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Calcium, potassium, and magnesium cycling in a Mexican tropical dry forest ecosystem

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Abstract. We estimated the fluxes, inputs and outputs of Ca, K, and Mg in a Mexican tropical dry forest. The study was conducted in five contiguous small watersheds (12–28 ha) gauged for long-term ecosystem research. A total of five 80 × 30 m plots were used for the study. We quantified inputs from the atmosphere, dissolved and particulate-bound losses, throughfall and litterfall fluxes, and standing crop litter pools. Mean cation inputs for a six-year period were 3.03 kg/ha for Ca, 1.31 kg/ha for K, and 0.80 kg/ha for Mg. Mean outputs in runoff were 5.24, 2.83, and 1.79 kg/ha, respectively. Calcium, K, and Mg concentrations increased as rainfall moved through the canopy. Annual Ca return in the litterfall (11.4 g/m^2) was much higher than K (2.3 g/m^2) and Mg (1.6 g/m^2). Litterfall represented 99% of the Ca, 84% of the Mg, and 53% of the K, total aboveground return to the soil. Calcium concentration in standing litter (3.87%) was much higher than K (0.38%) and Mg (0.37%). These concentrations were higher (Ca), lower (K), or similar (Mg) to those in litterfall. Residence times on the forest floor were 0.86, 1.17, and 1.77 yr for K, Mg, and Ca respectively. Compared to the residence time for organic matter at the site (1.31 yr), these results suggest slow mineralization for Ca in this ecosystem. Budget estimates were calculated for a wet and a dry year. Results indicated that nutrients accumulated in the dry but that nutrients were lost during the wet year. Comparison of Ca, K, and Mg losses in stream water with the input rates from the atmosphere for the six-year period show that inputs are lower than outputs in the Chamela tropical dry forest ecosystem.

Introduction

Tropical dry forests (TDF) represent more than 40% of tropical forest areas (Murphy & Lugo 1986). Biogeochemical processes in these ecosystems have

not been studied as extensively as in the tropical moist forest. Nutrient fluxes include deposition, throughfall, litterfall, weathering, and runoff losses. Although some of these have been studied individually in TDF, none of the studies have included a more general and integrated treatment of these fluxes.

Several studies have reported nutrient fluxes in litterfall of TDF (Díaz 1997; Esteban 1986; Lambert et al. 1980; Lugo & Murphy 1986; Singh & Singh 1991a, b, 1993), where it represents the major pathway of nutrient return to the soil and a more synchronized pulse of nutrient return than in the wet tropics. Litterfall nutrient concentrations directly feed back on soil over a relative short time and provide an indication of soil nutrient availability in tropical forests (Vitousek 1984).

Basic cations such as Ca, K, and Mg play important roles in a variety of plant functions. Calcium, a non-toxic mineral nutrient, is predominantly active in cell walls and plasma membranes and participates in control mechanisms of plant growth and development (Marschner 1995). Magnesium is a key element in chlorophyll and other enzyme molecules. In contrast, K is not a constituent of organic structures but functions mainly as an osmoregulator and in the regulation of enzyme activities. From a biogeochemical perspective the dominant source of these cations is rock weathering and their loss in streamwater relative to their concentration in bedrock tends to be among the highest of several elements (Schlesinger 1997).

Cycling processes differ greatly among Ca, K, and Mg. Throughfall has been reported of major importance for K transfer in tropical moist forest, whereas litterfall represented the major flux for Ca (Vitousek & Sanford 1986). Magnesium tends to be intermediate in its tendency to retranslocate from plant foliage (Parker 1983). Available evidence suggests that primary production in some TDF may be limited by P availability (Jaramillo & Sanford 1995). However, Ca, K, and Mg have also been reported as limiting in Amazonian forests (Cuevas & Medina 1986, 1988).

