Biogeochemistry **37:** 159–172, 1997.

The nutrient budgets of a watershed and its forest ecosystem in the Taï National Park in Côte d'Ivoire

J.J. STOORVOGEL[1], B.H. JANSSEN[2] & N. VAN BREEMEN[1]
[1]*Dept. of Soil Science and Geology, Agricultural University, P.O. Box 37, 6700 AA Wageningen, The Netherlands;* [2]*Dept. of Soil Science and Plant Nutrition, Agricultural University, P.O. Box 8005, 6700 EC Wageningen, The Netherlands*

Accepted 12 September 1996

Key words: Côte d'Ivoire, forest ecosystem, nutrient balance, nutrient cycling, rainforest, watershed

Abstract. Atmospheric inputs and stream water outputs of P, K, Ca and Mg were estimated for an undisturbed forested watershed and the forest ecosystem within it in Taï National Park, Côte d'Ivoire in 1990/91. The study included measurements of wet and dry deposition, and suspended sediments, organic debris and solutes in the water flows. Base flow as well as quick flow were sampled. The nutrient budgets of the entire watershed and the forest ecosystem (comprising vegetation and rooted soil layers) were distinguished on the basis of two assumptions (i) solutes in the base flow are derived from the soil layers below the rooted zone only, and hence not from the forest ecosystem; (ii) the total soil mass in the rooted zone remains constant, i.e. the export of topsoil material by erosion is compensated for by deepening the root zone. The first assumption was supported by the resemblance of the molar ratios of solutes in the base flow and those calculated for the weathering of the migmatite found in the soil layers below the rooted zone. It is concluded that the stocks of P, K, Ca and Mg in the watershed are decreasing with 1.4, 12.7, 15.3, and 8.1 kg ha^{-1} yr^{-1} respectively. Losses are mainly a result of nutrient exports by erosion and solutes in the base flow. Nutrient stocks for the forest ecosystem are also apparently decreasing, but to a much lesser extent, indicating the importance of distinguishing between the watershed and the forest ecosystem within.

Introduction

Nutrient cycling in tropical forest areas is a topic receiving increasing attention (Proctor 1989; Bruijnzeel 1991; Noij et al. 1993). Nevertheless, many aspects are still poorly understood and many data sets are incomplete (Proctor 1989). On the basis of their apparent stability, tropical forest ecosystems are often considered to be in a steady state with regard to their nutrient status. This implies that the sum of nutrient inputs would equal the sum of nutrient outputs. Bruijnzeel (1990) has shown, however, that the budget of tropical forest watersheds for specific major nutrients may be positive or negative (inputs $>$ or $<$ outputs).

Estimates of gross inputs and outputs of non-volatile nutrients usually refer to an entire forested watershed. Bruijnzeel (1991) suggested, however, that there may be a discrepancy between the nutrient budgets of a watershed and the budget of its biologically active part, the forest. The entire watershed and the forest ecosystem have the common inputs of dry and wet deposition, and the common outputs via erosion (loss of topsoil) and organic debris. The leaching output, however, is different for the systems. In the case of the entire watershed, it refers to the total export of solutes by the stream and in the case of the ecosystem to the export of solutes from the rooted soil only (see further under 'Materials and methods' for the estimation of these different leaching losses). When the roots enter the soil layer below the boundary of the rooted soil during the time period under study, the nutrients present in the newly rooted zone are considered as an input for the forest ecosystem. For the entire watershed, however, the tapping of a new soil layer by roots is an internal change.

In this paper, the term nutrient is used irrespective whether the nutrient is in an available form or not. The consequence of this decision is that processes like weathering of minerals and mineralization of organic matter are seen as internal nutrient transfers. The weathering of minerals in the soil, however, converts nutrients to a form prone to leaching and output as solutes.

This paper deals with both: it presents the nutrient budget of P, K, Ca and Mg for an entire forested watershed, and it gives a first approximation of the budget of the forest ecosystem (Figure 1). The latter is considered to include the vegetation and the rooting zone, i.e. the part of the soil profile from which the nutrients are taken up by the plant. The lower boundary of the proper forest ecosystem is in principle the imaginary borderline between the rooted and non-rooted soil, but in practice it may be difficult to identify that imaginary line. The maximum depth to which the soil is drained by the stream is seen as the lower boundary of the entire watershed. Hence, the soil layers below the rooted zone form the difference between the entire forested watershed and the proper forested ecosystem.

