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Biogeochemistry of an afrotropical montane rain forest on Mt. Kilimanjaro, Tanzania

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Abstract: In contrast to their well-studied counterparts in the Neotropics and in Asia, East African montane rain forests are surrounded by semi-arid savanna plains. These plains have a high erosion potential for salt crusts accumulated at the soil surface. Hence it may be hypothesized that East African montane forest ecosystems experience strongly enhanced nutrient inputs via dry deposition, which alters their overall biogeochemistry. The aim of our study was to test this hypothesis by investigating K, Mg, Ca, Na and N-forms in rainfall, throughfall, fine litter, litter percolate and soil solution of a montane rain forest at Mt. Kilimanjaro. Four forest plots situated at elevations between 2250 and 2350 m asl on the south-western slopes of Mt. Kilimanjaro were studied for 2 y. In contradiction to our hypothesis, inputs of K, Mg, Ca and Na via rainfall (7.5, 0.9, 2.3 and 6.2 kg ha^{-1} y^{-1}) and throughfall (35, 2.0, 3.5 and 11 kg ha^{-1} y^{-1}) were low on Mt. Kilimanjaro. Fluxes of NH_4-N and NO_3-N were within the range observed at other montane rain forests, with NO_3-N being the only nutrient partly absorbed in the forest canopies (2.9 kg ha^{-1} y^{-1} in rainfall, 0.9 kg ha^{-1} y^{-1} in throughfall). The highest overall nutrient concentrations in water samples occurred in litter percolate (1.4 mg l^{-1} K, 0.3 mg l^{-1} Mg, 0.8 mg l^{-1} Ca, 0.3 mg l^{-1} NH_4-N, 0.9 mg l^{-1} NO_3-N), with values still being low compared to other sites. Nutrient concentrations in seepage water strongly declined with increasing soil depth. Thus, both inputs and losses of base cations from the forest by water pathways are assumed to be low. N or P limitation of growth is not expected since high fluxes of N and P in fine litter (119 and 5.9 kg ha^{-1} y^{-1} for N and P respectively) indicate low within-stand efficiency.

Key Words: litter, montane rain forest, Mount Kilimanjaro, nutrient cycling, rainfall, soil solution, Tanzania, throughfall

INTRODUCTION

Tropical montane rain forests have received increasing scientific attention during the past decades due to their high biodiversity (Myers *et al.* 2000) and their value as water catchment areas (Bruijnzeel 2001, 2004). Most studies on biogeochemical cycling in montane rain forests have focused on South and Central America and Asia, where these forests cover large areas (Bubb *et al.* 2004).

In East Africa, montane rain forests only cover small areas. In Tanzania for example, less than 2% of the total area is covered by moist forests (Bjørndalen 1992). Nevertheless, they are of great ecological and economic value as they form isolated humid ecosystems providing water for regional agricultural production and hydroelectric power stations (Sarmett & Faraji 1991). Rainforests on isolated mountains, like on Mt. Kilimanjaro, are surrounded by semi-arid savanna plains. These tend to accumulate salt crusts at the soil surface and are at the same time strongly affected by wind erosion (Prospero 1999). Therefore, deposition of salts on the canopy of East African montane rain forests is potentially higher compared to montane rain forests growing in more humid regions, which potentially affects the whole nutrient cycle of these ecosystems.

Data on the nutrient status of montane rain forests in East Africa are extremely scarce. Above- and belowground biomass, litterfall, rainfall and soil properties in natural forests and forest plantations on Mt. Meru and in the Usambara Mts., Tanzania, were studied by Lundgren (1978) and Lundgren & Lundgren (1979).

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On Mt. Kilimanjaro, possible effects of the conversion of natural forests to forest plantations on major soil properties and changes in the run-off regime have so far only been analysed in the cultivated zone below the montane rain forests (Iseki *et al.* 1981, Maro *et al.* 1991, Mizota *et al.* 1988, Sarmett & Faraji 1991).

In our study, we wanted to investigate whether different aspects of the biogeochemistry of East African montane rain forests differ from montane rain forests elsewhere. In order to explore this question, a mature montane rain forest on the south-western slopes of Mt. Kilimanjaro, Tanzania was chosen as an example. In addition to concentrations and fluxes of main nutrients in rainfall, throughfall and litterfall, we analysed nutrient concentrations in the forest floor percolate, the soil solution and stream water. For our analysis, we were particularly interested in the following three questions:

(1) Due to the isolation of the humid afrotropical montane rain forests in a salt-affected semi-arid savanna environment, the forest ecosystems potentially experience high intakes of nutrients via wet and dry deposition from the surrounding savanna. Is this effect visible in nutrient fluxes via rainfall and throughfall?
(2) Are the assumed high nutrient inputs reflected in high nutrient concentrations in below-ground seepage water, or are nutrients widely retained within the forest ecosystem?
(3) N or P might be limiting factors in the tropical montane rain forest of Mt. Kilimanjaro due to low mineralization rates and a high P fixation capacity of volcanic soils. Is this evident from litter analyses?

METHODS

Study area

The study was conducted on the humid south-western slopes of Mt. Kilimanjaro above Machame village. At an altitudinal range between 2250 and 2350 m, four plots of old-growth forest with intact closed canopy were selected (3°8′S, 37°14′E).

According to Hemp (2002), the mature forest in the study area can be classified as middle montane *Ocotea–Podocarpus* forest dominated by *Ocotea usambarensis* Engl. trees in association with *Podocarpus latifolius* R. Br. Similarly, Lovett & Urono (1994) classified the forest at Mt. Kilimanjaro between 1600 and 2700 m as montane forest, and the area above 2400–2500 m as upper montane forest. The canopy reaches heights of 40 m, and the forest is characterized by a high density of epiphytes (Hemp *et al.* 1999), with lower portions of tree stems usually completely coated by an epiphytic layer. This layer mainly consists of bryophytes and reaches a thickness of more than 10 cm. A large number of pteridophytes are also contained within the epiphytic layers. The hydrological importance of the diversity and total biomass of lower plants in the forest of Mt. Kilimanjaro was emphasized by Pócs (1991). Lists of vascular plant species on the plots are presented in Axmacher (2003).

The Kilimanjaro region experiences a bimodal rainfall distribution with rainy seasons lasting from March to June and from November to December. For the most humid southern slopes of the mountain at 2200 m, Røhr & Killingtveit (2003) reported a rainfall maximum of more than 3500 mm. Temperature measurements carried out in the study area on 50 days from May to October and hence covering both parts of the main rainy season and the long dry season revealed a median daily minimum temperature of 8.7 °C and a maximum of 14.8 °C. The soils in the study area have developed in volcanic ash layers of different age deposited on lavas of the Lent Group (phonolites and trachyandesites; Downie & Wilkinson 1972).

Study design

The study was conducted on four plots of 400 m^2 each. The minimum distance between neighbouring plots was 130 m, the maximum distance 340 m. In order to avoid a strong influence of erosion, surface run-off and subsurface lateral flows, all plots had an inclination of less than 10°. A soil profile was established in the vicinity of each plot to a maximum depth of 2.3 m in order to assess main soil properties. Samples were taken by horizon from three sides of the pit walls for laboratory analyses. Homogeneity of soils on the plots was verified by soil coring. Litter was collected from the organic soil layers separately for the L, Oi and Oa horizons at five locations per plot.

