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Long-term effects of rainforest disturbance on the nutrient composition of throughfall, organic layer percolate and soil solution at Mt. Kilimanjaro

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Abstract

At the lower parts of the forest belt at Mt. Kilimanjaro, selective logging has led to a mosaic of mature forest, old secondary forests (~60 years), and old clearings (~10 years) covered by shrub vegetation. These variations in the vegetation are reflected by differences in nutrient leaching from the canopy and in both amount and quality of litter reaching the ground, thereby also influencing mineralization rates and the composition of seepage water in litter percolate and soil solution. The aim of this study was to investigate how above- and belowground nutrient dynamics vary between regeneration stages, and if forest regeneration at the clearings is hampered by a deterioration of abiotic site conditions. K, Mg, Ca, Na and N compounds were analysed in rainfall, throughfall, organic layer percolate and the soil solution to a depth of 1.00 m at three clearings, three secondary forest and four mature forest sites. Element fluxes via throughfall showed only small variations among regeneration stages except for K and NO_3-N. With 57–83 kg ha^{-1} a^{-1}and 2.6–4.1 kg ha^{-1} a^{-1} respectively, K and NO_3-N fluxes via throughfall were significantly higher at the clearings than at the mature forest sites (32–37 and 0.7–1.0 kg ha^{-1} a^{-1} for K and NO_3-N). In organic layer percolate and in soil solution at 0.15-m soil depth, concentrations of K, Mg, Ca and N were highest at the clearings. In the organic layer percolate, median K concentrations were e.g. 7.4 mg l^{-1} for the clearings but only 1.4 mg l^{-1} for the mature forests, and for NO_3-N, median concentrations were 3.1 mg l^{-1} for the clearings but only 0.92 mg l^{-1} for the mature forest sites. Still, differences in annual means between clearings and mature forests were not always significant due to a high variability within the clearings. With the exception of NO_3-N, belowground nutrient concentrations in secondary forests ranged between concentrations in mature forests and clearings. Vegetation type-specific differences decreased with increasing soil depths in the soil solution. Overall, the opening of the forest led to a higher spatial and seasonal variation of nutrient concentrations in the seepage water. These results suggest differences in both mineralization rates and in nutrient budgeting at different regeneration stages. Since nutrient availability was highest at the clearings and no compaction of the soil was observed, deterioration of soil properties did not seem to be the main reason for the impeded regeneration on the clearings.

Keywords: Litter percolate; Montane rainforest; Nutrient cycle; Regeneration; Soil solution; Throughfall

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1. Introduction

Due to its wealth in natural resources, the Kilimanjaro district became the most densely populated rural area in Tanzania (Bjørndalen, 1992). The remaining forest belt on Mt. Kilimanjaro is restricted to elevations between 1800 and 3000 m a.s.l. and plays a vital role in the regional water supply (Newmark, 1991). While large sections of the lower reaches of the forest belt were logged in the course of the Second World War (Wood, 1964) and are now covered in secondary forest, selective logging and fire have led to a further opening of the lower forests in recent decades (Lambrechts et al., 2002). This created a mosaic of secondary vegetation of varying ages, with the species composition significantly differing from the former natural forests (Mwasaga, 1991). Especially at large openings dominated by *Pteridium aquilinum* L. and *Rubus steudneri* Schweinf., regeneration seems strongly impeded. According to local foresters, these species may cover the plots for many years or even decades. In contrast to natural forest gaps, logging often causes more severe disturbance of both undergrowth and soil properties on affected sites (Chandrashekara and Ramakrishnan, 1994). The question hence arises whether a degradation of the soil or nutrient limitations also hinder the regeneration on the large clearings at Mt. Kilimanjaro, and if the nutrient cycle of plots covered by secondary vegetation differs from that of mature forest sites.

Immediate effects of logging and burning on nutrient cycling have been investigated in a number of tropical lowland rainforest ecosystems mainly in the Amazon Basin. After disturbances, a general increase in nutrient concentrations in the soil and soil solution was observed (Uhl and Jordan, 1984; Eden et al., 1991; Klinge, 1997). N mineralization and nitrification, as well as P availability were enhanced (Matson et al., 1987; Palm et al., 1996; Giardina et al., 2000), leading also to increases in stream water concentrations (Malmer, 1996). The peak of these effects usually occurred within 6 months after disturbance and declined again to initial levels soon afterwards (Klinge, 1997).

When disturbed forest sites are abandoned, natural regeneration sets in. Five years after burning of a tropical lowland rainforest, Uhl and Jordan (1984) found that nutrient concentrations in the soil solution had returned to pre-burning levels. It can nevertheless be assumed that in cases like the tropical mountain rainforest at Mt. Kilimanjaro, where forest disturbance leads to a pronounced long-term change in plant species composition and vegetation structure, nutrient dynamics could be altered for extensive time periods. In forest ecosystems, nutrients are transported to the soil as litter and via throughfall fluxes, with both pathways being strongly affected by the vegetation type. Amount and chemical composition of throughfall fluxes depend on the vegetation structure, which determines the ability of plants to intercept rainfall, capture dry deposits from the atmosphere, and affects the direct leaching of nutrients from leaves (Tukey, 1970; Parker, 1983). Thus, regenerating forests differing in vegetation composition and structure presumably have an altered nutrient composition in throughfall fluxes. Epiphytes typically occur at great densities in montane rain forests, with thick layers of mosses and ferns often completely covering stems and branches. These plants are well known to extract significant amounts of nutrients, especially nitrogen components, from passing rain- and throughfall (Liu et al., 2002; Clark et al., 2005). Their presence or absence in secondary vegetation hence further influences nutrient fluxes.

The amount and chemical composition of litter reaching the soil is determined by vegetation type, annual biomass production and nutrient availability at individual sites (Veneklaas, 1991; Hafkenscheid, 2000; McDonald and Healey, 2000). Thus, it is supposedly also altered during forest regeneration (McDonald and Healey, 2000). This will in turn affect litter mineralization rates and thus, combined with differences in throughfall fluxes entering the soil, alter the chemical composition of water percolating through the litter layer (Tobón et al., 2004). Finally, nutrient demand and uptake by the vegetation will be altered during forest regeneration due to differences in annual biomass production. This further affects the composition of water percolating through the mineral soil and determines the amount of nutrients leached below the rooting zone.

The growth of tropical montane rainforests is often said to be limited by nutrient availability, for example of nitrogen and phosphorous (Vitousek, 1984; Tanner et al., 1998). Nutrient losses following forest disturbance hence potentially hamper forest regeneration. The montane rainforest on the southern slopes of Mt. Kilimanjaro receives only small amounts of nutrients via dry deposition and rainfall, but high cycling rates of both N and P via leaf litter indicate that these nutrients might not be a limiting factor in the forest (Schrumpf et al., 2006). Base cations, especially K, on the other hand are recycled more effectively, suggesting their potentially more important role (Schrumpf et al., 2006). Though it is known that the type of vegetation cover can affect internal nutrient cycling and nutrient retention in forest ecosystems in general, hardly any study has looked at regenerating montane tropical rainforests (e.g., McDonald and Healey, 2000; Hölscher et al., 2003; Dezzeo and Chacón, 2006). With regard to the increase in the extent of secondary vegetation in the forest belt of Mt. Kilimanjaro, the main focus of the investigations was to compare soil properties and different aspects of the nutrient cycle among disturbed and mature forest sites. The following hypotheses were addressed:

A. Nutrient amounts reaching the ground via throughfall are higher beneath forests as compared to plots covered by shrub vegetation. This hypothesis is based on the expectation that the higher biomass of forests leads to an increased accumulation of dry deposits and overall higher leaching rates from the leaves.
B. The composition of seepage water in the soil differs between regeneration stages. This hypothesis relates not only to initial differences in nutrient fluxes via throughfall and litterfall, but also to microclimatic differences between clearings and forests which affect mineralization rates.
C. Forest regeneration on the clearings is hindered by a loss in soil fertility due to a deterioration of physical and chemical soil properties following forest disturbance.