One way to evaluate the relative importance of the soil as a nutrient source to an ecosystem is to compare the rates of nutrient inputs from the atmosphere with the rates of nutrients leaching out of the system (Jordan 1985). Input-output budgets for tropical forest ecosystems have been reviewed by Bruijnzeel (1991) but none of the studies included a tropical dry forest site. Also, a recent review of nutrient cycling in tropical dry forests (Jaramillo & Sanford 1995) did not report nutrient budget studies for this ecosystem. This suggests that comprehension of nutrient cycling in dry tropical regions is far from complete.

A long-term study on the structure and functioning of a tropical dry forest ecosystem in México (Sarukhán & Maass 1990) has included measurements of the rates of nutrient inputs and outputs, and of nutrient dynamics associated

with organic matter. In this paper we consider the cycle of the base cations Ca, K, and Mg. A first objective of our study was to estimate the cation input by precipitation and output in stream water. For this input-output study we used the watershed-ecosystem method (Likens & Bormann 1995). A second objective was to determine the relative importance of throughfall, litterfall, and litter decomposition in cation cycling of this tropical dry forest.

Study site

The study was conducted at the Chamela Biological Station, on the Pacific coast of Mexico (19°30′N, 105°01′W). This area is characterized by a mean temperature of 24.9 °C, with less than a 5 °C difference between the coolest and warmest months. Mean precipitation is 679 mm (García-Oliva et al. 1995), distributed mainly from June to October. Average runoff is 5.1% of the annual rainfall, and the mean infiltration rate is 13.7 mm/15 min (Cervantes et al. 1988; López Guerrero 1992).

The landscape consists of low hills (50–160 m in elevation) with convex slopes (26° in average). The predominant lithology includes Tertiary volcanic of rhyolitic and rhyodacitic composition and their tuff (Campo 1995). The annual weathering rate is over 600 kg/ha and the secondary mineral in soil is authogenic kaolinite (Campo 1995). The soils are young, shallow (0.5–1 m depth), poorly structured sandy loams (Orthens; Solís 1993). Organic matter content in the upper soil profile (20 cm) is 2.9%. Exchangeable cation concentrations are 1744 mg/kg for Ca, 163 mg/kg for K and 435 mg/kg for Mg and the pH is 6.2 (Maass 1985).

The forest is dominated by deciduous trees, 6 to 10 m in height (Lott et al. 1987). Lott (1985) reports 758 plant species from 107 families for the Biological Station. Floristically, the Leguminoseae is the most important family with 15% of the species. Aboveground biomass is 85 Mg/ha (Martínez-Yrízar et al. 1992) and below-ground biomass ranges from 17 to 31 Mg/ha (Castellanos et al. 1991; Rentería 1997). With few exceptions, the species are leafless for several months each year and their phenology is driven by water availability (Bullock & Solís Magallanes 1990). Leaf area index varies between 1 m^2/m^2 and 4.5 m^2/m^2 during the year (Maass et al. 1995).

Methods

Five contiguous small watersheds (12–28 ha) were gauged for long-term ecosystem research (Sarukhán & Maass 1990). Three permanent plots were established along the altitudinal gradient on one of the watersheds (Watershed I). The rest of the watersheds (Watershed II to V) included only one

permanent plot at the middle position. Only the five middle position plots were used to study the nutrient fluxes in litterfall and throughfall, and the standing litter (see below). Each plot was 2400 m^2 (80 $\times$ 30 m) with the long axis perpendicular to the stream channel.

Input from the atmosphere

Calcium, K, and Mg entering the ecosystem by bulk deposition were measured during a 6-yr period (1990–1995). Samples were collected in six polypropylene bulk precipitation collectors maintained in cleared areas within a radius of 2 km from the study site. The precipitation collectors were made with polypropylene funnels (12 cm diameter) connected to 2 l polypropylene reservoirs by tygon tubing. Each reservoir was attached to a vapor trap and a vapor barrier formed by a loop in the tubing to prevent evaporation and gas exchange with the atmosphere. The entrance to the collector was covered with a thin layer of glass wool to prevent contamination from insects and bird excrement. The reservoir and tubing were kept from sunlight to avoid algal growth. Samples were stored in polypropylene containers, analyzed for pH and kept refrigerated. The collectors were cleaned with 10% HCl solution, rinsing with deionized water. The deionized water used for washing and rinsing the collectors was periodically analyzed to check for contamination through washing and manipulation.

