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Solute fluxes in throughfall and stemflow in four forest ecosystems in northwest Amazonia

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Abstract. The contribution of throughfall and stemflow as pathways for solute inputs into the forest floor in four mature forests in northwest Amazonia was investigated. Total solute inputs, resulting from the changes of atmospheric deposition after rainfall passes through the forest canopy, are presented in the form of throughfall and stemflow nutrient inputs and their possible sources are discussed. Throughfall is by far the most important solute input into the forest floor of the forests studied. On average, it represents about 98% of the total solute inputs. Although trends in solute enrichment varied among the forests, there is a general tendency in all ecosystems towards a distinct enrichment of SO_4, K, Cl, NO_3 and NH_4 in throughfall and stemflow and a small increase of protons, Mn, orthoP and Fe. When comparing the net enrichment between the forests, the relative increase of solutes in throughfall and stemflow was higher in the flood plain and low terrace than in the high terrace and sedimentary plain forests. While highest values for total cation inputs were observed in the flood plain, the low terrace showed the highest value for total inorganic anions. The length of the antecedent dry period was the main factor affecting throughfall and stemflow composition, concentrations increasing with increasing length. A second, less important factor was the amount of throughfall and stemflow, which showed a poor and negative correlation with solute concentrations. The increased activity of frugivores in the canopy during fruiting periods seemed to lead to temporary increased solute concentrations in throughfall and stemflow as a result of the wash off of deposited faecal materials and detritus in the canopy. Leaching from leaves and wash off of exudes, of solutes deposited on the foliage after evaporation of intercepted rainfall and of dry deposited materials were all found to contribute to the concentration of solutes in the throughfall and stemflow. Gross rainfall enrichment after passing the forest canopy, mainly by nutrient leaching, is considerably lower than the amounts of nutrients released in litterfall implying a tight nutrient cycling and nutrient conserving mechanisms by forests studied.

Introduction

Nutrients are expected to be a more limiting factor in the tropics than in other latitudes and within the tropics, it is in the lowlands that the most prominent oligotrophism is encountered (Walter 1971; Jordan 1985). In Amazonia, one of the largest lowland forested areas, inputs of nutrients through atmospheric deposition appeared to be of low magnitude (Jordan 1982; Brouwer 1996). Connected to this low input, some forest ecosystems developed a very tight internal nutrient cycle and related nutrient conserving-mechanisms (Jordan and Herrera 1981; Bruijnzeel 1991). Under such conditions, the top-down solute fluxes play an important role in forest nutrient cycling and probably also in the sustainability of the forests. Transfer of nutrients to the forest floor occurs through litterfall, by atmospheric deposition and by the enrichment of rainfall after passing through the forest canopy as throughfall and stemflow. Rainfall chemistry is altered with this passage, mainly by canopy exchange, wash-off of dry deposited solutes, leaching and uptake of solutes (Lovett and Lindberg 1984; Potter et al. 1991; Brouwer 1996). The magnitude of the nutrient fluxes associated with these processes is determined mainly by the type of forest and its nutrient stocks, the internal biochemical processes, hydrological fluxes and human activities (Potter et al. 1991). Therefore, understanding of the nutrient exchange at canopy level and the net rainfall enrichment after its passage through the forest canopy, contributes to the understanding of the internal processes in and functioning of forest ecosystems and to the evaluation of the impact of forest clearance on nutrient cycling and the potentials for its subsequent recovery.

In the Amazon basin, a number of forest types have been investigated for their throughfall and stemflow (Poels 1987; Franken et al. 1992; Lesack 1993; Jetten 1996; Ubarana 1996; Hölscher et al. 1997; Tobón et al. 2000). Although, solute fluxes in gross rainfall and their partitioning after impacting the forest canopy received some attention (Jordan et al. 1980; Brinkmann 1985; Franken et al. 1985; Jordan 1985; Poels 1987; Forti and Moreira 1991; Brouwer 1996), these studies are largely limited to the central Amazon (Brazil) and San Carlos (Venezuela) and pay most attention to nutrients in throughfall. The foregoing implies that for the forests in the more humid western part of the Amazon, notably Colombian Amazonia, studies on solute fluxes in throughfall and stemflow are virtually inexistent. Consequently, very little is know about the processes in the canopy controlling the amounts of fluxes, such as wash-off of dry deposited solutes, leaching and uptake of solutes (Lovett and Lindberg 1984; Potter et al. 1991; Brouwer 1996). The same holds for the contribution of the fluxes to the nutrient cycle in these often strongly nutrient limited systems.

This study deals with the throughfall and stemflow chemistry and their temporal dynamics in four adjacent forest ecosystems in the Colombian Amazonia. These systems differ from each other with respect to their vegetation (structure and number of species) and litterfall (Duivenvoorden and Lips 1995), and to other relevant characteristics such as canopy water storage, leaf area index, litter decomposition and soil nutrient status (Tobón 1999). Therefore, attention is also paid to differences in element enrichment among forest types and the role of canopy leaching and wash off of dry deposition. The study forms part of a larger project on the nutrient and water cycling in virgin forest ecosystems in the Caquetá area, Colombian Amazonia by the University of Amsterdam, executed within the Tropenbos Colombia program. The precipitation chemistry in these forests and the nutrient fluxes through the forest floor are dealt with in another paper by Tobón et al. (2004).

Study area

The study was executed in four plots with pristine forest used as research sites by Tropenbos Colombia and located near Peña Roja (Nonuya Indian community), Middle Caquetá (Colombia), between 0°37′ and 1°24′S, 72°23′ and 70°43′W (see Figure 1). The landscape in this part of Amazonia comprises a large dissected Tertiary sedimentary plain (about 250 m.a.s.l.) and the alluvial system of the River Caquetá, which includes high and low terraces and a recent floodplain at about 200 m.a.s.l.. The four plots cover the sequence from the floodplain to the Tertiary sedimentary plain, with distances between the plots of 4–5 km.

The soils from this part of the Amazon have been extensively studied on their soil distribution and chemical properties (Proradam 1979; Duivenvoorden and Lips 1995) and for their physical and hydraulic properties (Tobón 1999). Except for the very recent soils of the floodplain, these generally have a clay loam to sandy clay loam topsoil over a clayey subsoil. The floodplain soils that regularly receive fresh sediments from the River Caquetá, which originates from the Andes, are relatively nutrient rich, contain significant amounts of weatherable minerals, lack a distinct litter layer (Fluvaquents and Dystrochrepts) and have rather randomly distributed roots. While the soils of the low terrace hold an intermediate position, the strongly weathered and leached soils of the high terrace and sedimentary plain have a very low base saturation, contain very low amounts of weatherable minerals, have a thick litter layer (Paleudults and Kandiudults) and have roots that are largely concentrated in a superficial root mat.

In all plots, the vegetation is mature pristine rain forest (ombrophilous tropical rain forest). Vegetation in the various landscape units differs in total standing biomass, species diversity and tree density (Duivenvoorden and Lips 1995). Other important differences between plots pertain to the structure of the forest canopy, such as canopy cover and LAI (Tobón 1999). The gap fraction was 16.8% on the sedimentary plain, 15.4% on the high terrace, 11.7% on the low terrace and 9% on the flood plain and the LAI ranged from 4.4 to 4.9, 5.6 and 6.7, respectively. The floodplain forest is less sclerophyllic and has more abundant epiphytes, a trend gradually reversing towards the forest of the sedimentary plain. The canopy reaches a height of 25–30 m above the forest floor with some emergent trees reaching up to 45 m in the rarely inundated flood plain. There are 3–4 canopy layers, but the bulk of the vegetation is in the form of large tree crowns in the upper canopy. The lower canopy mainly consists of small palms reaching a height of 2–4 m. Species diversity is lowest in the flood plain and highest in well drained upland areas, like the sedimentary plain and high terrace (Duivenvoorden and Lips 1995).