To test these hypotheses, soils as well as concentrations and fluxes of nutrients in rainfall, throughfall, organic layer percolate and the soil solution were compared among clearings, secondary and mature forest sites at Mt. Kilimanjaro.

2. Material and methods

2.1. Study area

Ten sampling sites were selected between 2075 and 2320 m a.s.l. on the southwestern slopes of Mt. Kilimanjaro in the rainforest above Machame village. Geologically, the area belongs to the Lent Group (phonolites and trachyandesites, Downie and Wilkinson, 1972), but the soils mainly developed on overlaying layers of volcanic ashes.

Four sites were located in mature forest, three in secondary forests and another three in forest clearings covered by shrub vegetation. As the lower slopes up to 2150 m essentially consisted of secondary forest and shrubs, the mature forest plots had to be selected at a slightly higher elevation (Fig. 1). The least vertical distance between mature forest sites and regenerating sites was hence 140 m. According to the forest zonation

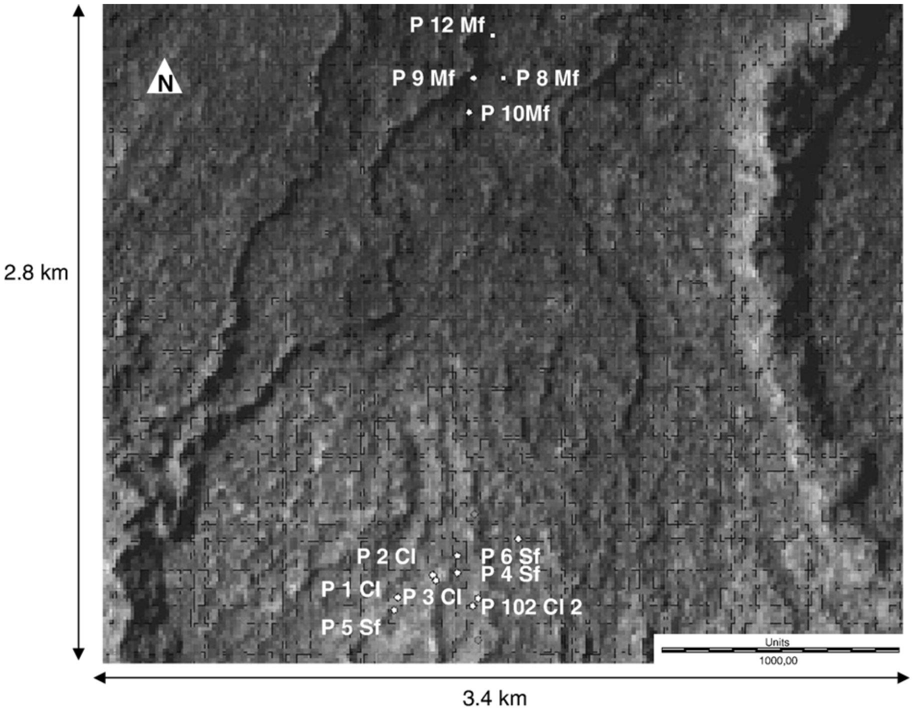

Fig. 1. Satellite image showing the location of the study sites in the forest belt on the southwestern slopes of Mt. Kilimanjaro above Machame village (Landsat 7TM+, Channel 8, 21.2.2000, 15 m × 15 m resolution, UTM coordinates of the section: 303600-307000, 9650750-9653500). Mf: mature forest, Cl: clearing, sf: secondary forest.

Table 1
Characteristics of soils under mature forest (Mf), secondary forest (Sf), and clearings (Cl) in the montane rainforest belt on Mt. Kilimanjaro at soil depths, where instruments were installed (means with standard error in parenthesis below, $n=4$ for mature forests, $n=3$ for clearings and secondary forests)

Soil depth	0.10–0.20 m			0.25–0.35 m			0.95–1.05 m		
	Mf	Sf	Cl	Mf	Sf	Cl	Mf	Sf	Cl
pH (H_2O)	4.4	4.6	4.1	4.7	4.7	4.7	4.6	4.9	5.0
	(0.1)	(0.3)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)
pH ($CaCl_2$)	4.0	4.0	3.9	4.3	4.5	4.4	4.9	5.0	5.0
	(0.1)	(0.2)	(0.1)	(0.1)	(0.1)	(0.3)	(0.0)	(0.1)	(0.1)
C (g kg^{-1})	144	139	163	123	106	102	58.8	57.2	74.8
	(21)	(15)	(13)	(13.3)	(7.0)	(2.7)	(9.3)	(6.1)	(9.3)
N (g kg^{-1})	8.1	9.0	10.6	6.2	6.1	6.8	2.6	2.9	3.7
	(1.4)	(1.2)	(0.4)	(0.4)	(0.1)	(0.4)	(0.5)	(0.1)	(0.6)
NO_3 (mg kg^{-1})	13.2	6.5	14.1	5.8	2.4	8.0	8.5	3.6	4.7
	(1.2)	(1.2)	(2.2)	(0.7)	(0.6)	(1.6)	(1.3)	(2.4)	(0.7)
NH_4 (mg kg^{-1})	26.4	15.0	23.3	12.0	9.4	12.5	5.2	3.6	5.6
	(7.5)	(1.9)	(1.6)	(2.2)	(1.2)	(2.3)	(0.5)	(0.3)	(0.6)
Sand (g kg^{-1})	97	213	104	142	142	169	179	146	134
	(26)	(82)	(28)	(21)	(31)	(70)	(71)	(21)	(35)
Silt (g kg^{-1})	156	273	311	224	365	318	327	291	272
	(25)	(16)	(8)	(37)	(7)	(29)	(43)	(6)	(15)
Clay (g kg^{-1})	747	514	585	634	493	513	494	563	594
	(71)	(62)	(69)	(126)	(52)	(70)	(70)	(9)	(12)
BD (g cm^{-3})	0.32	0.37	0.30	0.40	0.38	0.35	0.56	0.61	0.53
	(0.1)	(0.09)	(0.02)	(0.04)	(0.03)	(0.06)	(0.05)	(0.02)	(0.01)
ECEC ($cmol_c$ kg^{-1})	6.16	6.53	8.54	2.52	1.93	1.36	0.48	0.70	0.37
	(2.4)	(2.0)	(0.8	(0.5)	(0.1)	(0.4)	(0.1)	(0.1)	(0.1)
K ($cmol_c$ kg^{-1})	0.13	0.19	0.35	0.05	0.09	0.14	0.11	0.03	0.05
	(0.1)	(0.06)	(0.04)	(0.01)	(0.00)	(0.03)	(0.02)	(0.00)	(0.02)
Mg ($cmol_c$ kg^{-1})	0.11	0.12	0.24	0.03	0.05	0.03	0.01	0.02	0.00
	(0.1)	(0.04)	(0.01)	(0.01)	(0.02)	(0.01)	(0.00)	(0.00)	(0.00)
Ca ($cmol_c$ kg^{-1})	0.21	0.18	0.57	0.10	0.12	0.09	0.02	0.06	0.06
	(0.1)	(0.02)	(0.12)	(0.02)	(0.02)	(0.01)	(0.01)	(0.02)	(0.02)
Al ($cmol_c$ kg^{-1})	5.2	5.7	7.1	2.2	1.6	1.1	0.3	0.5	0.2
	(1.9)	(1.8)	(0.84)	(0.43)	(0.04)	(0.36)	(0.06)	(0.13)	(0.11)