Wet and dry depositions were sampled together after every rainfall event, thus a slight underestimation of nutrient input may have occurred as a result of an infrequent sampling of dry deposition during the rainless period.

Calcium, K, Mg, and Na entering the ecosystem were calculated by multiplying the rainfall amount by the element concentrations. Sodium measurements were included to determine the potential sources of the cations (Drever 1982). Rainfall amount was determined with two rain gauges and one recording rain gauge.

Losses from the watershed

Dissolved Ca, K, and Mg exported from the ecosystem were evaluated for a 6-yr period (1990–1995), in the five small watersheds. Coschocton wheels were used to sample the runoff water, which was stored in polypropylene containers (50 l capacity) following the same procedure as for the rain samples (see above). Drain water was collected after each event and analyzed accordingly. Nutrients were analyzed in 160 ml aliquots of drain water from each of the three containers and the five watersheds, for every runoff event. Fifty microliters of phenyl mercuric acetate solution (0.1 g in 15 ml dioxane diluted to 100 ml) were added to the samples which were kept refrigerated.

The volumes of drainage water were gauged with one water level recorder located at the mouth of each watershed.

Losses of particulate-bound Ca, K, and Mg, were estimated by collections of sediments and particulate organic material trapped at the mouth of the gauged watershed-ecosystem. Material was collected in three 10 cm, 5 cm and 2 cm mesh nets from water passing through the gauged weir and in a sediment trap behind the net at the weir during a 2-yr period (1993–1994). All organic material or sediments were collected, oven-dried (80 °C) and weighed after every runoff event. Particulate organic matter was ground in a Wiley Mill. Dissolved Ca, K, and Mg fluxes leaving the watershed were calculated as the product of the nutrient concentration in the runoff by the amount of water drained from the watershed. The particulate-bound Ca, K, and Mg exported from the watershed were estimated as the product of the nutrient concentration by the amount of organic matter or sediment output from the watershed.

Cation flux in throughfall

Throughfall was collected during the 6-yr period (1990–1995) from six collectors at the plot on Watershed I. Each collector consisted of a polyvinyl chloride (PVC) channel 0.1 × 2.0 m, drained by a tygon tubing into a polypropylene reservoir (22.5 l capacity). The PVC channel was covered with a thin mesh, 1 × 1 mm, and glass wool was placed at the mouth of the drainage tubing to prevent contamination from litterfall and litter debris. The reservoir was attached to a vapor trap similar to bulk precipitation collectors. Reservoir and tubing were kept from sunlight to avoid algae growth. Water samples were treated as described for the rainfall samples. Collectors were cleaned after every sample collection with a 10% HCl solution, rinsing with deionized water. The deionized water used for washing and rinsing the collectors was periodically analyzed to check for contamination through washing and manipulation.

Calcium, K, and Mg returned to soil in throughfall was determined by multiplying the throughfall amount by its element concentration. Net nutrient throughfall was calculated by subtracting element mass in the bulk deposition. As bulk precipitation collectors are inefficient in collecting dry deposition, the results could overestimate nutrient flux to the soil by canopy leaching.

Cation flux in litterfall

Flux was calculated multiplying litterfall production by its cation concentrations. Production data came from a long-term study (A. Martínez-Yrízar pers.

comm.) in which 24 litter traps (50 cm in diameter), located in each of the five plots previously described, are collected monthly. Cation concentration was determined in samples for a one-year period (1991).

