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Change in water quality during the passage through a tropical montane rain forest in Ecuador

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Abstract. We studied five 20-m transects on the lower slope under tropical lower montane rain forest at 1900–2200 m above sea level. We collected samples of soil and of weekly rainfall, throughfall, litter leachate, and stream water between 14 March 1998 and 30 April 1999 and determined the concentrations of Al, total organic C (TOC), Ca, Cl^-, Cu, K, Mg, Mn, NH_4^+-N, NO_3^--N, total N (TN), Na, P, S, and Zn. The soils were shallow Inceptisols; pH ranged 4.4–6.3 in the O horizons and 3.9–5.3 in the A horizons, total Ca (6.3–19.3 mg kg^{-1}) and Mg concentrations (1.4–5.4) in the O horizon were significantly different between the transects. Annual rainfall was 2193 mm; throughfall varied between 43 and 91% of rainfall, cloud water inputs were ≤ 3.3 mm a^{-1} except for one transect (203). The volume-weighted mean pH was 5.3 in rainfall and 6.1–6.7 in throughfall. The median of the pH of litter leachate and stream water was 4.8–6.8 and 6.8, respectively. The concentrations of Ca and Mg in litter leachate and throughfall correlated significantly with those in the soil (r = 0.76–0.95). Element concentrations in throughfall were larger than in rainfall because of leaching from the leaves (Al, TOC, Ca, K, Mg), particulate dry deposition (Cu, Cl^-, NH_4^+-N), and gaseous dry deposition (NO_3^--N, total N, S). Net throughfall (= throughfall-rainfall deposition) was positive for most elements except for Mn, Na, and Zn. High-flow events were associated with elevated Al, TOC, Cu, Mn, and Zn concentrations.

1. Introduction

Tropical montane rain forests protect downslope areas from flooding, prevent soil erosion, and maintain a constant baseflow during dry periods (Hamilton et al. 1995; Bruijnzeel 2000). Among the neotropical forests, the north Andean montane forests are the richest in plant species (Henderson et al. 1991). Nevertheless, by 1991 already more than 90% of the original forest cover in this region had been lost (Henderson et al. 1991; Hamilton et al. 1995). The protection of the remaining native forests and the development of sustainable land-use practices require the understanding of its functioning. Although tropical montane forests have now been studied for two decades, still little is known about their functioning (Bruijnzeel 2000). We are not aware of any study on the water and nutrient cycles of the montane forests on the verges of the Amazonian basin.

Rainfall in tropical montane forests ranges between several hundreds and several thousands of mm per year (Bruijnzeel & Proctor 1995; Cavelier et al. 1997; Bruijnzeel 2000). All of these forests are affected by low clouds and many of them receive considerable cloud water inputs (Asbury et al. 1994; Clark et al. 1998; Bruijnzeel 2000). Bruijnzeel and Hamilton (2000) suggested to classify tropical montane forests on large mountains according to the decreasing stature and increasing cloud impact in the order, lower montane rain forest, lower montane cloud forest, upper montane cloud forest, and subalpine cloud forest.

During the passage through the forest, the quantity and chemical composition of the water that enters the forest with rainfall and clouds changes (Parker 1983; Bruijnzeel 1990; Likens & Bormann 1995). The chemical quality of throughfall and stemflow is controlled by intensity of rainfall and by gaseous and particulate dry deposition (Parker 1983; Schaefer & Reiners 1990; Veneklaas 1990). There are indications that soil fertility also influences the quality of throughfall and stemflow (Parker 1983). The few studies on litter leachate in tropical montane forests indicate that the concentrations of all plant nutrients increase compared with rainfall and throughfall (Steinhardt 1979; Bruijnzeel et al. 1993; Hafkenscheid 2000). In stream water draining tropical rain forests, nutrient concentrations are smaller than in litter leachates except for elements which are released by weathering mainly from geologically young bedrock (Bruijnzeel et al. 1993; McDowell 1998).

Our study was conducted on five 20-m transects in similar topographic position in a c. 30 ha area of a lower montane rain forest according to Bruijnzeel and Hamilton (2000) in south Ecuador. We determined physical and chemical properties of the soil, quantified the water input and assessed the chemical composition of throughfall, litter leachate, and stream water.

2. Materials and methods

2.1 *Site description*

We selected three microcatchments on a 30–50° steep slope at an altitude of 1900–2200 m above sea level (a.s.l.) between the cities of Loja and Zamora

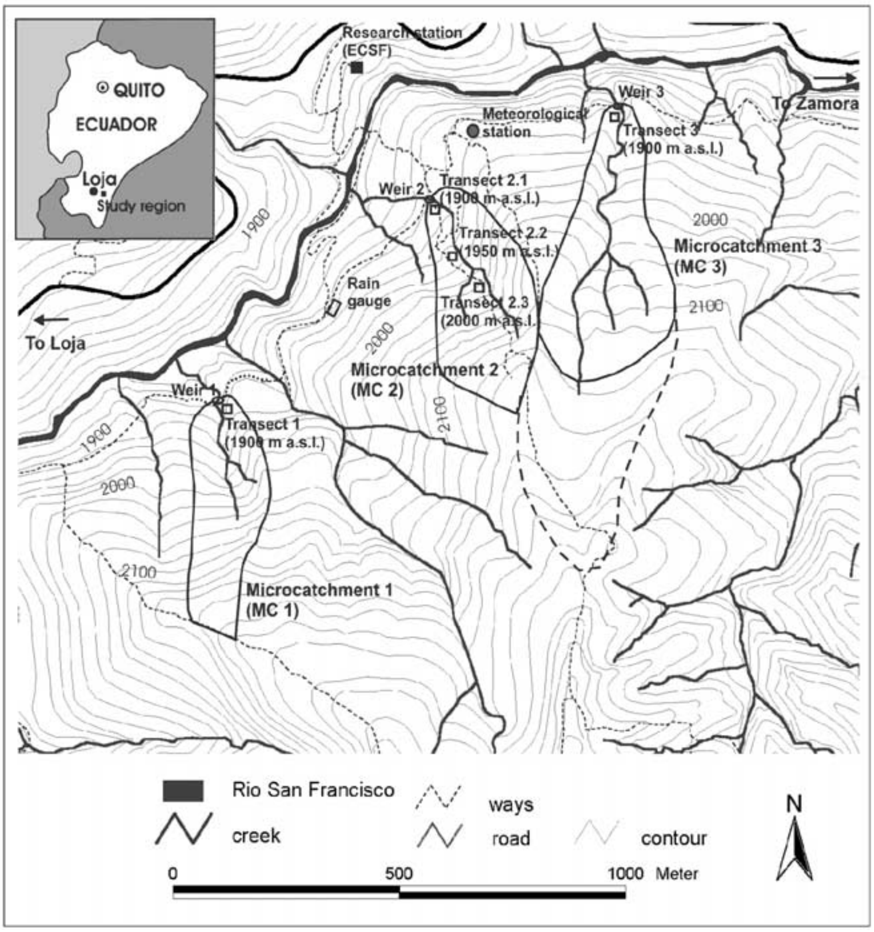

Figure 1. Location of the studied transects.

in the south Ecuadorian Andes (Figure 1). The site is at 4°00′ S and 79°05′ W. Microcatchment (MC) 1 covers c. 8 ha, MC 2 c. 10 ha, and MC 3 c. 13 ha. All MCs are drained by small tributaries to the Rio San Francisco which flows into the Amazonian basin. The slope faces north and is on the shoulder of the Rio San Francisco valley. We installed scientific equipment within each MC on transects, about 20 m long with a vertical altitude difference of 10 m, on the lower part of the slope at 1900–1910 m a.s.l. (transects MC1, MC2/1, and MC3) and in MC2 also at 1950–1960 (MC2/2) and 2000–2010 m a.s.l. (MC2/3).

Between April 1998 and April 2000, the mean annual temperature at 1950 m a.s.l. on a ridge between MC2 and MC3 was 16.2 °C. The mean annual temperature gradient was −0.6 to −0.7 °C per 100 m increase in altitude.

The coldest month was July with a mean temperature of 14.9 °C, the warmest month was November with a mean temperature of 17.3 °C. Mean annual precipitation was 2220 mm. On average, 300 mm of precipitation fell in April, the wettest month, and 70 mm in November, the dryest month. The mean annual air humidity was 85% (90% in April and 80% in November). The prevailing directions of the synoptic wind (above 2850 m a.s.l.) were easterly during $>80\%$ of the observed time while the air circulation in the study area was dominated by valley-mountain wind systems. As available data cover 24 months these results still have to be considered as preliminary (P. Emck, personal communication).

The bedrock consists mainly of Palaeozoic weakly metamorphosed schists and sandstones with some quartz veins. Recent soils are developed from periglacial cover beds. Furthermore, postglacial landslides are common modifying the substrate for soil development.