BD: bulk density; ECEC: effective cation exchange capacity, NO_3: KCl extractable NO_3-N, NH_4: KCl-extractable NH_4-N.

suggested by Hemp (2005), all plots are located within *Ocotea usambarensis* Engl.-dominated forest types. A comparison of the vegetation composition between small mature forest remnants within the secondary vegetation mosaic and the mature forest plots furthermore showed a very strong resemblance (Axmacher, 2003; Axmacher et al., 2004), so that it can be safely assumed that the potential natural forest vegetation at the study plots is highly similar. All plots had a size of 400 m^2 and an inclination of less than 10° in order to avoid substantial effects of lateral flow and erosion.

Canopy trees reached heights exceeding 40 m, and the forest was furthermore characterised by a high density and diversity of epiphytic plants (mainly mosses and ferns). Secondary forest plots belonged to a logging phase occurring during the Second World War, when a sawmill operated at 2000 m a.s.l. above Machame village (Wood, 1964). The canopy layer of these plots consisted mainly of the pioneer tree species *Macaranga kilimanjarica* Pax and some regrowth of *O. usambarensis*. Overall tree stem diameters were smaller (maximum 0.7 m in the secondary forest versus 1.6 m in the mature forest), the number and diversity of epiphytes were reduced and the moss layer at the tree trunks was thinner and partly lacking as compared to the mature forest plots (personal observation).

According to regional foresters, some of the clearings had an age of more than 10 years. They were dominated by bracken fern (*P. aquilinum* L.) and blackberry (*R. steudneri* Schweinf.) in varying proportions, with the latter becoming more important in apparently older clearings, where the liana *Begonia meyeri-johannis* Engl. was also abundant. A tree layer and subsequently epiphytic plants were widely missing at these plots, but the shrub vegetation reached a height of more than 2 m at some places. A complete species list of the vascular plants at the plots was provided in Axmacher (2003).

Table 2
Mean C and N stocks in the organic soil horizons and the mineral soil up to a soil depth of 1.0 m (standard error in parenthesis) under mature forest sites (Mf), secondary forest sites (Sf) and clearings (Cl) in the montane rainforest belt at Mt. Kilimanjaro

		C	N
		(t ha^{-1})	
Organic soil horizons	Cl	98 (18)^{ab}	6.3 (1.3)^{ab}
	Sf	62 (13)^{a}	3.7 (0.8)^{a}
	Mf	164 (22)^{b}	10.3 (1.2)^{b}
Mineral soil	Cl	474 (8)^{a}	30.0 (1.4)^{a}
	Sf	471 (33)^{a}	27.4 (0.4)^{a}
	Mf	565 (44)^{a}	25.6 (2.8)^{a}
Total soil	Cl	572 (13)^{ab}	36.4 (1.1)^{a}
	Sf	533 (35)^{a}	31.1 (0.9)^{a}
	Mf	729 (54)^{b}	35.9 (3.1)^{a}

Different letters indicate significant differences between vegetation types (Scheffé-test, $p < 0.05$).

Northern Tanzania has a bimodal rainfall distribution with a short rainy season from November to December and a long rainy season from March to May, with an overall high annual variability in rainfall amounts (Hedberg, 1964). For the most humid southern slopes of the mountain, Røhr and Killingtveit (2003) reported a rainfall maximum of more than 3500 mm at 2200 m. Periodic temperature measurements at 50 days between May and October 2001 resulted in a median of 8.7 °C for the daily minimum temperature and of 14.8 °C for maximum temperatures in the mature forest at 2330 m. At 18 days in February 2001, parallel temperature measurements were performed at all treatments. In the secondary forest, temperatures were on average 1.6 °C higher than in the mature forest. Highest variability between day and night temperatures was found in the shrub vegetation, where maximum daily temperatures in this comparatively dry month were on average 14 °C higher than in the adjacent secondary forest.

2.2. Instrumentation of the plots

Rainfall was collected at three clearings with a diameter of more than 40 m, two situated at lower elevations and one close to the mature forest plots. At each clearing, five rainfall collectors were installed 1.5 m above the ground after removal of the shrub vegetation. Furthermore, all plots were equipped with eight to ten randomly distributed throughfall collectors. Rain collectors as well as throughfall collectors consisted of 2-l collection bottles and a sharp-rimmed funnel with a diameter of 115 mm, all made of polyethylene. The collection bottles of the throughfall collectors were half buried in the ground so that the rims of the funnels were approximately 0.3 m above the ground surface. The ground of the funnel was covered by a 1-mm polyethylene net to reduce the contamination of the samples with litter and insects. Additionally, a table tennis ball was placed in the funnel mouth to reduce evaporation losses. If necessary, the funnel was cleaned after each sampling, and twice a year all collecting bottles were cleaned using deionised water.

Organic layer percolate was collected using four to five collectors per plot placed below the root mat within the organic layer. The collectors consisted of plastic boxes (285-mm side length, 80-mm height), covered with a 1-mm polyethylene mesh. A silicon tube connected the boxes to a buried 2-l polyethylene sampling bottle in a closeable bucket. Soil solution from deeper soil layers was extracted by ceramic suction cups (SKL 100, ceramic cup K100, UMS Munich) in 0.15, 0.30 and 1.00 m depths. Three cups, one at each depth, were installed in the form of a triangle with 1-m side length in three replicates at each plot. The groups were arranged at maximal distance to each other, and all had a horizontal distance of 5 m from the pump system (Vacuum case VK-3, UMS Munich) placed together with 1-l sampling bottles (Duranglass) in a box in the plot centre. Soil solution collected by suction cups was stored in one bottle for each soil depth.

Although stemflow was collected on 8 trees during 1 year, conservative estimates of stemflow fluxes proved that it contributes less than 1% to throughfall amounts. Due to this and to sampling problems, measurements were cancelled in the second year and will not be considered further here.