Cation pools in litter

Cation pools were calculated multiplying standing litter mass by cation concentrations. Standing litter on the forest floor was sampled in Watersheds I and IV during 1991 (Martínez-Yrízar & Sarukhán 1993). Litter was collected from twelve 20 cm diameter microplots in January, May, September, and November. The material was oven-dried at 80 °C, weighed, and ground in a Wiley Mill.

Chemical analysis

Rainfall, throughfall, and runoff samples were filtered to remove the suspended material. Sediment samples were air-dried and ground to pass a 2 mm sieve. Exchangeable Ca, K, and Mg were extracted with 1 N NH_4OAC (pH 7). Calcium, K, and Mg in particulate organic matter, litterfall and litter samples, were determined with 0.5 g samples and were dry-ashed at 500 °C for 2 hs. The ash was dissolved in 5 ml of 4 N HCl solution. The solution was filtered and then diluted to 50 ml with deionized water. Potassium and Na were analyzed by flame emission, and Ca and Mg by atomic absorption, atomizing in air-acetylene flame. One ml of lanthanum (La) solution (29 g La_2O_3 in 250 ml HCl, diluted to 500 ml) was added per 10 ml sample (APHA 1992). Concentrations were corrected with deionized water blanks.

Statistical analysis

Differences in concentrations of Ca, K, and Mg between bulk deposition and runoff waters were determined by a one-way analysis of variance (ANOVA). Correlations among throughfall fluxes with rainfall depth, throughfall depth, open rain concentrations of each mineral and rain pH were performed. Spatial and temporal variation of cation fluxes in litterfall and throughfall and pools in the forest soil were analyzed by ANOVA. The Honest Significant Difference (HSD) test was used when statistical differences ($p < 0.05$) were observed.

Results

Nutrient inputs and outputs

Inputs from the atmosphere

The annual mean rainfall during 1990–1995 was 753 mm, slightly higher than the mean of 679 mm for the period 1983–1990 (García-Oliva et al. 1995). Rainfall variation between years was very high (Table 1). Its pH during the study period was 4.7 ± 0.2 (mean and S.E.). Mean nutrient inputs by bulk deposition were 3.03, 1.31, and 0.80 kg/ha·yr for Ca, K, and Mg, respectively. Monthly Ca inputs, but not K and Mg, correlated positively to the rainfall pattern ($r = 0.66$, $p < 0.005$).

Losses of nutrients from the watershed

Water does not flow continuously in the Chamela experimental watershed streams. Between one and six runoff events per year occurred during the study period with a mean annual runoff of 86 mm (Table 1). Concentrations of dissolved Ca, K, and Mg in stream water were higher than in bulk deposition. A yearly comparison of runoff losses from the ecosystem with input rates from the atmosphere showed that leaching loss was generally higher.

The amounts of organic particulate matter and sediments transported from hillslopes were highly dependent on large runoff events ($r = 0.74$ and $r = 0.62$, $p < 0.01$). Some 75% of total particulate matter losses were as sediments (Table 2). Interestingly, between 72% and 82% of minerals exported were bound to organic particulate matter. Particulate matter and sediments represented a minor cation loss (1.2, 0.1, and 0.3% of Ca, K, and Mg total losses, respectively) during a wet year (1993). However, their contribution to total nutrient output in a dry year (1994) was 39.1, 3.2, and 38.5% for Ca, K, and Mg total losses, respectively.

Intrasystem cycling

Ca, K, and Mg in throughfall

The proportion of the rainfall which reached the forest floor as throughfall between 1990 and 1995 was 76.5 ± 2.1% (S.E.). Concentrations of Ca, K, and Mg increased as rainfall moved through the canopy. The annual mean values (with S.E.) for this period were 0.93 ± 0.07 for Ca, 5.67 ± 0.52 for K, and 0.99 ± 0.14 mg/l for Mg. The amounts of minerals in throughfall were 0.127 ± 0.048, 2.066 ± 0.260, and 0.294 ± 0.054 g/m^2, for Ca, K, and Mg, respectively (mean and S.E.).

