Biogeochemistry **32:** 115–142, 1996.

Mass balance of major solutes in a rainforest catchment in the Central Amazon: Implications for nutrient budgets in tropical rainforests

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Received 18 May 1995; accepted 13 September 1995

Key words: Central Amazon, nutrient budgets, tropical rainforests

Abstract. A solute mass balance for a 23.4 ha catchment of undisturbed rainforest in the central Amazon Basin was computed from detailed measurements of water and solute fluxes via rainfall, streamflow, and subsurface outflow over an annual cycle. Annual atmospheric deposition fluxes are lower than previously reported among mass balance studies conducted in the Amazon. Nutrient export fluxes are lower than previously reported for the Amazon, despite the fact that export fluxes via flow paths not previously measured were included. Given that climatic conditions were representative of a one in 10 wet year, the ecosystem was expected to show a net loss of nutrients rather than net gain. Instead, an excess of nutrient inputs via rainfall over ecosystem outflows was detected, ranging in annual quantities from 0.30 to 0.50 of the measured input. Among several mechanisms that could reconcile this budget, two are supported by the information presently available while two others cannot be evaluated without further research. Interannual variability in the amount of water available for runoff at the spatial scale of small catchments varies by a factor of two, in contrast to rainfall variability of ±20%, and may be a critical control on the apparent changes in ecosystem storage detected by annual-scale nutrient budgets in rainforests. Entrainment of materials from the terrestrial ecosystem to the atmosphere, including particulates containing elements which do not exist as gases, may be a particularly important loss pathway in rainforests existing on deeply weathered or nutrient poor soils.

Introduction

Atmospheric deposition has been widely accepted as a major input path for important nutrients in terrestrial ecosystems (e.g. Likens et al. 1977; Lindberg et al. 1989; Hedin et al. 1995). Jordan (1982) introduced the idea that the rainforest at San Carlos, in the northern Amazon, was maintained on nutrients derived from the atmosphere while input of nutrients from weathering of parent material was minimal, and later suggested (Jordan 1985) that despite the high potential for nutrient loss from leaching in rainforests, the potential for nutrient replenishment through precipitation may also be high. Important distinction has subsequently been made in recent reviews (Vitousek &

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Sanford 1986; Proctor 1987; Bruijnzeel 1991) between rainforests growing on nutrient-poor or deeply-weathered soils which receive nutrients mostly via rainfall (*cf.* Jordan 1982) versus forests located on soils where nutrients are also supplied from incompletely weathered parent material within the rooting zone (*cf.* Proctor 1989).

Bruijnzeel (1991) observed that considerable differences in annual-scale nutrient budgets have been reported among sites that may reflect differences in soil fertility, but also that there is considerable variability among sites with similar soils and moisture regimes that may reflect widespread methodological problems. In particular, the soils of the central Amazon are infertile and deeply-weathered, and represent a situation where site-specific differences in ecosystem-scale nutrient budgets should be minimal among sites (Bruijnzeel 1991; Lesack 1993a). Bruijnzeel further postulated that inconsistencies of mass balance results among sites that should behave similarly may be caused by chemical analysis problems, overestimation of atmospheric deposition inputs, underestimation of ecosystem export because of subsurface leakage, or because of differences in degree of basin incision by the outflowing stream relative to the bedrock weathering front. To this list, Lesack (1993a) added that underestimation of ecosystem export could also occur because of inadequate sampling of stream water chemistry during the frequent storms associated with rainforests.