Materials and methods

The study area

This study was carried out in a 117 ha watershed in Taï National Park in the south west of Côte d'Ivoire at 5°52′ W longitude and 7°20′ N latitude during the period between 18 May 1990 and 15 March 1991 (Stoorvogel 1993; Stoorvogel et al. 1997). Impermeable ironstone occurs in approximate 12% of the watershed area, but generally the weathering zone is found below the rooting zone. Nutrients released in the weathered layer below the rooted zone are most probably leached to the stream. It is unlikely that there are

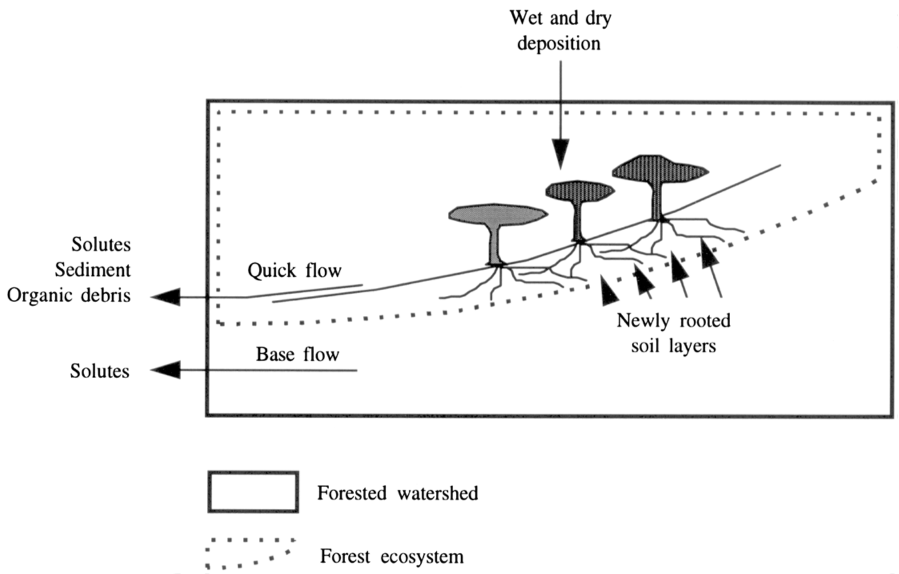

Figure 1. Gross inputs and outputs of a forested watershed (solid box) and its subsystem, the forest ecosystem (dotted box).

leaching losses to deep aquifers, because the weathered zone is underlain by essentially impermeable rocks of the Precambrium Basement Complex, consisting of granites and associated metamorphic rocks (Papon 1973; Bos 1964).

The watershed is covered with a humid evergreen forest (Van Rompaey 1993). The soils of the area form a toposequence from gravelly clay, plinthic Acrisols on the highest terrain positions to gravelly sandy clay, plinthic Ferralsols on the slopes and coarse sandy, dystric Gleysols in the valley bottom. This toposequence is typical for much of the humid tropical zone of West Africa (De Rouw et al. 1990). All soils are deeply weathered with few weatherable minerals at depths shallower than 3 m, but rooting depth may in some cases be restricted by hardened plinthic layers. The topography of the watershed is characterised by predominantly convex slopes of around 10% close to the crests and concave slopes of around 5% near the valley bottom. The valley bottom is flat to almost flat and around 200 meters wide with the creek in the centre. The creek originates from 4 small springs in the middle and upper slopes. The slightly meandering main stream channel is filled with coarse quartz sand, covered locally with a thin layer of decomposing organic debris. At the point were the creek leaves the watershed the valley bottom narrows to 88 meters.

The average annual rainfall is 1833 mm with a standard deviation of 338 mm, and the average annual temperature is 26 °C. Roughly two seasons can be distinguished. In the dry season between December and February when the Intertropical Convergence Zone (ITCZ) lays south of the area, winds are mainly northeastern and Harmattan dust is transported over West Africa. During the long rainy season from February to November, the ITCZ is situated north of the area and southwestern winds are dominant. The rainy season is usually interrupted by a short dry spell from August to October.