Table 3
Nutrient concentrations in the litter layer (Oi) of mature rain forest sites (Mf), secondary rain forest sites (Sf) and clearings (Cl) at Mt. Kilimanjaro (standard error for field replicates in parenthesis, $n = 3–4$)

	Total	K	Mg	Ca	Na	N	P	S
		(g kg^{-1})						
Oi layer	Mf	1.5 (0.1)^{b}	0.4 (0.1)^{a}	1.9 (0.1)^{ab}	13 (1.1)^{a}	16 (0.0)^{b}	1.1 (0.2)^{a}	1.8 (0.0)^{a}
	Sf	1.6 (0.0)^{b}	0.3 (0.0)^{a}	1.6 (0.1)^{b}	7.0 (0.2)^{a}	15 (0.1)^{b}	1.3 (0.2)^{a}	1.7 (0.0)^{a}
	Cl	2.9 (0.3)^{a}	0.2 (0.0)^{a}	2.2 (0.4)^{a}	7.9 (1.4)^{a}	21 (0.2)^{a}	1.2 (0.1)^{a}	1.8 (0.0)^{a}

Different subscripts within columns indicate significant differences among vegetation types ($p < 0.05$).

2.3. Sampling procedure

Measurements of the rainfall and throughfall collectors, suction cups and stream water were started in May 2000. Organic layer percolate sampling started by November 2000. In the first year (June 2000–May 2001), samples were taken twice a week. On one day, the rainfall and samples of organic layer percolate were taken. Water volumes were recorded for all individual collectors, and a composite volume weighted sample of 100 ml was taken from each plot. Pumps for the suction cups operated to create a constant vacuum of 40 kPa until the next day when soil solution samples were taken. Due to a fire experiment in the second study year, three more clearings were added to the study, and the sampling procedure had to be changed. The burning experiment is out of the scope of this study, so only the unburned sites will be considered, inducing a replacement of one clearing sampled in the first year (Cl 2 in Fig. 1) by another one (Cl 102). From June 2001 until October 2001, samples were taken on a weekly basis on all sites. For logistical reasons, mature forests were sampled 2 days after the regenerating sites. From November 2001 until the end of the second study year, samples of the lower plots were again taken on a biweekly basis, while the weekly mode was continued at the mature forest plots.

Soil solution was obtained continuously at all plots at soil depths between 0.15 and 0.30 m with the exception of a very dry period in 2001 when no solution could be extracted for up to 5 weeks at single plots. The suction cups at 1.00 m were less effective in extracting soil solution and sampling failed frequently during drier periods especially at the overall drier secondary forest sites.

2.4. Treatment and analysis of samples

Composite samples were made in the laboratory for 14-day periods. This allowed having similar time steps for the treatments for both years. Rain, throughfall and organic layer percolate samples were mixed volume weighted for each 14-day period while soil solution samples were equally weighted as no reliable data on the belowground water fluxes existed. Missing soil solution samples due to dry soils were ignored in the mixed samples. At three occasions when either samples or data were missing for individual plots, samples were excluded. Composite samples were made for the whole period independent of the sampling frequency. Water samples were stored frozen until analysed.

Prior to further analysis, rain and organic layer percolate samples were filtered through an ash-free paper filter, pore size <2 μm (Schleicher and Schuell, blueband 589^3). NH_4-N as well as NO_3-N and NO_2-N were measured using a Segmented Flow Analyser (SKALAR, SA 2000/4000). As NO_2-N concentrations were considered to be negligible, they are not listed separately but included in the NO_3-N concentrations. To determine the element concentrations of Mg, K, Ca and Na, atomic absorption spectrometry (AAS; Varian SpectrAA 400) was employed.

2.5. Soil sampling and analyses

The plots were tested for homogeneity using a soil auger. Then a soil profile was established at one edge of each 20 m × 20 m plot and samples were taken by horizon from three sides of the pit walls for laboratory analyses. For the determination of the bulk density, three undisturbed soil cores with a volume of 100 cm^3 each were taken from all horizons.

Analyses of the mineral soil were carried out on air-dried samples (40 °C) of the fraction <2 mm. The 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 and 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. Particle size

Table 4
Amounts of rainfall, throughfall and intercepted water (standard error in parenthesis) at mature forest sites (Mf) secondary forest sites (Sf) and clearings on Mt. Kilimanjaro during 2 years from June 2000 to June 2002

	Rainfall		Throughfall			Interception		
	2100 m	2250 m	Mf	Sf	Cl	Mf	Sf	Cl
	(mm)		(mm)			(mm)		
Year 1	2600	2480	2040 (27)	1890 (100)	2490 (80)	438 (33)	712 (100)	110 (80)
Year 2	2210	1960	1370 (20)	1500 (20)	2010 (40)	590 (20)	710 (20)	210 (40)

Table 5

Volume weighted mean annual concentrations of rainfall and throughfall, means of the median nutrient concentrations of organic layer percolate and the soil solution in 0.15 and 1.00 m depth in mature rain forest sites (Mf), secondary forest sites (Sf) and clearings (Cl) at Mt. Kilimanjaro for 2 years (June 2000 to June 2002)

	K			Mg			Ca			Na			NH_4-N			NO_3-N		
	Cl	Sf	Mf	Cl	Sf	Mf	Cl	Sf	Mf	Cl	Sf	Mf	Cl	Sf	Mf	Cl	Sf	Mf
	(mg l^{-1})			(mg l^{-1})			(mg l^{-1})			(mg l^{-1})			(mg l^{-1})			(mg l^{-1})		
Year 1																		
Rf	0.65	0.03		0.03	0.04		0.08	0.09		0.33	0.30		0.15	0.16		0.09	0.13	
Tf	3.06^{a}	2.98^{a}	1.50^{b}	0.09^{a}	0.09^{a}	0.08^{a}	0.14^{a}	0.16^{a}	0.13^{a}	0.43^{a}	0.51^{a}	0.53^{a}	0.23^{a}	0.21^{a}	0.19^{a}	0.15^{a}	0.04^{b}	0.05^{b}
	(0.09)	(0.07)	(0.20)	(0.01)	(0.01)	(0.02)	(0.01)	(0.01)	(0.01)	(0.06)	(0.04)	(0.09)	(0.03)	(0.01)	(0.02)	(0.03)	(0.00)	(0.01)
Lp																		
Ss15	1.53^{a}	0.20^{b}	0.15^{b}	0.40^{a}	0.14^{a}	0.15^{a}	1.41^{a}	0.16^{b}	0.27^{b}	0.43^{a}	0.51^{a}	0.42^{a}	0.04^{a}	0.03^{a}	0.03^{a}	2.18^{a}	0.62^{b}	1.48^{a}
	(0.44)	(0.04)	(0.04)	(0.05)	(0.03)	(0.06)	(0.45)	(0.02)	(0.10)	(0.03)	(0.09)	(0.07)	(0.01)	(0.00)	(0.00)	(0.32)	(0.23)	(0.34)
Ss100	0.35^{a}	0.21^{a}	0.15^{a}	0.29^{a}	0.20^{a}	0.13^{a}	0.59^{a}	0.21^{a}	0.21^{a}	0.31^{a}	0.40^{a}	0.31^{a}	0.07^{a}	0.07^{a}	0.03^{a}	0.42^{a}	0.34^{ab}	1.11^{b}
	(0.11)	(0.02)	(0.02)	(0.05)	(0.05)	(0.02)	(0.17)	(0.04)	(0.06)	(0.02)	(0.04)	(0.03)	(0.01)	(0.00)	(0.00)	(0.11)	(0.14)	(0.12)
Year 2																		
Rf	0.33	0.05		0.05	0.05		0.11	0.15		0.35	0.36		0.15	0.16		0.15	0.17	
Tf	3.04^{a}	4.41^{b}	2.97^{a}	0.12^{a}	0.14^{a}	0.16^{a}	0.25^{a}	0.24^{a}	0.34^{a}	0.59^{a}	0.93^{a}	0.90^{a}	0.18^{a}	0.21^{a}	0.19^{a}	0.14^{a}	0.05^{a}	0.05^{a}
	(0.27)	(0.24)	(0.15)	(0.04)	(0.03)	(0.03)	(0.11)	(0.05)	(0.05)	(0.06)	(0.05)	(0.11)	(0.00)	(0.02)	(0.01)	(0.02)	(0.01)	(0.01)
Lp	7.41^{a}	3.21^{ab}	1.44^{b}	0.92^{a}	0.31^{ab}	0.32^{b}	1.95^{a}	0.80^{ab}	0.79^{b}	0.93^{a}	0.93^{a}	0.81^{a}	0.64^{a}	0.45^{ab}	0.27^{b}	3.08^{a}	0.62^{a}	0.92^{a}
	(0.61)	(0.36)	(0.50)	(0.20)	(0.01)	(0.06)	(0.48)	(0.05)	(0.15)	(0.09)	(0.06)	(0.05)	(0.02)	(0.07)	(0.04)	(1.69)	(0.07)	(0.25)
Ss15	2.09^{a}	0.29^{a}	0.19^{a}	0.57^{a}	0.18^{ab}	0.11^{b}	1.59^{a}	0.28^{b}	0.25^{b}	0.36^{a}	0.74^{a}	0.41^{a}	0.04^{a}	0.05^{a}	0.04^{a}	3.92^{a}	1.07^{a}	1.54^{a}
	(1.22)	(0.03)	(0.04)	(0.20)	(0.04)	(0.02)	(0.45)	(0.05)	(0.06)	(0.10)	(0.12)	(0.08)	(0.00)	(0.00)	(0.00)	(2.25)	(0.17)	(0.55)
Ss100	0.43^{a}	0.21^{a}	0.21^{a}	0.34^{a}	0.18^{a}	0.13^{a}	0.77^{a}	0.25^{a}	0.27^{a}	0.46^{a}	0.57^{a}	0.40^{a}	0.08^{a}	0.13^{a}	0.04^{a}	0.99^{a}	0.40^{a}	1.07^{a}
	(0.18)	(0.02)	(0.04)	(0.09)	(0.04)	(0.03)	(0.20)	(0.05)	(0.08)	(0.05)	(0.01)	(0.05)	(0.02)	(0.03)	(0.00)	(0.55)	(0.14)	(0.17)