For throughfall measurement, all plots were equipped with 8–10 randomly distributed collectors consisting of a sharp-rimmed funnel (115-mm diameter) and a 2-l collecting bottle (polyethylene). The lower 100 mm of the collectors were buried in the ground so that the funnel rim was about 350 mm above the ground. The funnel outlet was covered by a 1-mm plastic mesh to avoid contamination of the samples by litter, and a table-tennis ball was placed in the funnel to reduce evaporation. If necessary, the funnel was cleaned after each sampling, whereas all collecting bottles were cleaned at least twice a year using a brush and deionized water. In a nearby forest gap, five raincatchers of similar construction were installed 1.5 m above the ground for rainfall sampling.

Four free-draining litter percolate collectors were installed below the dense root mat in the Oa horizon of the litter layer at each plot. These consisted of square plastic boxes with a side length of 285 mm and a height of 80 mm. Each box was covered with a 1-mm mesh net and

connected via a silicon tube to a polyethylene sampling bottle. Suction cups (SKL100, ceramic cup K100, UMS, Munich) for soil water extraction were installed at soil depths of 0.15, 0.30 and 1.00 m in three replicates per plot. Cups from different depths were grouped in a triangle with 1 m side length, with three triangles situated in a larger triangle with a distance of 5 m to a pump (Vacuum case VK-3, UMS, Munich) located at the plot centre. Suction cups were installed in holes created by a soil corer with a similar diameter as the suction cups. As the hole diameter increased by several mm at the uppermost part during the extraction of the corer, the immediate surroundings of the suction cups were filled with suspended soil material of the corresponding soil horizon to prevent preferential flow along the sampler tube and to ensure direct contact with the soil. The shaft was further sealed with a silicon ring (0.1-m diameter) at the soil surface. One day before sampling, the pumps were started to create a constant suction of 400 hPa for 24 h. On each plot, samples of equal soil depth were combined in one Duran glass bottle. Stream water samples were collected regularly using polyethylene bottles submersed in a small catchment at 2220 m elevation, some 400 m away from the study plots in mature forest.

Square litter collectors with 0.5 m side length covered with a polyethylene net (1-mm mesh) were placed horizontally 0.25 m above the ground on three plots in two replicates each in order to estimate litterfall.

Sampling procedure and sample treatment

All samples collected during the first 2 mo were discarded to avoid effects caused by the installation of the equipment. Starting from May 2000, water samples from raincatchers, throughfall gauges, litter percolate collectors and suction cups were sampled twice a week (alternating every 3 and 4 d). Installation of the litter percolate collectors was only completed in October 2000, so that the respective data are lacking for the first 5 mo. Whilst water volumes were reported separately for each rain and litter percolate collector, volume-weighted composite samples representing the whole plot were taken in the field. Later on, water samples from individual sampling dates were combined to composite samples of 14-d periods and stored frozen. Samples of rain and litter percolate were mixed volume-weighted, while equal portions were used for the soil solution samples as no reliable information about the below-ground water fluxes was available. On three sampling occasions, samples had to be excluded from mixed samples as either data on volume or samples were missing. Suction cups extracted soil water regularly except for dry periods mainly in September and October. Whenever no soil solution was available for individual times and soil depths, mixed samples were made of the remaining samples of the 14-d period. From May 2001 onwards, sampling frequency was reduced to weekly collections.

Litterfall samples were taken on a monthly basis starting from November 2000. Litter samples were also combined for each plot and stored after air-drying.

Chemical analyses

Analyses of the mineral soil were carried out on air-dried samples (40 °C) of the fraction < 2 mm. pH was determined using H_2O and 0.01 M $CaCl_2$ at a soil : solution ratio of 1 (m) : 2.5 (v) with a standard combined electrode with integrated temperature probe (WTW SenTix 41 pH 330). Total carbon (C_t) and nitrogen (N_t) contents were analysed on ball-milled samples using a total element analyser (Elementar Vario EL). Exchangeable cations (K, Ca, Mg, Na, Al) were extracted by a 0.5 M NH_4Cl solution (Trüby & Aldinger 1989) and measured by atomic absorption (Varian SpectrAA 400). The ECEC was calculated as the sum of the exchangeable base cations and exchangeable Al. Dissolution of Al was tested in a 0.2 M oxalate solution at pH 3 (Schwertmann 1964) to get Al bound in metal-humus complexes, allophane, imogolite and ferrihydrite (Al_o). Al in extracts was measured by atomic absorption. Particle size distributions were analysed using field moist samples, which were stored at temperatures around 4 °C. Soil samples were dispersed by shaking 5 g of soil in 20 ml 0.1 M $Na_4P_2O_7$ solution added to 500 ml water overnight. Sand-size particles were removed by sieving, silt and clay contents were determined using the pipette method (Gee & Bauder 1986). The P retention capacity was measured in only one soil profile following the method of Burt (1996).

Rainfall, throughfall and litter percolate solutions were filtered through ash-free filter paper with a pore size < 2 μm prior to analyses (Schleicher & Schuell, blue band 589^3). Therefore, overall solute concentrations were probably slightly overestimated since not only dissolved elements (< 0.45 μm), but also elements in particles < 2 μm were involved in chemical analyses. Litter samples from the soil litter layer as well as from the litter collectors were oven-dried in the laboratory (70 °C), ground, and digested with concentrated HNO_3 under pressure for nutrient analysis (after Heinrichs *et al.* 1986). Determination of total N and S concentrations was conducted on ball-milled samples using a total element analyser (Elementar Vario EL). Flame absorption spectrometry (AAS; Varian SpectrAA 400) was used to measure element concentrations of K, Mg, Ca and Na in water samples and plant extracts. NO_3-N and NH_4-N in rain and soil solution samples were analysed with a Segmented Flow Analyser (SAN plus SYSTEM, SKALAR), as were the P concentrations in plant extracts. For one

Table 1. Selected soil properties (mean ± SE, n = 4, texture: n = 3) of four soil profiles in the montane rain forest on Mt. Kilimanjaro at three different soil depths (0.1–0.2, 0.25–0.35 and 0.95–1.05 m, representing depths of suction for soil water sampling) and in the Oa organic soil layer.

			Soil depth (m)		
		Oa	0.10–0.20	0.25–0.35	0.95–1.05
pH (H_2O)		3.8 ± 0.3	4.0 ± 0.1	4.6 ± 0.1	4.7 ± 0.1
pH (KCl)		3.1 ± 0.2	3.3 ± 0.1	4.3 ± 0.1	5.0 ± 0.1
C	(g kg^{-1})	369 ± 19	188 ± 28	117 ± 12	70 ± 7
N	(g kg^{-1})	26 ± 1	11 ± 2	6.2 ± 0.4	3.0 ± 0.5
Clay	(g kg^{-1})		747 ± 71	634 ± 126	494 ± 70
Alo*	(g kg^{-1})		9.3 ± 2.2	37.4 ± 5.5	57.5 ± 6.8
ECEC*	(cmol (+) kg^{-1})	16 ± 1.7	3.0 ± 0.4	0.7 ± 0.9	0.6 ± 0.2
K	(cmol (+) kg^{-1})	0.78 ± 0.15	0.23 ± 0.04	0.06 ± 0.01	0.06 ± 0.02
Mg	(cmol (+) kg^{-1})	2.58 ± 0.65	0.24 ± 0.03	0.03 ± 0.01	0.01 ± 0.01
Ca	(cmol (+) kg^{-1})	4.96 ± 1.51	0.40 ± 0.04	0.10 ± 0.02	0.19 ± 0.17
Na	(cmol (+) kg^{-1})	0.28 ± 0.06	0.09 ± 0.02	0.05 ± 0.02	0.03 ± 0.01
Al	(cmol (+) kg^{-1})	6.15 ± 0.81	1.13 ± 0.18	0.38 ± 0.03	0.32 ± 0.07

*Al_o: acid oxalate extractable Al; ECEC: effective cation exchange capacity.

year, Cl concentrations were analysed in rainfall samples using an ion chromatograph.