Nutrient input by wet deposition

Rainfall quantities were measured using three hand-operated rain gauges placed in natural gaps in the forest. To avoid contamination of rain water, samples were taken on a 2 ha open field used for meteorological observations and surrounded by primary forest, 3 km south of the watershed. Rain water was collected in a plastic hand-operated rain gauge, which was cleaned daily and of which the container was renewed daily. Due to the absence of rainfall in the dry season, no special measures were necessary to avoid contamination of rainfall samples with Harmattan dust. To preserve the samples two drops of chloroform were added and the samples were stored refrigerated at 11 °C. The electrical conductivity (EC) and pH were measured for all 98 samples within two weeks after sampling. Nineteen rain water samples were selected in such a way that they covered the whole range in rainfall and time and analyzed for P, Al, Si, NH_4 (by Autoanalyser Technicon II), Ca, Mg, Fe, Mn, K, Na (by AES Perkin Elmer 560), Cl, NO_3, SO_4 (by HPLC Waters 510), C_{total} and $C_{inorganic}$ (by TOC analyser Thermo Instruments type 555) within three months after sampling.

Nutrient input by newly rooted soil layers

It was assumed that the total soil mass in the rooted zone remained constant, i.e. that the export of topsoil material by erosion was compensated for by deepening the root zone. The nutrients present in the newly rooted zone were considered as an input into the forest ecosystem. This input was calculated as the product of soil mass in the newly rooted zone and nutrient mass fractions. Soil mass was set equal to the mass of suspended sediments leaving the catchment (see ‘Nutrient output by sediment’). Nutrients mass fractions were derived from Fraters (1986); they refer to the fine earth of weathered subsoil material sampled at a depth of 1.3 m at the middle slope. These samples were chosen as reference because erosion was strongest at this position on the slope.

Nutrient output by solutes

The hydrology of the watershed had been studied by Casenave et al. (1980, 1981, 1984), who provided complete water balances for the period 1979–

1982. They had constructed a 88 meters long weir in the valley bottom and measured water flow continuously in the outlet point. In addition, rainfall was measured at six locations within the watershed. The hydrographs of the watershed are characterised by a continuous low discharge base flow, and distinct quickflow peaks during and shortly after rainfall. On the basis of the discharge data collected by Casenave et al. (1980, 1981, 1984), the hydrological balance was modeled to obtain appropriate hydrological data for the study period between 18 May 1990 and 15 March 1991 (Stoorvogel 1993). The model calculates daily base flow and quickflow discharges using rainfall data of the previous 90 days and the relative water storage in the watershed. The model was verified by water level measurements in the study period. The modeled discharges showed correlation coefficients of 0.92 and 0.88 for base flow and quick flow respectively. Although no data are available to check the constancy in hydrology for the watershed, these high correlation coefficients indicate that no major changes in hydrology occurred between 1979 and 1991.

Whereas all solutes are exported from the watershed, they only partially originate from the forest ecosystem. Quick flow is mainly the result of surface runoff. It is, therefore, likely that solutes exported with quick flow originate from the forest ecosystem proper. Base flow, on the other hand, passes deep soil layers and the weathering zone. In view of the low soil fertility in the catchment, we assumed that most of the solutes in base flow originate from the relatively rich weathering zone (see below). Solutes in an organic form in base flow, however, are leached from the root zone.

Water samples from the base flow were taken daily. Quickflow water was sampled for every 25 cm of rise and drop of the water level using automatic water samplers. In all water samples the pH and EC were measured. A part (13%) of the samples, covering the entire range of water levels and sampling dates, was selected for chemical analysis. The same procedures were used as for the rain water samples. In 10 base flow samples the total (inorganic plus organically-bound) P was analyzed after 0.4 M HNO_3 digestion of freeze-dried water residues.