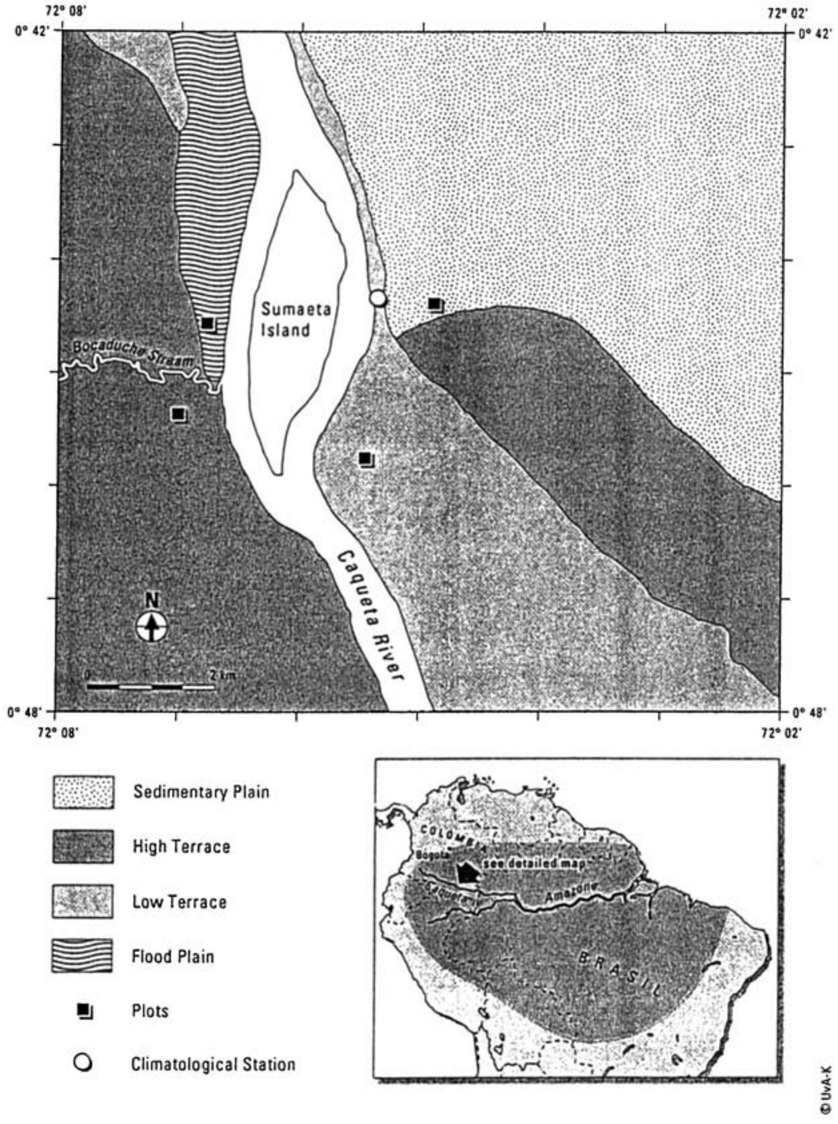

Figure 1. Location of the research sites in the different landscape units in the Middle Caquetá, Colombian Amazonian. The detail map (deduced from Duivenvoorden and Lips 1995) shows the location of a climatological station (AWS) and the four sites in the different physiographic units: the Tertiary sedimentary plain (SP), high terrace (HT), low terrace (LT) and the flood plain (FP) of the river Caquetá.

Based on data collected during the period between 1992 and 1997, mean annual rainfall was about 3400 mm. This value is higher than the mean value of 3100 mm based on the less reliable data from Araracuara (at about 20 km north of the research sites, and 320 m.a.s.l.), for the preceding 20 years. The period December–February is relatively dry, mean monthly rainfall still exceeding 100 mm. The relative humidity is generally above 75% and close to saturation (> 95%) during the nights. The mean daily temperature is around 24 °C. During the day, inside the forest the temperature is slightly lower than outside, but the humidity is always higher and the radiation is low and patchy. A hydrological study showed that amounts of throughfall and stemflow differed between events and among ecosystems, depending on rainfall characteristics (volume, intensity and duration) and forest structure (Tobón 1999). Throughfall ranged from 47 to 93% of gross rainfall depending on rainfall size, while among the forests studied the average throughfall relative to gross rainfall ranged from 82% in the flood plain to 87% in the sedimentary plain and stemflow from 1.0 to 1.5% (Tobón et al. 2000).

Methodology

Within the hydrological study, gross rainfall, throughfall, stemflow and litterflow were manually measured during 2 years on daily basis in the four forests (Tobón 1999). Total rainfall in the open area was measured every 20 min by a tipping bucket rain gauge with a resolution of 0.2 mm. Gross rainfall in each forest plot was measured in two ways: 1 – automatic measurements, every 20 min, with one tipping bucket installed in the top of an emergent tree crown, after clearing all branches, 2 – daily manual measurements with six rain gauges per plot suspended from cords attached to two emergent trees in small gaps within the forest. Throughfall was measured on daily basis with 60 randomly located collectors per forest plot. For stemflow, 45 collectors were connected to a plastic collar around trees (45) with a diameter (DBH) >10 cm (Tobón et al. 2000). In each collector, a fine plastic mesh (240 μm) was placed between funnel/collar and collector to prevent that any solid material entered the collectors. All collectors were painted black to prevent internal algae growth. Each collector was washed with a solution of HCl (10%) and rinsed with abundant distilled water prior to their installation for sampling. When contaminants were found in the collector's mesh (decomposed leaves, insects or animal deposition) that collector was not sampled. For a full explanation of the methodology used for the estimation of throughfall and stemflow reference is made to Tobón et al. (2000).

The time of sampling was based on the temporal distribution of gross rainfall in such a way that samples were collected at roughly monthly intervals and contiguous with the sampling of gross rainfall at the same sites. Sampling dates cover all wet and dry periods during the 2-year period and follow rainfall patterns in the area. In total, per collector, 35 samples were taken: 11 during dry and 24 during wet periods, between January 1995 and August 1997. Separate samples of throughfall and stemflow from each collector and each sampling occasion were bulked per plot. 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 (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.

The strategy of bulking samples of fixed volume was followed because sampling a fixed proportion of throughfall or stemflow from each collector and bulking these would have been logistically impossible. Field conditions were quite difficult, particularly during the wet season, and large but variable amounts of water were found in the throughfall and stemflow collectors. This implies that the chemical composition of bulk throughfall or stemflow could not be corrected for any volume-related differences in chemical composition of individual samples. However, the chemical composition of throughfall and stemflow was not found to depend on their volume as will be described further on. Therefore, bias due to the sampling methodology must be of very minor importance if relevant at all.