Data analysis and statistical evaluation

Plots were monitored for a total of 2 y from June 2000 to June 2002. Since no reliable data on soil water fluxes were available, the median nutrient concentration of 14-d samples was used as annual mean for the soil solution, while volume-weighted means were calculated for nutrient concentrations in rainfall and throughfall. The annual mean for litter percolate was volume-weighted according to throughfall fluxes, assuming that water uptake by roots was comparable among sites. Nutrient fluxes in rainfall and throughfall were calculated by multiplying recorded water fluxes with the respective element concentrations. Net throughfall fluxes were determined as the difference between throughfall and rainfall fluxes. Nutrient fluxes for litter percolate and soil solution could not be determined since no reliable information on water fluxes was available because of a lack of climate and runoff data.

Conservative estimates of stemflow fluxes from measurements on one *Podocarpus latifolius* and three *Ocotea usambarensis* trees over 1 y proved that it contributes less than 1% to rainfall amounts. Tree stems were surrounded by a pipeline of foam rubber, which was connected to 50-l plastic containers via plastic tubes. Median concentrations for K, Mg, Ca and Na were 8.2, 0.46, 1.74 and 0.63 mg l^{-1} respectively for *P. latifolius* and 4.48 ± 0.78, 0.17 ± 0.04, 0.37 ± 0.05 and 0.86 ± 0.10 mg l^{-1} respectively for *O. usambarensis*. Thus, although enriched in nutrients, stemflow was not considered to be of great relevance for total nutrient fluxes in the forest. Since there were continual problems with blockage of the collection channel around the tree and a lot of water bypassed the channel by dropping from the thick moss layers above the collector, stemflow fluxes were not always accurately determined and measurements were abandoned in the second study year. Hence, results of nutrients fluxes in stemflow are not considered further in this paper.

Statistical analyses were conducted using STATISTICA 5.0 (Statsoft, Inc., Tulsa, OK). Correlation analyses were done as Pearson Product-Moment Correlations.

RESULTS

Soil properties

The soils in the study area were classified as Placaquands and Fulvudands (Soil Survey Staff 2003, http://soils.usda.gov/technical/classification/taxkeys/). Overall soils were characterized by low pH values, high concentrations of C and N and high clay contents with huge amounts of non-crystalline Al oxides and hydroxides (Table 1). Mean carbon and nitrogen stocks were high and accounted for 164 and 10 t ha^{-1} respectively in the organic soil horizons and for 565 and 26 t ha^{-1} in the mineral soil. The P retention capacity was measured in only one soil profile where it varied between 96 and 100%. Due to low pH values, corresponding low effective cation exchange capacity and base saturation, periodic water stagnation and a high P fixation capacity of the soils, the available pool for most nutrients was relatively poor. Highest amounts of exchangeable nutrient cations were detected in the organic soil horizons (Table 1). Total concentrations of nutrients in the Oi litter layer were 16.2 g kg^{-1} for N, 1.1 g kg^{-1} for P, 1.5 g kg^{-1} for K, 1.9 g kg^{-1} for Mg, 12.6 g kg^{-1} for Ca and 0.36 g kg^{-1} for Na. The C/N ratio was 30.

Rainfall and throughfall amounts

Between June 2000 and June 2002, rainfall amounts were 2480 mm in the first and 1960 mm in the second,

Table 2. Annual means of nutrient concentrations (mg l^{-1}) in different ecosystem compartments of a montane rain forest at Mt. Kilimanjaro (± SE, n = 4). For rainwater and throughfall, volume-weighted mean concentrations for each year (1 and 2 from June 2000 until May 2002) were calculated, while the median concentration was used for litter leachates, soil solution and stream water.

	Year	K	Mg	Ca	Na	NH_4-N	NO_3-N
Rainfall	1	0.30	0.04	0.09	0.30	0.16	0.13
	2	0.50	0.05	0.15	0.36	0.16	0.17
Throughfall	1	1.50 ± 0.20	0.08 ± 0.02	0.13 ± 0.01	0.53 ± 0.09	0.19 ± 0.02	0.05 ± 0.01
	2	2.97 ± 0.15	0.16 ± 0.03	0.34 ± 0.05	0.90 ± 0.11	0.19 ± 0.01	0.05 ± 0.01
Litter percolate	1	–	–	–	–	–	–
	2	1.63 ± 0.36	0.32 ± 0.06	0.89 ± 0.18	0.87 ± 0.04	0.30 ± 0.04	0.89 ± 0.13
Soil solution							
0.15 m	1	0.15 ± 0.04	0.15 ± 0.06	0.27 ± 0.10	0.42 ± 0.07	0.03 ± 0.00	1.48 ± 0.34
	2	0.19 ± 0.04	0.11 ± 0.02	0.25 ± 0.06	0.41 ± 0.08	0.04 ± 0.00	1.54 ± 0.55
0.30 m	1	0.16 ± 0.04	0.14 ± 0.06	0.25 ± 0.08	0.35 ± 0.07	0.02 ± 0.00	1.42 ± 0.13
	2	0.18 ± 0.03	0.15 ± 0.06	0.26 ± 0.08	0.38 ± 0.09	0.04 ± 0.00	1.41 ± 0.31
1.00 m	1	0.15 ± 0.02	0.13 ± 0.02	0.21 ± 0.06	0.31 ± 0.03	0.03 ± 0.00	1.11 ± 0.12
	2	0.21 ± 0.04	0.13 ± 0.03	0.27 ± 0.08	0.40 ± 0.05	0.04 ± 0.00	1.07 ± 0.17
Stream	1	0.70	0.07	0.14	1.18	0.05	0.60
	2	0.84	0.08	0.16	1.25	0.06	0.56

Table 3. Mean nutrient fluxes (kg ha^{-1} y^{-1}) via rainfall and throughfall in a montane rain forest on Mt. Kilimanjaro, Tanzania. Net fluxes were calculated as difference between throughfall and rainfall fluxes (± SE, n = 4).

	Year	K	Mg	Ca	Na	NH_4-N	NO_3-N
Rainfall	1	6.9	0.9	2.1	6.7	3.6	3.0
	2	8.0	0.8	2.4	5.7	2.5	2.7
Throughfall	1	32.2 ± 4.0	1.8 ± 0.4	2.8 ± 0.3	11.5 ± 2.0	4.2 ± 0.4	1.0 ± 0.3
	2	37.2 ± 1.8	2.0 ± 0.3	4.2 ± 0.6	11.2 ± 1.2	2.4 ± 0.1	0.7 ± 0.2
Net throughfall	1	25.3	0.9	0.7	4.8	0.6	−2
	2	29.2	1.2	1.8	5.5	−0.1	−2

drier year. Annual throughfall amounts reached 2040 and 1370 mm, respectively, resulting in a total rainfall interception (rainfall-throughfall) of 18% in the first and 30% in the second year. Standard deviations for collected water amounts in individual throughfall collectors within one plot were usually in the range 10–20% of the mean. This error was not included in the standard errors presented for the means among sites in Tables 2 and 3.