Four causal factors were tested against the throughfall fluxes: (1) rainfall depth, (2) throughfall depth, (3) open rain concentrations of each mineral,

Table 1. Annual nutrient inputs via bulk deposition and output in stream water for the Chamela tropical dry forest, Mexico. Values are averages and standard errors in parentheses.

Year	Rainfall/	Ca		K		Mg	
	Runoff (mm)	(mg/l)	(kg/ha)	(mg/l)	(kg/ha)	(mg/l)	(kg/ha)
Inputs							
1990	563	0.36	1.61	0.44	1.76	0.15	0.63
		(0.06)	(0.21)	(0.06)	(0.19)	(0.02)	(0.06)
1991	709	0.34	2.54	0.14	1.02	0.12	0.51
		(0.04)	(0.31)	(0.03)	(0.13)	(0.02)	(0.06)
1992	1094	0.54	3.49	0.21	1.54	0.12	1.36
		(0.08)	(0.42)	(0.04)	(0.23)	(0.03)	(0.15)
1993	960	0.82	7.42	0.17	1.83	0.07	0.79
		(0.11)	(0.89)	(0.02)	(0.19)	(0.01)	(0.04)
1994	435	0.64	1.82	0.36	1.12	0.24	0.83
		(0.04)	(0.11)	(0.07)	(0.22)	(0.01)	(0.03)
1995	757	0.35	1.30	0.19	0.61	0.18	0.68
		(0.04)	(0.14)	(0.03)	(0.08)	(0.02)	(0.06)
Average			**3.03**		**1.31**		**0.80**
Outputs							
1990	17	8.28	2.05	5.00	1.01	1.85	0.62
		(0.79)	(0.48)	(0.41)	(0.14)	(0.22)	(0.12)
1991	<1	14.82	0.03	4.59	0.01	1.08	<0.01
		(2.74)	(0.02)	(0.57)	<(0.01)	(0.12)	<(0.01)
1992	216	6.92	15.19	3.35	6.44	1.06	2.51
		(0.92)	(1.09)	(0.30)	(0.71)	(0.14)	(0.34)
1993	119	7.54	9.48	3.74	4.82	2.97	3.57
		(1.02)	(1.40)	(0.31)	(0.80)	(0.31)	(0.51)
1994	2	4.34	0.07	3.91	0.06	1.05	0.01
		(0.23)	(0.02)	(0.16)	(0.02)	(0.12)	<(0.01)
1995	163	3.68	4.64	3.37	4.62	3.01	4.04
		(0.56)	(0.82)	(0.38)	(0.43)	(0.35)	(0.45)
Average			**5.24**		**2.83**		**1.79**

Table 2. Nutrient output in particulate organic matter and in sediments for the Chamela tropical dry forest, Mexico. Values are averages and standard errors in parentheses.

Year	Dry mass		Ca		K		Mg
Particulate	(kg/ha)	(%)	(kg/ha)	(%)	(kg/ha)	(%)	(kg/ha)
1993	4.33	2.74	0.120	0.14	0.004	0.25	0.011
	(0.46)	(0.13)	(0.018)	(0.02)	(0.001)	(0.01)	(0.001)
1994	1.26	3.50	0.045	0.13	0.002	0.27	0.004
	(0.36)	(0.12)	(0.012)	(0.01)	<(0.001)	(0.01)	<(0.001)
Average			**0.083**		**0.003**		**0.008**
Sediments	(kg/ha)	(ppm)	(kg/ha)	(ppm)	(kg/ha)	(ppm)	(kg/ha)
1993	19.31	2067	0.040	140	0.002	303	0.006
	(1.44)	(100)	(0.005)	(14)	<(0.001)	(14)	<(0.001)
1994	1.22	1783	0.002	119	<0.001	287	<0.001
	(0.74)	(576)	<(0.001)	(22)	<(0.001)	(70)	<(0.001)
Average			**0.021**		**0.001**		**0.003**