Net enrichment in throughfall and stemflow, after rainfall passes through the canopy in each ecosystem, was calculated from the bulk concentration (in mol l^{-1}) of the i solute in throughfall and stemflow relative to that in the corresponding gross rainfall for each sampled event. Solute fluxes in throughfall and stemflow were calculated for individual rainfall events by multiplying the bulk concentration of each element in the sample by the measured volume of throughfall or stemflow during that specific event. To determine gross inputs, daily solute fluxes in throughfall and stemflow during the entire period or the volume weighted mean concentration (VWMC) of each solute in throughfall and stemflow were calculated separately from the paired measurements of solute concentrations and amounts of throughfall and stemflow for each sampled event.

$$\mathrm{VWMC}_i = \frac{\sum_{j=1}^{n} C_{ij}\,\mathrm{Th}_j}{\sum_{j=1}^{n} \mathrm{Th}_j} \tag{1}$$

Where C_{ij} is the i-solute concentration in throughfall (or in stemflow, St) during the j-event, Th_j is the total amount of throughfall (or stemflow) in a given event. The last equation was calculated for each of the n-events sampled. Total yearly inputs of elements ($\mathrm{kg\,ha^{-1}\,year^{-1}}$) were calculated from the VWMC of each element and the annual values of throughfall and stemflow during the studied period. Although the concentrations of most elements were relatively low, mainly those in the sedimentary plain forest, the concentration of most elements in throughfall and stemflow were within the detection limits.

After calculating annual element fluxes, the enrichment or depletion ratios, as indicated by numbers larger or lower than 1.0, respectively (canopy recycling rate), were defined separately by dividing the fluxes in throughfall and stemflow by those in bulk rainfall:

$$\frac{E}{D} = \frac{[\mathrm{Throughfall} + \mathrm{stemflow}] - \mathrm{rainfall}}{\mathrm{Rainfall}} \tag{2}$$

Lovett and Lindberg (1984) studied the possible sources for the enrichment in throughfall relative to rainfall using a multiple linear regression approach. They assumed that elements derived from canopy exchange are correlated with the storm-size (P in mm) and those from dry deposition with the length of the antecedent dry period (A in days) for events sampled. The model requires well defined single event samples of gross rainfall and throughfall, as it was the case in this study. The model allows for an estimation of the contribution of dry deposition (a) and canopy exchange by leaching and uptake (b), assuming that:

$$\mathrm{Th} = aA + bP \tag{3}$$

Additionally, factor analysis (principal component method) after Varimax Rotation was used to estimate the contribution of individual sources. To know whether the means of the value sets in each forest differ between them (spatial variability of throughfall and stemflow composition), we applied the Student's t-test (by paired forest at the time). Product–moment Pearson correlation, linear simple and bi-varied regressions were applied after log-transformation of the concentrations using the length of the antecedent dry period and the intensity and duration of the corresponding rainfall, employing the SPSS program.

Results and discussion

Solute concentrations in throughfall and stemflow

Mean ratios of throughfall and stemflow solute concentrations relative to those in rainfall (in $\mu\mathrm{mol\,l^{-1}}$) and their standard deviations (SD) are presented in

Table 1. Mean ratios of solute concentrations ($\mu mol\,l^{-1}$) in throughfall (Th) and stemflow (St) versus those in rainfall and their standard deviation ($n = 35$) in four forest ecosystems in the Colombian Amazonian, and rainfall (Pg) solute concentrations in $\mu mol\,l^{-1}$(except for pH). DOC values are expressed in $\mu mol\,l^{-1}$. Values larger than 1.0 indicate element enrichment, and values below 1.0 indicate depletion.

		Sedimentary plain			High terrace		Low terrace		Flood plain	
		Pg	Th	St	Th	St	Th	St	Th	St
pH	Mean	5.03	1.03	0.87	1.09	0.93	1.05	0.93	1.1	0.94
	SD	0.3	0.06	0.06	0.11	0.24	0.1	0.1	0.08	0.12
H	Mean	13.6	0.9	5.7	0.8	6.0	1.2	4.2	0.5	3.8
	SD	12.0	0.7	4.3	1.4	8.6	2.3	5.7	0.4	4.6
K	Mean	9.0	3.6	5.5	5.0	7.6	4.9	6.4	4.6	8.7
	SD	7.5	2.1	2.6	4.8	7.2	4.0	5.5	2.9	5.7
Na	Mean	20.0	1.2	1.4	1.4	1.5	1.4	1.6	1.3	1.6
	SD	7.3	0.7	0.8	0.6	0.7	1.0	1.1	0.5	0.9
NH_4	Mean	11.5	2.4	5.8	3.1	5.4	2.8	4.5	2.8	8.1
	SD	8.4	2.4	8.3	5.3	7.3	4.3	7.3	2.8	19.4
Ca	Mean	6.8	1.3	2.2	1.4	2.9	1.5	2.0	2.2	4.9
	SD	2.3	0.5	2.6	0.9	3.9	1.1	1.0	1.4	3.3
Mg	Mean	2.8	2.9	3.7	2.7	6.1	3.2	6.7	5.1	11.2
	SD	1.7	1.5	1.9	1.5	4.6	1.6	3.9	3.0	6.7
Fe	Mean	0.7	1.5	4.8	1.9	6.7	2.1	3.7	1.7	7.1
	SD	0.4	0.7	5.5	2.0	15.4	1.9	6.2	1.4	7.4
Mn	Mean	0.3	3.0	3.4	0.5	2.2	2.1	6.7	1.7	7.3
	SD	0.4	3.0	4.4	0.5	1.9	1.8	12.1	2.7	6.6
Si	Mean	2.5	2.9	12.8	2.7	4.3	4.1	14.7	3.0	8.3
	SD	1.5	2.7	13.2	1.9	3.8	4.5	16.2	2.3	5.3
Cl	Mean	25.4	0.9	1.6	1.5	2.4	1.4	1.8	1.6	2.3
	SD	12.1	0.4	0.8	1.1	2.7	0.8	1.3	1.0	1.1
NO_3	Mean	6.4	3.7	5.2	2.6	8.1	5.2	7.4	6.1	11.4
	SD	4.0	4.7	4.7	3.9	21.7	8.4	13.7	15.4	22.1
OrthoP	Mean	0.3	3.3	5.1	2.4	6.0	3.7	3.7	5.1	8.0
	SD	0.3	6.2	8.9	2.4	7.2	5.3	5.7	12.9	12.7
SO_4	Mean	36.9	1.6	2.8	2.1	2.8	2.3	2.7	1.9	3.4
	SD	25.1	0.8	2.0	1.8	2.4	2.2	2.3	1.9	2.6
Cations	Mean	62.9	1.5	3.3	1.7	3.1	1.8	2.8	1.9	4.2
	SD	24.2	0.6	1.2	0.9	1.3	0.9	1.6	0.9	1.6
Anions	Mean	73.7	1.3	2.1	1.6	2.3	1.7	2.0	1.7	2.8
	SD	29.3	0.5	1.1	0.9	1.1	0.9	0.9	0.8	1.3
DOC	Mean	328.3	1.4	2.7	1.7	2.7	1.7	2.5	1.6	4.7
	SD	135.1	0.5	1.0	1.0	1.3	0.7	1.2	0.6	2.7

Table 1. After rainfall passage through the forest canopy, mean concentrations of nearly all elements increased. As illustrated by ratios larger than 1.0 in Table 1, trends in element enrichment varied between forests, the relative increase in throughfall and stemflow being higher in the forests of the flood plain and low terrace than in those of the high terrace and sedimentary plain. Moreover, the average enrichment of NO_3, K, Si, orthoP, Mg and NH_4 in

throughfall and stemflow was relatively strong in all ecosystems, while that of Cl, Na, Ca and Fe was relatively weak. Silica was very strongly enriched in stemflow in the forests on the floodplain and high and low terraces. Furthermore, increases in concentrations of Mg, NO_3 and orthoP in the flood plain forest were about twice as strong as in the sedimentary plain forest. Although element concentrations in rainfall increased in throughfall and stemflow, in some events, solute levels were lower reflecting lesser leacheates or even net uptake by the canopy. These concentration decreases were more common in throughfall than in stemflow and were also element-specific.