Water chemistry in ecosystem compartments

Concentrations and fluxes of nutrients in rainfall were highest for K and decreased in the order K > Na > NH_4-N, NO_3-N > Ca > Mg (Tables 2 and 3). Annual mean Cl concentrations in rainfall were 0.86 mg l^{-1}. Annual mean concentrations of all base cations were higher in throughfall than in rainfall, except for NO_3-N, where throughfall concentrations were lower. Thus, although total water fluxes declined, net fluxes of all basic cations were positive, indicating a net enrichment of these ions during their passage through the canopy (27 kg ha^{-1} y^{-1} K, 1.1 kg ha^{-1} y^{-1} Mg, 1.3 kg ha^{-1} y^{-1} Ca, 5.2 kg ha^{-1} y^{-1} Na). The highest enrichment rates (throughfall fluxes divided by rainfall fluxes) were obtained for K (5), followed by Mg (2.4) > Na (1.8) > Ca (1.6). NH_4-N showed net fluxes close to zero (0.3 kg ha^{-1} y^{-1}) while negative net fluxes of NO_3-N (–2 kg ha^{-1} y^{-1}) indicated a net retention in the forest canopy for both years.

In litter percolate, concentrations exceeded throughfall values for all nutrients except K and Na (Figure 1, Table 2). The greatest increase was observed for NO_3-N (0.1 mg l^{-1} in throughfall and 0.9 mg l^{-1} in litter percolate). In the soil solution, all concentrations with the exception of NO_3-N were distinctly lower than in the litter percolate (Figure 1, Table 2). Overall concentrations in the soil solution decreased in the order NO_3-N > Na > Ca > K, Mg > NH_4-N. Cation concentrations in the soil solution were generally very low (K: 0.15–0.21 mg l^{-1}, Mg: 0.11–0.15 mg l^{-1}, Ca: 0.21–0.27 mg l^{-1}, Na: 0.31–0.42 mg l^{-1}, NH_4-N: 0.02–0.04 mg l^{-1} as minimum and maximum annual means at all three soil depths). With increasing soil depth NO_3-N concentrations decreased, whereas no general trend occurred for cations. NO_3-N, Ca and Mg concentrations were lower in the stream water than in the soil solution, while Na, K and NH_4-N concentrations were higher (Table 2).

Correlation analyses of throughfall fluxes

A positive correlation between throughfall amount and nutrient fluxes was observed for all nutrients. The closest

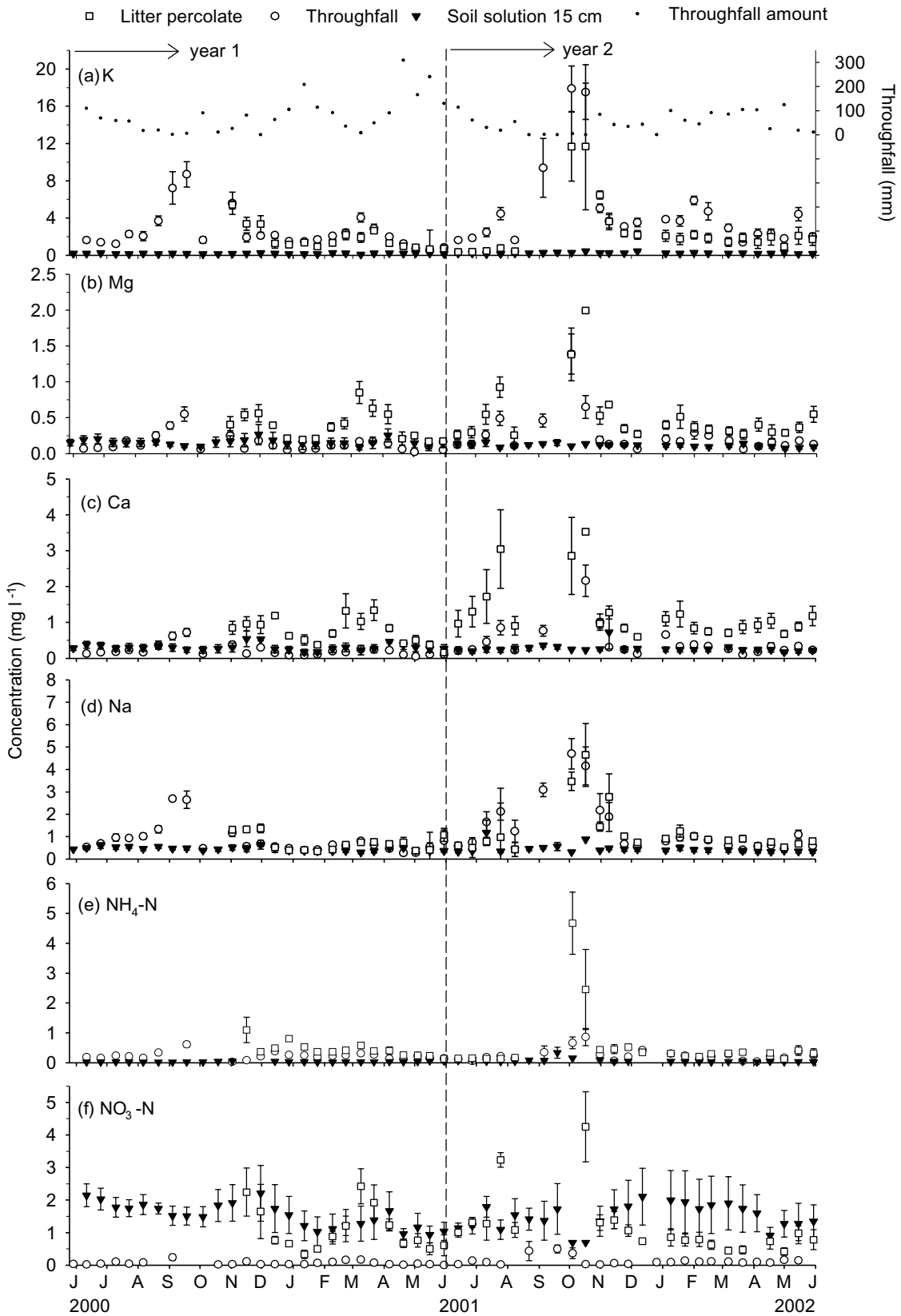

Figure 1. Seasonal variation of concentrations in throughfall, litter percolate and soil solution in a montane rain forest at Mt. Kilimanjaro for 2 consecutive y from June 2000 to May 2002 (± SE, n = 4).

Table 4. Results of Pearson Product-Moment correlations between net throughfall fluxes and rainfall amounts at the left side and net throughfall fluxes per mm rain and rainfall concentrations at the right side. Correlation coefficients are given together with the level of significance (n = 17–23).