Microcatchments 2 and 3 are entirely under forest, the upper part of MC1 is open grassland under natural succession. This part had been used for subsistence agriculture until about 10 years ago. The forest is tall-statured lower montane rain forest (Bruijnzeel & Hamilton 2000). It has an upper 15–20 m-tall storey with few trees reaching 35 m, a lower 10–15 m-tall tree storey, and a <5 m-tall shrub storey. The canopy coverage of the uppermost storey is 50–60% and that of the second storey is 10–50%. The shrub storey covers 50–80%. The forest has a stem density of c. 1000 stems ha^{-1} with a diameter at breast height (dbh) >0.1 m and of c. 6000 stems ha^{-1} with a dbh >0.05 m. The gentle lower slopes are dominated by species of the families Euphorbiaceae, Solanaceae, Cecropiaceae, and Lauraceae; the steeper higher slopes carry mainly Melastomataceae, Lauraceae, Euphorbiaceae, and Rubiaceae. The most abundant tree species between 1800 and 2200 m is *Graffenrieda emarginata* (Ruiz&Pav.) Triana (Melastomataceae). The ground flora is dominated by large ferns, particularly Dryopteridaceae and some large herbs (mainly Lobeliaceae, R. Bussmann, J. Homeier & D.A. Neill, personal communication). The forest, though mainly natural has been disturbed by man as indicated by an old path connecting Loja and Zamora, electric cables, an about 2 m wide water channel of an electricity plant, some small landslides, and the open area in the upper part of MC1.

2.2 *Sampling*

We sampled O, A, and B horizons of three soils on each of the five transects (15 soils in total). The soils were located at the lower end, in the center, and at the higher end of the transects. Samples were taken from the walls of a soil pit in a manner to be representative for the horizons. Soil samples were air-dried, O horizon samples were additionally ground, mineral soil samples were sieved to <2 mm. All samples were stored in closed plastic bags at room temperature until analysis.

At the outlet of each catchment, we installed 90° V-notch metal weirs, the water levels were read once per week. At the same time, a 100-ml water sample was taken from the center of the stream before it passed through the weir.

Furthermore, each of the five study transects was equipped with five throughfall collectors which were evenly distributed on the transect. On the three lowermost transects in each catchment, four trees of the uppermost layer and one tree fern belonging to the second tree layer were equipped with stemflow collectors made of polyurethane foam and connected with plastic tubes to a 10-l container (Likens & Eaton 1970). To collect litter leachate, three zero-tension lysimeters were installed at the lower end, in the center, and at the upper end of the transects next to the locations where soil samples were taken. The lysimeters, consisting of plastic boxes covered with a polyethylene net (0.5 mm mesh), had a surface area of 0.20 m × 0.14 m and were 0.15 m high. The boxes were connected to a 1-l polyethylene sampling bottle with plastic tubes. The lysimeters were installed from a soil pit below the organic layer parallel to the surface. The organic layer was not disturbed, most roots in the organic layer remained intact. Rainfall samples were collected with five collectors at an unforested site between MC1 and 2 (Figure 1). The unforested area was caused by a landslide. Throughfall and rainfall collectors consisted of a 2-l polyethylene sampling bottle and a funnel with a diameter of 115 mm. The opening of the funnel was at 0.3 m height above the soil surface. Each sampling bottle was protected against larger particles and small animals with a polyethylene net (0.5 mm mesh width). A table-tennis ball was used to reduce evaporation. The rainfall collectors were additionally wrapped with Al foil to reduce the radiation impact on samplers and collected solution. Solution samples were collected weekly between 14 March 1998 and 30 April 1999. The water volume was recorded individually for each collector or lysimeter, rainfall samples and, on each transect, the five throughfall and three litter leachate samples were bulked, respectively, and two 100-ml aliquots were removed of each bulk sample. After each collection, the rainfall and throughfall collectors were cleaned with the remaining solution or deionized water. One of the aliquots was used to measure pH and Cl^- concentrations in the unfiltered solution and to produce a filtered combined monthly sample (ashless white ribbon paper filters, pore size, 4–7 μm; Nr. 300111, Schleicher and Schuell). The monthly sample consisted of aliquots from 4 weeks in 30-d months and from 5 weeks in 31-d months. The other aliquot was filtered and frozen immediately after collection.

2.3 *Chemical analyses*

The following parameters were determined in the soil samples: soil pH in water (soil:solution ratio 1:2.5) with a standard pH electrode (Orion U402-S7), total C, N, and S concentrations with a CHNS-analyzer (Vario EL, Elementar Analysensysteme), effective cation-exchange capacity (ECEC) by extraction with 1 M NH_4NO_3 (Zeien & Brümmer 1989), base saturation (BS) by calculating the proportion of charge equivalent of extractable Ca + K + Mg + Na of the ECEC, and total Al, Ca, K, Mg, Mn, Na, P, and Zn concentrations in the mineral soil samples by digestion with concentrated HNO_3/HF (4:1 v/v, Zeien & Brümmer 1989) and in the organic samples by digestion with concentrated HNO_3 under pressure (Heinrichs et al. 1986). The ECEC and exchangeable cations were only determined in a single bulked A horizon and a bulked B horizon sample from the three soil pits on each transect. The concentrations of P in the extracts were determined with inductively-coupled plasma-atomic emission spectrometry (ICP-AES, GBC Integra XMP), those of the metals with flame atomic absorption spectrometry (AAS, Varian SpectrAA400).

In the solution samples, Cl^- concentrations were determined with a Cl^--specific ion electrode (Orion ionplus 9617BN) and pH with a standard pH electrode (the measurement was conducted in a subsample which was afterwards discarded because of the contamination with K released by the pH electrode). After export of the filtered 100-ml aliquots from Ecuador to Germany in frozen state, total organic C (TOC) concentrations were determined with an automatic TOC analyzer (TOC-5050, Shimadzu), NH_4^+ and NO_3^- concentrations with a rapid flow analyzer (RFA-300, Alpkem), total N (TN) concentrations with a total N analyzer (ABIMED TN-05), and Cu with a graphite tube AAS (Varian SpectrAA400Z). In the solution samples and in soil extracts, Al, Mn, and Zn were determined with inductively-coupled plasma-mass spectroscopy (ICP-MS, VG PlasmaQuad PQ2 Turbo Plus, VG Elemental), total S and P with ICP-AES, and Ca, K, Mg, and Na concentrations with flame AAS. As TN determination required a large sample volume, we performed TN analyses only in the composite monthly samples. Phosphorus and Cu concentrations were only determined in the monthly samples, except between 14 March and 24 April 1998 when Cu was measured in the weekly samples.

2.4 *Calculations and statistical evaluation*

The instantaneous stream discharge was calculated by using the empirical equation for 90° V-notch weirs: $Q = 1.35\ h^{2.48}$ where Q is the instantaneous stream discharge in $m^3\ s^{-1}$ and h the water level in m (Dyck & Peschke 1995).

The empirical constants were found to be adequate by manual flow measurements with container and stop watch. Mean values of the soil parameters were tested for differences between the various transects with Tukey's honest significant difference (HSD) mean separation test. The correlation analyses followed the least squares method. To compare average metal concentrations in solution between the transects, the Wilcoxon matched-pairs test for connected data rows was used. Significance was set at $p < 0.05$. Statistical analyses were performed with STATISTICA for Windows 5.1 (StatSoft 1995, Hamburg, Germany). We removed not more than one outlier from any data row. Values below the detection limit were taken as zero for calculations.

3. Results

3.1 *Soils*

The soils on transect MC1 were Humic Eutrudepts, those on transects MC2/1, 2/2, and 2/3 were Humic Dystrudepts, and on transect MC3 Oxyaquic Eutrudepts (USDA-NRCS 1998). All soils had a thick and densely rooted organic layer; the thickness ranged from 5 to 16 cm. In all organic layers, three horizons could be distinguished. The Oi horizon consisted of fresh litter, the Oe horizon mainly contained mechanically fragmented litter, and the dark brown Oa horizon had lost all plant structure. The mean bulk density of the organic horizons in the study area increased in the order, Oi (0.08 g cm^{-3}) < Oe (0.11) < Oa (0.23, Wilcke et al. 2001). In the mineral soil, the bulk density increased abruptly to *c.* 1.0 cm^{-3} in the A horizons and to *c.* 1.3 cm^{-3} in the B horizons. The mineral soil contained many stones and considerably less roots than the organic layer.

All soils were acid and showed a highly variable pH. In most soils, the pH decreased between the organic layer and the mineral soil and increased between A and B horizons of the mineral soil (Table 1). The effective cation-exchange capacity in the mineral soil was correlated with the C concentration ($r = 0.75$). Although all mineral soils were strongly acid, the base saturation covered a broad range of values reaching up to 95% in the A horizons on transects MC1 and 3. Exchangeable Ca, Mg, K, and Na concentrations in the A horizons ranged between 0.7, 2.4, 1.3, 0.3 and 63, 74, 3.2, 3.2 $mmol_c\ kg^{-1}$, respectively. Exchangeable Al concentrations were negatively correlated with exchangeable base metal concentrations ($r = -0.84$).

Total C, Ca, Mg, N, P, and S concentrations were larger in the organic layer than in the mineral soil, Mn and Zn concentrations were comparable, Al, Fe, K, and Na concentrations were larger in the mineral soil. In most

Table 1. Average properties and element storages of the studied soils ($n = 3$ on each transect, except effective cation-exchange capacity (ECEC), base saturation (BS), and exchangeable Al (Al_{ex}) which were only analyzed in one combined sample per transect). The O horizon properties are according to the depth weighted means of the respective Oi, Oe, and Oa horizon properties. Different letters indicate significant differences of the means between the transects according to Tukey's HSD test ($p < 0.05$).