This larger increase in element concentration in throughfall and stemflow in the flood plain and low terrace forests could be partly explained by the evaporation of intercepted rainfall, which causes an increase on ion concentration in the canopy, in concordance with the amount of water intercepted. The decreases of the leaf area index from the flood plain forest through the sedimentary plain (Tobón 1999) is likely to reduce the amount of dry and wet deposition in the respective forest canopy, with a considerable reduction of ions in throughfall and stemflow.

Contrary to that occurring at temperate forest (Oyarzun et al. 1998; Moreno et al. 1994), average throughfall pH slightly increased relative to rainfall (0.46), mainly during the dry periods and only in some events it decreased (18% on average for the four forests). This indicates that studied forests have a low canopy contribution to throughfall enrichment with organic acids. Contrary, pH in stemflow decreased considerably relative to that of rainfall in these forests and in most events, as indicated by ratios lower than 1.0 in Table 1. Moreover, changes in proton concentrations were larger in throughfall than in stemflow. The decreases on the pH in stemflow indicate that part of the organic acids observed at the litter percolates are leached from the stems rather than from the foliage.

In throughfall, Cl ratios pointed to uptake in 29–71% of the events sampled, NO_3 ratios in 23–35% except for the flood plain where these ratios were distinctly 1 and Na ratios in 29–40% of the events. The forests fixed ions such as Mg and orthoP, particularly that on the sedimentary plain (85 and 35% of the measure > d events). In stemflow, Na uptake occurred in 26–43% of the events and Cl uptake in 18–29%. However, a net accumulation of elements was not observed for protons in all forests and mainly at the canopy (ratios <1.0), Cl in the sedimentary plain and Mn in the high terrace.

In general, there were considerable increases in the concentration of K in throughfall and stemflow in all forests, which can easily be attributed to the high mobility of this element and its abundance in leaves. However, lower values in its increases in both throughfall and stemflow were observed in the forest at the sedimentary plain, which can be related to the high Al^{3+} content in the mineral soil at this landscape (Duivenvoorden and Lips 1995). Al^{3+} is capable of blocking the transport channels in fine roots cell plasmatic membranes, thus limiting the uptake of K (Kochian 1995; Lüttge 1997), which can be also applied for P.

The increase of phosphorous levels in throughfall and stemflow in our sites was of minor magnitude, with low fluxes in throughfall and stemflow and even negative values (ratios <1) during some events. Evidently, its net leachability in our forests is low, which can be attributed to its low availability, both in the soil compartment and the plant tissues (Duivenvoorden and Lips 1995). Moreover, many species in tropical rain forests on soils with very low nutrient status have high levels of silica in their biomass (Ludlow 1969; Köeppen 1978; Norman 1979), ascribed to substitution of phosphorous by silica in plant tissues in strongly phosphorous-limited systems (D'Hoore and Coulter 1972). In our forests, we observed that Si was indeed released in throughfall and stemflow, but in some events (16%) some uptake occurred, mainly in the forests on the sedimentary plain and high terrace. This apparent Si uptake occurred when the concentration of orthoP in incoming rainfall was very low (less than $0.2\,\mu\text{mol}\,\text{l}^{-1}$) and ratios in throughfall were also very low, that is, under conditions that P-limitations will indeed have been very pronounced. However, the low Si concentrations in stemflow and its relatively high concentration in throughfall, indicates that this element is mainly leached from the foliage rather than from the stems.

Substantial decreases in the concentration of NH_4 in throughfall occurred in only 18% of all events, implying that during some events this ion was taken up by the foliage or transformed into NO_3, where NH_4 is taken up by the forest canopy and nitrified at the leaf surfaces (Chen et al. 1983; Wilson 1992), while the overall release was considerable. In stemflow, the overall releases were even higher and only in 7% of the sampled events NH4 ratios were <1. Evidently, in case that NH_4 is transformed into NO_3, a corresponding increase in NO_3 concentrations might be expected. This occurred in the long lasting and large storms during the wet periods, but the behaviour of absorption or leaching of these ions by the vegetation did not show any seasonal pattern or relationship with antecedent rainfall history or event size. Considerable differences existed between mean NH_4 and NO_3 enrichment in throughfall versus stemflow, stemflow exhibiting distinctly higher ratios than throughfall. On the sedimentary plain and high terrace, the NO_3 ratios of throughfall and stemflow were distinctly lower than in the other two forests.

In several studies on nutrient enrichment of throughfall and stemflow in non-tropical forest, a net uptake of NH_4 and NO_3 was found (e.g., Parker 1983; Kloeti et al. 1989; Veneklaas 1990; Potter et al. 1991; Crockford et al. 1996; Cavalier et al. 1997), which was mostly related to the N absorption by epiphytes and bryophytes (Bruijnzeel and Proctor 1995; Hafkenscheid 2000). Contrary, net releases of N were observed in our forests, including the flood plain forest, which is consistent with the low amounts of epiphytes upland forests. Though, the flood plain forests present large number of epiphytes (Duivenvoorden and Lips 1995), they may not be considerably larger to absorb the atmospheric N inputs and those washed off from the canopy. Additionally, increases of N in throughfall in other Amazonian forests (Edwards 1982; Brouwer 1996) have been attributed to the large stocks in plant tissues and its release by decay from leaves that are still attached to the tree (Duivenvoorden and Lips 1995).

Concentrations of DOC in throughfall, increasing by a factor of more than 2 relative to rainfall, ranged from 424 to 543 μmol l^{-1}, while in stemflow they were even larger, ranging from 775 to 1317 μmol l^{-1}. These increases might be partly due to wash-off of organic matter deposited on leaves during the dry periods, given its rather abundant occurrence in the atmosphere above the Amazon basin (Talbot et al. 1988), but additionally will have been due to the release of organic acids from leaves, bark and decomposing organic matter (e.g., insect excrements) in the canopy.

Our results concerning the enrichment of throughfall and stemflow are similar to those in pristine forest in Guyana (Brouwer 1996), except for Na and Cl, which appeared to be higher in those forest in Guyana, mainly due to the larger maritime aerosol deposition. However, these results differ from those found by Jordan et al. (1980) in Rio Negro (Venezuela) where large amounts of nutrients were found in rainfall but concentrations of most ions decreased in throughfall, implying the existence of large differences of nutrient absorption at the forest canopy by forests within the Amazonia. Results here also differ from those for montane forests in Panama and Colombia, where the nutrient concentrations in throughfall and stemflow did not differ significantly from those in rainfall (Veneklaas 1990; Cavalier et al. 1997). The relative strong nutrient enrichment in throughfall and stemflow in our forests, as compared to some sites in the tropical montane forests, might be explained by the fact that tropical lowland forest stores most of its nutrients in the biomass as a nutrient conserving mechanism (Jordan 1985), while in montane and temperate forests nutrients are primarily stored in the soil compartment (Fölster et al. 1976; Tanner 1977; Veneklaas 1990).