	Correlation coefficients			
	Net throughfall fluxes vs. rainfall amounts		Net throughfall flux per mm rain vs. rainfall concentrations	
	Year 1	Year 2	Year 1	Year 2
K	0.77****	0.62****	0.31 n.s.	−0.17 n.s.
Mg	0.72****	0.60***	−0.07 n.s.	−0.49*
Ca	0.63****	0.36 n.s.	−0.81****	−0.73****
Na	0.65****	0.37 n.s.	−0.69****	−0.39 n.s.
NH_4-N	0.37 n.s.	0.19 n.s.	−0.62****	−0.76****
NO_3-N	0.11 n.s.	−0.05 n.s.	−0.95****	−0.97****

**** $P < 0.001$, *** $P < 0.005$, ** $P < 0.01$, * $P < 0.05$, n.s., not significant.

correlations for both years were obtained for NH_4-N ($r = 0.84$, $P < 0.001$), the weakest for Ca ($r = 0.45$, $P < 0.001$). Analysis of net throughfall fluxes gives information on the origin and fate of nutrient ions in the forest canopy. Whilst net fluxes of basic cations were correlated with rainfall amounts in the first year, flux of neither N form was (Table 4). In the second year, correlations for basic cations were weaker and only significant for K and Mg. Besides rainfall amounts, the net gain and loss of nutrients in throughfall upon passing the canopy may also be related to the concentrations of individual nutrients in rainfall. On Mt. Kilimanjaro, no significant correlations between concentrations in rainfall and net fluxes per mm rainfall were obtained for K and Mg, but for NO_3-N, these correlations were very strong ($r = -0.95$, $P < 0.001$). Ca, Na and NH_4-N showed intermediate trends (Table 4).

Nutrient input to the forest floor via fine litterfall

The total amount of fine litterfall was 7.4 t ha^{-1} y^{-1}, and it comprised 68% leaves, 10% twigs < 2 mm diameter, 4% mosses and lichens, and a huge part of 18% consisting of unidentified material such as flowers, other reproductive parts and small leaf parts. Total annual nutrient fluxes of N, P, K, Mg, Ca, Na and S via fine litter were 119, 6, 25, 16, 69, 4 and 12 kg ha^{-1} y^{-1} respectively. The seasonal pattern of nutrient fluxes followed the monthly amounts of fine litterfall, with the highest inputs between the end of the dry season and the beginning of the minor rains in December and January (Figure 2). While annual nutrient fluxes via fine litter exceeded the fluxes in throughfall for Ca and Mg, the opposite held true for K and Na (Tables 3 and 5).

Nutrient concentrations in fine litter samples did not correlate with the corresponding amount of litterfall. Mean concentrations of base cations in fine litter were higher than in the litter layer, while there were no differences in the case of N, and P concentrations were even higher in the litter layer (Table 5).

DISCUSSION

Rainwater chemistry on Mt. Kilimanjaro

Possible sources for solutes in rainfall on Mt. Kilimanjaro are volcanic emissions, oceanic sprays or terrestrial dust. Terrestrial dust sources include ashes from burning of organic material (forest fires, burning of harvest residues, house fires) and eroded soil particles. Most natural forest and savanna fires occur at the end of the dry seasons, which is also the time when vegetation residues are burnt on the fields below the forest belt, leaving them unprotected against wind erosion. Different from many other tropical montane rain forests of the more humid tropics, Mt. Kilimanjaro is surrounded by a semi-arid environment where salt accumulation frequently occurs at ephemeral ponds, the edges of salt lakes and on irrigated fields (Wakatsuki & Mizota 1992). As shown by Prospero (1999), the African savanna plains have a high wind-erosion potential, and dust is often transported over great distances. Thus, additions of salt-rich particles to dry deposition seem likely on Mt. Kilimanjaro. Mizota *et al.* (1988) detected an addition of soil particles from the savanna plains to a soil profile in Machame (a village below the study area) at 1600 m. Their results were supported by the frequent occurrence of dust storms and vortices of different magnitudes in the savanna, especially during the dry season.

Thus, it might be assumed that comparatively high amounts of salts may enter the studied forest at Mt. Kilimanjaro via rainfall. But a comparison with a

Table 5. Volume weighted mean nutrient concentrations in the Oi litter layer and in fine litterfall collected in a montane rain forest at Mt. Kilimanjaro and annual nutrient fluxes via fine litterfall (± SE, n = 3).

	K	Mg	Ca	Na	N	P	S
Oi-layer							
(g kg^{-1})	1.54 ± 0.10	1.92 ± 0.05	7.93 ± 1.37	0.36 ± 0.06	16 ± 0.2	1.09 ± 0.15	1.82 ± 0.03
Fine litter							
(g kg^{-1})	3.45 ± 0.23	2.17 ± 0.11	9.42 ± 0.95	0.49 ± 0.05	16 ± 1.1	0.82 ± 0.08	1.69 ± 0.09
(kg ha^{-1} y^{-1})	25.3 ± 3.6	15.8 ± 1.4	68.5 ± 9.1	3.6 ± 0.7	119 ± 13	5.9 ± 0.5	12.4 ± 1.5

