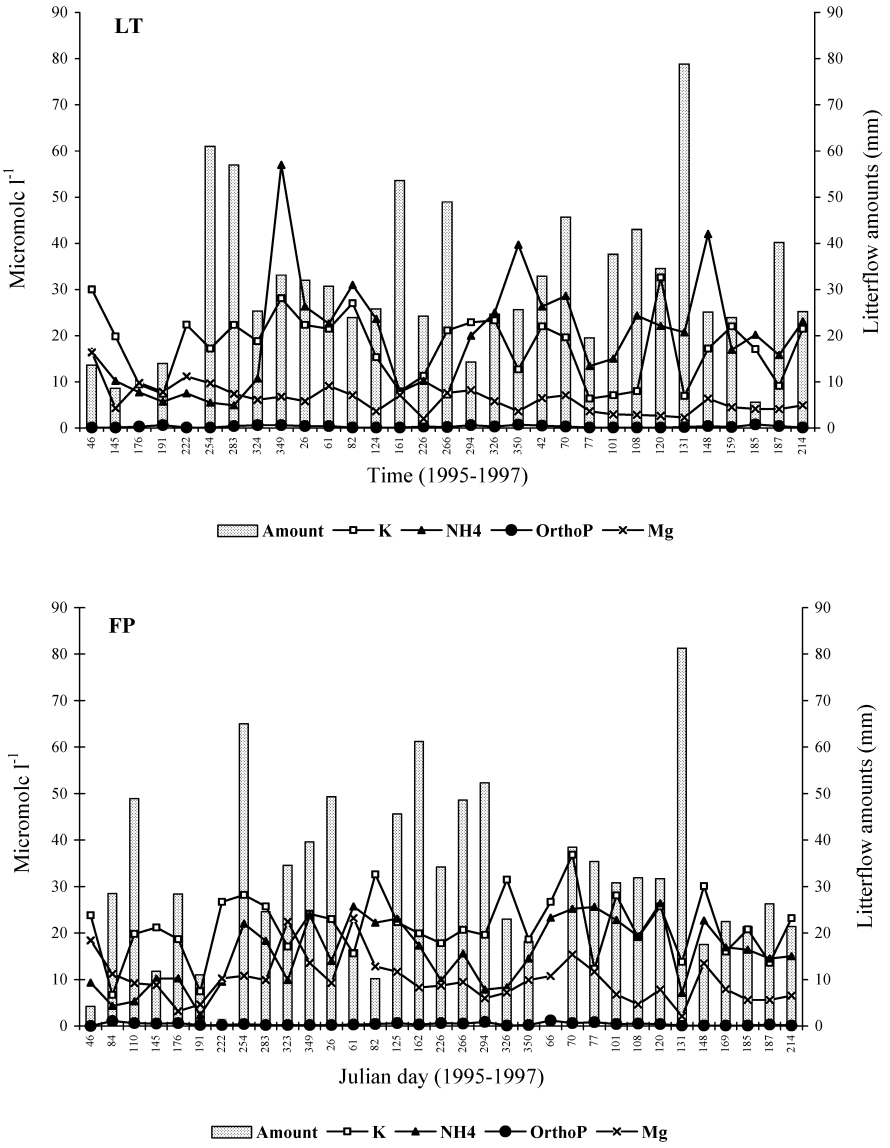


Figure 2. (continued).

poorly correlated with rainfall intensity. Only Mg in the sedimentary plain and K in the high terrace showed a relative high correlation ($p > 0.95$). Since K inputs in throughfall and litterfall were small, the latter correlation is probably related to the high leachability of K from living and dead plant tissues. Although correlations between net element concentration in litterflow and length of the antecedent dry

period were not significant (even at the 0.05 level), K also showed a high correlation with the length of the dry period in all ecosystems. In most forests, H, Ca, Mn, Na, and Si exhibited a relatively strong inverse correlation pointing to a dissolution effect. DOC concentrations were not significantly related to any of the above mentioned variables.