Standard errors for field replicates ($n=3$, 4) are presented in parenthesis below. Different subscripts within rows indicate significant differences among means ($p<0.05$).

Table 6
Nutrient fluxes via rainfall and throughfall (standard error in parenthesis, $n=3–4$) at mature forest sites (Mf), secondary forest sites (Sf) and clearings (Cl) on Mt. Kilimanjaro for two consecutive years (June 2000 to June 2002)

	Year 1					Year 2				
	Rainfall		Throughfall			Rainfall		Throughfall		
	2300 m	2100 m	Mf	Sf	Cl	2300 m	2100 m	Mf	Sf	Cl
	(kg ha^{-1} year^{-1})					(kg ha^{-1} year^{-1})				
K	6.9	15.8	32.2 (4.0)^{c}	62.5 (1.9)^{b}	83.0 (3.0)^{a}	8.0	6.2	37.2 (1.8)^{b}	61.6 (3.8)^{a}	57.2 (4.3)^{a}
Mg	0.9	0.8	1.8 (0.4)^{a}	1.9 (0.1)^{a}	2.5 (0.3)^{a}	0.8	1.0	2.0 (0.3)^{a}	1.9 (0.4)^{a}	1.9 (0.4)^{a}
Ca	2.1	1.9	2.8 (0.3)^{a}	3.2 (0.2)^{a}	3.9 (0.4)^{a}	2.4	2.2	4.2 (0.6)^{a}	3.3 (0.6)^{a}	4.7 (1.9)^{a}
Na	6.7	8.0	11.5 (2.0)^{a}	10.5 (0.5)^{a}	11.5 (1.1)^{a}	5.7	6.7	11.2 (1.2)^{a}	12.9 (0.9)^{a}	11.1 (1.5)^{a}
NH_4-N	3.6	3.6	4.2 (0.4)^{a}	4.5 (0.3)^{a}	6.1 (0.6)^{a}	2.5	2.8	2.4 (0.1)^{b}	2.9 (0.2)^{ab}	3.3 (0.1)^{a}
NO_3-N	3.0	2.1	1.0 (0.3)^{b}	0.8 (0.1)^{b}	4.1 (0.6)^{a}	2.7	2.8	0.7 (0.2)^{b}	0.7 (0.2)^{b}	2.6 (0.3)^{a}

Different subscripts within rows for each year indicate significant differences among vegetation types ($p<0.05$).

distributions were analysed using field moist samples, which were stored at temperatures around 4 °C. Soil samples were dispersed overnight by shaking 5 g of soil in 20 ml 0.1 M $Na_4P_2O_7$ solution added to 500 ml of water. Sand-size particles were removed by sieving, while silt and clay contents were determined using the pipette method (Gee and Bauder, 1986).

Material of the litter layer was digested with concentrated HNO_3 under pressure (Heinrichs et al., 1986). To determine the element concentrations of Mg, K, Ca and Na in extracts, atomic absorption spectrometry (AAS; Varian SpectrAA 400) was employed.

2.6. Calculations and statistical evaluation

Fluxes of rainfall and throughfall were calculated by multiplying the amount collected with the respective element concentrations. Volume weighted means were calculated by dividing the product of element concentration and flux depths by the annual total flux depth for each

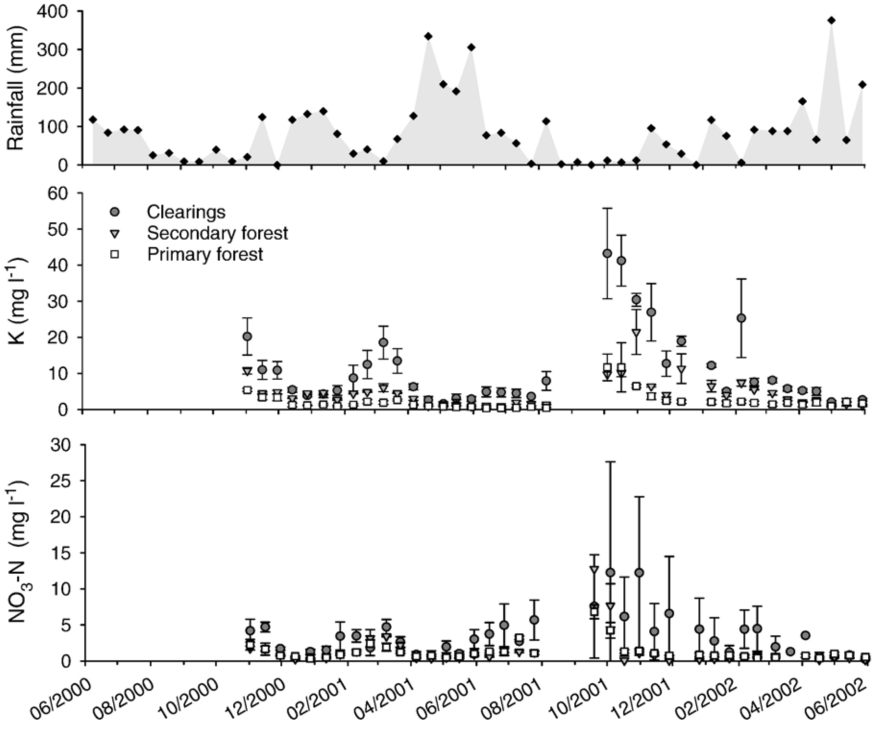

Fig. 2. Rainfall amounts and nutrient concentrations in organic layer percolate under mature forest, secondary forest and clearings in the rain forest belt of Mt. Kilimanjaro. Error bars provide standard errors ($n=3$ for clearings and secondary forest, $n=4$ for mature forest).