Temporal variability in throughfall and stemflow chemistry

Temporal trends in solute concentrations differed considerably from those in rainfall and at the same time differed between forest types (Figure 2), which is comparable to those results found by Hansen et al. (1994) in other forests. In throughfall, variability was highest in the sedimentary plain forest, whereas for stemflow variability was highest in the flood plain forest. Na, Cl, Si and SO_4 concentrations were most variable, while those of orthoP and NO_3 were least. The product–moment Pearson correlation and regression analysis indicate that the correlation coefficients for some elements were very low, the length of the antecedent dry period was found to be the dominant factor. It explained a significant part ($r^2 = 0.43$) of the variability in throughfall chemistry, particularly of Ca, orthoP and Mg, suggesting that during a dry period these elements accumulate on leaves and branches, probably by atmospheric deposition and eventually by leaf exudation. Relative high ion concentrations occurred in events sampled after some dry periods, in particular those that lasted more

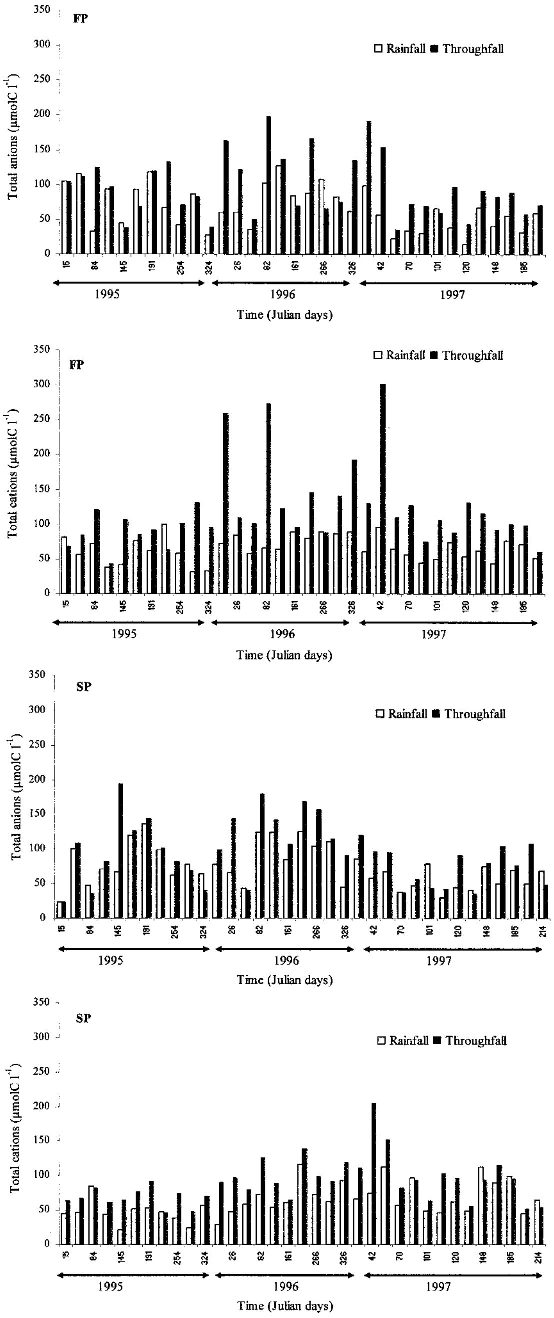

Figure 2. Temporal dynamics of the concentration of total cations and anions in throughfall as compared to those in respective rainfall in two contrasting forest ecosystems in Colombian Amazonia.

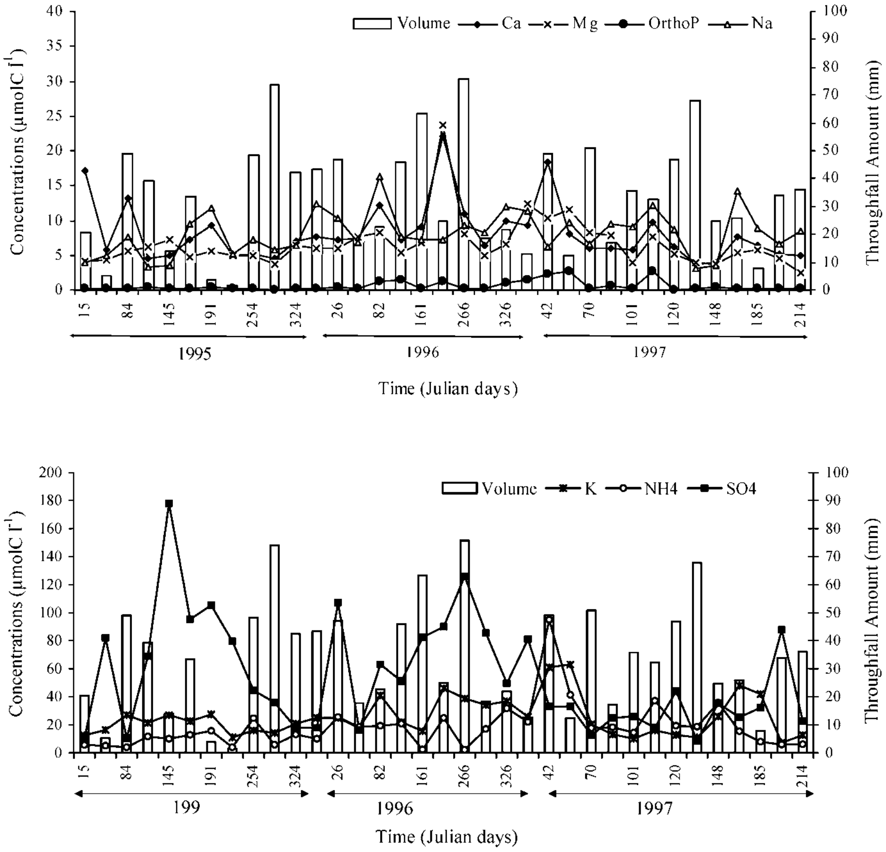

Figure 3. Relationships between main element concentration in throughfall and throughfall volumes in the sedimentary plain forest (as an example), during the period between 1995 and 1997.

than 6 days (Figure 3). This can be illustrated by data on two events with similar amounts of precipitation (events 226/96 and event 148/97 with an average throughfall of 25 and 24.7 mm, respectively) but with different length of the antecedent dry period (9 and 0.6 days, respectively). For stemflow the length of the antecedent dry period also explained a considerable part of the variability ($r^2 = 0.51$) mainly of Na, SO_4, Si, Mg, protons and DOC.

Separately correlation coefficients of throughfall and stemflow amounts versus solute concentration were negative and non-significant ($p > 0.95$), which is quite evident from Figure 3. In throughfall Si was the element with the highest correlation, exhibiting a significant correlation (at the 0.05 level) in all ecosystems, followed by Na, K, orthoP, Mg and SO_4, pointing to canopy leaching as a partial source. K and H were best correlated with stemflow volume in all ecosystems, followed by orthoP and NH_4. Moreover, seasonal trends in these concentrations were not observed.