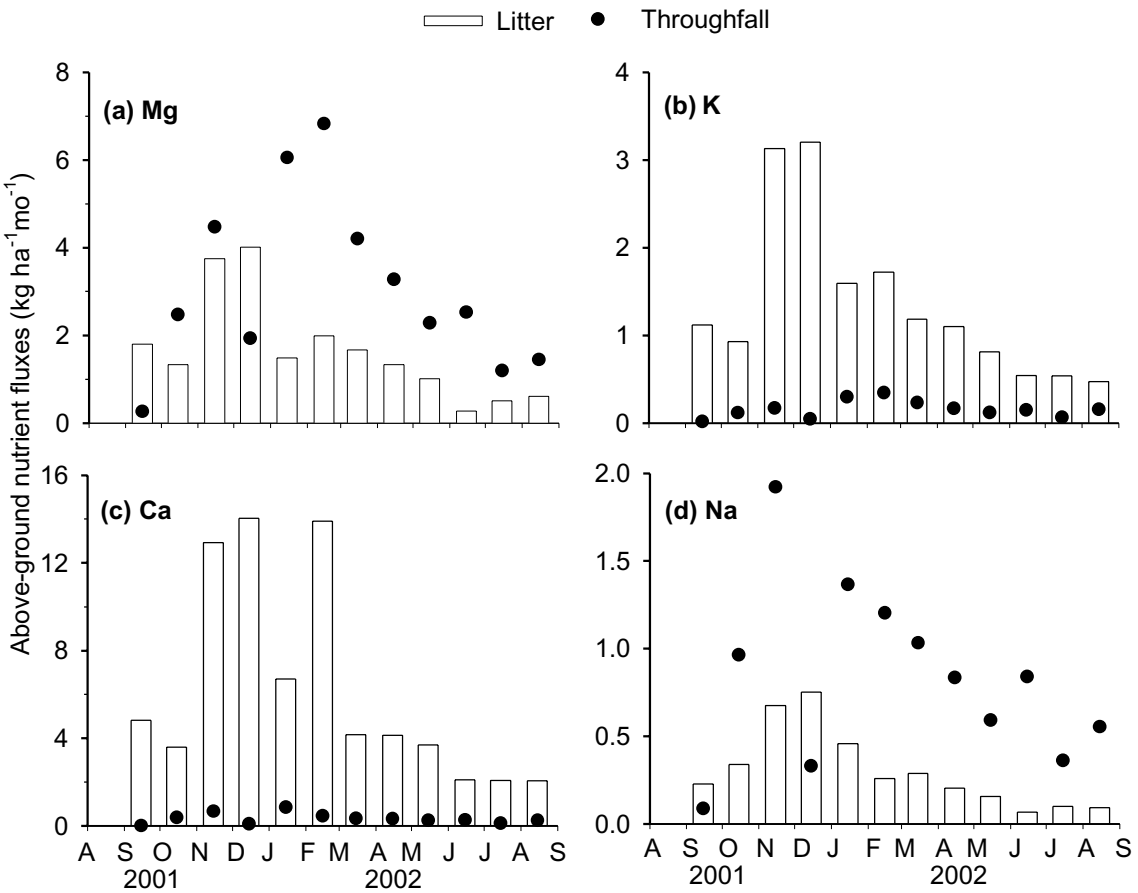

Figure 2. Comparison of the seasonal distribution of monthly fluxes in fine litterfall and throughfall in a montane rain forest at Mt. Kilimanjaro from September 2001 to August 2002.

number of other montane rain forests summarized in Table 6 reveals in contrast that fluxes for Ca and Mg were quite low at Mt. Kilimanjaro. While Ca exhibited overall lowest values (2 kg ha^{-1} y^{-1} compared with 4–47 kg ha^{-1} y^{-1} at other sites), only an upper montane rain forest (UMRF) in Costa Rica revealed lower Mg fluxes than the study sites on Mt. Kilimanjaro, and also Na fluxes were at the lower end of fluxes encountered in tropical montane rain forests. N and K fluxes on the other hand were within the range typically observed in these forests.

One explanation for the low input of salts via rainfall is a strong decrease in dry deposition with increasing elevation on Mt. Kilimanjaro. At about 1500 m, the vertical difference between the savanna plains (around 800 m) and the study sites (2250 m) is large. As the area below the forest belt at the southern slope of Mt. Kilimanjaro is managed as agroforest, the soil surface is permanently covered and hence protected against erosion. Similarly, ion additions from marine sources seem to be low, which is probably due to the distance to the coast (around 200 km). For the detection of possible impacts of sea water on the nutrient composition in rainfall, an 'excess amounts' approach suggested by Eriksson (1960) has often been used in the literature (Bruijnzeel 1989, Waterloo *et al.* 1997, Wilcke *et al.* 2001). Applied to the present study, this method reveals that Na and Mg concentrations in rainfall did not match the Cl content during both the wet and dry seasons (although differences were smaller during the wet season). Bruijnzeel (1989) also observed a surplus of Cl over expected values of Na in rainwater of Java and ascribed this to additional non-maritime inputs by volcanic activity. This might also have been the case on Mt. Kilimanjaro, which is part of the volcanically active East African rift valley. For K and Ca on the other hand, concentrations by far exceeded supposed maritime concentrations, thus indicating a high contribution of dust to total fluxes (at least 80% for Ca and 95% for K). As in the present study a coarser water filter was used than in many other studies (< 2 μm instead of 0.45 μm), solute concentrations are rather over- than underestimated so that it can be concluded that cation inputs in the forest belt on the south-western slopes of the mountain are unexpectedly low.

Table 6. Nutrient fluxes in rainfall and throughfall of different tropical montane rain-forest ecosystems. For details on forest types, elevation, annual rainfall amounts and soil types, see footnotes.

	Rainfall flux (kg ha^{-1} y^{-1})						Throughfall flux (kg ha^{-1} y^{-1})					
	K	Mg	Ca	Na	NH_4-N	NO_3-N	K	Mg	Ca	Na	NH_4-N	NO_3-N
Ecuador[1]	3.7	1.2	3.9	19	2.6	3.0	76–166	7–21	15–28	10–22	3–7	5.9–8.6
Venezuela[2]	2.6	5.2	5.6	3.3			70	3.3	6.9	4.4		
Malaysia[3]	4	1.2	4		2.5	5	23	7	12		9	10
Puerto Rico[4]	4.7	8.5	13	63	0.7	1.2	52	13	23	81	3.3	0.2
Costa Rica[5]	5.8	0.7	4.0	3.0	1.4	1.7	62	5.6	15	3.2	3.4	0.6
Jamaica 1[6]	8.3	2.0	9.0	21	3.9	1.7	44	5.9	13	30	4.8	0.7
Jamaica 2[7]	8.3	2.0	9.0	21	3.9	1.7	33	6.4	12	23	3.9	0.7
Tanzania[8]	6.9–8.0	0.8–0.9	2.1–2.4	5.7–6.7	2.5–3.6	2.2–3.0	32–37	2.0	3–4	11	2–4	0.7–1.0
Published range in Hafkenscheid (2000)												
LMRF n = 5	2.6–14	1.3–5.2	3.6–28	3.3–64	1.7–18	1.7	63–95	3.3–12	6.9–35	4.4–131	1.3–22	0.6
Intermediate												
UMRF n = 3	6.9–8.3	2.0–5.0	5.5–9.0	16–21	3.9–11	1.7	33–56	5.9–9.8	11–19	14–30	4.8–12	0.7
Stunted												
UMRF n = 3	7.1–27	2.0–30	5.5–47	20–247	3.9–6.9	1.7–5.3	24–77	6.4–91	12–109	23–692	3.9–5.1	0.7–15

[1] Wilcke *et al.* (2002): Ecuador, 1900–2010 m, LMRF, 2190 mm, Dystrudepts, Eutrudepts.
[2] Steinhardt (1979): Venezuela, 2300 m, LMRF, 1500 mm, Humitropepts.
[3] Bruijnzeel *et al.* (1993): Malaysia, 870 m, LMRF, 2130 mm, Dystropepts, approximation from 6 wk.
[4] McDowell (1998): Puerto Rico, 390 m, LMRF, 3500 mm, Ultisols.
[5] Hölscher *et al.* (2003): Costa Rica, 2900 m, UMRF, 2830 mm, Humic Andosols.
[6] Hafkenscheid (2000): Jamaica, 1800 m, intermediate UMRF, 2310 mm, Dystric Cambisols.
[7] Hafkenscheid (2000): Jamaica, 1800 m, stunted UMRF, 2180 mm, Folic Histosols.
[8] This study: Tanzania, 2300 m, TMF, 2220 mm, Endoaquands, Fulvaquands.
LMRF: lower montane rain forest, UMRF: upper montane rain forest, TMF: tropical montane rain forest.

Throughfall chemistry

The composition of rainfall is usually altered during the passage through the forest canopy by processes like wash-off of wet- and dry-deposited material, passive leaching from plant tissues, ion exchange or adsorption. Further, leaching from or ion exchange in canopy humus can add to throughfall fluxes (Nadkarni *et al.* 2002).