Horizon	Transect	ECEC	Al_{ex}	BS	pH	Al	C	Ca	Fe	K	Mg	Mn	N	Na	P	S	Zn
		($mmol_c$ kg^{-1})		(%)	(H_2O)						(g kg^{-1})						
O	MC1				6.3a	5.8	404	19a	2.4	3.8	4.1ab	0.67	26	0.05	1.2	3.0	0.05
	MC2/1				4.4b	6.0	408	5.4b	3.8	3.3	1.4c	1.1	23	0.06	1.0	3.0	0.05
	MC2/2				4.4b	20	338	6.3b	6.4	6.6	2.8bc	0.50	20	0.15	0.9	2.3	0.04
	MC2/3				4.7b	7.9	403	10bc	3.0	3.9	3.2abc	0.45	24	0.09	1.1	2.9	0.05
	MC3				6.2a	7.1	394	15ac	2.7	4.0	5.4a	0.56	24	0.12	1.2	2.8	0.05
A	MC1	47	2.1	95	5.1ab	55	28	0.4	24	21	1.1	0.50	3.2	1.3	0.7	0.5	0.07
	MC2/1	83	77	6.3	4.3ab	49	44	0.3	23	13	0.5	0.23	3.6	2.1	0.7	0.5	0.04
	MC2/2	92	79	10	3.9b	46	62	0.5	20	16	0.8	0.42	4.7	2.1	0.7	0.6	0.04
	MC2/3	49	19	62	4.7ab	44	22	0.6	20	15	0.7	0.63	2.3	1.2	0.7	0.4	0.05
	MC3	150	6.5	95	5.3a	43	52	2.1	20	17	1.3	0.73	4.8	2.5	0.9	0.6	0.08
B	MC1	39	29	22	5.1	55	12	1.0	24	21	1.1	0.49	1.6	1.1	0.6	0.3	0.07
	MC2/1	68	64	6.1	4.8	52	19	0.4	24	14	0.6	0.31	1.8	1.8	0.4	0.3	0.04
	MC2/2	135	128	4.8	4.4	52	37	0.4	20	17	0.8	0.25	2.8	1.9	0.5	0.4	0.06
	MC2/3	37	22	35	4.8	45	12	1.2	20	15	0.7	0.55	1.5	1.4	0.6	0.3	0.07
	MC3	35	5	81	5.8	48	21	1.3	20	17	1.1	0.41	2.4	2.5	0.6	0.4	0.05
						Element storage (kg ha^{-1})											
O	MC1					523	29400	1430	221	295	304	55	2000	4.6	92	226	3.5
	MC2/1					837	49100	584	520	430	152	134	2910	7.7	129	368	6.0
	MC2/2					3831	44900	671	1120	1140	325	64	2700	25	136	315	6.7
	MC2/3					1187	52800	1200	446	520	380	55	3230	12	151	392	6.4
	MC3					826	34500	1340	296	403	472	58	2190	12	114	253	4.7
0–0.3 m	MC1					194000	59200	2760ab	83200	73900a	3680ab	1650ab	7230	4150	2180	1130	238
	MC2/1					183000	93100	1220b	84400	50000b	2070c	1040b	8190	6690	1690	1240	147
	MC2/2					178000	165000	1470b	72100	61000ab	2870bc	1250ab	12400	6700	2030	1660	204
	MC2/3					160000	53600	3580ab	71000	53700ab	2330c	2050a	6100	4800	2200	1080	216
	MC3					160000	122000	5470a	69400	59800ab	4130a	1940ab	12100	8800	2470	1640	214

mineral soils, Al and Ca concentrations increased with depth, those of Fe, K, Na, and Zn did not show differences between A and B horizons, and those of C, Mn, N, P, and S decreased.

The uppermost 0.3 m of the mineral soil had a larger storage of all studied elements than the organic layer. It contained, on average, between 67% (C) and almost 100% (Na) of the total element storage in the organic layer and the uppermost 0.3 m of the mineral soil. Although the total nutrient storage in the mineral soil was larger than in the organic layer, there were much less roots in the A than in the O horizons.

The soils on transects MC1 and MC3 had a significantly higher pH in the O horizon than the soils on the other transects and a still higher pH in A and B horizons although the differences were partly not significant. The higher pH coincided with larger Ca and Mg concentrations in the O horizon and a substantially higher base saturation in the A and B horizons.

3.2 *Water*

Between 3 April 1998 and 2 April 1999, the first complete year after all equipment was installed, 2193 mm of rainfall were recorded. During the monitored period, five weeks had more than 100 mm of rainfall and only two weeks were without rain (Figure 2). During the whole monitored period, the average throughfall ranged between 43 (MC1) and 91% (MC2/1) of the rainfall. The stemflow ranged between 0.9 and 1.1% of the rainfall on all transects. Weekly throughfall on all transects and weekly stemflow at the 15 monitored trees were closely correlated with weekly rainfall ($r = 0.58$–0.96). The stemflow was not further considered in this paper, because of its small contribution to the total soil water input.

On transect MC2/1, on 21 sampling weeks higher throughfall than rainfall was recorded during the monitored period (Figure 3). On transects MC2/2 and MC3 more throughfall than rainfall was recorded during two weeks, on transect MC1 during one week, on transect MC2/3 never. If the difference between throughfall and rainfall volumes is interpreted as cloud water input, on transect MC2/1 203 mm of cloud water contributing 8.5% to the total water input were recorded between 3 April 1998 and 2 April 1999. On all other transects, the annual cloud water input was ≤ 3.3 mm. These estimates represent minimum values because cloud water that evaporates without appearing in the throughfall was not included. Between 3 April 1998 and 2 April 1999 we collected, on average, 106 mm ± standard error, 20 mm of litter leachate with our zero-tension lysimeters. This represented 4.8% of the rainfall. Litter leachate fluxes correlated significantly with throughfall on most transects ($r = 0.54$–0.73) except for MC3 (0.31). During dry phases, we frequently could not collect litter leachate.

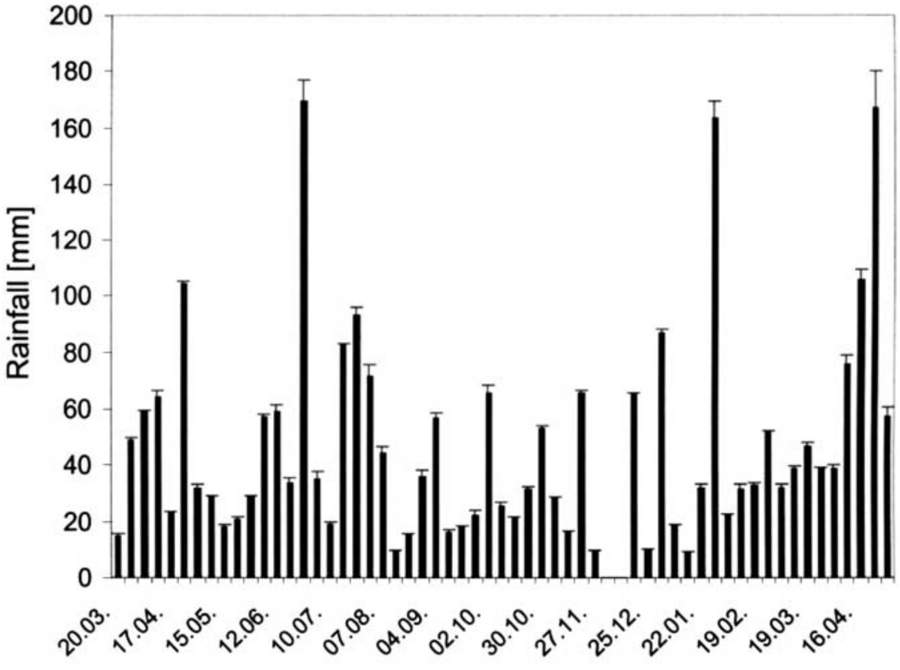

Figure 2. Average weekly rainfall. (Mean of five rain collectors and standard error.)

Our estimate of the water flow through the litter was too low because the used type of lysimeter only collected a variable part of the total flow during nearly water-saturated conditions (Jemison & Fox 1992). A reliable quantification of the water yield of the catchments was also not possible because this would require a measurement with a much higher time resolution (Likens & Bormann 1995).

3.3 *Chemical composition of solutions*

pH. The volume-weighted mean (VWM) pH of the rainfall was 5.3 ranging from 4.0 to 5.7. During the passage through the canopy, the pH was buffered to a VWM of 6.1–6.7 in throughfall (Figure 4(a)). The pH of the throughfall reflected the acidity of the soil. It increased in the order MC2/2 = MC2/3 (6.1) < MC2/1 (6.4) < MC1 (6.5) < MC3 (6.7).