As part of a study of the biogeochemistry of the central Amazon floodplain (Lesack 1988; Melack & Fisher 1990; Lesack & Melack 1995), we measured the mass balance of major nutrients and ionic solutes for a catchment of undisturbed rainforest adjacent to the Amazon floodplain over a one year period. Critical new information not available from previous studies includes propagation of measurement errors and evaluation of the representativeness of the measurements at time scales beyond the duration of the study period. Major findings published thus far are that our measurements of annual atmospheric deposition are lower than previously reported among mass balance studies conducted in the Amazon (Lesack & Melack 1991). This result is in reasonable agreement with recent estimates of atmospheric deposition fluxes derived from short-term observations during the wet and dry seasons by Andreae et al. (1990a). Our estimates of solute export flux are lower than previously reported for the Amazon, despite that export fluxes via flow paths not previously measured, such as subsurface flows and storm conditions, were included in our study (Lesack 1993a, 1993b). We report here the results of our mass balance measurements, evaluate possible mechanisms that could reconcile measurements of apparent nutrient retention during a one in 10 wet year, and evaluate the implications of these results for interpreting nutrient budgets in tropical rainforests.

Study area and methods

Our study was conducted on a 23.4 ha terra firme sub-basin within the local drainage basin of Lake Calado (3°15′ S, 60°34′ W), a floodplain lake in the central Amazon Basin, which is located 80 km upriver from the confluence of the Solimões (main stem of the Amazon) and the Negro River. Terra firme soils (beyond the geomorphological limit of the floodplain and never flooded by the river) within the area have been classified on the Projeto Radambrasil (1978) map series as yellow latosols. They probably fall within the oxisol category of the USDA (1975) soil taxonomy system and are similar to the forest soils of Reserva Ducke (to the north of the Negro River and 25 km northeast of Manaus), which have been studied previously by Nortcliff & Thornes (1978, 1981), Nortcliff et al. (1979), and Brinkmann & Santos (1973). Mean rainfall within the area during the previous 18 years was 2400 mm, with 1 in 10 wet and dry years respectively of about 2800 mm and 2000 mm (Lesack & Melack 1991). A complete description of the study area, soils, climate, and hydrology is provided by Lesack (1993b). A description of the hydrology of Lake Calado and its relation to the present study area is provided by Lesack & Melack (1995).

The mass balance of elements (or solutes) available to the biota in a catchment-scale unit of ecosystem can be represented as:

$$\delta S = I_P + I_W + I_B - E_R - E_B \tag{1}$$

where S is the mass of elements stored in the ecosystem; I_P, I_W, and I_B are the masses of elemental input to the ecosystem respectively via atmospheric deposition, rock weathering, and biotic processes; and where E_R and E_B are the masses exported respectively via hydrologic outflows and biotic processes. In the "classic" rainforest paradigm, I_W is considered to be small relative to the other terms because the soils are presumed to be highly leached and weathered to considerable depth. In the case of elements which do not have biologically mediated input and export pathways, the change in storage of the ecosystem reduces to the difference between the input flux via atmospheric deposition (I_P) and the export flux via hydrologic outflows (E_R). Over annual time scales, the change in storage or net balance approximates the net retention of elements in the ecosystem.

Considerable effort was made to obtain high-quality estimates of the solute input fluxes via rainfall (Lesack & Melack 1991) and export fluxes via hydrologic outflows (Lesack 1993a, 1993b), and to evaluate potential measurement errors (Table 1). To estimate the mass of solutes exported from the rainforest ecosystem, a calibrated v-notch weir and water level recorder was installed on a first-order stream draining a 23.4 hectare terra firme catchment. The

Table 1. Summary of expected errors for each of the parameters measured for the solute mass balance of the rainforest ecosystem. The total cumulative error was calculated assuming independence of component variances and standard propagation of error techniques (Taylor 1982), then was expressed as a fraction of the input flux via rainfall. The expected error assigned to parameters for propagation calculations are accepted literature values (*cf.* Winter 1983) for the measurement techniques employed. Sampling error is our best estimate of potential error in the representativeness of the water samples. Greater detail on propagation calculations is provided by Lesack (1993a, 1993b).