To test the assumption that base-flow nutrients originate from the weathering process, one sample of migmatite representative for the bedrock of the watershed was analysed by X-ray fluorescence spectroscopy, and the ratios of solutes that would result from its weathering were calculated. The method of Brown & Skinner (1974) was followed for the calculation of the normative mineralogical composition, assuming that typical granite minerals were present, viz. quartz, K, Na, and Ca feldspars, Mg or Mg-Fe^{II} biotite, and either augite ($Na(Al_1Fe^{II}_{0.75})(Si_{0.5}Al_{1.5})O_6$) and hornblende

$(Ca_3Fe^{II}_5(Al_2Si_6)O_{22}(OH)_2)$, or an amphibole with an Al_2O_3-$6SiO_2$-H_2O skeleton.

Nutrient output by sediment

Erosion may play an important role in Taï forest. Several large gullies of more than 2 m deep occur in the watershed and sheet erosion was observed in the field during heavy rainfall. Casenave et al. (1980) assessed the erosion rate for 1979 at 1.5 ton ha^{-1}. In this study suspended sediment concentrations were assessed using the same sampling scheme as for solutes, taking samples of 3 liters during base flow and samples of 2 liters during quickflow. All samples were filtered over a Whatman 542 ashless filter and the residues were dried and weighed. A part (5%) of the samples was selected covering the entire range of sediment concentrations and water levels. In the selected samples, loss on ignition (900 °C) was determined, after which the samples were melted with lithium borate and analyzed for their elemental composition on a Philips X-ray fluorescence spectroscopy assembly.

Nutrient output by organic debris

Organic debris leaving the watershed through the creek was collected using two bow nets which were placed in the creek. The first bow net was made of 5 cm wire netting and the second was made of fine 1 mm netting. These nets collected all material leaving the watershed through the creek. Three nets of the last type were placed on the flood plain to sample organic debris during very high runoff when the valley bottom was submerged, which occurred 10 times during the study period. The collectors in the creek were emptied daily, whereas the collectors on the flood plain were emptied after high floods occurred. A sub-sample was taken for each of the collectors which was divided over three categories of organic debris: leaves, branches and fruit (including flower material). The samples were dried and weighed and about 10% was selected for chemical analysis. After digestion in a H_2SO_4-Se-Salicyclic acid mixture with addition of H_2O_2, N and P were determined by absorption spectrophotometry, K and Ca by flame photometry and Mg by atomic absorption spectrometry (Walinga et al. 1989).

Results

Nutrient input by wet deposition

The total amount of rainfall in the study period was 1238 mm, which is slightly under the average. The pH of the rain water varied between 4 and 5

Table 1. Average concentrations (mmol m^{-3}) of solutes in rain water (17 samples) and creek water (53 samples). Standard deviations in parentheses.

	Rain	Creek
P	0.04 (0.2)	0.9 (1)
K	3 (3)	55 (12)
Ca	6 (5)	107 (40)
Mg	1 (1)	70 (25)
Na	4 (2)	232 (77)
Fe	1 (2)	26 (12)
Mn	0 (0)	0 (0)
Al	0 (0)	4 (5)
$N\text{-}NH_4$	5 (7)	1 (3)
$N\text{-}NO_3$	6 (7)	3 (8)
Cl	7 (6)	75 (19)
SO_4	2 (5)	4 (5)
Si	1 (2)	580 (288)
C_{total}	719 (748)	2731 (918)
$C_{inorganic}$	105 (60)	526 (214)

and the EC between 4 and 10 μmho cm^{-1}. Average nutrient concentrations are presented in Table 1. Significant relations were found between rainfall and EC (slightly negative, $r^2 = 0.82$) and between EC and concentrations of K ($r^2 = 0.58$), Ca ($r^2 = 0.49$) and Mg ($r^2 = 0.82$). All regression slopes were significant at a 95% confidence level. These correlations were used to estimate nutrient inputs. No significant correlation was found for P, and therefore an average P concentration was used to estimate P inputs by rain water. Using daily rainfall figures from 1966–1991, the average annual nutrient input by rain was estimated to be 0.02 kg of P, 3.5 kg of K, 6.5 kg of Ca and 0.9 kg of Mg per ha.

Nutrient input by dry deposition (Harmattan dust)

Stoorvogel et al. (1997) reported dry deposition inputs of 80 kg ha^{-1} yr^{-1} with a nutrient input by dust deposited in the 1990/1991 season estimated at 0.11 kg of P, 2.5 kg of K, 3.5 kg of Ca and 0.4 kg of Mg per ha.