As we do not know the total volume of the vertically percolating water, we did not calculate VWMs for the litter leachate but used the median for comparison. The median of the pH in litter leachates on transects MC2/1, 2/2, and 2/3 (4.8, 5.4, and 5.9, respectively), was lower than the VWM pH in throughfall. On transects MC1 and MC3 there was no difference in pH between throughfall and litter leachate (6.4 and 6.8, respectively). The pH of

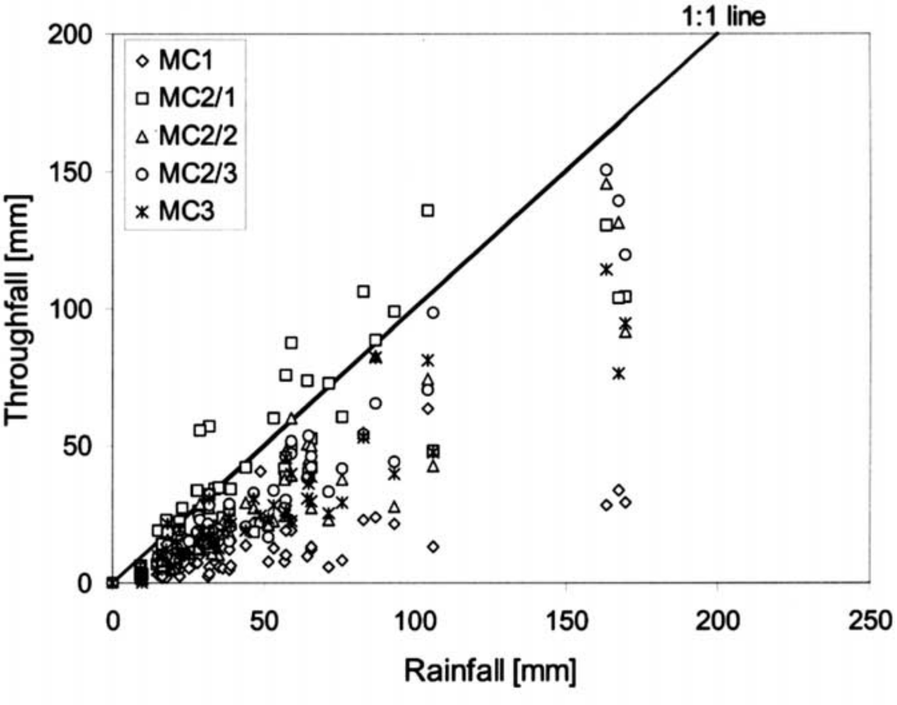

Figure 3. Relation between rainfall and throughfall on the five transects.

the litter leachates correlated significantly with that of the O horizons (r = 0.88).

Although the mineral soils were strongly acid (Table 1), the median of the pH of the stream water (where the total volume is also unknown) was 6.8 in all three streams. There were only few sampling dates with a pH in stream water below 6.0 (Figure 4(b)). Low pH was related with storm events.

The pH of the rainfall showed seasonal variations. Between 31 July and 30 October 1998, it was lower (<5 on most sampling dates) than during the rest of the monitored period. During the first monitored year, we observed an increase in pH of rainfall. While in March 1998 there was a difference of up to 3 pH units between rainfall and throughfall, in March 1999 there was almost no difference anymore.

Element concentrations. The concentrations of most elements increased in the order, rainfall < throughfall < litter leachate but decreased substantially between litter leachate and stream water (Table 2). Exceptions of this general trend were the Na concentrations which continuously increased from rainfall to stream water and the H^+ concentrations. The differences in Cl^-, K,

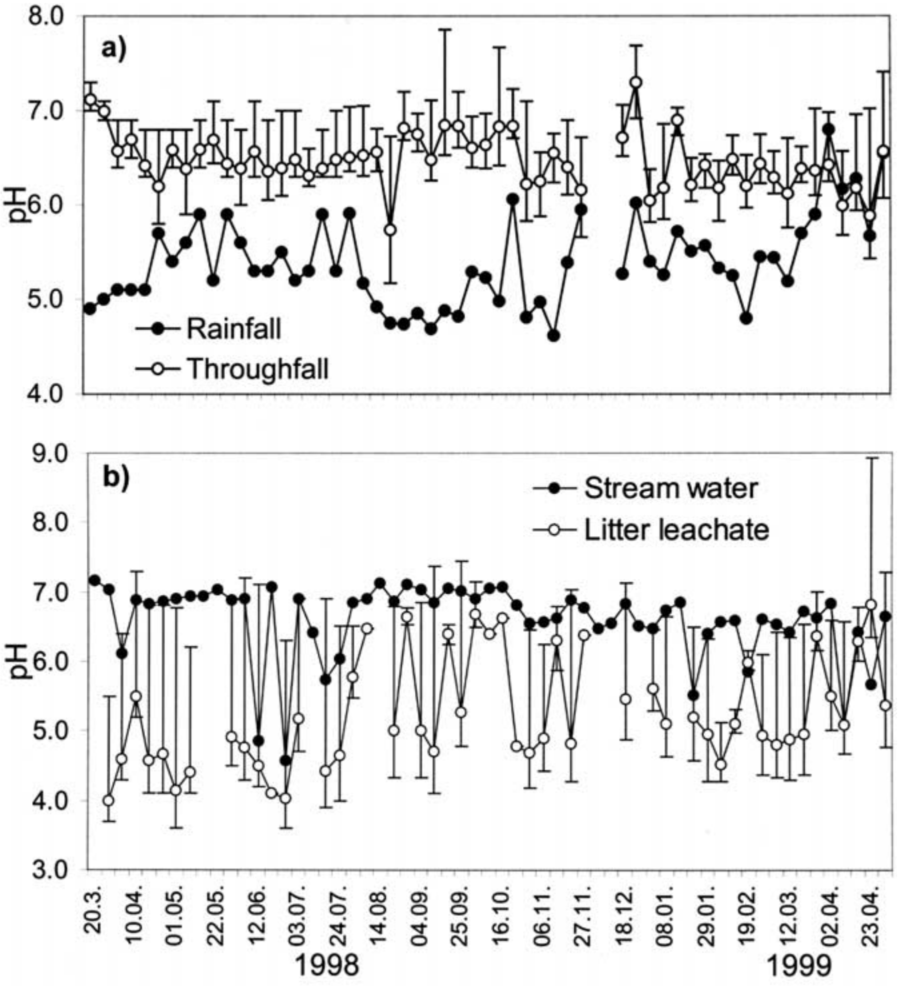

Figure 4. Temporal course of pH in (a) rainfall and throughfall and (b) litter leachate and stream water.

and NH_4^+-N concentrations between throughfall and litter leachate were not consistent.

Most element concentrations in throughfall and litter leachates were significantly different among the five transects (Table 2). Calcium, Cl^-, Mg, NO_3^--N, and TN concentrations were largest on transect MC3, Al and Mn concentrations were smallest.

The Ca, Mg, Mn ($r = 0.82$), Na (0.90), and P (0.77) concentrations in the O horizon correlated significantly with their VWM concentrations in throughfall ($r = 0.77$–0.95, Figure 5). Furthermore, significant correlations existed

Table 2. Volume-weighted mean element concentrations in rainfall and throughfall and median concentrations in litter leachate and stream water (where the total volume is not known) in an Ecuadorian lower montane rain forest between 14 March 1998 and 30 April 1999 and in literature (see text for explanations). Values for TOC refer to a filter pore size of 4–7 μm in our study and of 0.45 μm in literature, values for S refer to total S in our study and SO_4^{2-}-S in literature. Different letters indicate significant differences of the data rows between transects according to the Wilcoxon matched-pairs test ($p < 0.05$). ND is not detected.