Parameter	Estimated values	% Error
Catchment area[a]	23.4 ha	3–4
Rainfall[b]	2870 mm	5–7
Element concentrations*	0.05–17 μM	
Sampling error[c]		10
Analytical error[c]		3
Baseflow runoff[d]	1562 mm	5
Element concentrations*	0.03–24 μM	
Sampling error[e]		4–18
Analytical error[c]		3
Stormflow runoff[d]	88 mm	15
Element concentrations*	0.04–39 μM	
Sampling error[f]		50
Analytical error[c]		3
Subsurface outflow[g]	42 mm	75
Element concentrations*	0.05–24 μM	
Sampling error[h]		50
Analytical error[c]		3
Total cumulative error/input flux		15–25

[a]Ground survey plus 1:30,000 stereo aerial photos (Lesack 1993b).
[b]One recording rain gauge plus two non-recording gauges (Lesack 1993b).
[c]Estimated from 123 samples of rainfall events and 60 samples representative of concurrent accumulations of bulk precipitation (Lesack & Melack 1991).
[d]V-notch weir calibrated in the field (Lesack 1993b).
[e]Estimated from 32 stream water samples (Lesack 1993a).
[f]Estimated from 36 stream water samples during 8 storms (Lesack 1993a).
[g]Nests of three piezometers installed to depths of 1 m, 2 m, and 4 m beneath the stream bed at three locations (Lesack 1993b).
[h]Estimated from 18 groundwater samples from the piezometer nests (Lesack 1993a).
*Representative concentrations for the range of elements.

drainage area is accurately known from extensive ground survey and interpretation of 1:30,000 stereo aerial photographs. To evaluate subsurface loss of groundwater from the catchment through the deeply weathered tropical soils, three nests of piezometers were installed into the stream bed. To estimate the mass flux of solutes exported from the catchment during baseflow conditions, the concentration of stream water solutes was measured every week to two weeks over a one year period (February 1984 through February 1985). To estimate the flux of solutes exported during the frequent storms that occur in the central Amazon, streamwater concentrations were measured during eight storms, which included five storms where multiple measurements of streamwater concentration were made during the course of the storm. The hydrograph separation technique of Hewlett & Hibbert (1967), and a two-source mixing model were used to partition the inferred contribution of solutes by stormflow water, from the background of solutes contributed by baseflow water. Estimates of solutes exported during the sub-set of storms where solute concentrations were measured were then extrapolated to the complete set of storms that occurred during the study period by regression techniques. To evaluate the potential flux of solutes exported in subsurface outflow from the basin, samples of groundwater were obtained from the piezometer nests installed into the stream bed during the period of maximum annual outflow, while concurrent measurements of hydraulic conductivity and hydraulic head were obtained to estimate groundwater flow rates. Complete methodological details and evaluation of the representativeness of the estimates of the water balance components and solute export fluxes are provided by Lesack (1993a, 1993b, 1988).

To estimate the input flux of solutes via rainfall at the gauged terra firme catchment, a combination of recording and non-recording rain gauges was installed near the weir site and samples from discrete rain events were collected from a floating laboratory that was anchored in the middle of Lake Calado. The rain collector was maintained clean, kept covered, and was only open during the course of storms. The concentration of solutes in rainwater was measured for 123 storms, ranging in size from 1 to 90 mm and representing *ca.* 60% of the total rainfall volume. Comparison of the frequency distributions of all storms that occurred, against the storms that were sampled indicated that the sampling was quantitatively representative. Average concentrations of bulk precipitation samples (wet plus dry) concurrently collected in the middle of the lake over 60 intervals during the same period were either not significantly different or were slightly lower, with the exception of P, than the event samples. Despite lack of universally accepted methods to measure dry deposition, bulk samples are prone to overestimate the deposition flux of large aerosols and particulates (Lindberg et al. 1989). Our data

therefore indicate no evidence of substantial dry deposition relative to the wet deposition flux at our study site. A complete description of the sampling methods, and evaluation of the representativeness of our estimates of atmospheric deposition are provided by Lesack & Melack (1991).