and (4) rain pH. The quantities of Ca and K leached were correlated with the amount of throughfall ($r = 0.48$ and $r = 0.42$, respectively; $p < 0.001$), and correlations with rainfall depth were slightly lower ($r = 0.29$ to 0.35, $p < 0.05$). Magnesium flux was significantly correlated only to the ion concentration in the rainfall ($r = 0.45$, $p < 0.01$). No significant correlations were observed between minerals in throughfall and pH ($r = 0.01$–0.12; $p > 0.5$).

Ca, K and Mg in litterfall

Nutrient concentrations in the litterfall varied during the year except for Ca (Table 3). Potassium concentration was higher in the dry than in the rainy season ($F = 191.82$, $p < 0.0001$). However, Mg concentration was greater in the wet than in the dry season ($F = 39.14$, $p < 0.0001$). Variation among plots was generally very low and the differences were not significant ($p > 0.05$).

Annual litterfall production during 1991, the year from which samples were chemically analyzed, did not differ significantly from long-term litterfall production (395 g/m^2·yr) at the study site (Martínez-Yrízar & Sarukhán 1990; Martínez-Yrízar 1995; Table 3). The annual Ca return was much higher than K and Mg. Differences between wet and dry periods in cation returns largely

Table 3. Concentrations and amounts of minerals in litterfall in the Chamela tropical dry forest, Mexico. All values are averages and standard errors in parentheses.

Period	Dry weight	Ca		K		Mg	
	(g/m^2)	(%)	(g/m^2)	(%)	(g/m^2)	(%)	(g/m^2)
Dry season							
(January–June)	127.31	2.96	3.914	0.82	1.015	0.34	0.433
	(13.81)	(0.11)	(0.455)	(0.02)	(0.106)	(0.01)	(0.051)
Rainy season							
(July–December)	261.87	2.84	7.484	0.49	1.296	0.44	1.156
	(8.12)	(0.13)	(0.432)	(0.02)	(0.060)	(0.01)	(0.049)
Annual	389.17	2.90	11.398	0.66	2.311	0.39	1.589
	(16.19)	(0.08)	(0.662)	(0.02)	(0.130)	(0.01)	(0.077)

reflected litterfall mass variation. Thus, larger amounts of these minerals were returned in the wet season (F = 5.40 to 107.51, $p < 0.05$). Calcium and K amounts in litterfall were higher in Watershed II than in the other watersheds (F = 3.75, $p < 0.01$; F = 6.87, $p < 0.001$; respectively).

Pools in standing litter

Mean annual cation concentrations in standing litter followed the order Ca > K ≈ Mg (Table 4). The differences among sampling dates were significant (F = 11.28 to 113.53; $p < 0.0001$). Potassium and Mg concentrations were higher in the litter collected during January and May. Calcium concentrations were highest in May and September.

Potassium concentration in standing litter (Table 4) was lower than in the litterfall material (Table 3). Calcium concentration however, was about 1.3 times that in litterfall.

The amounts of minerals in the litter fluctuated through the year (Table 4). The differences reflected changes in the standing crop (F = 3.51, $p < 0.05$). Thus, lower amounts of minerals were observed during the rainy season (September and November), while the highest amounts were present in the dry season (F = 10.85 to 104.91, $p < 0.001$).

Table 4. Litter standing crop and cation concentrations and pools in the Chamela tropical dry forest, Mexico. All values are averages and standard errors in parentheses.