	Al	TOC	Ca	Cl^-	Cu	H	K	Mg	Mn	NH_4^+-N	NO_3^--N	TN	Na	P	S	Zn
	(μgl^{-1})															
Rainfall	1.6	4114	177	535	0.7	4.9	168	56	1.9	119	136	264	856	27	51	5.8
Forti& Neal 1992	–	–	<50–1500	140–4500	–	2.0–100	20–1330	<20–250	–	30–490	–	–	70–1700	–	ND–1020	–
Hafkenscheid 2000	–	–	100–790	920–4500	–	10–40	90–380	30–330	–	50–860	5.0	170–850	210–1810	10–70	370–1240	–
Throughfall:																
MC1	19c	15200abc	1990b	1740d	3.1ab	0.4b	12500a	1060b	1.9ab	274a	631b	1650ab	1080ab	450ab	361a	8.4c
MC2/1	26b	13300abc	939d	1900b	3.8a	0.4b	8290c	413d	2.3a	359a	431c	1250b	1070a	186c	338a	6.6ab
MC2/2	23b	17600a	1160d	1770c	2.2b	0.9a	9700b	539d	1.8b	431a	535c	1480b	1550a	274bc	329b	9.9a
MC2/3	32a	12900c	1180c	1030c	2.6ab	0.9a	5330d	657c	1.7ab	377a	554c	1250b	1110a	588abc	153b	5.6b
MC3	11d	14600b	2250a	2410a	2.6a	0.2c	11300a	1680a	1.4b	327a	986a	2330a	1230b	642a	373a	7.7ac
Forti & Neal 1992	–	–	60–5600	370–2880	–	–	260–12500	80–8300	–	62–2240	–	–	240–18300	–	150–830	–
Hafkenscheid 2000	–	–	550–1600	1960–2260	–	1.5–2.5	2890–5530	260–580	–	70–1160	40	330–1400	350–5940	110–120	280–2200	–
Litter leachate:																
MC1	230b	56100b	5800ab	1700bc	5.4a	2.5b	11700c	2090c	14cd	262bc	674c	2550a	1530a	290a	1070c	17b
MC2/1	944a	42600c	1890c	834d	4.3a	17a	3730d	1580d	56a	376b	893bc	1570a	1320b	86a	960bc	25ac
MC2/2	203b	35600d	2290c	1360cd	3.1b	4.2a	5890d	1380d	21bc	246c	602bc	1570a	1400a	–	635d	16b
MC2/3	246b	63700a	5320b	2780b	7.0ab	1.2c	16500b	3010b	43b	320ab	903b	5830a	1360a	2370a	1740bc	25ac
MC3	26c	42400bc	8030a	4410ab	4.5ab	0.2d	27700a	5030a	5.5d	709a	5740a	–	1440a	1620a	1250ab	15bc
Forti & Neal 1992	–	–	20–1100	70–2500	–	–	300–2100	60–700	–	16–311	–	700–2900	–	70–1130	–	
Steinhardt 1979	1060	–	5080	–	–	4.6	38400	2090	101	–	4560	415	291	–	–	
Hafkenscheid 2000	<190	–	1650–2540	2750–4240	–	2.1–8.5	2870–4140	930–1100	–	130–220	<170	810–1050	1560–1980	<40–53	<1320–1940	–
Stream water:																
MC1	5.3ab	2270c	1030a	279b	1.9a	0.2ab	295a	400b	<2a	59a	81a	112a	3990a	22a	361a	2.6c
MC2	6.3a	2810b	770b	328a	1.2a	0.2a	345a	453a	<2a	65a	47b	207a	3450b	117a	<300b	3.4b
MC3	5.9b	3110a	530c	396a	1.8a	0.2b	330a	385b	<2a	58a	54ab	107a	2770c	67a	<300b	4.3a
McDowell & Asbury 1994	–	1860–4010	1110–5040	5040–8350	–	0.1–0.3	280–460	940–4420	–	12–18	60–69	222–237	3100–6460	2.0	776–932	–
Forti & Neal 1992	–	–	ND–19000	400–1100	–	–	30–1400	ND–5100	–	8–70	–	–	210–10800	–	27–1270	–

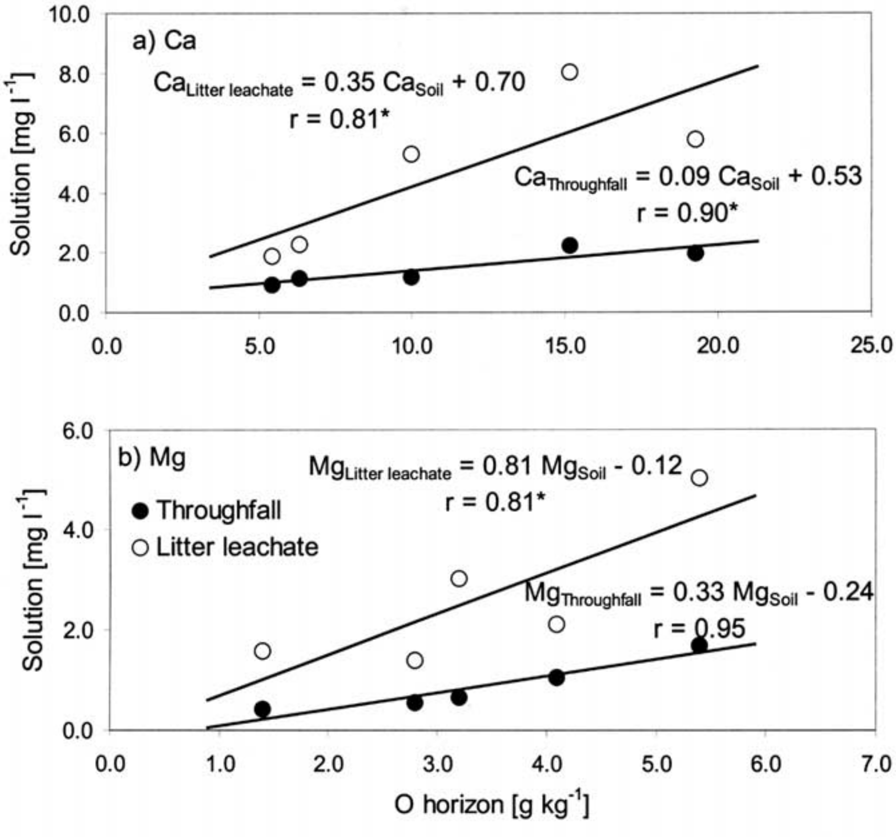

Figure 5. Relation between the mean Ca and Mg concentrations in the O horizons and the volume-weighted mean Ca and Mg concentrations in throughfall and between the mean Ca and Mg concentrations in the O horizons and the median of the Ca and Mg concentrations in litter leachate.

between the Ca and Mg concentrations in the O horizon and the median of their concentrations in litter leachate. There were only few significant correlations between the instantaneous stream discharge and element concentrations which were not consistent between the three microcatchments.

The Ca, Cl^-, Mg, Na, and NH_4^+-N concentrations in rainfall showed seasonal variation (Figure 6). Between 31 July and 30 October 1998, when the pH was lower, the concentrations of these elements were smaller than during the rest of the monitored period. During this time the mean molar ratio of Na/Cl^- was 1.05. There was no seasonality of the Al, TOC, K, Mn, NO_3^--N, and Zn concentrations in rainfall. Copper, TN, and P concentrations were measured in too few samples to detect temporal trends.

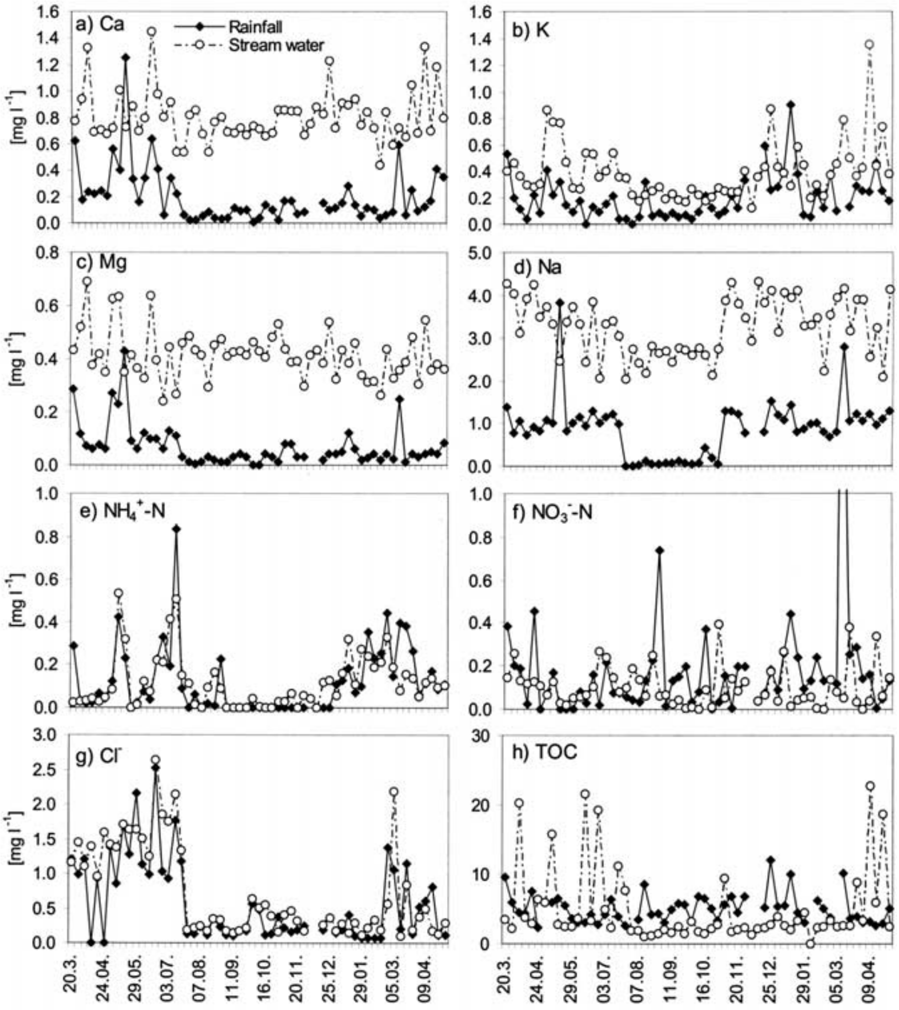

Figure 6. Temporal course of the mean (a) Ca, (b) Mg, (c) K, (d) Na, (e) NH_4^+-N, (f) NO_3^--N, (g) Cl^-, and (h) TOC concentrations in rainfall (n = 1) and stream water (n = 3).