During the period of study we did not observe any clear indication for seasonality in solute concentrations in the litterflow. Nevertheless, we observed that immediately after some relative long dry periods (a.o. event on day 145/95) K, Ca, Mg and orthoP concentrations in the litterflow increased with the exception of the flood plain forest, while on most sampling dates during wet periods these concentrations were low. This relative increase in the concentration of specific elements in the litterflow was probably related to an increase in their leachability from the litter and fine roots, as the rate of litterfall increased during the relative dry periods (Edwards 1982; Scott et al. 1992; Duivenvoorden and Lips 1995). These results are also in line with the observation that the flood plain forest lacks clear seasonality in litterfall (Duivenvoorden and Lips 1995). Elements in relatively fresh litter, released by decomposers, are probably leached during the first rainfall events after the dry periods. Furthermore, during small events root uptake seems to be important since net element values in litterflow (litterflow minus net precipitation concentration) showed consistently negative values during rainfall events smaller than 10 mm.

Element fluxes to the mineral soil

To quantify the net solute outputs from the forest floor and to test the differences between ecosystems in element fluxes from the forest floor to the mineral soil, the total yearly element fluxes ($kg\,ha^{-1}\,year^{-1}$) in each forest were calculated and compared. Some significant differences were found ($p > 0.95$) in the total yearly element fluxes in litterflow between the forests. These differences mainly pertain to the amounts of total cations transferred to the mineral soil, being the largest in the flood plain, followed by those in the high terrace (Table 2) and total anions, being larger in the sedimentary plain and the high terrace than in the other forests, implying a largest soil acidification in those ecosystems. In general, large fluxes were observed for DOC, SO_4, Cl, NO_3, K, Na and Si. However, when compared with solute inputs in net precipitation, the elements that decreased most in our forests were orthoP, K, Mn, N and Mg. Those fluxes of orthoP have to be interpreted with some care is evident, considering the expected contribution of organic phosphorous in both throughfall and litterflow (see above).

Although concentrations of several elements such as Na, Cl and Ca increased considerably in the litterflow relative to that in throughfall (see Table 1), their net fluxes to the mineral soil ($kg\,ha^{-1}\,year^{-1}$) were in balance with net inputs. From the element balance it appears that Na inputs to the forest floor are mainly by throughfall and stemflow, and that outputs are slightly higher than total inputs. As described elsewhere (Tellez et al., in preparation), atmospheric deposition contributes most to the sodium input ($15.43\,kg\,ha^{-1}\,year^{-1}$ on average) while canopy

Table 2. Net annual solute fluxes from the litterflow (kg ha^{-1} $year^{-1}$) and their coefficient of variation (between brackets, $n = 35$) in four undisturbed forests in Colombian Amazonia.

Element	Sedimentary plain	High terrace	Low terrace	Flood plain
H	3.38 (0.76)	2.24 (0.83)	2.67 (0.99)	1.73 (1.04)
K	17.91 (1.08)	21.37 (1.19)	19.15 (1.52)	26.57 (1.50)
Na	14.00 (1.42)	14.92 (1.32)	14.09 (1.78)	16.66 (1.46)
NH_4	11.85 (1.05)	8.44 (1.26)	10.18 (1.28)	8.91 (1.31)
Ca	4.84 (1.26)	5.48 (0.75)	4.98 (1.60)	8.24 (1.55)
Mg	1.52 (1.28)	2.96 (1.25)	2.01 (1.31)	3.33 (1.21)
Fe	3.09 (0.98)	4.79 (0.83)	3.18 (1.32)	2.93 (1.41)
Mn	0.16 (0.94)	0.44 (0.63)	0.23 (1.23)	0.34 (1.21)
Si	12.11 (1.40)	11.12 (1.03)	14.75 (1.69)	14.52 (0.99)
Cl	26.83 (1.26)	25.01 (1.27)	26.67 (1.27)	26.82 (1.20)
NO_3	24.95 (1.14)	22.28 (1.07)	19.37 (1.31)	21.74 (0.87)
OrthoP	0.61 (1.15)	0.68 (0.81)	0.76 (1.31)	0.75 (1.43)
SO_4	93.56 (1.28)	91.85 (1.17)	78.16 (1.46)	68.79 (1.29)
Σ Cations	56.75 (0.95)	60.60 (1.06)	56.05 (1.15)	68.7 (1.19)
Σ Anions	145.91 (1.18)	139.80 (1.39)	125.00 (1.19)	118.10 (1.07)
DOC	310.70 (1.33)	369.10 (1.29)	293.80 (1.35)	217.49 (1.36)