Although overall correlations were negative and non-significant, we observed that throughfall enrichment depended on the amount of precipitation in a rather complex way. In small events that were large enough to produce throughfall and in large-size events, solute ratios were generally lower than in the medium-size events ($5 < P < 25\,\mathrm{mm}$). At first sight, one would expect that elements of atmospheric origin (dry deposition) or exuded by leaves would be washed off at the beginning of the events, producing relatively concentrated throughfall, mainly in small ones (Reiners and Olson 1984; Skiba et al. 1986). However, during the small-size events a considerable part of the rainfall is intercepted and evaporated from the forest canopy (41–53% of gross rainfall) and other part (9–17%) passes through canopy gaps (Tobón et al. 2000) to reach the forest floor without being intercepted. Therefore, in these events large part of atmospheric deposition in rainfall precipitates onto foliage and part of the collected throughfall will in fact be non-intercepted rainfall and thus not or only marginally be enriched through wash-off. Moreover the contact time and the amount of water in the canopy in these events may be too small for a dominant ion exchange effect in the foliage. During medium-size events, water remains in contact with the foliage for longer periods and therefore both wash-off and leaching/uptake by the canopy will be rather optimal. This may, for example, explain why the concentration of Cl decreased during these events, as under such conditions the foliage can take up this element. During long-lasting and large-size storms, the effect of wash-off will decrease, the exchange by the foliage will decline and concentrations will be more near to those in rainfall, except for those elements that are actively taken up or leached from the foliage.

In contrast to throughfall, where correlations between solute concentration and rainfall intensity and event duration were poor and non-significant, good correlations between stemflow concentrations and intensity and duration were found, these concentrations increasing considerably in large-size and long-lasting events. Only during medium or large-size and long-lasting events we observed significant amounts of stemflow for most trees and only during such events trunks of trees with fibrous bark were slowly wetted (Tobón 1999). This probably explains the observed correlations.

Even though no clear seasonality in throughfall and stemflow concentrations was observed, element concentrations in samples collected during April and September were relatively high, particularly in the alluvial plain forest. During these periods we did not find a correlation with rainfall inputs nor with any of the other tested variables such as antecedent dry period and measured amounts, suggesting that other factors are involved. Many tree species in the forests studied exhibited a peak in their flowering and fruiting during the early part of the rainy season, that is, about April, and a smaller peak between mid-August and mid-September. During these periods animal activity in the canopy increases considerably (e.g., pollinators, primates, birds, bats and insects predators). Through their excrements and the damage done to the leaves and fruits, wash-off is likely to increase as well as release of solutes from decomposing plant material (leaves and fruits). This would be fully in line with results from other studies, where insect and frugivore consumption in the canopy was found to be responsible for increases in solute concentration of throughfall and stemflow (Tukey and Morgan 1963; Carslile et al. 1966; Crossley and Seastedt 1981; Föster 1982). Such animal activity might also explain the differences in solute concentration between our forest types, especially between that of the sedimentary plain and of the alluvial plain. The first lacks distinct fruiting season, has lesser fruits and consequently lesser animal activity in the canopy. In the flood plain forest the fruiting seasons are very clear and a considerably large number of frugivores have been observed.

Net solute fluxes

As nutrient use efficiency and limiting nutrients in a forest are more easily highlighted by comparing the total volume of nutrients cycling through the forest and arriving to the forest floor or topsoil (throughfall, stemflow, litterfall and root decay), and the net nutrients percolating through this forest floor or in the water drainage, which will deals with in a following paper (Tobón et al., in press), the nutrient budget here will concentrate on the essentials related to nutrient fluxes associated with leaching, dry and wet deposition and absorption by the forest canopy.

Annual solute inputs by throughfall and stemflow in our four forests over the period 1995–1997 are presented in Table 2. The Student's *t*-test showed that significant differences ($p > 0.95$) existed between throughfall inputs in all forests, but that differences in inputs of cations between the high and low terrace forests were not significant (at the 0.05 level). The largest differences in throughfall inputs occurred between the low terrace and sedimentary plain forests, followed by those between the flood plain and sedimentary plain forests. As to stemflow, inputs in the flood plain and low terrace forests differed significantly (at the 0.05 level) from those in the sedimentary plain and high terrace forests, particularly those of K, Ca, and Mg, while in the flood plain and low terrace forests stemflow inputs were similar.

The enrichment/depletion ratios (Figure 4) show that in the low terrace and flood plain forests, the solute fluxes were highest, particularly of K, Mg orthoP, Si and DOC, while the sedimentary plain forest exhibited the lowest inputs, though its throughfall volume was the largest of the forests studied (Tobón et al. 2000). Thus, in the flood plain forest, net inputs of K, Mg and orthoP were 1.5 times higher than in the sedimentary plain forest. Na and Cl appeared to be taken up by most forests, whereas Mn was only depleted in the high terrace forest. The largest total cation input was observed in the flood plain forest, while the forest in the low terrace received the largest inorganic anion input. The data show that particularly SO_4, K, Cl, NO_3 and NH_4 were enriched in throughfall and stemflow, indicating that throughfall and stemflow were important pathways of these solutes in the systems studied, while fluxes of Mn, Fe and orthoP were low. This large nutrient enrichment in throughfall and

Table 2. Solute fluxes in throughfall and stemflow (kg ha^{-1} year^{-1}) in four undisturbed forest ecosystems in Colombian Amazonia.

Ion	Sedimentary plain		High terrace		Low terrace		Flood plain	
	Throughfall	Stemflow	Throughfall	Stemflow	Throughfall	Stemflow	Throughfall	Stemflow
H	0.01	0.02	0.19	0.02	0.29	0.02	0.16	0.02
K	27.51	0.37	36.64	0.56	37.74	0.68	38.76	0.75
Na	13.28	0.15	16.61	0.19	15.32	0.28	15.92	0.21
NH_4	9.72	0.18	12.08	0.17	10.81	0.21	12.98	0.26
Ca	4.75	0.06	5.12	0.11	5.30	0.11	7.53	0.20
Mg	2.29	0.03	2.40	0.06	2.55	0.08	3.86	0.10
Fe	0.73	0.03	1.06	0.04	0.94	0.02	0.86	0.04
Mn	0.26	0.002	0.08	0.003	0.20	0.01	0.22	0.01
Si	3.29	0.14	4.99	0.09	4.15	0.27	5.43	0.19
Cl	24.70	0.38	26.87	0.41	35.46	0.73	28.01	0.50
NO_3	23.64	0.32	17.07	0.32	31.98	0.62	21.08	0.54
PO_4	1.51	0.04	1.89	0.04	2.08	0.03	2.92	0.04
SO_4	71.79	0.97	78.30	1.08	79.39	1.39	65.63	1.41
Cations	58.61	1.02	74.20	1.22	73.10	1.71	85.70	1.83
Anions	121.62	1.73	124.10	1.81	148.90	2.83	117.10	2.52
DOC	148.43	2.82	190.42	3.02	174.48	4.52	175.56	6.14

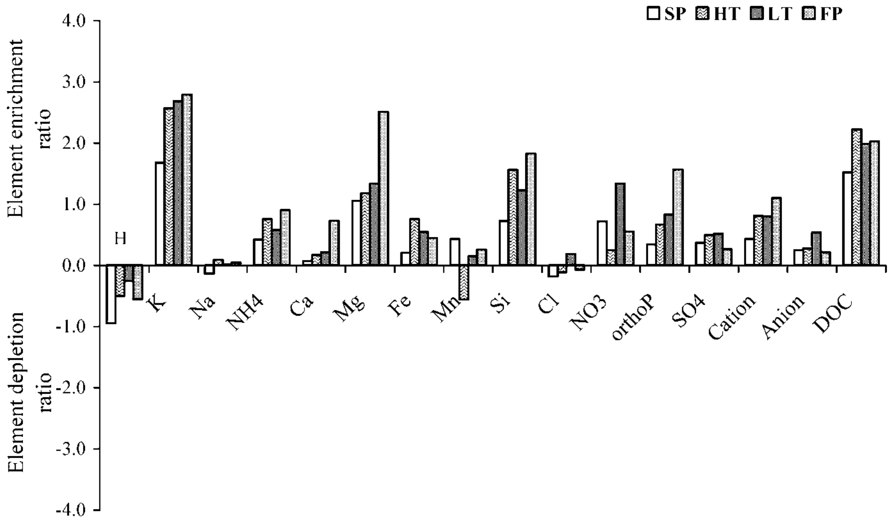

Figure 4. Ratios of element enrichment or depletion in net precipitation after rainfall pass through the canopy (throughfall + stemflow) in four pristine forests in Colombian Amazonia, as deduced from Equation (2). Tertiary sedimentary plain (SP), high terrace (HT), low terrace (LT) and the flood plain (FP) of the river Caquetá.

stemflow in the flood plain forest, compared to the upland forests, are consistent with trends of high nutrient contents in litter fall in this forest and the declining litterfall nutrient concentrations and the increases in sclerophyllic leaves according to the soil nutrient limitation across the ecotonal gradient.