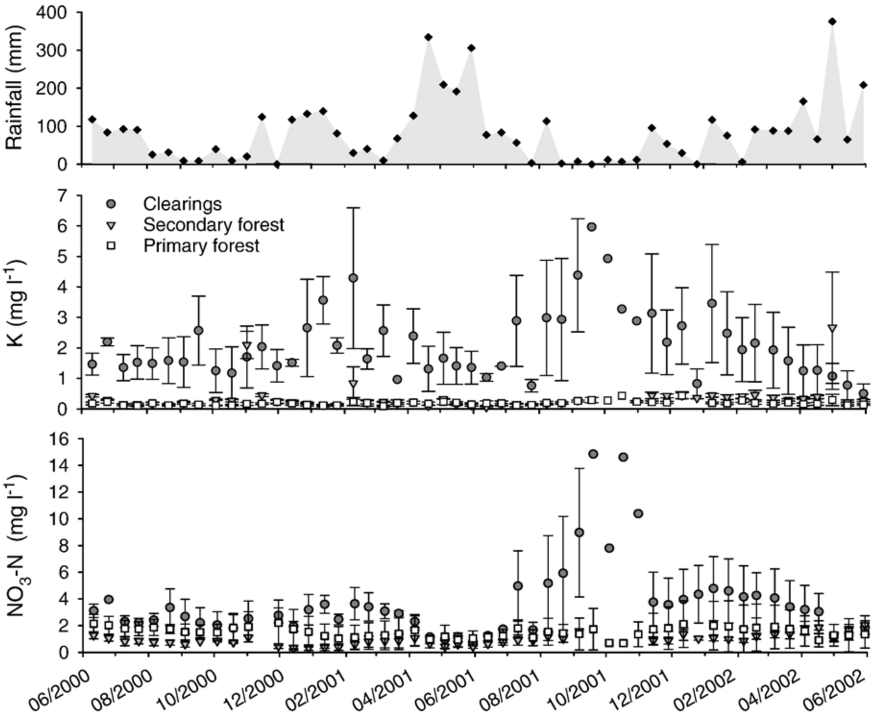

Fig. 3. Rainfall amounts and nutrient concentrations in the soil solution (0.15 m) under mature forest, secondary forest and clearings in the rain forest belt on Mt. Kilimanjaro. Error bars provide standard errors ($n = 3$ for clearings and secondary forest, $n = 4$ for mature forest).

two week period and summing the terms. Net throughfall fluxes were determined as difference between throughfall and rainfall fluxes. Nutrient fluxes for organic layer 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.

Statistical analyses were conducted using the program Statistica 5.0 (Statsoft, Inc., Tulsa, UK). The annual means of the different sites were compared by solution type using one-way analyses of variance (ANOVA), followed by a post hoc separation of means by the Scheffé-test ($p < 0.05$). ANOVA was conducted on log-transformed data to avoid a correlation between mean values and respective standard deviations.

3. Results

3.1. Soil properties and comparability of sites

Soils in the study area were classified as Fulvudands and Epiaquands (Soil Survey Staff, 2003). Mineral soils were overlain by organic layers varying in thickness within sites as well as between the treatments with an average thickness for Oi, Oe and Oa horizons of 6, 8 and 8 cm respectively for the clearings, 4,1 and 8 cm for the secondary forest and 3, 1 and 22 cm for the mature forest sites. Buried soils could be found on every plot below 0.3 m. Despite overall high C contents, the ECEC was generally low with values ranging between 6.2–8.5 cmol$_c$ kg^{-1} in the topsoil and 0.4–0.7 cmol$_c$ kg^{-1} at 1-m soil depth (Table 1). Al dominated the cation exchange sites in all horizons, resulting in a low base saturation of 13–35%. For all except the deepest analysed soil layer, KCl-extractable NO_3-N pools were significantly lower in soils under secondary forests and slightly lower in mature forests as compared to clearings (Table 1).

While most soil properties did not differ among different regeneration stages (Table 1), the sand content in the topsoil (0.05–0.10 m) was significantly higher in the secondary forests as compared to the mature forests. Clearings took a position between the two forest types. Chemical and mineralogical analyses indicated no differences in parent materials of these horizons, and radiocarbon dating of charcoal found in fossil horizons indicated a similar age of soil surface layers (Zech, unpublished data). Soil erosion following disturbance might be another explanation, but does not seem to have been substantial due to the huge organic layer covering the mineral soil. Andisols are known to irreversibly form stable, sand-size aggregates after drying below a critical value between pF 3 and 4 (Wada, 1989; Shoji et al., 1993). Thus, an alternative hypothesis might be that topsoil drying of the exposed disturbed forest sites led to the formation of stable aggregates which could not be dispersed by the methods applied in this study. Bulk density did not differ significantly between regeneration stages.

Stocks of C and N did not exhibit significant differences in the mineral soil to a depth of 1.0 m (Table 2). In the organic layers, total C and N stocks were lowest under secondary forests. This difference was significant between mature and secondary forest plots ($p < 0.05$). The chemical composition of the litter layer (Oi layer, Table 3) revealed no significant differences between the sites for P, S and Mg, while litter concentrations for K, Ca and N were higher at the clearings as compared to the forest sites.

3.2. Nutrient concentrations and fluxes in rainfall and throughfall

Annual rainfall amounts collected varied between 2000 and 2600 mm, with the second year being overall drier than the first year (Table 4). Rainfall amounts collected in clearings in the area of the mature forest sites were 5% smaller than in the area of the disturbed forest sites in the first year, and 11% smaller in the second year. Interception was low at the clearings, but reached up to 30% of incident rainfall in the forests. Thus, highest throughfall amounts were recorded at the soil surface of the clearings (Table 4).