Season/ month	Dry weight (g/m^2)	Ca (%)	Ca (g/m^2)	K (%)	K (g/m^2)	Mg (%)	Mg (g/m^2)
Dry season							
January	565.19 (48.96)	3.16 (0.31)	18.666 (3.052)	0.69 (0.04)	3.636 (0.233)	0.44 (0.02)	2.399 (0.178)
May	580.23 (41.33)	5.43 (0.37)	32.111 (3.793)	0.53 (0.03)	2.905 (0.182)	0.37 (0.01)	2.105 (0.127)
Rainy season							
September	431.58 (34.13)	5.14 (0.26)	21.489 (1.622)	0.10 <(0.01)	0.436 (0.041)	0.33 (0.01)	1.444 (0.141)
November	468.04 (31.92)	1.76 (0.08)	8.546 (0.815)	0.21 (0.01)	0.941 (0.067)	0.33 (0.02)	1.512 (0.123)
Annual	511.26 (20.27)	3.87 (0.20)	20.203 (1.527)	0.38 (0.03)	1.980 (0.156)	0.37 (0.01)	1.865 (0.081)

Discussion

Sources of Ca, K and Mg for the ecosystem

There are at least three potential sources of nutrients in the rainwater: (a) sea salts, (b) aerosols and suspended particles from biomass burning, and (c) soil particles and biogenic gases from the terrestrial ecosystems and perturbed areas. Since the study area is only 2 km in-land from the Pacific coast, we expected that the potential contribution of solutes from marine sources would be important during the rainy season. However, cation/Na ratios in Chamela's bulk deposition were enriched above sea-salt ratios (Table 5). This suggests that the origin of Ca and K present in the bulk deposition at Chamela is predominantly terrestrial.

Annual Ca, K, and Mg inputs in bulk deposition (Table 1) are comparable to the lower end inputs of tropical moist forests reviewed by Bruijnzeel (1991). On the other hand, mineral concentrations in rainfall at Chamela are in the upper-end of those in tropical moist forests (Bruijnzeel 1989). Thus, the lower inputs may be due to the lower rainfall and not to lower cation levels.

Table 5. Nutrient: Na concentrations ratio in bulk deposition at Chamela, Mexico.

Year	Ca/Na	K/Na	Mg/Na	Reference
Sea salt	0.038	0.037	0.120	(1)
1990–1992	0.512	0.293	0.153	(2)
1993–1995	0.710	0.262	0.154	(2)

(1) Drever 1982; (2) this study.

Table 6. Annual dry mass and mineral content of litterfall in tropical dry forests; "n.d." indicates no data.

Site	Rainfall	Mass	Ca	K	Mg	Reference
	(mm)	(g/m^2)				
Mexico	753	389	11.4	2.3	1.6	(1)
India	821	578	3.6	1.6	n.d.	(2)
Mexico	826	489	6.9	3.9	4.1	(3)
Puerto Rico	860	480	n.d.	3.6	n.d.	(4)
Belize	1030	1260	37.3	5.9	3.2	(5)
Mexico	1100	422	12.0	6.2	1.2	(6)

(1) This study, Chamela; (2) Singh & Singh 1991a, b; (3) Jaramillo & Sanford 1995, Chamela; (4) Lugo & Murphy 1986; (5) Lambert et al. 1980; (6) Whigham et al. 1991, Yucatan.

Intrasystem cycling

Mineral fluxes in throughfall and litterfall

Total annual Ca, K, and Mg flux to the forest soil (net throughfall plus litterfall) was 11.5, 4.4 and 1.9 $g/m^2 \cdot yr$, respectively. Litterfall is the main pathway for Ca and Mg return to the soil in this tropical dry forest ecosystem (Table 3). Of the total aboveground return, 99% of Ca and 84% of Mg occurred in the litterfall. These figures are in the upperbound reported for tropical humid forests (80–90% for Ca and 65–85% for Mg; Parker 1983).

The amounts of Ca and K in litterfall in Chamela (this study; Jaramillo & Sanford 1995) were generally higher than in a tropical dry forest in an infertile site in India (Table 6), despite their similar annual litterfall production. In contrast, the dry forest of Belize showed an average litterfall production of 1260 $g/m^2 \cdot yr$ (Lambert et al. 1980) and a Ca flux considerably higher than in Chamela.