In agreement with increased nutrient concentrations, the amounts of solutes in throughfall plus stemflow (kg ha^{-1} year^{-1}) were larger than those in gross rainfall. On average, about 98% of the total solute inputs in the forests studied was in the form of throughfall, of which about 38% originated from dry deposition and canopy exchange and 62% from rainfall. The contribution of stemflow was very low, but we have to take into account that its input is very local, that is, around stem bases where fine roots are concentrated. This contribution ranged from 0.8 to 4.7% of the total input depending on the type of solute and forest ecosystem. Comparing the total inputs of cations and anions in throughfall and stemflow, anions are in excess, with an annual cation deficit of 64 kg ha^{-1} year^{-1} in the sedimentary plain, 51 in the high terrace and 77 in the low terrace, while the flood plain forest had the smallest deficit (33 kg ha^{-1} year^{-1}).

Differences in throughfall and stemflow chemistry among nearby forests have been attributed to different factors. If climate and topographic position are similar, factors such as forest type and structure, stand age and soil fertility are generally considered to be the most important variables (Mahendrappa and Ogdem 1973; Jordan et al. 1980; Cole and Rapp 1981). Rainfall chemistry did

Table 3. Net solute inputs by throughfall (kg ha^{-1} year^{-1}) in some Neotropical rain forests as compared with the average values from the four forest types (this study) in Colombian Amazonia.

Site	K	Ca	Mg	Na	NH_4	Cl	orthoP	Reference
Rio Negro – Venezuela	4.3	30.6	0.4		11.6		10.7	Jordan et al. (1980)
Reserva Duke – Brazil	22.1	1.0	7.8		0.7	16.3	0.1	Franken et al. (1985)
Reserva Duke – Brazil	11.8	10.2	6.6		20.0	13.7	0.5	Brinkmann (1985)
Belém de Para – Brazil	15.8	5.1	4.4	2.3	3.5	3.5	0.1	Hölscher (1995)
Mabura Hill – Guyana	6.8	2.0	1.9	11.6	2.4	6.6	0.2	Brouwer (1996)
Montane forests – Panama	63.2	35.1	7.6	131.2	7.2	49.6	2.2	Cavalier et al. (1997)
Montane forest – Colombia	95.2	27.1	10.7	26.9	21.5	36.3	1.7	Veneklaas (1990)
Lowland forest – Colombia	35.2	5.7	2.8	15.3	11.4	28.7	2.1	This study (average values from the four sites)

not differ between the forests studied (Tobón et al., 2004) and climate and topographic position are highly similar. Consequently, most of the variability in net precipitation chemistry between sites must be attributed to differences in dry deposition and canopy exchange, which can be linked to differences in nutrient status of leaves, aboveground litter and soils as found by Duivenvoorden and Lips (1995), as well as in LAI and forest cover (Tobón 1999). Another possible cause might be the differences in interception of rainfall, causing differences in the concentration of solutes in the fraction of rainfall passing through the forest canopy (Parker 1983) and deposition. We found clear differences in the amounts of rainfall intercepted by the canopy in the forests studied, values for the flood plain forest being twice as high as those for the sedimentary plain forest (Tobón et al. 2000).

Yearly throughfall fluxes in our study were compared with those found by others in Amazonian and Andean tropical mountain forests (Table 3). Fluxes of K, orthoP, Na and Cl appeared to be higher than those from other sites within the basin, while amounts of Ca and Mg were lower or about similar. When compared with Venezuelan forests (Jordan et al. 1980), it appeared that solute inputs in forest studied were higher. However, they were considerably lower than those in the Andean montane forests studied by Veneklaas (1990), except for orthoP whose inputs were much higher in our forests. The solute inputs in stemflow were considerably lower than in San Carlos, Venezuela (Jordan 1978), which may be related to the differences in tree species composition and the possible absorption by epiphytic algae and lichens on the bark. It can be concluded, therefore, that element fluxes through these nearby forests are among the highest reported from similar forest in central Amazonia and Rio Negro Venezuela.

Element sources

Enrichment of rainfall after passing through the forest canopy has been attributed to two main processes: exchange of solutes by the canopy through leaching and absorption, and wash off of dry deposition from the leaves (Lovett and Lindberg 1984; Alcock and Morton 1985; Bruijnzeel 1990; Potter et al. 1991). The model by Lovett and Lindberg (1984) was applied using the calculated throughfall inputs. Although results indicated that a large proportion of the solutes in throughfall resulted from canopy exchange with the highest proportion in the flood plain ecosystem, the model could not explain the provenance of some solutes. Therefore we complemented this analysis with a factor analysis to identify the factors determining the composition of the throughfall.

Combined results from the Lovett and Lindberg's model and factor analysis (Table 4) indicated that although solute concentrations correlate poorly with water amounts, canopy exchange (factor 1) had a major control over net throughfall chemistry in most forests (this factor explained in average the 52% of the throughfall composition), with slightly higher values in the flood plain forest, mainly for elements such as K, Ca, SO_4, Mg, Na, Si, Cl and DOC. In general this predominant source for nutrient enrichment of net precipitation is likely to be connected to the losses of element in shedding leaves and small dying branches and twigs, while they are still attached to the trees; nevertheless, high nutrient retranslocation from these leaves, before abscission, is expected to occur (Cuevas and Medina 1986; Scott et al. 1992; Duivenvoorden and Lips 1995). Contrary, the larger amounts of nutrient leached from the canopy at the flood plain forest are likely related to the larger amounts of nutrient on leaves and branches (Duivenvoorden and Lips 1995), which appeared to be linked to the relative higher nutrient status in the mineral soil.

Although sodium and chloride are often inferred to be of atmospheric origin as oceanic air masses (Parker 1983; Beier et al. 1992), mainly in Amazonian forests (Brouwer 1996), and Ca is often immobilised in structure tissues (Parker 1983), in this study we found that they largely originate from canopy leaching, as inputs in rainfall were relatively small and our forests are located at a very large distance from the ocean. In this context, it is not surprising that Na was a dominant ion in throughfall in pristine forest in Guyana (Brouwer 1996) and that its concentration was considerably higher compared to the studied sites in this part of the Amazonia. These results agree with the findings of Parker (1983), who concluded that K and Na enrichment in throughfall could be the result of leaching and more specific, leaching of Na from the leaves occurred in most studied forests (Tukey 1970). However, for forests growing on oligotrophic soil conditions this has been questioned (Jordan et al. 1980).