exchange of Na is of very minor importance. Therefore, root uptake of Na must be of very minor importance and roots might even loose some Na to the forest floor.

When compared the litter percolates from studied forest floors with those from the Pinus plantation in Viti Levu, Fiji (Waterloo 1994) and in tropical montane rain forests in Jamaica (Hafkenscheid 2000), the net amount of elements transferred to the mineral soil are considerably lower in our forests, except for NH_4, NO_3, SO_4 and Si, implying a high nutrient efficiency by these Amazonian forests, which can be partly attributed to the high root mat content in our forest floors and the relatively lower nutrient availability both in the mineral soil and in living biomass.

Towards a forest floor solute budget

Information on the contribution of elements from decomposing litter and fine roots in the forest floor is essential to understand the solute dynamics in the forest floor and to asses the nutrient balance at the forest floor compartment. Once incoming solutes in throughfall and stemflow reach the forest floor they could diminish by root uptake and immobilisation, but also increase by litter and fine root decay. According to Jordan (1985) the sum of element concentrations in the litter or in the forest does not tell much about the leachability potential in tropical rain forests. He stated that in order to determine the annual element leaching reference, the concentrations of elements in the litterflow must be multiplied by the annual amount of water percolating (litterflow) through the forest floor. Therefore we include the available data on the annual average litterfall inputs (Table 3), fine root content (Table 4) and their main element

Table 3. Annual fine litter input to the forest floor (gr) and main element concentration in litter ($g\,m^{-2}$) in four forest ecosystems in the Middle Caquetá, Colombian Amazonia, as deduced from Duivenvoorden and Lips 1995 (D and L = Duivenvoorden and Lips).

	Annual fine litter input (g) and its CV	K	Na	N	Ca ($g\,m^{-2}$)	Mg	OrthoP	Reference
Sedimentary	6920 (16.1)	1.8	0.04	11.4	1.1	0.8	0.24	Overman (1994)
plain	6800 (12.6)	1.4	0.02	14.9	0.9	0.7	0.17	Duivenvoorden and Lips (1995)
High terrace	7640 (15.9)	2.6	0.03	11.7	1.4	0.9	0.15	Overman (1994)
	8600 (16.5)	3.0	0.03	12.1	1.7	1.2	0.13	Duivenvoorden and Lips (1995)
Low terrace	8110 (36.8)	2.3	0.07	13.3	1.7	1.1	0.29	Overman (1994)
	6900 (12.1)	2.2	0.04	15.5	2.1	1.2	0.17	Duivenvoorden and Lips (1995)
Flood plain	9770 (10.0)	3.1	0.15	13.5	7.1	1.9	0.45	Overman (1994)
	10700 (8.1)	3.4	0.04	16.7	11.6	2.5	0.37	Duivenvoorden and Lips (1995)

Table 4. Fine root amounts in the forest floor ($kg\,m^{-2}$) and their main element concentration ($g\,m^{-2}$) in four pristine forests in the Middle Caquetá, Colombian Amazonia (deduced from Wassenaar 1995; de Vente 1999).