In throughfall, there was only a seasonal variation of Na and on the transects of MC2 also of the Cl^- concentrations which were smaller between 31 July and 30 October 1998 (VWM Na: 0.15–0.19 mg l^{-1} for all transects; Cl^-: 0.52-0.84 mg l^{-1} for the transects in MC2) than during the rest of the monitored period. Simultaneously, Ca, K, Mg, and NH_4^+-N concentrations tended to be larger. After the two weeks without rain in early December 1998 (Figure 2), an increase of most element concentrations except for H^+, NO_3^--N, and Na in throughfall was observed. The mean ratios of the concentrations on 18.12.1998 to the VWM concentrations ranged between 2.19 (Zn) and 6.52 (Cl^-) and were 1 or lower for H^+, NO_3^--N, and Na.

In litter leachates and stream water, only the Na concentrations showed a seasonal variation. During the time when the concentrations of many elements were smaller in rainfall, smaller TOC, NH_4^+-N, and Cl^- concentrations in streamwater were observed (Figure 6). High-flow events were associated with decreased pH and increased TOC, Al, Cu, Mn, and Zn concentrations in stream water (Figure 7).

3.4 *Element fluxes*

Our study design only allowed for the quantification of input fluxes. For most elements, throughfall deposition was higher than rainfall deposition. Thus, the net deposition, i.e. throughfall-rainfall deposition, was positive for most elements (Table 3). However, the net deposition of H^+ on all transects and that of Mn, Na, and Zn on some transects were negative. Positive net deposition is reflected by deposition ratios, i.e. the ratio of throughfall to rainfall deposition rates, higher than 1, negative net deposition by deposition ratios lower than 1. The highest deposition ratios were observed for the base metals decreasing in the order, $K > Mg > Ca$.

To assess the relative importance of element leaching from leaves as reason for throughfall enhancement, we correlated the weekly rainfall with the weekly net throughfall rates. Close correlations existed for Al, the base metals, and TOC (Table 4). The correlation coefficients of P ranged between 0.22 and 0.58.

Ulrich (1983) suggested the use of the deposition ratio of Cl^- to estimate the dry deposition. Chloride is believed to be only taken up or leached from leaves to a negligible extent. Thus, the throughfall enhancement of Cl^- exclusively results from dry deposition. If it is furthermore assumed that all other elements are scavenged by the canopy to the same extent, the contributions of dry deposition (particulate or gaseous) and leaching of the leaves to the throughfall enhancement may be estimated. Similar deposition ratios as for Cl^- were observed for NH_4^+-N, TOC, and Cu (Table 3). The deposition ratios of all other elements were higher than those of Cl^-.

4. Discussion

4.1 *Soils*

Thick organic layers and the acid soil reaction are typical for soils under tropical montane forests (Bruijnzeel & Proctor 1995; Grubb 1995; Tanner et al.

Table 3. Rates of rainfall and throughfall deposition, net throughfall deposition, and deposition ratios in an Ecuadorian lower montane rain forest between 3 April 1998 and 2 April 1999 and in literature (see text for explanations). In Hafkenscheid (2000), the P values represent PO_4^{3-}-P and the S values SO_4^{2-}-S. Different letters indicate significant differences of the data rows between transects according to the Wilcoxon matched-pairs test ($p < 0.05$).

	Al	TOC	Ca	Cl^-	Cu	H	K	Mg	Mn	NH_4^+-N	NO_3^--N	TN	Na	P	S	Zn
							($kg\ ha^{-1}\ a^{-1}$)									
Rainfall	0.04	90	3.9	12	0.02	0.11	3.7	1.2	0.04	2.6	3.0	5.8	19	0.6	1.1	0.13
Hafkenscheid 2000	–	–	3.6–28	19–59	–	0.32–0.84	2.6–14	1.3–5.2	–	1.7–18	1.7	6.5–18	3.3–64	0.05–1.1	12–260	–
Throughfall:																
MC1	0.18b	143c	19b	16c	0.03c	0.00c	118c	9.9bd	0.02b	2.6d	5.9b	16c	10c	4.2b	3.4bc	0.08cd
MC2/1	0.52a	266a	19b	38a	0.08a	0.01a	166a	8.3c	0.05a	7.2ab	8.6b	25abc	22a	3.7b	6.8a	0.13a
MC2/2	0.30a	232a	15b	23b	0.03bc	0.01b	128b	7.1cd	0.02c	5.7a	7.1b	20b	20a	3.6b	4.3b	0.13ab
MC2/3	0.45a	183b	17b	15c	0.04b	0.01a	76d	9.3b	0.02abc	5.4bc	7.9b	18bc	16b	8.4ab	2.2c	0.08d
MC3	0.14b	183b	28a	30ab	0.03bc	0.00c	142ab	21a	0.02bc	4.1c	12a	29a	15b	8.0a	4.7b	0.10bc
Hafkenscheid 2000	–	–	6.9–35	36–50	–	0.04–0.05	63–95	3.3–12	–	1.3–22	0.6	7.2–36	4.4–131	0.48–3.0	6.1–41	–
Net throughfall:																
MC1	0.14b	53c	15b	4.7c	0.01c	−0.10c	114c	8.7bd	−0.02b	0.0d	2.9b	9.8c	−8.6c	3.6b	2.3bc	−0.05cd
MC2/1	0.49a	176a	15b	26a	0.06a	−0.10a	162a	7.0c	0.00a	4.6ab	5.7b	19abc	2.7a	3.1b	5.7a	0.01a
MC2/2	0.27a	142a	11b	12b	0.01bc	−0.10b	124b	5.9cd	−0.02c	3.1a	4.1b	14b	1.7a	3.0b	3.2b	0.00ab
MC2/3	0.42a	93b	13b	3.0c	0.02b	−0.09a	72d	8.1b	−0.02abc	2.7bc	4.9b	12bc	−2.8b	7.8ab	1.1c	−0.05d
MC3	0.10b	92b	24a	19ab	0.02bc	−0.10c	138ab	20a	−0.02bc	1.5c	9.4a	23a	−3.4b	7.5a	3.2b	−0.03bc
Hafkenscheid 2000	–	–	1.3–19	15–17	–	50–87	−1.9–11	–	−0.4–3.2	−1.1	−1.0–3.0	1.1–68	0.43–2.5	−7.1–15	–	
Deposition ratios:																
MC1	5.1ab	1.6c	4.8b	1.4b	1.9b	0.03c	32c	8.1bcd	0.43b	1.0c	2.0c	2.7b	0.5c	7.1b	3.0a	0.6bc
MC2/1	15a	3.0a	4.8b	3.2a	5.0a	0.07b	45a	6.7c	1.1a	2.8a	2.9bc	4.3a	1.1a	6.3b	6.1ab	1.0a
MC2/2	8.7a	2.6a	3.9b	2.0b	1.9b	0.11a	35b	5.8d	0.57a	2.2a	2.4b	3.4a	1.1a	6.1b	3.9ab	1.0a
MC2/3	13a	2.0b	4.3b	1.3c	2.4b	0.12ab	21d	7.6b	0.58ab	2.1b	2.6bc	3.1a	0.9b	14a	1.9b	0.6c
MC3	3.9b	2.0b	7.3a	2.6a	2.1b	0.02c	38ab	17a	0.42b	1.6bc	4.1a	5.0ab	0.8b	14a	4.2ab	0.8ab
Parker 1983	–	–	2.9	3.0	–	–	11	4.0	–	1.6	1.3	1.9	2.4	3.9	2.3	–
Hafkenscheid 2000	–	–	1.2–6.3	1.4–1.9	–	–	4.7–27	0.64–9.4	–	0.8–1.2	0.4	0.9–5.6	1.1–2.1	1.3–9.6	0.5–1.6	–

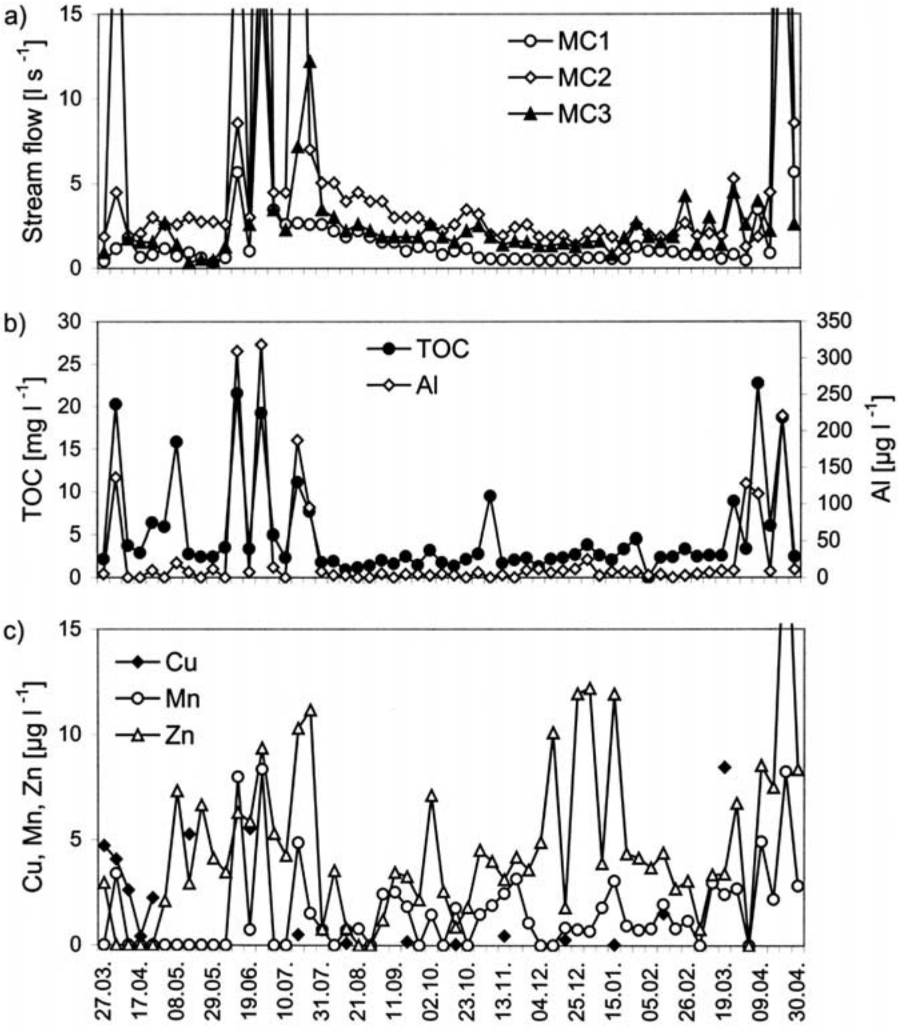

Figure 7. Temporal course of (a) the instantaneous stream discharge of three microcatchments, (b) mean Al and TOC concentrations in stream water, and (c) mean Cu, Mn, and Zn concentrations in stream water.