A high accumulation of dust particles on plant tissues was expected during the dry season on Mt. Kilimanjaro, which should lead to increased throughfall concentrations and fluxes following wash-off and dilution. But similar to rainfall fluxes, throughfall fluxes of base cations were unexpectedly low on Mt. Kilimanjaro as compared to other tropical montane rain-forest sites (Table 6). Throughfall fluxes for Mg and Ca were the lowest values observed and K fluxes were also at the lower end. A comparison of the enrichment factors (throughfall fluxes divided by rainfall fluxes) reveals that with a value of 5, the enrichment factor for K was also low on Mt. Kilimanjaro compared with lower montane rain forest (LMRF) elsewhere (5–45, values from Hafkenscheid (2000) and calculated from Table 6) and was closer to values of UMRF (3–11). At one montane rain-forest site in Venezuela (Steinhardt 1979), a net absorption of Mg was observed, while an enrichment between 1.5 and 17.5 was measured for other LMRF. With 2.4, the enrichment factor for Mg was again at the lower end at Mt. Kilimanjaro. Enrichment factors were also low for Ca (1.6) but within the range at other sites (1.2–7.2). Highest overall values were always observed at a LMRF in Ecuador (Wilcke *et al.* 2001), which had a distinctly lower tree height than the forest on Mt. Kilimanjaro and grew on acidic soils developed on Palaeozoic schists and sandstones. Otherwise, rainfall regime and altitude were comparable to Mt. Kilimanjaro. Unfortunately, Wilcke *et al.* (2001) present no explanation for their high enrichment factors, which might partly be related to fires and volcanic activity in the region. On Mt. Kilimanjaro, no fires occurred in the vicinity of the plots during the study period. That might be different during dry El Niño years, when forest fires are more frequent (Hemp & Beck 2001). Overall it seems that similar to low rainfall fluxes, low throughfall fluxes of base cations result from the great altitudinal and vertical distance between various dust sources and the studied forest sites during most years, leading to low nutrient additions via dry deposition.

The contribution of internal and external sources to ion enrichment in rainfall during the passage through the forest canopy can only indirectly be assessed from the available data. Ion additions to throughfall water by dry deposition are not expected to depend on rainfall amounts as long as the rainfall amount is high enough to remove all the deposited material. Thus, the dependency of net throughfall fluxes of base cations on rainfall amounts observed in our study indicates that passive leaching processes from leaves or ion exchange do contribute to throughfall fluxes on Mt. Kilimanjaro. The

relation between net throughfall fluxes of Ca and Ca concentrations in rainfall further hints that ion exchange is involved in Ca enrichment on the passage of rain through the forest canopies. In a lowland rain forest in the Amazon Basin with low nutrient fluxes in rainfall, Filoso *et al.* (1999) observed high contributions of canopy leaching to net throughfall fluxes of Mg and Ca.

Nitrogen fluxes in throughfall were low but overall within the range of other tropical montane forest sites (Table 6). In the majority of forests presented in Table 6, NO_3-N was not leached, but absorbed in the forest canopies. The absorption of NO_3-N by montane forest canopies has usually been ascribed to the epiphytic coverage (Clark *et al.* 1998, Liu *et al.* 2002). Unlike the base cations, net throughfall fluxes of NO_3-N and NH_4-N did not show a dependency on water fluxes. Negative correlations with rainfall concentrations indicate that ion uptake or release depends on N concentrations. High N concentrations in rainfall result in a net absorption of N in the canopy, while lower concentrations lead to net leaching. Veneklaas (1990) made similar observations in an upper montane cloud forest in Colombia.

Table 7. Nutrient concentrations (mg l^{-1}) in litter percolate of different tropical montane rain-forest ecosystems. For details on forest types, elevation, annual rainfall amounts and soil types, see footnotes.

	K	Mg	Ca	Na	NH_4-N	NO_3-N
Ecuador[1]	0.4–28	1.4–5.0	0.3–8.0	1.4–1.5	0.3–0.7	0.6–5.7
Venezuela[2]	38	2.1	5.1	0.4		4.6^{+}
Malaysia[3]	5.1	2.5	4.6	5.2	1.0	8.4
Malaysia[4]	3.6	2.7	5.7	3.6	1.0	6.5
Jamaica[5]	4.1	1.1	2.5	2.0	0.2	0.2
Jamaica[6]	2.9	0.9	1.7	1.6	0.1	0.0
Tanzania[7]	1.4	0.3	0.8	0.8	0.3	0.9

[1] Wilcke *et al.* (2002): Ecuador, 1900–2010 m, LMRF, 2190 mm, Dystrudepts, Eutrudepts.
[2] Steinhardt (1979): Venezuela, 2300 m, LMRF, 1500 mm, Humitropepts.
[3] Bruijnzeel *et al.* (1993): Malaysia, 680 m, LMRF, 2130 mm, Dystropepts, approximation from 6 wk.
[4] Bruijnzeel *et al.* (1993): Malaysia, 870 m, LMRF, 2130 mm, Dystropepts, approximation from 6 wk.
[5] Hafkenscheid (2000): Jamaica, 1800 m, intermediate UMRF, 2310 mm, Dystric Cambisols.
[6] Hafkenscheid (2000): Jamaica, 1800 m, stunted UMRF, 2180 mm, Folic Histosols.
[7] This study: Tanzania, 2300 m, TMF, 2220 mm, Endoaquands, Fulvaquands.
LMRF: lower montane rain forest, UMRF: upper montane rain forest, TMF: tropical montane rain forest.

Water chemistry in litter percolate and soil solution

Very few studies on nutrient cycling in tropical montane ecosystems include the chemistry of below-ground seepage water. A limitation of the present study and some others for the comparability among different rain-forest sites is that only concentrations, not fluxes, are available due to a lack of climatic and runoff data. The composition of litter percolate was determined with two different approaches in the literature. In Jamaica (Hafkenscheid 2000) and Malaysia (Bruijnzeel *et al.* 1993) litter percolate was collected directly below the leaf-litter-layer (Oi-horizon), thus providing information on the leaching of nutrients from freshly shed litter. In other studies, the focus was more on the input of nutrients from the litter layer into the mineral soil. Thus, litter percolate was collected between the Oa-horizon and the mineral soil in studies in Ecuador (Wilcke *et al.* 2001), Venezuela (Steinhardt 1979) and the present study. Since the composition of seepage water is altered on the passage through different parts of the litter layer by further leaching from organic material or root uptake, the concentrations in litter percolate between the different sites summarized in Table 7 are not fully comparable.

Keeping that problem in mind, the concentrations of nutrients in the litter percolate of the forest on Mt. Kilimanjaro, especially those of basic cations, were low compared with other montane rain-forest sites. Since throughfall amounts are often correlated to the amounts of litter percolate (Wilcke *et al.* 2001), and these were within the range of other forest sites at Mt. Kilimanjaro, it might be assumed that fluxes of K, Ca and Mg in litter percolate were also comparatively low. Among possible reasons are low inputs via throughfall (see section above), a low release from the organic layer or a high nutrient uptake.

A comparison of the nutrient composition of the litter layer reveals that concentrations of K, Mg and Ca were lower in the Oi layer at Mt. Kilimanjaro (1.5, 1.9 and 7.9 g kg^{-1} respectively) compared with the forest in Venezuela (2.1, 2.5 and 10 g kg^{-1}, Steinhardt 1979) and Ecuador (2.6, 3.4 and 10 g kg^{-1}, Wilcke *et al.* 2002). N concentrations exhibited intermediate values in the litter layer (16 g kg^{-1} in the present study versus 11 g kg^{-1} in Venezuela and 17 g kg^{-1} in Ecuador).