Overall results here also agree with the observations by Duivenvoorden and Lips (1995) that K, Ca, Mg and Na were easily leached from decomposing litter in studied forests. This indicates that elements present in large amounts in the leaves are also leached in larger amounts and transported as soluble ions, while the leaves are being decomposed (Eaton et al. 1973; Alcock and Morton 1985; Potter et al. 1991; Brouwer 1996). However, the opposite can also occur, where forest growing on more nutrient poor soil conditions or having elements limiting, notably the sedimentary plain forest, can retain and retranslocate

Table 4. Grouping the element sources through factor analysis (principal component method, after Varimax Rotation) of net solute inputs in throughfall to pristine forests in Colombian Amazonia. Factor 1 indicates that the source of these elements is mainly due to canopy exchange. Factor 2 indicates a source of dry deposition and Factor 3 indicates different sources.

Factor	Sedimentary plain			High terrace			Low terrace			Flood plain		
	1	2	3	1	2	3	1	2	3	1	2	3
Exp. var (r^2)	0.52	0.17	0.08	0.51	0.18	0.09	0.52	0.19	0.07	0.58	0.24	0.07
H	0.02	−0.15	−0.03	0.003	0.72	−0.05	0.07	−0.10	0.94	0.27	0.06	0.88
K	0.69	0.55	0.25	0.87	0.22	0.10	0.70	0.04	−0.11	0.57	0.23	0.38
Ca	0.78	0.53	0.15	0.19	0.72	0.49	0.62	0.13	0.02	0.89	0.16	0.09
Mg	0.78	0.42	0.29	0.28	0.76	0.39	0.83	0.14	0.03	0.78	0.23	0.29
Na	0.69	0.06	0.53	0.89	0.25	0.20	0.85	−0.003	0.18	0.62	0.51	0.33
NH_4	0.05	0.88	0.21	0.86	−0.08	0.20	0.04	0.88	0.02	0.49	0.72	−0.01
Fe	0.62	0.14	0.62	0.08	0.55	0.65	0.33	0.68	0.05	0.15	0.83	0.19
Mn	0.76	−0.11	0.19	0.11	0.27	0.91	0.80	0.23	0.34	0.09	0.11	0.77
Si	0.66	0.32	0.26	0.71	0.44	−0.01	0.45	0.27	0.31	0.06	0.31	0.61
Cl	0.27	0.09	0.83	0.74	0.31	0.31	0.73	−0.11	0.05	0.83	0.13	0.01
NO_3	0.27	0.64	0.55	0.17	−0.03	0.95	0.38	0.71	0.02	0.28	0.78	−0.01
OrthoP	0.09	0.89	0.14	0.73	−0.01	0.01	0.03	0.91	−0.14	0.32	0.86	0.08
SO_4	0.79	−0.04	0.19	0.51	0.45	0.53	0.79	0.30	0.02	0.84	0.27	0.18
DOC	0.87	0.23	0.21	0.28	0.81	0.22	0.90	0.14	0.05	0.79	0.40	0.22

larger amounts of its nutrients before leaf abscission (Gauch 1972), as a mechanism to avoid nutrient losses.

Although the poor soil nutrient conditions, there is a relatively larger annual losses by leaching of these forests when compared with those within the Amazonia (Franken et al. 1985; Hölscher 1995; Brouwer 1996), which can be associated with the rather high annual rainfall, as compared to other sites. However, except for Na, the releases of nutrients by the forest canopies (leacheates) were considerably lower than those in litterfall (Duivenvoorden and Lips 1995), stressing the large nutrient conservation mechanisms by these forests. The implication of this nutrient use efficiency and conserving mechanisms, mainly by upland forests (sedimentary plain and high terrace) is that they are less susceptible to loose nutrients by drainage and can recycle more efficient those elements from atmospheric deposition, as it is concluded in the following paper on forest floor nutrient fluxes (Tobón et al., in press).

Dry deposition was the second factor determining the solute inputs, particularly of NH_4, NO_3, Ca, orthoP and Fe and explaining on average 19% of its composition. These results are in line with the observed positive relationship between the concentrations of these solutes and the length of the antecedent dry period, discussed above. They also agree with the findings by Talbot et al. (1988) in the sense that nitrate and other volatile elements largely originate from dry deposition, depending on their abundance in the surrounding atmosphere. As to phosphate, it has been argued that orthoP in throughfall is mainly due to animal defecation in the canopy (López-Hernández 1989), which seems highly applicable to our forests. The particularly large contribution of dry deposition in the flood plain forest (0.24) may be due to its higher ability to capture nutrients, because of its relatively large LAI and connected larger capacity to intercept rainfall (Tobón 1999). The considerable effect of dry deposition on throughfall and stemflow chemistry is somewhat questionable, since nutrient inputs in rainfall appeared to be of low magnitude. Therefore, this relative high contribution of dry deposited elements can be probably be partly ascribed to dissolution of salts, formed by evaporation of intercepted water and leaf exudes in the canopy. Moreover, as large amounts of nutrient enrichment were derived from the wash off of dry deposited elements in the canopy and leacheates, the lowest enrichment occurring in the sedimentary plain, mainly for elements such as K, Mg, Si, orthoP and DOC, suggests that the trapping efficiency of this forest is distinctly less than the other forests.

Factor 3 groups solutes of which the provenance cannot be identified with certainty, but probably also largely originate from canopy leaching (e.g., K). This might be due to the sampling methodology employed, which in fact does not allow for an optimal discrimination between canopy exchange and dry deposition. However, the contribution of this factor is small and in general more than 70% of the variance can be explained by the first two factors.

Conclusions

This study demonstrates the importance of throughfall and stemflow as pathways for nutrient inputs into the forest floor in the Amazonian forests studied. Throughfall formed the most important flux, on average contributing 98% of the total solute input. Although stemflow contribution was very low, its localised inputs around trunk bases were large.

Solute dynamics in throughfall and stemflow differed considerably from that in rainfall, which implies that processes occurring in the canopy had a strong control over throughfall and stemflow inputs. In general, concentrations of most solutes increased, though rates clearly differed between the four forest ecosystems studied, which differ with respect to their structure, composition and soil nutrient status.

Net nutrient fluxes in throughfall and stemflow in the low terrace and flood plain forests differed considerably from those in the sedimentary plain. While cation inputs were largest in the flood plain forest, being 1.5 times larger than those in the sedimentary plain, the largest input of inorganic anions occurred in the low terrace forest, which additionally had the largest total input. K, SO_4, NH_4 and NO_3 increased significantly in all forests, while Mn and orthoP decreased in some events and forests. The trend in the release of orthoP among the forests is related to the phosphorus availability in the soils, which decreases from the flood plain to the sedimentary plain.

The length of the antecedent dry period was the dominant factor affecting the temporal variability in throughfall and stemflow chemistry in these forests, and amounts of throughfall and stemflow showed a poor and negative correlation with solute concentration. Flowering and fruiting of forest trees appeared to have considerable influence on the enrichment of rainfall, most probably due to the high biological activity of frugivores in the canopy. However, the main processes causing this enrichment are solute exchange processes in the canopy (uptake/exudation/leaching). Dry deposition contributed to a lesser extent, which is in line with the low concentrations of solutes in rainfall.

Although the large spatial variability observed for throughfall chemistry between forests and the estimates of the deposition of some ions (e.g., N) onto forest are open to debate, with most canopies absorbing deposited N, this study, along others carried out within the Amazon basin, provides useful information on the changes of the element concentration after rainfall passes the canopy of contrasting forests, which can be used for large scale estimations (long-range transport models) of atmospheric deposition and the contribution of wash off, foliar leaching and nutrient absorption by the canopies.

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