Nutrient concentrations in rainfall generally increased upon passage through the vegetation cover (Table 5, Fig. 4). This resulted in higher nutrient fluxes via throughfall as compared to rainfall for most elements

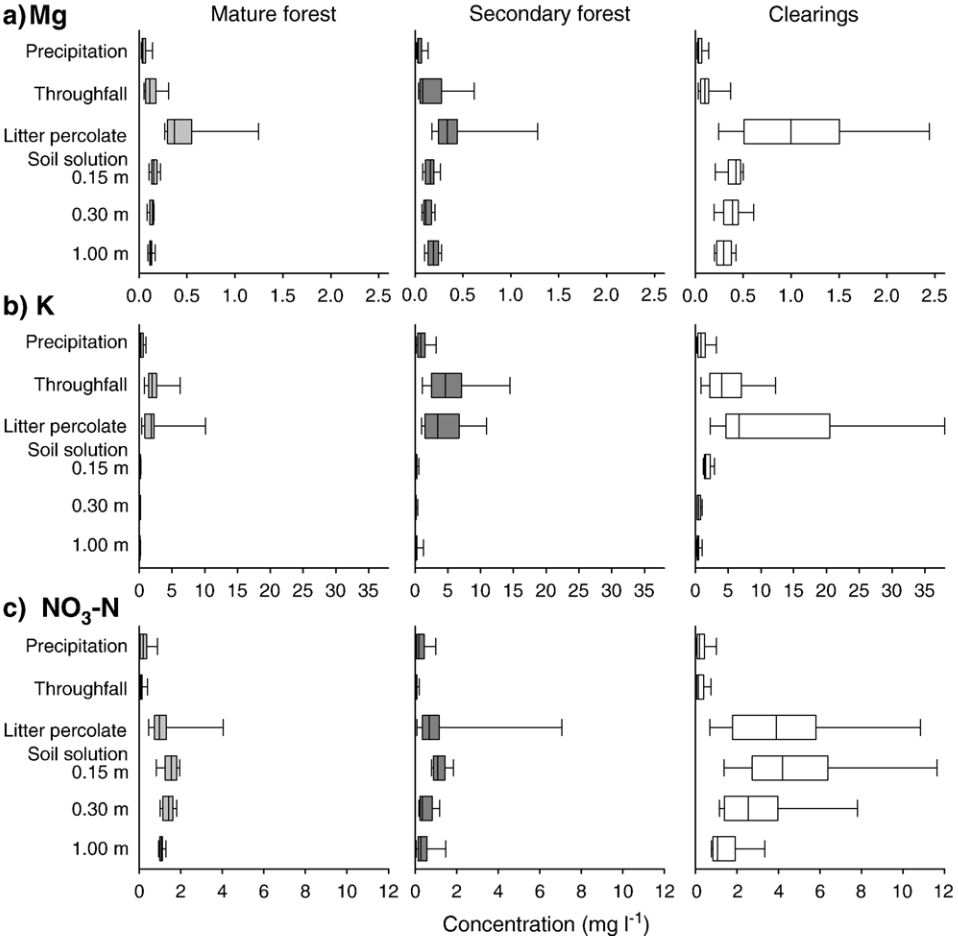

Fig. 4. Annual variability of nutrient concentrations in water flows through different ecosystem compartments (rainfall, throughfall, organic layer percolate, soil solution) in mature forest sites, secondary forest sites and clearings on Mt. Kilimanjaro. Box-whisker diagrams include the means of fortnight samples of the different vegetation types in the second year, with vertical lines showing the median, boxes the 25 and 75% quantiles and whiskers showing the 5 and 95% quantiles.

(Table 6). Overall nutrient concentrations and fluxes in throughfall under the shrub vegetation of the clearings matched the ones of the two forest types. For K, NO_3-N and NH_4-N throughfall concentrations and fluxes under shrub vegetation even significantly exceeded those of the forests during some years (Tables 5 and 6).

3.3. Composition of water in organic layer percolate and soil solution

Nutrient concentrations in organic layer percolate and soil solution differed strongly between regeneration stages. As sampling of organic layer percolate only started in late November 2000, data for the first 5 months are missing. For all nutrients with the exception of Na, the highest concentrations in organic layer percolate were generally found in the clearings (Fig. 2, Table 5). Differences between clearings and forest plots were most pronounced during dry periods, when concentrations at the clearings increased stronger than at the forest sites (Fig. 2). This effect was most pronounced for K, but also observable for Mg, NO_3-N and Ca. Only Na concentrations did not show major differences between treatments. The high standard error of concentrations measured for 14-day periods at the clearings, especially during dry periods, indicates that the spatial variability was also higher among these sites as compared with the forests. Ion concentrations in the soil solution at 0.15 m generally followed the pattern observed in the organic layer percolate (Fig. 3). Still, overall seasonal changes induced by rainy and dry seasons were less pronounced compared to organic layer percolate (Figs. 2 and 3).

Median annual concentrations of K, Mg, Ca and NH_4-N, but not NO_3-N in organic layer percolate were significantly higher in the clearings as compared to mature forest (Table 5). For the secondary forests, no significant differences to mature forests or clearings were observed. In the soil solution, median annual K concentrations at 0.15-m soil depth on the clearings were on average 1.5 mg l^{-1} in the first and 2.1 mg l^{-1} in the second study year, while mean values for the forests ranged between 0.2 and 0.3 mg l^{-1} for both years. Due to the high spatial variability of K concentrations at the clearings, the median concentrations between clearings and forests were significantly different, only in the first, but not in the second year. Significant differences in Mg concentrations between forests (0.1–0.2 mg l^{-1}) and clearings (0.4–0.6 mg l^{-1}) were only apparent in the second study year again due to a high variability within field replicates. Ca concentrations were significantly higher at clearings (1.4–1.6 mg l^{-1}) than in the forests (0.2–0.3 mg l^{-1}) during both years. While lowest nutrient concentrations in the organic layer percolate as well as in the soil solution usually occurred in the mature forest, lowest concentrations for NO_3-N were recorded at secondary forest plots. Due to the high variability, mean NO_3-N concentrations in the soil solution at 0.15-m depth were only significantly lower in secondary forest sites than in the clearings in the first year (Fig. 4). At 1-m soil depth, nutrient concentrations in the soil solution were overall very low, and with the exception of NO_3-N, differences were not significant (Table 5).

4. Discussion

4.1. Aboveground nutrient fluxes under different regeneration stages

The observed high similarity of nutrient concentrations and fluxes in throughfall of clearings and forest plots for most elements, and the elevated fluxes for K and NO_3-N under shrub vegetation clearly contradict our first hypothesis. Similarly, only small differences between throughfall nutrient fluxes under old growth and secondary forests were observed in Costa Rica (Hölscher et al., 2003) and Venezuela (Dezzeo and Chacón, 2006), but in these cases the forests were in an advanced stage of regeneration as compared to the clearings at Mt. Kilimanjaro.

The ability of plants to filter aerosols and dust particles from the atmosphere depends on vegetation coverage, roughness and leaf structure. Axmacher (2003) estimated the %vegetation cover at the study plots on Mt. Kilimanjaro within four layers between 0.5 and >10 m height. When sums of all layers were compared, the total coverage of the forests was not significantly different from the dense shrub vegetation (110–165% for forests and 115–155% for clearings). Furthermore, comparisons with other montane rainforest sites revealed that nutrient fluxes of base cations via rainfall and throughfall under mature forests are generally very low at Mt. Kilimanjaro (Schrumpf et al., 2006), so that overall dry deposition is also supposed to be low.