Nutrient input by newly rooted soil layers

The total soil mass in the root zone was assumed to be constant for the proper forest ecosystem. The soil mass in newly rooted soil layers was, therefore, set equal to the sediment export. Sediment export was estimated at 1.8 t ha^{-1} per

Table 2. Chemical composition (mass fractions of the oxide components in %) of Harmattan dust, sediment and Migmatite. Standard deviations in parentheses.

	Harmattan dust	Sediment	Migmatite
SiO_2	48 (3.4)	51.6 (4.3)	70.6
Al_2O_3	24 (3.6)	13.4 (1.6)	14.4
CaO	6.1 (0.6)	0.5 (0.1)	2.5
Fe_2O_3[1]	1.9 (0.4)	3.7 (0.6)	4.5
MgO	0.9 (0.0)	0.2 (0.0)	1.7
K_2O	3.7 (1.0)	0.6 (0.2)	2.1
Na_2O	0.7 (0.2)		3.2
TiO_2	0.3 (0.0)	0.9 (0.1)	0.5
P_2O_5	0.3 (0.0)	0.2 (0.0)	0.2
MnO	0.1 (0.0)	0.1 (0.0)	0.0
L.I.	11.4 (1.1)	28 (4)	0.9
Total	97 (0.0)	99 (1)	101

[1] Fe_2O_3 + FeO, expressed as % Fe_2O_3.

year (see below). According to Fraters (1986), mass fractions in weathered subsoil were 0.01, 0.05, 0.00 and 0.04%, for P, K, Ca and Mg, respectively. Hence, the mean annual inputs of these nutrients via the newly rooted soil layers are estimated at 0.18, 0.9, 0.0 and 0.7 kg ha^{-1} respectively.

Nutrient output by solutes

Base flow discharge varied between 0 and 2 l s^{-1}. The mean EC decreased with increasing discharge from 80 to 40 μmho cm^{-1}. The pH increased with increasing discharge and varied between 6.5 and 7. Table 1 gives the average stream water concentrations for the dissolved nutrients.

Assuming that the 1990/1991 solute concentrations are representative, the nutrient output between 1966–1990 was estimated on the basis of regression equations between simulated discharge and EC (r^2 = 0.62) and equations between nutrient concentrations and EC (with r^2 of 0.50, 0.55, 0.92, and 0.90 for P, K, Ca and Mg respectively). The average concentrations of major non-volatile nutrients in base flow are listed in Table 3. The export in base flow during an average year was 0.16 kg of P (of which 0.06 kg organically bound P), 5.8 kg of K, 13.9 kg of Ca and 5.5 kg of Mg per ha.

Water discharge during quickflows varied from 2 l s^{-1} to 1500 l s^{-1}. In general, the water level started to rise just after the beginning of a rainstorm and returned to the base flow level within 7 hours after the rain storm ceased. During quickflow the EC varied between 20 and 40 μmho cm^{-1} and the

Table 3. Flux weighted average nutrient concentrations in creek water (mmol m^{-3}).

	Quickflow	Base flow		
		Total	Inorganic	Organic
P	0.8	1.9	1.2	0.7
K	45	55		
Ca	65	128		
Mg	48	83		

Table 4. Mass fractions of nutrients in organic debris (g kg^{-1}). Standard deviations in parentheses.

	Branch	Leaf	Flower & fruit
N	8.1 (2.3)	10.2 (4.3)	13.1 (0.1)
P	0.3 (0.1)	0.6 (0.3)	0.6 (0.2)
K	0.7 (0.0)	1.5 (2.7)	1.1 (0.5)
Ca	14.8 (4.3)	7.0 (2.8)	12.1 (1.9)
Mg	1.4 (0.5)	1.2 (0.5)	1.7 (0.4)
Na	0.2 (0.1)	0.3 (0.3)	0.3 (0.1)

pH between 6 and 6.5. The average nutrient concentrations in quickflow are listed in Table 3. The average annual export (1966–1990) of nutrients with the quickflow, estimated on the basis of regression equations similar to the procedure followed for the base flow (with r^2 of 0.90, 0.93, and 0.95 for K, Ca and Mg respectively; for P no significant relation was found and an average value has been used), was 0.05 kg of P, 3.5 kg of K, 5.2 kg of Ca and 2.3 kg of Mg per ha.