1998). A detailed discussion of the soil organic layer properties is presented in Wilcke et al. (2001). The pH covered a large part of the range of pH values in topsoil horizons (including organic and mineral horizons) from various tropical montane forests of 3.2–7.0 collected by Bruijnzeel and Proctor (1995). The C concentrations in the A horizons were larger than the mean of humid tropical Inceptisols (Kauffman et al. 1998). This is frequently the case in soils of tropical montane forests (Bruijnzeel & Proctor 1995; Tanner et al. 1998;

Table 4. Significant correlation coefficients of the relation between rainfall and net throughfall deposition on the five transects between 20 March 1998 and 2 April 1999 ($p < 0.05$).

Transect	Al	C	Ca	Cl^-	Cu	H	K	Mg	Mn	NH_4^+-N	NO_3^--N	TN	Na	P	S	Zn
MC1			0.42			0.35	0.57	0.34					0.58			
MC2/1	0.73	0.67	0.45			0.30	0.63									
MC2/2	0.30	0.58	0.54			0.28	0.64	0.46								
MC2/3	0.76	0.62	0.74	0.33			0.55	0.61		0.53						
MC3	0.60	0.72	0.81	0.45		0.31	0.49	0.78			0.29		0.33		0.45	

Hafkenscheid 2000). The correlation between the C concentrations and the ECEC illustrated the importance of soil organic matter for the storage of bioavailable cations, particularly of the base metals. The N concentrations in the A horizons were at the lower end of the range of data (2–25 g kg^{-1}) in Bruijnzeel and Proctor (1995). This was also the case for the exchangeable base metal concentrations in the A horizons. In contrast, exchangeable Al concentrations were larger than the mean of tropical Inceptisols (Kauffman et al. 1998).

Increasing metal concentrations with soil depth, except for Mn, were the result of the decrease in weathering intensity and of a more pronounced leaching in the topsoil than in the subsoil (Filipinski & Grupe 1990). Smaller Mn concentrations in the subsoil than in the topsoil may be the result of the increase in soil moisture with increasing soil depth and thus more pronounced reduction of Mn. Decreasing element concentrations with soil depth indicated that the element input from the atmosphere and the vegetation was higher than the leaching.

The reason for much less roots in the mineral soil than in the organic layer may be that only a small part of the total nutrient storage in the mineral soil was available to the plants possibly because of slower mineralization of organically bound nutrients and strong binding of nutrients to minerals. Furthermore, most mineral soils were more acid than the organic layers which increased the risk of Al toxicity (Savory & Wills 1991).

The finding that soil properties under tropical forests are highly variable has also been reported from other locations (Silver et al. 1994; Burghouts et al. 1998). Silver et al. (1994) observed a systematic variation in soil properties in a tropical rain forest in Puerto Rico. Along a catena from riparian valley to ridge top positions, pH and exchangeable base metal concentrations decreased while exchangeable acidity and the concentrations of exchangeable Fe and soil organic matter increased. At our site, however, all sampled soils were located in similar positions. Thus, topographic position may not explain the marked difference in pH and Ca and Mg concentrations among the studied soils.

4.2 *Water*

Our rainfall estimate is close to the independently measured mean of 2220 mm for the period April 1998 to April 2000 at the meteorological station between MC2 and MC3 (P. Emck, personal communication). Steinhardt (1979) and Veneklaas (1990) reported a bimodal rainfall distribution in the Sierra de Mérida in Venezuela and in the Cordillera Central in Colombia north of our study area. Veneklaas (1990) stated that this was common in the northern Andes which is not supported by our data. However, the monitored period followed a strong El Niño event in late 1997 and may therefore not be representative for the average long-term rainfall distribution.

The throughfall percentage of the rainfall on all transects except for MC2/1 (43–65%) was at the lower end of the range of the data in Bruijnzeel and Proctor (1995) and Bruijnzeel (2000) of 55 to 101% for lower montane forests. Scatena (1990) reported a similar high mean evaporation loss of intercepted water (42%) in a Puerto Rican rain forest and suggested that this was related with a high frequency of low-intensity rainfall which is also the case at our study site. Recent evidence of Schellekens et al. (1999), however, indicated that this low value was caused by advected energy from the nearby ocean. Ataroff (1998) assumed that the high number of epiphytes of a tropical montane forest in Venezuela was responsible for a througfall as low as 55% of the rainfall. As our study site was characterized by both high epiphyte load and frequent low-intensity rainfall, high evaporation rates of the intercepted water may be expected which were partly compensated by cloud water inputs on transect MC2/1. If results of Lloyd and Marques (1988) for lowland forests are valid for our study site, the error of the measured mean throughfall on the individual transects may be around 20%. Even if we assumed that we measured throughfall systematically too low the clear finding of comparatively high evaporation losses of intercepted water from the canopy for all transects except for MC2/1 still would hold. The contribution of stemflow to the total soil water input at our site was at the lower end of the range of data for tropical montane forests of 0.1–18% of the rainfall (Bruijnzeel & Proctor 1995; Bruijnzeel 2000).

The reason for the higher cloud water input on transect MC2/1 may be its location near a depression and a small forest clearing which was caused by the construction of the channel of the electricity plant. This assumption was supported by the qualitative observation that transect MC2/1 was more frequently in the clouds than the other transects. The cloud water contribution of 203 mm or 9.3% of the rainfall on transect MC2/1 was at the lower end of the range of cloud water inputs to lower montane forests of 31–887 mm a^{-1} or 6–35% of the rainfall in Bruijnzeel (2000). However, the possible error in the throughfall measurements may also affect our estimate of cloud water input.

4.3 *Chemical composition of solutions*

pH. The range of the volume-weighted mean (VWM) pH in rainfall was comparable to that in rainfall in the Amazonian lowland rainforest (Forti & Neal 1992). The pH of rainfall in our study was also similar to that in other montane forests of the northern Andes (4.4–5.6, Steinhardt 1979; Veneklaas 1990). The partly low pH of rain water in the Amazonian basin results from large concentrations of low molecular organic acids like acetic and formic acid released by the forest canopy (Forti & Neal 1992). In montane forests, low pH in rain water may also be caused by contributions of cloud water which is frequently strongly acid (Clark et al. 1998).

The higher pH of the stream water than of the mineral soil indicated that H^+ were buffered in the subsoil by mineral weathering and possibly also consumed by chemical reduction processes. During storm events, water travelling rapidly in macropores which is more acid than matrix flow because of less equilibration time with the mineral soil reached the stream (Cozzarelli et al. 1987; Neal et al. 1989; McDowell & Asbury 1994). Furthermore, during storm events more acid contributions of near-surface water become more important for the stream water recharge. A similar course of pH during the passage of water through a tropical rain forest in Puerto Rico was observed by McDowell (1998).

The beginning of the monitored period followed an El Niño event associated with forest fires in the Amazonian basin. Thus, besides the organic acids released by the forest canopy NO_x and SO_2 produced by the fires may have contributed to low pH in rain water which may have been transported with the prevailing winds from the Amazonian basin to our study site.

Element concentrations. The VWM concentrations of most elements in rainfall were at the lower end of the range of concentrations reported by Forti and Neal (1992) for various tropical rain forests and by Hafkenscheid (2000) for a range of tall-statured lower montane rain forests mainly in Central and South America (Table 2). The reason for small element concentrations in rainfall was the location far away from anthropogenic emission sources and from the sea. The large distance to the sea was reflected by a far higher mean molar Na/Cl^- ratio of 4.99 than in sea water (0.85, Eriksson 1960).