	Fine root content and its CV ($kg\,m^{-2}$)	K	Na	N ($g\,m^{-2}$)	Ca	Mg	OrthoP	Reference
Sedimentary plain	1.2 (0.67)	7.40	0.03	20.4	0.66	1.26	0.69	Wassenaar (1995)
High terrace	0.6 (0.35)	6.40	0.03	26.7	0.65	1.02	0.81	Wassenaar (1995)
Low terrace	0.5 (0.41)	8.90	0.31	29.0	0.61	1.91	1.10	de Vente (1999)
Flood plain	0.3 (0.18)	8.58	0.28	25.3	1.91	2.45	0.87	de Vente (1999)

concentration, as deduced from Overman (1994); Wassenaar (1995); Duivenvoorden and Lips (1995) and de Vente (1999).

According to Duivenvoorden and Lips (1995), these forests clearly differed in both the quality and quantity of their litterfall and thus the actual supply of elements from the litter to the litterflow might be quite specific for the ecosystem concerned. Except for the flood plain forest, litterfall in these forests peaked in July–September and during December and January, which seems to be related to the occurrence of short dry seasons in the area, and differences in composition and input of litterfall and in element leachability ratios were quite limited. Moreover, elements in the litterflow did not exhibit seasonality, which indicates that there was a continuous contribution of elements from decomposed litter to the forest floor and a negligible influence of litterfall seasons. The mean residence time for the fine litter in the forest floors studied was found to vary among forests, ranging from 1.0 to 1.3 years from the flood plain to the sedimentary plain and Ca, Mg, N and P were

the elements that disappeared faster (Overman 1994; Duivenvoorden and Lips 1995).

de Vente (1999) and Wassenaar (1995) investigated the dynamics of fine roots in the forest floor and in the mineral soil in these ecosystems (fine root distribution and content, root mortality rates and element concentrations). They observed that fine root stocks differed between ecosystems with the lowest amount in the flood plain (Table 4) and that the rate of fine root decomposition was similar between forests studied, being around 1.3 in all plots. Element concentrations in fine roots in the flood plain and low terrace were much higher than in the other forests, but total amounts of elements released by fine root decomposition were higher in the sedimentary plain and the high terrace forests because of their larger amounts of fine roots. Additionally, The rate of nutrient release appeared to be much faster in the sedimentary plain than in the other forests. This partly explains the larger enrichment of net precipitation in litter percolates in these forests, as stated earlier in this paper.

Considering that the residence time for most elements is less than one year (except for P and N) and that the forests concerned are pristine mature forests, it is appropriate to assume that annual element inputs by litterfall (kg ha^{-1} $year^{-1}$) are equal to the elements released by decomposition. Therefore, the annual element fluxes in litterfall were calculated by multiplying annual fine litter input and its element concentrations. Additionally, the annual element release by fine roots were deduced from the values of fine root content in each forest floor, their rate of decomposition and from their element contents.

Available data on litterfall and root chemical composition pertained to six major elements only, for which reason only for these elements annual inputs to the forest floor and nutrient balance could be established, expressed as the sum of elements released by fine litter decomposition, fine root decay and solute inputs in throughfall and stemflow (Table 5) and the outputs in the drainage from these forest floors. N, K, Ca and Mg were the most abundant elements in litterfall and in the fine roots, while N, K and Na dominated in throughfall and stemflow. The low inputs of Na and P in litterfall are balanced by the relative large inputs in throughfall and stemflow, which leads to a positive input–output balance in the forest studied.

Although the evaluation of the nutrient use efficiency of a forest must be done through the comparison of the net primary production (NPP) with the net uptake on yearly basis (Vitousek 1982; Gholz et al. 1985), in this study we evaluate this efficiency by comparing the net inputs and outputs from the forest floor. Combining the Tables 2 and 5, the trend in element recycling rates appeared to be similar among the forests studied and were in the order of $Na > orthoP > Mg > K > Ca > N$, though amounts differ between them. When expressing the total outputs as percentage of the total input (throughfall, stemflow, litterfall and root decomposition), the largest value was observed in the high terrace forest (26%), which indicates that the other three forests were more effectively recycling the solutes, their rates being similar (around 80% of total element inputs). However, in the flood plain forests the net amounts of elements recycled (net uptake from the forest floor) were in the order of 1.3 times larger than on the sedimentary plain and high terrace,

Table 5. Annual inputs (kg ha^{-1} year^{-1}) of major elements to the forest floor in fine litterfall, fine root decay and by net precipitation (throughfall + stemflow) in four forest ecosystems in Colombian Amazonia.