For both base flow and quick flow, the variation found among the calculated values for the individual years was less than 10%. The apparent absence of extreme years makes the use of average years reasonable.

Nutrient output by sediment

The concentrations of suspended sediment did not exceed 15 mg l^{-1} in base flow, but they increased to 500 mg l^{-1}during quickflow. Highest sediment concentrations occurred at the beginning of the quickflow when it was still raining. Using the hydrological model and relationships between water level and mass fractions of suspended sediments for rising water levels (r^2 = 0.67) and falling water levels (r^2 = 0.78), the average annual (1966–1991) sediment export was calculated to be around 1.8 t ha^{-1}. The mass fractions of elements in the sediments are listed in Table 2. The total amounts of nutrients exported with 1.8 t of sediment were 1.35 kg of P, 9.4 kg of K, 6.2 kg of Ca and 1.6 kg of Mg.

Nutrient output by organic debris

The export of organic debris was 0.6 kg ha^{-1} for the study period. Using a relation between drainage and organic debris export the average annual export was calculated to be 0.8 kg ha^{-1}. The organic debris consisted of leaves (40%), branches (40%), and fruit and flower material (20%). Table 4 shows the mass fractions of nutrients for the different categories of organic debris. The high N/P ratios point to P being the limiting factor, thus confirming the findings by Jaffré (1985) and Van Reuler & Janssen (1989[A,B]). Total annual export of nutrients by organic debris will be less than 10 g ha^{-1} of P, K, Ca and Mg.

Discussion

The inputs and outputs for the entire forested watershed and for the forest ecosystem within it are summarized in Table 5. The balance of the entire watershed is negative for all four nutrients P, K, Ca and Mg. The values of the losses are in the same order as those reported by Bruijnzeel (1991). The largest outputs for P and K were via suspended sediments, and for Ca and Mg via solutes in base-flow.

Theoretically, the actual outputs of the watershed may have been still higher, because bed load was not considered. However, the fact that mass fractions of suspended sediments, on two occasions sampled simultaneously at five different points across the stream, varied less than 5%, suggests that bed load was not a big flux (Stoorvogel 1993).

We assumed that the base-flow nutrients were derived mainly from the soil layers below the rooting zone, where they go into solution by mineral weathering. A first indication that this assumption may be correct is the high Ca concentration in the base flow, whereas Ca is very low in the soil (Fraters 1986). The second indication is based on the composition of the migmatite bedrock (Table 2). Depending on the assumptions made, calculated normative quartz contents of the rock varied from 31 to 44%. For the calculation of the solute ratios, the quartz content was set at 37%, and further it was assumed that quartz was inert and all Al would be conserved in kaolinite, in accordance with the general mineralogy of the soils in the area. Molar ratios found in the base flow resembled those calculated for migmatite weathering (Table 6), with the exception that the values for K and Mg in the base flow were lower and corresponded better with those found in water draining from granite in Sierra Nevada. These data do not incontrovertibly demonstrate that the root

Table 5. Nutrient budgets of the entire forested watershed (I), and of the proper forest ecosystem (II) (kg ha^{-1} yr^{-1}).

	P	K	Ca	Mg
I Entire watershed				
Inputs				
Wet deposition	0.02	3.5	6.5	0.9
Dry deposition	0.11	2.5	3.5	0.4
Total	0.13	6.0	10.0	1.3
Outputs				
Solutes				
Quick flow	0.05	3.5	5.2	2.3
Base flow	0.16	5.8	13.9	5.5
Sediment	1.35	9.4	6.2	1.6
Organic debris	0.00	0.0	0.0	0.0
Total	1.56	18.7	25.3	9.4
Balance	**−1.43**	**−12.7**	**−15.3**	**−8.1**
II Forest ecosystem				
Inputs				
Wet deposition	0.02	3.5	6.5	0.9
Dry deposition	0.11	2.5	3.5	0.4
Newly rooted layers	0.18	0.9	0.0	0.7
Total	0.31	6.9	10.0	2.0
Outputs				
Solutes				
Quick flow	0.05	3.5	5.2	2.3
Base flow	0.06			
Sediments	1.35	9.4	6.2	1.6
Organic debris	0.00	0.0	0.0	0.0
Total	1.46	12.9	11.4	3.9
Balance	**−1.15**	**−6.0**	**−1.4**	**−1.9**