On Mt. Kilimanjaro, concentrations of Mg, Ca and NO_3-N in litter percolate were higher overall than in throughfall, indicating that additional ion release in the litter layer exceeded the ion uptake by roots for these ions. On the other hand annual mean K concentrations in litter percolate were lower than in throughfall water. This was unexpected since K is easily leached from freshly fallen litter (Lundgren 1978, Tukey 1970) and should thus be further enriched in the litter percolate. Potential sinks for K are adsorption and exchange processes with soil organic material or ion uptake by roots and mycorrhizas. As organic matter preferentially binds polyvalent cations, the ion exchange sites were dominated by Al, Mg and Ca (Al: 10.45, Ca: 6.08, Mg: 3.15, K: 0.89 and Na 0.33 $cmol_c$ kg^{-1}). Therefore, cation exchange is not likely to be a strong sink for K. This indicates that a large

quantity of K is readily taken up by roots or mycorrhizas in the uppermost litter layers.

A pronounced decrease in ion concentrations from the litter layer to the mineral soil was similarly observed at other sites with nutrient-depleted, weathered soils in the humid tropics (Bruijnzeel *et al.* 1993, Hafkenscheid 2000, Lilienfein *et al.* 2000). Still, solute concentrations obtained by zero-tension litter percolate collectors and suction cups are not totally comparable. Firstly, by using negative pressure, additional solution is extracted that would not be obtained with free draining lysimeters, which can lead to different concentrations depending on the suction applied (Marques *et al.* 1996). Furthermore, collectors for litter percolate accumulated seepage water for the whole period between two sampling days, while suction cups only collected water during one day. Thus, individual peaks of nutrient concentrations during the week might not be registered with the suction cups.

Similar to litter percolate, also concentrations of K, Mg, Ca and Na in the soil solution in 0.2 m soil depth were higher at a tall LMRF in Venezuela (1.4, 0.6, 0.8 and 0.6 mg l^{-1} respectively, Steinhardt 1979) than on Mt. Kilimanjaro (0.2, 0.1–0.2, 0.3, 0.4 mg l^{-1} respectively in 0.15 m soil depth). Similarly, with 0.9–1.0 g kg^{-1} K, 0.5–0.8 g kg^{-1} Mg, 0.5–0.6 g kg^{-1} Ca and 1.7 g kg^{-1} Na, concentrations were also higher at two UMRF of contrasting stature in Jamaica. In the present study, soils are already in an advanced stage of weathering with a low cation exchange capacity and base saturation. This indicates that the stocks of nutrients easily available to plants in the mineral soil as well as its retention capacity for nutrients leached from the organic layer are rather low. The same was true for the other two montane rainforest sites. Thus, plant uptake seems to be more important for the reduction of ion concentrations in the soil solution than the sorption of ions to particles in the mineral soil. Low concentrations of base cations in the soil solution indicate that the overall losses of these ions via leaching will be low at Mt. Kilimanjaro, especially for K. The only exception for the general trend of reduced concentrations in the soil solution as compared to the litter percolate was the concentration of NO_3-N, which increased from litter percolate to the soil solution. This may be related to N mineralization and nitrification of NH_4-N below the litter layer. Since the concentration of base cations in the soil solution was low, Al and H were most likely the cations accompanying NO_3-N for charge compensation.

Nutrients in fine litterfall

Nutrient concentrations in fine litterfall are widely believed to be a suitable indicator for the nutrient status of a forest and the tightness of the nutrient cycle (Vitousek 1984). The concentrations of K, Mg, Ca and Na in litterfall on Mt. Kilimanjaro were within the range observed at other tropical montane rainforests as summarized in Hafkenscheid (2000). Litter P concentrations (0.82 g kg^{-1}) were at the higher end and N concentrations (16.3 g kg^{-1}) were higher than the range of 0.17–0.95 g kg^{-1} P and 6–15 g kg^{-1} N presented in Hafkenscheid (2000) for a number of montane rain forests. On the other hand, litter N, P and S concentrations of a montane rain forest in Ecuador (Wilcke *et al.* 2002) exceeded the values measured on Mt. Kilimanjaro with values between 19–22 g kg^{-1} N, 0.9–1.6 g kg^{-1} P and 2.3–2.4 g kg^{-1} S. In a montane rain forest in the West Usambara Mts., Lundgren (1978) measured similar litter concentrations than the ones obtained on Mt. Kilimanjaro (17.6 g kg^{-1} N, 1.0 g kg^{-1} P, 4.3 g kg^{-1} K, 12, 7 g kg^{-1} Ca and 3.0 g kg^{-1} Mg in Mazumbai Forest Reserve at 1400–1900 m, LMRF with canopy heights of 35–40 m situated about 300 km south-east of Mt. Kilimanjaro).

Tanner *et al.* (1998) found a positive correlation between canopy height and N concentrations in leaves. A similar, but weaker correlation was obtained for litter P concentrations. The combination of tall canopy height and high N and P concentrations of the litter at Mt. Kilimanjaro fit well in the correlations presented by Tanner *et al.* (1998).

Montane rain forests exhibit an overall tendency for low N concentrations and fluxes in litterfall as compared to lowland rain forests (Bruijnzeel & Proctor 1995, Tanner *et al.* 1998). Vitousek (1984) suggested the litter amount/nutrient flux ratio as a measure of the nutrient use efficiency of a forest. According to his reference forests, montane rain forests usually have lower N and P cycling rates and a higher within-stand efficiency. With canopy heights of over 40 m for some *Ocotea* trees, the stature of the forest on Mt. Kilimanjaro more resembles statures of lower montane rain forests (Grubb 1977). Accordingly, also the ratio between litter dry mass/nutrient flux of the forest on Mt. Kilimanjaro (62 for N and 1254 for P) more strongly resembles lower montane rain forests with a higher N and P circulation. The overall results from Mt. Kilimanjaro indicate that N and P are not major growth-limiting factors for the montane rain forest.

CONCLUSIONS

Contrary to expectations, above-ground nutrient fluxes of base cations in rainfall and throughfall were very low on Mt. Kilimanjaro compared to other tropical montane rain forests. This was especially true for Mg and Ca. The low fluxes are most likely related to the large altitudinal distance between forest and surrounding savanna plains, which otherwise form an extensive source for terrestrial salt-rich dust. Furthermore, the large distance to the sea limits inputs from this potential source. Thus, the

amount of base cations reaching the soil via throughfall was comparatively low. The pronounced decline in cation concentrations from litter percolate to the soil solution indicates that these ions are retained within the ecosystem. K in particular seems to be held in a relatively closed cycle between forest canopy and soil litter layer.

Nutrient concentrations and annual fluxes of fine litterfall on Mt. Kilimanjaro were in the range observed in other tropical montane forests. However, high litter N and P concentrations and fluxes indicate high circulation rates, so that N or P limitations are not expected to be an important factor in this ecosystem.

In order to get a better insight into the nutrient availability and usage by plants, biogeochemical studies in montane rain forest should also include analyses of below-ground water and soil chemistry. For studying internal nutrient transfers within ecosystems as well as for comparisons between different sites, nutrient fluxes are more meaningful than concentrations, since they are independent of the amount of the transport medium: water. Therefore, it is important that future studies on seepage water will also include estimates of water fluxes.

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