Element	Sedimentary plain			High terrace (kg ha^{-1} year^{-1})			Low terrace			Flood plain		
	Litterfall	Fine roots	Th + St	Litterfall	Fine roots	Thr + St	Litterfall	Fine roots	Thr − St	Litterfall	Fine roots	Thr + St
K	12.5	42.1	27.9	19.9	13.3	37.2	18.6	17.4	42.1	30.3	14.8	39.5
Na	0.3	0.2	13.4	0.2	0.1	16.8	0.6	0.7	15.6	1.5	0.5	16.1
N	78.9	116.0	34.1	89.4	55.2	29.6	107.8	84.1	43.6	131.9	46.1	34.8
Ca	7.2	3.8	4.81	10.7	1.4	5.23	13.8	1.5	5.4	69.4	4.3	7.7
Mg	5.8	7.2	2.32	7.0	2.1	2.46	8.9	4.2	2.6	18.6	5.2	4.0
OrthoP	1.1	4.0	1.55	1.2	1.7	1.95	2.4	2.6	2.4	4.4	1.6	3.0

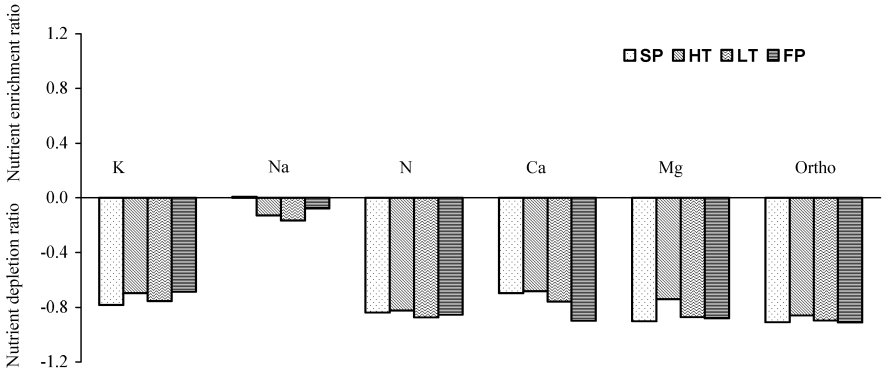


Figure 3. Ratios of ion enrichment and depletion in litterflow, as the relationship between litterflow outputs minus total inputs (throughfall + stemflow + litterfall + fine root decay) divided by total solute inputs in four pristine forests in Colombian Amazonia. (SP, tertiary sedimentary plain; HT, high terrace, LT, low terrace and FP, flood plain of the river Caquetá).

due to the considerably larger inputs in that forest. This large nutrient use efficiency by these forests differ from the stunted montane forests in Jamaica, whose capacity for nutrient uptake appeared to be restricted, although nutrients were available (Hafkenscheid 2000).

Element enrichment or depletion in litterflow relative to inputs is shown in Figure 3. Negative values indicate that roots in the forest floor scavenged most nutrients coming in as throughfall and stemflow and released by the decomposition of litter and fine root decay, implying that these forest floors act as a sink for the elements concerned. Depletion ratios were not significantly different between forests ($p > 0.99$), which imply that the relative larger nutrient availability in soils in the flood plain and low terrace are not sufficient to compensate the nutrient demands from the vegetation growing under these nutrient soil conditions. Moreover, there appears to be no relationship between root mat amounts in the forest floor and net uptake of main nutrients, neither in the nutrient efficiency associated to soil nutrient status, as these forests did not show significant differences in the depletion ratios of these main nutrients.