Table 6. Molar ratios of major solutes relative to Na in drain water from weathering granite in Sierra Nevada (Garrels & Mackenzie 1971), in Taï base flow, and as calculated for Taï migmatite weathering.

	Na		K		Ca		Mg		Si
Granite weathering	1	:	0.18	:	0.62	:	0.2	:	2.5
Taï base flow	1	:	0.21	:	0.46	:	0.3	:	2.7
Taï bedrock	1	:	0.45	:	0.43	:	0.41	:	2.7

Table 7. Approximate minimum and maximum values for inputs and outputs based on estimated ranges for the individual measurements (in kg ha^{-1} yr^{-1}).

	P		K		Ca		Mg	
	Min	Max	Min	Max	Min	Max	Min	Max
Inputs								
Wet deposition	0.01	0.10	0.9	4.0	3.2	9.3	0.7	1.8
Dry deposition	0.06	0.18	1.8	3.1	2.6	4.5	0.3	0.5
Total	0.07	0.28	2.7	7.1	5.8	13.8	1.0	2.3
Outputs								
Solutes								
Quick flow	0.01	0.09	3.1	4.4	4.6	6.8	1.9	2.8
Base flow	0.08	0.18	5.2	7.2	11.0	16.2	4.4	6.3
Sediment	1.25	1.44	7.6	11.1	5.1	7.4	1.4	1.8
Organic debris	0.00	0.00	0.0	0.0	0.0	0.0	0.0	0.0
Total	1.34	1.71	15.9	22.7	20.7	30.4	7.7	10.9
Balance for watershed	**−1.6**	**−1.1**	**−20**	**−9**	**−25**	**−7**	**−10**	**−5**

zone contributed little to the solutes in the base flow, but they support the distinction of the leaching losses from the entire forested watershed vs. those from the forest ecosystem within it. Using this assumption, we calculated that the balance of the forest ecosystem is less negative than that of the entire watershed due to the absence of base flow solute output plus the small input associated with newly rooted soil layers. The absolute values of the balance terms, however, are small: given the difficulties experienced during sampling and analysis, we are not able to conclude that the forest ecosystem nutrient stocks are decreasing.

Rough estimates for the error ranges in the various input and output terms of the watershed were established using the 95% confidence intervals for the different regression parameters and ranges in observed values (Table 7). Although the uncertainties in some of the measurements are high, the negative nutrient balances for the watershed are confirmed. The balance of the forest ecosystem is more uncertain due to the assumptions related to leaching losses (e.g. part of the nutrients in base flow may originate from the rooted zone and part of the nutrients released by weathering may be taken up by roots). Nevertheless, these results suggest that watershed scale analysis of nutrient balances do not necessarily reflect the conditions experienced by forests within the watershed. Our results indicate that nutrient stocks of the forest ecosystem in the Taï National Park may be in a steady state or slightly decreasing, whereas the nutrient stocks of the entire forested watershed appear to be decreasing, mainly because of nutrient exports from the soil layers below the rooted zone, and because of erosion from the middle slope area.

Acknowledgements

This study was carried out within the framework of the Tropenbos Programme, which is funded by the Tropenbos Foundation in Wageningen, The Netherlands. The intention of the Tropenbos Programme is to generate scientific data and tools for management and policy related to the conservation and wise use of tropical rain forests.

Soil and water samples were analysed at the Department of Soil Science and Geology, and vegetation and organic debris samples at the Department of Soil Science and Plant Nutrition of the Wageningen Agricultural University.

Dr. W.A. Blokhuis provided the sample of Taï migmatite representative for the bedrock of the watershed, and Edward M. Meijer calculated its normative mineralogical composition.

Two anonymous reviewers are acknowledged for their valuable comments.