Rates of nutrient release in the forest floor

Surface litter decomposition has been considered one of the main pathways for nutrient cycling in tropical dry forest ecosystems (Kundu 1990). Mineral elements in the forest floor at Chamela increase during the dry season, possibly as a result of reduced microbial activity and leaching (Campo et al. 1998), and an increase in the litter standing crop (Martínez-Yrízar & Sarukhán 1993). The estimated mean residence time for organic matter in Chamela, calculated as the ratio of the litter standing crop to the annual litterfall production (Vogt et al. 1986), was 1.31 yr (A. Martínez-Yrízar pers. comm.). Annual mineral residence times calculated from Tables 3 and 4 were 1.77 yr for Ca, 0.86 yr for K, and 1.17 yr for Mg. The difference in residence times between organic matter and minerals reflect different rates of mineralization. A high leaching of K in the forest floor during the rainy season could explain its lower residence time. Potassium pools were very low in September (Table 4), when rainfall was high. Previously, Jaramillo and Sanford (1995) calculated residence times for foliar minerals in the forest floor of 1.71 yr for Ca, 0.39 yr for K, and 0.55 yr for Mg. The higher residence times for K and Mg in our study may be explained by a slower mineralization of these nutrients in woody litter. However, the residence times of Ca in the forest floor were similar in both studies and revealed the slow mineralization of this nutrient in the ecosystem.

The turnover times of Ca, K, and Mg in the forest floor of Chamela were higher than those reported for a fertile site in Belize (0.77, 0.48 and 0.76 yr, respectively; Lambert et al. 1980). These differences in nutrient release of nutrients to the forest soil could be related to a higher rainfall in Belize (1260 mm) than in Chamela.

Mineral balance

Our results showed that aboveground return (litterfall production) was large relative to atmospheric inputs and runoff water losses (Tables 1 and 3). Including the mineral flux in throughfall, average inputs represented about 2.6, 3.0 and 4.2% of the annual Ca, K, and Mg aboveground loss from the vegetation, respectively. Mean runoff nutrient losses were also lower than the aboveground plant nutrient return. Annual amounts of dissolved Ca, K, and Mg lost in stream water were only 4.5, 6.5 and 9.5% of the throughfall plus litterfall fluxes. This suggests that Ca, K, and Mg are held tightly within the ecosystem. Moreover, a comparison of inputs and streamwater losses to soil pools of 507, 98.5, and 165 kg/ha for Ca, K, and Mg in the first 6 cm of soil (García-Oliva & Maass 1998) indicates that soil nutrient supply greatly exceeds atmospheric inputs and losses in Chamela.

Although we do not have an accurate estimation of dry deposition, our measurements of particulate and sediment losses (Table 2) allow us to estimate approximate budgets for a wet (1993) and a dry (1994) year. During the dry year nutrient accumulation occurred (1.70, 1.06, and 0.82 kg/ha, for Ca, K, and Mg, respectively; calculated from Tables 1 and 2). However, net losses of Ca, K, and Mg were observed in the wet year (2.22, 3.00, and 2.80 kg/ha, respectively). Thus, wet years may produce losses that affect the nutrient economy of the ecosystem. Comparison of Ca, K, and Mg losses in stream water with the input rates from the atmosphere for a six year period (Table 1), show that inputs are lower than outputs in Chamela. The annual values probably represent fluctuations around a long-term mean input-output balance. If the ecosystem is not in succession or at least the soil is not aggrading, as the Chamela TDF appears to be, this could mean that the soil is being weathered at rates that exceed the nutrient uptake capacity of the plants (Jordan 1982). Preliminary weathering estimates suggest this may be true at least for Ca in this ecosystem (Campo 1995).

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