In the throughfall, VWM concentrations of all elements were well within the range of concentrations in tropical lowland and montane rain forests (Forti

& Neal 1992; Hafkenscheid 2000). However, the concentrations of N, P, and K in the throughfall at our study site were at the upper end of this range. The throughfall in the other north Andean studies was more acid, and in the study of Steinhardt (1979) also contained more Al (191 $\mu g\,l^{-1}$) and Mn (26 $\mu g\,l^{-1}$). Thus, the canopy of our study forest showed a high buffer rate resulting in the consumption of most deposited H^+ and in the release of base metals. The particularly strong increase in K concentrations after the passage of rainfall through the forest canopy has frequently been observed. It is attributable to the high leachability of K from leaves (Tukey 1970). Proton buffering and element leaching may be enhanced at our site due to the large leaf damages as a result of animal activity.

The median of the Ca, Cl^-, K, Mg, and NH_4^+-N concentrations in litter leachate was at the upper end or higher than the range of concentrations in soil solution and groundwater under some tropical forests (Forti & Neal 1992). In a Venezuelan lower montane rain forest (Steinhardt 1979) and in two Jamaican upper montane cloud forest types (Hafkenscheid 2000), similar Ca, Cl^-, Mg, TN, and partly also P concentrations in litter leachate were found. The Venezuelan litter leachate was, like the throughfall, more acid and contained larger concentrations of Al, K, and Mn. The soils on transects MC2/2 and MC3 had particularly large P concentrations in the litter leachate. However, the median of the P and TN concentrations in litter leachate was based on only one to four samples of which a sufficient volume of solution was available for all analyses and therefore have to be interpreted with caution. In nutrient-depleted strongly weathered tropical soils, nutrient concentrations in litter leachates are generally larger than in the mineral soil solution because of larger nutrient concentrations in organic than in mineral horizons (Steinhardt 1979; Bruijnzeel et al. 1993; Lilienfein et al. 2000). In the mineral soil, nutrients are sorbed or taken up by plants resulting in smaller solution concentrations.

In the stream water, the median of the Ca, Cl, K, and Mg concentrations was at the lower end of the range of values in Forti and Neal (1992) for surface waters of some tropical forests. Only the NH_4^+-N concentrations were near the upper end. The median of the Ca, Cl^-, Mg, TN, and Na concentrations was at the lower end of the range of flow-weighted means in three Puerto Rican streams draining forested catchments, that of the TOC, H^+, K, and NO_3^--N concentrations was comparable and that of NH_4^+-N, and P concentrations was higher at our study site (McDowell & Asbury 1994; McDowell 1998). Large Ca and Mg concentrations in the Puerto Rican stream water were explained by metal release by weathering of the bedrock. Furthermore, the nutrient deposition at the Puerto Rican site was greater than at our site because of the proximity of the sea.

The increase in element concentrations between rainfall and throughfall is known as "throughfall enhancement" (Parker 1983). The reasons include concentrations because of evaporation of intercepted water, particulate and gaseous dry deposition, hidden depositions with cloud water which does not reach the soil surface because of complete evaporation, and canopy processes. The most important canopy processes are leaching from the plant tissue, N fixation, decomposition of plant debris in the crown, and insect excretions (Parker 1983; Schaefer & Reiners 1990).

The correlation of the Ca, Mg, Mn, Na, and P concentrations in the O horizon with their VWM concentrations in throughfall indicated that these elements were taken up from the organic layer and recycled by leaching from the leaves (Figure 5).

The seasonal fluctuations of the Ca, Cl^-, Mg, Na, and NH_4^+-N concentrations in rainfall indicated that during the relatively dry period between 31 July and 30 October air masses differing in chemical composition from those of the rest of the monitored period reached the study area (Figure 2). During this time the average molar ratio of Na/Cl^- was closer to the molar Na/Cl^- ratio in sea water pointing at a larger contribution of marine aerosols to the deposited elements.

The larger Ca, K, Mg, and NH_4^+-N concentrations in throughfall during the relatively dry period may be related with less rainfall resulting in a concentration effect. The increase in most element concentrations in throughfall after the two weeks without rain in early December 1998 resulted probably from dry deposition during the time without rain which was washed off the canopy with the first rain thereafter.

The decrease in Cl^- concentrations in stream water during the time when the concentrations of many elements were lower in rainfall may be explained by the simultaneous decrease in Na concentrations. In stream water, Cl^- was probably the major accompanying anion of Na while in throughfall and litter leachate organic anions were more important for the compensation of the positive charge. Small NH_4^+-N concentrations probably indicated that the soil during this relatively dry period was well aerated and rapid oxidation of NH_4^+ to NO_3^- occurred. Although the NO_3^--N concentrations in stream water were elevated on few sampling dates during this time, no consistent trend was observed. This may be related with the large variation in NO_3^--N concentrations in stream water. Another explanation for small NH_4^+-N concentrations in stream water during this time may be a low biological activity which could also explain the smaller TOC concentrations because the release of soluble low molecular organic compounds is related to mineralization rates (McGill et al. 1986).

The considerable change in the chemical quality of the stream water during storms (Figure 7) indicated that high-flow events had a particular importance for the export of Al and micronutrients from the studied ecosystem probably as organic complexes (König et al. 1986; Stevenson & Vance 1989).

4.4 *Element fluxes*

The rainfall deposition of most elements at our study site was at the lower end of those of the througfall deposition well within the range of data collected by Hafkenscheid (2000) for lower montane rain forests. The N, P, and K deposition in throughfall was at the upper end or higher than the range of values given in Hafkenscheid (2000) reflecting their elevated concentrations in throughfall. Low rainfall deposition and high throughfall deposition of Ca, K, Mg, NO_3^--N, TN, P, and S resulted in higher deposition ratios than the global mean given in Parker (1983) and the range of data for lower montane rain forests in Hafkenscheid (2000). The deposition ratios of Cl^-, NH_4^+-N, and Na in our study were similar or lower than the values used for comparison in Table 3.

The negative net deposition rates of H^+ on all transects and those of Mn, Na, and Zn on some transects indicated uptake in the canopy. The reason for the uptake of Na, which is not an essential nutrient, may be small Na concentrations in the leaves because of small Na concentrations in the soil (Table 1). It has been shown that leaves may take up micronutrients like Mn and Zn (Berrow & Burridge 1991). Thus, our results may indicate that there was a limitation of forest growth by lack of Mn and Zn. This seems to be particularly true for the soils with higher pH in the organic layer and larger base metal concentrations on transects MC1, MC3, MC2/3. This assumption is further supported by the finding of Wilcke et al. (2001) that during incubation of the weakly acid organic layers on transects MC1 and MC3 Mn and Zn, which were added to soil with a percolation solution, were immobilized on balance. However, the uncertainties concerning the representativity of our throughfall sampling also affected our estimate of net deposition. Therefore, further experiments are needed to support the hypothesis of Mn and Zn limitation for plant growth.

The close correlations of Al, base metal, and TOC concentrations between weekly rainfall and weekly net throughfall indicated that the throughfall enhancement of these elements may mainly be explained by leaching from the leaves partly as result of H^+ buffering (Table 4). This may also be the case for P although the correlation coefficients were not significant because of the small data set for P. For the other elements with positive net throughfall, leaching was not the major reason for throughfall enhancement. The similar mean deposition ratios of NH_4^+-N and Cu and of Cl^- indicated that their throughfall enhancement may mainly be explained by particulate dry deposition. The higher mean deposition ratios of NO_3^--N, TN, and S than of Cl^- and the lack of correlation between net deposition and rainfall deposition pointed at additional sources of N and S to the canopy. Such sources may be gaseous dry deposition of NO_x, HNO_3, and S and N_2 fixation in the canopy. Vance and Nadkarni (1990) found a similar microbial biomass in organic matter accumulated in the canopy as in the organic layer in montane forest in Costa Rica which may be capable of fixing N_2 from the atmosphere. Gaseous deposition of N and S have been shown to be substantial in a temperate deciduous forest ecosystem (Lindberg et al. 1986).

5. Conclusions

The soil properties varied much among the five study transects. Although the mineral soils were strongly acid, the pH reached up to 6.3 in the organic layer and the base saturation up to 95% in the mineral soil. This variation was reflected by the chemical quality of the water during its passage through the studied forest. The mean Ca, Mg, Mn, Na, and P concentrations in throughfall and the median of the Ca and Mg concentrations in litter leachate were related to the concentrations of these elements in the O horizons as indicated by significant correlations.

The concentrations of most elements, except Mn, Na, and Zn which were retained in the canopy increased in the order, rainfall $<$ throughfall $<$ litter leachate. Correlations between the weekly rainfall and the weekly net throughfall and the comparison of deposition ratios of the elements with those of Cl^- were used as indication of the reasons of the increase in concentrations between rainfall and throughfall. Our results indicated that leaching from the leaves was particularly important for Al, TOC, Ca, K, and Mg, particulate dry deposition for Cu, Cl^-, and NH_4^+-N, and gaseous dry deposition for NO_3^--N, TN, and S. The uptake of Mn and Zn by the canopy may indicate micronutrient limitation of plant growth, that of Na may be the consequence of small Na concentrations in the leaves. However, further experiments are necessary to support this hypothesis because of the limited accuracy of our throughfall measurement.

Element concentrations in stream water were smaller than in litter leachate indicating that most elements were taken up by the vegetation or retained in the soil. However, during high-flow events the pH decreased and the concentrations of TOC, Al, Cu, Mn, and Zn increased illustrating that high-flow events may contribute significantly to the export of these elements from the studied catchments.

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