Elements such as P, Cl and N were massively taken up (ratios around 0.1). The relatively low values for N output in litterflow implied a high demand for this nutrient by the trees, which can be attributed to the high losses through litterfall, which need to be compensated for. The mechanisms involved clearly include an effective uptake by roots and probably also a slow release from decomposing litter, preventing serious drainage losses. Moreover, the leaching of elements from the decomposed material and from death roots and animals in the litter layer releases relative large amounts of elements which are more readily to be taken by roots in the litter layer or on the top of the mineral soil, so preventing losses (Swift and Anderson 1989).

Duivenvoorden and Lips (1995) observed such slow release of N by the forest floor of the forests studied, in conformance with an earlier study on similar forests by Gosz

et al. (1976). The low amounts of P in litterfall (total P) and throughfall (orthoP) and its small losses (orthoP) from the forest floor demonstrated the high P use efficiency of our forests, though this might be somewhat less efficient than suggested by our results, since fluxes of organic phosphorous to the mineral soil were not established (see above) and according to Burslem et al. (1994) mycorrhiyza can immobilise large amounts of P. Potassium was also very efficiently recycled through uptake by roots, in spite of its high mobility and leachability from plant tissues and litter (Burghouts 1993). Moreover, this net accumulation of P in these forests largely reflects the low mobility of this element due to the complexation process occurring in the soils (Sanchez 1976).

According to the findings of the high use nutrient efficiency by the forests studied, the nutrient cycling between trees and soils in these forests most likely will decouple, as found by Hertel et al. (in press) in Costa Rican secondary forest, to a large degree from the mineral soil (Leuschner et al. 2001), due to the relatively larger pool of nutrient availability on the forest floor, when compared to those in the mineral soil (Proradam 1979).

The concentration of main elements, such as Ca, Mg, K, Na and OrthoP both in the litterfall and in the net precipitation were among the lowest measured values in different upland tropical rain forests (Edwards 1982; Golley 1983; Jordan 1985; Cuevas and Medina 1986; Scott et al. 1992). Moreover, the low soil nutrient availability in these well drained upland forests, notably the sedimentary plain and high terrace, the low concentration and fluxes of element as orthoP, Ca, Mg, K, Na and Mn in litterfall and fine roots in the forest floors and their low inputs both in gross and net precipitation and the high nutrient demand (nutrient use efficiency) by these forests questions the assumption that the western part of the Amazon basin is less oligotrophic than central Amazonia as presented by Fittkau et al. (1975).

Conclusions

Our results clearly demonstrate the efficiency of pristine forests in Colombian Amazonia to scavenge nutrients from the forest floor, which entered this forest floor by throughfall, stemflow, litterfall and fine root litter input. Outputs of all major nutrients (excluding S) are very small. Although this efficiency slightly varied between forest ecosystems, significant differences lacked.

Element concentration in litterflow did not show any clear relationship with litterflow amounts, antecedent dry period or rainfall intensity. However, some elements showed unexpected increases after some dry periods and a somewhat larger uptake during small rainfall events, which need further research to be fully explained. Other than often described in the literature, which emphasises the role of litter input and fine root decay, throughfall and stemflow were the most important sources of nutrients for the forest floors. N forms an exception, for which litterfall and fine root decay are indeed the main sources.

The element enrichment–depletion ratios showed that the forest floor acts a sink of elements and their depletion occur in the order of Na, orthoP $>$ Mg $>$ K $>$ Ca $>$ N. This depletion was similar in most forests (around 80%), except for

the high terrace forest where the depletion was relatively less (74%). The major uptake of elements such as P, Mg and N strongly suggests that these are limiting nutrients in the forests studied. Na is hardly cycled, atmospheric inputs passing through the forest floor and being leached into the mineral soil.

Among the nutrients studied, S is the only nutrient with relatively large fluxes in throughfall, stemflow, litterfall and litterflow. This is attributed to the nature of the parent material, containing pyrites and related iron-sulphides. S therefore is amply available to plants and, other than often reported, does not constitute a limiting nutrient.

Although differences exist between the amount of litter inputs, root mat content, mainly between the forest at the sedimentary plain and the other forests, the nutrient uptake efficiency per volume of fine root content in the forest floors was not significantly different in these forests.

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