References

Bos J (1964) Rapport de fin de levé des coupures Taï 4A-4C. B.R.G.M., SODEMI, Abidjan, Côte d'Ivoire

Brown TH & Skinner BJ (1974) Theoretical prediction of equilibrium phase assemblages in multicomponent systems. Am. J. Sci. 274: 961–986

Bruijnzeel LA (1990) Hydrology of Moist Tropical Forests and Effects of Conversion: A state of Knowledge Review. Free University, Amsterdam

Bruijnzeel LA (1991) Nutrient input-output budgets of tropical forest ecosystems: A review. J. of Trop. Ecol. 7: 1–24

Casenave A, Flory J, Mathieux A & Simon JM (1984) Etude hydrologique des bassins de Taï. Campagne 1981. ORSTOM, Adiopodoumé, Côte d'Ivoire

Casenave A, Flory J, Ranc, N & Simon JM (1981) Etude hydrologique des bassins de Taï. Campagne 1980. ORSTOM, Adiopodoumé, Côte d'Ivoire

Casenave A, Flory J, Guiguen N, Ranc N, Simon JM, Toilliez J & Tourne M (1980) Etude hydrologique des bassins de Taï. Campagnes 1978–1979. ORSTOM, Adiopodoumé, Côte d'Ivoire

De Rouw A, Vellema HC & Blokhuis WA (1990) Land unit survey of the Taï region, south-west Côte d'Ivoire. Tropenbos Technical Series 7. The Tropenbos Programme, Ede, The Netherlands

Fraters D (1986) A study of a catena in the Taï forest, Ivory Coast. MSc Thesis, Department of Soil Science and Geology, Agricultural University, Wageningen

Garrels RM & Mackenzie FT (1971) Evolution of Sedimentary Rocks. W.W. Norton, New York

Jaffré T (1985) Composition minérale et stocks de bioéléments dans la biomasse épigée de recrûs forestiers en Côte d'Ivoire. Acta Oecol. Plant. 6: 233–246

Noij IGAM, Janssen BH, Wesselink LG & Van Grinsven JJM (1993) Modelling nutrient and moisture cycling in tropical forests. Tropenbos Series 4. The Tropenbos Programme, Wageningen

Papon A (1973) Géologie et minéralisations du Sud-Ouest de la Côte d'Ivoire; synthèse des travaux de l'opération SACSA 1962–1986. SODEMI, Abidjan, Côte d'Ivoire
Proctor J (Ed) (1989) Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Blackwell Scientific Press, Oxford
Stoorvogel JJ (1993) Gross inputs and outputs of a forest ecosystem, Taï area, Côte d'Ivoire. Tropenbos Series 5, The Tropenbos Programme, Wageningen
Stoorvogel JJ, Van Breemen N & Janssen BH (1997) The nutrient input by Harmattan dust to a forest ecosystem in Côte d'Ivoire, Africa. Biogeochem. 37: 145–157.
Van Reuler H & Janssen BH (1989[A]) Nutritional constraints in secondary vegetation and upland rice in south-west Ivory Coast. In: Proctor J (Ed) Mineral Nutrients in Tropical Forest and Savanna Ecosystems (pp 371–382). Blackwell Scientific Press, Oxford
Van Reuler H & Janssen BH (1989[B]) Nutrient fluxes in the shifting cultivation system of south-west Côte d'Ivoire. I. Dry matter production, nutrient contents and nutrient release after slash and burn for two fallow vegetations. Plant & Soil 154: 169–177
Van Rompaey, RSAR (1993) Forest gradients in West Africa. A spatial gradient analysis. PhD thesis, Agricultural University, Wageningen
Vrins ELM, Hofschreuder P, ter Kuile WM, Oeseburg F & Alderliesten PT (1985) Het vangstrendement voor grof stof van de mens en van meetinstrumenten in de buitenlucht. Vakgroep Luchthygiëne en – verontreiniging. Landbouwhogeschool Wageningen
Walinga I, van Vark W, Houba VJG & van der Lee JJ (1989). Soil and Plant Analysis. Part 7: Plant Analysis Procedures. Department of Soil Science and Plant Nutrition, Agricultural University Wageningen