Thus, differences in the susceptibility of leaves for passive leaching from plant tissues might be more important. This is supported by the fact that the greatest difference in throughfall fluxes among all three vegetation types was measured for K, an element easily leached from leaves (Parker, 1983). The dominant tree species of the mature forest is *O. usambarensis* (Lauraceae) with mostly scleromorphous leaves. Leaves of *M. kilimanjarica* (Euphorbiaceae), the most abundant tree in the canopy of the secondary forests, are larger and thinner, and hence probably more easily susceptible to leaching. The leaves of *P. aquilinum*, *R. steudneri* and other lianas on the clearings may cause the highest concentrations in throughfall. This hypothesis is supported by studies in an oak forest in Britain, where a high contribution of ground vegetation, consisting mainly of *P. aquilinum*, to total throughfall fluxes of K in the forest was observed (Carlisle et al., 1967). Moreover, a comparatively large amount of standing dead biomass within the shrub vegetation on the clearings might have further increased the nutrient content in throughfall through leaching of nutrients from the decomposing material.

Another reason for differences in throughfall fluxes might be the presence of epiphytic bryophytes at individual sites. These plants are known to absorb nitrogen, especially nitrate, but also other nutrients from passing and intercepted rainfall (Clark et al., 1998; Liu et al., 2002; Clark et al., 2005). Thus, nutrient absorption by the dense layers of bryophytes covering stems and branches of the old growth and to a lesser extent of the secondary forest trees might have reduced net enrichment of nutrients on the passage through the forest canopies as compared to the clearings where epiphytes were absent. This could be especially the case for NO_3-N, which was retained in the canopy of the forests at Mt. Kilimanjaro, but leached from the vegetation on the clearings.

4.2. High nutrient concentrations in seepage water on the clearings

In accordance to the second hypothesis, nutrient composition varied in seepage water between regeneration stages with overall highest nutrient concentrations for the organic layer percolate under shrub vegetation. As the water fluxes via throughfall were greatest at the clearings due to the reduced interception, the water fluxes via organic layer percolate are also expected to be greater in the clearings than in the forests. This was confirmed by the amount of water collected in the organic layer percolate collectors, but as these amounts do probably not reflect the true quantities of seepage water, they were not used to calculate nutrient fluxes. Still, with both concentrations and expected water fluxes being higher at the clearings, nutrient fluxes in the organic layer percolate predictably make the differences measured in solute concentrations between the vegetation types even more apparent.

The organic layer percolate was collected below the root mat at the lower boundary of the Oa horizon. This implies that the concentration of the seepage water is the result of elements leached from fresh litter or released by mineralization, nutrient uptake by plants or mycorrhiza, and ion exchange with soil constituents. Water and nutrient demand, and thus uptake, are both expected to be lower on the clearings as compared to the adjacent forest. Since uptakes of water and nutrients counteract on nutrient concentrations, the overall effect on differences between vegetation types is not predictable from the present data. Another reason for the enhanced concentrations on the clearings may be related to differences in mineralization rates. The latter is usually raised by an increase in temperature, moisture and litter quality (Prescott, 2005). Higher temperatures together with higher nutrient contents in the litter (N, K, Ca) observed on the clearings could have enhanced the decomposition in the litter layer. But besides mineralization, also accumulation of SOM seemed to occur on the clearings, since on clearings dominated by *P. aquilinum*, hardly decomposed fern litter accumulated at the soil surface. Following the invasion of *P. aquilinum*, Johnson-Maynard et al. (1997) observed higher organic matter enrichment at these sites as compared to forests. This indicates that leaves of *R. steudneri* and other lianas present on the clearings at Mt. Kilimanjaro might be easier decomposable than bracken litter and hence more important for the nutrients in the organic layer percolate. It is possible that also older material from the former forest litter layer is mineralized on the clearings.

While concentrations of the topsoil soil solution for some ions also differed significantly between regeneration stages, these differences decreased with increasing soil depths and overall decreasing concentrations probably in relation to further plant uptake or adsorption to soil particles. The soil profiles reveal that on all study plots, roots are found to a depth of at least 1 m, where the deepest suction cups were buried. But these were far less numerous (1–10 roots per dm^2) than in the topsoil and the organic horizons (6 to >50 roots per dm^2). From forest sites in Panama there is some evidence for extensive lateral root systems of mature forest trees (Meinzer et al., 1999). Thus, it cannot be ruled out that some roots found at the clearings might also have invaded from the adjacent forest and removed additional nutrients from the soil solution.

4.3. Possible causes for the impeded forest regeneration on the clearings

The case of arrested succession in forest glades has often been reported in East Africa (Kasenene, 1987;

Chapman and Chapman, 1997; Babaasa et al., 2004). From the results obtained by our study, a degeneration of the soil nutrient status following forest clearance, as suggested by the third hypothesis, can be ruled out as a possible cause for the impeded forest regeneration. Contrarily, nutrient availability was even higher on clearings as compared to adjacent forests, while soil compaction hinting at a deterioration of physical soil conditions was also not observed. Thus, alternative reasons for the impeded forest regeneration might be ongoing disturbance by fire and other agents favouring bracken and suppressing natural regeneration (Kramer et al., 1995; Hemp, 2001; Hemp and Beck, 2001), or the absence of aggressive pioneer forest species able to compete with the current shrub vegetation on the clearings (Chapman et al., 1999).

4.4. Nutrient conservation

In the mature forests, most studied nutrients and especially base cations (K) exhibited low concentrations in the organic layer percolate and the soil solution, indicating overall low losses (see also Schrumpf et al., 2006). The litter produced by the forests has lower nutrient contents than that of the clearings, and leaching rates from the canopy were also small, indicating a better nutrient conservation. The nutrient cycle of the clearings on the other hand seemed to be more open with higher leaching rates from the vegetation as well as from the topsoil as compared to the forest sites. The scheme of enhanced nutrient cycling by higher litter nutrient contents and increased litter turnover rates are also known from a number of invasive exotic plant species which enter new ecosystems (Allison and Vitousek, 2004; Ehrenfeld, 2003). While the shrub vegetation on the clearings is not exotic, it still consists of highly competitive invasive species which might use a similar strategy to take advantage of the higher nutrient availability following forest disturbance and to hinder the regeneration of the natural forest at those sites. Overall, the impeded regeneration of forest vegetation on the clearings leads to long-term alterations of the nutrient cycle at those sites.

5. Conclusion

Our study showed that different aspects of the nutrient cycle on disturbed sites at Mt. Kilimanjaro are not only affected immediately after disturbance, but altered for decades by the impeded regeneration on the clearings. Nonetheless, and in contradiction to our first hypothesis, nutrient fluxes in throughfall appear not to be reduced when forest is replaced by shrub vegetation. Overall, the opening of the forest at lower elevations, resulting in a domination of shrub vegetation and secondary forests, led to a higher spatial and seasonal variability of nutrient concentrations in seepage water in the area, with an overall increase in concentrations of dissolved nutrients apparent in the upper soil layers. The higher nutrient concentrations in seepage water observed on clearings support- our second hypothesis and is probably the result of higher litter turnover rates caused by higher litter nutrient contents and warmer temperatures on the clearings. The overall differences in nutrient cycling between different forest regeneration stages with a closed nutrient cycle of the old growth forest and a more open nutrient cycle at the clearings with invasive pioneer species clearly deserve further attention in the light of ongoing deforestation in the tropics, leading to a strong increase in areas covered by secondary shrub and forest vegetation. Finally and in contradiction to our third hypothesis, the arrested regeneration on the clearings cannot be linked to nutrient deficiencies.

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