Chemical analysis of the water samples and quality assurance procedures followed during the course of this study are well described by Lesack (1993a) and Lesack & Melack (1991) and are summarized only briefly below. Considerable effort was taken to ensure that the analytical results were high quality and representative. Sample filtrations, subsampling, and measurement of pH were performed promptly after collection and thereafter samples were kept refrigerated at 4 °C until analyzed. pH and acid titrations were performed on aliquots of unfiltered water, while measurements for major solutes were performed on aliquots of water filtered through thoroughly rinsed Gelman A/E glass fiber filters and an all-plastic filtration apparatus. Within a day or two of sample collection, NH_4^+ was measured by the indophenol blue method (Strickland & Parsons 1972), NO_3^- by cadmium-copper reduction followed by formation of an azo dye (Wood et al. 1967), and PO_4^{3-} by the molybdenum blue-ascorbic acid method (Strickland & Parsons 1972). Total and total dissolved fractions of nitrogen (TN and TDN) and phosphorus (TP and TDP) were measured, respectively from unfiltered and filtered aliquots of sample, by the acid persulfate digestion technique of Valderrama (1981) with subsequent measurement of nitrogen as NO_3^- and phosphorus as PO_4^{3-}. Particulate fractions (PN and PP) were considered to be the difference between the total and the total dissolved fractions. Organic fractions (DON and DOP) were determined as the difference between the total dissolved and the inorganic fraction. The remaining major ions were measured in the laboratory at the University of California, Santa Barbara. Na^+ K^+, Ca^{2+}, and Mg^{2+} were measured by atomic absorption spectrophotometry. Cl^- and SO_4^{2-} were measured by Dionex ion chromatography. Based on the precision of the above methods (summarized in Lesack & Melack 1991), the ionic charge balances of the water samples (sum of measured cations less the sum of measured anions) have an analytical error equal to about 5% of the ionic sum. However, most samples showed a deficit of anions relative to ionic balance (DEF) which was significantly larger than the analytical error and probably reflects a variety of organic acids that were present in the samples but not measured (Lesack & Melack 1991).

Propagation of component measurement errors to obtain estimates of overall error associated with the total export fluxes of solutes are described in Lesack (1993a). Propagation of errors associated with the rainfall input fluxes and the net mass balance have not been previously published but followed the same procedures.

Results and discussion

Mass balance results and comparison with previous work

The mass balance results are based on stream gauging and water chemistry measurements obtained over the period from 21 February 1984 through 24 February 1985. Propagation of measurement errors associated with each component of the mass balance (Table 1) indicate that the net balance ($I_P - E_R$) of most of the solutes typically have expected errors equivalent to 15–25% of the input flux. Hence, we are not confident that solutes which show a net balance ranging from -0.25 to $+0.25$ of the input are distinguishable from measurement error. However, the values for almost all of the solutes are outside of this range and therefore appear to represent a real change in the storage of nutrients within the ecosystem.

Among the solutes measured during this study, only the net balance of H^+ is within the estimated range of measurement error (Figs. 1 and 2; flux values summarized in Table 2). Each of Na^+, Cl^- and NO_3^- show net losses from the catchment, while all of the remaining solutes in Figs. 1 and 2 accumulated within the catchment in significant quantities over the observation period. If all forms of nitrogen are treated together (TN), there is also net accumulation of nitrogen within the ecosystem.

An ideal characterization of the mass balance of a catchment-scale unit of forest ecosystem would be based on a long-term study where all the inputs and outflows were monitored through a full range of natural conditions including unusually wet and dry years. We are not aware of any study which meets this criteria that has yet been conducted in a relatively pristine system in the wet tropics. More typically, studies have thus far consisted of short-term investigations, rarely longer than 1–2 years, and where supporting data are not usually available to properly classify the observation period as representing wet, dry, or normal conditions (*cf.* Bruijnzeel 1991). This, in particular, has been the case for small catchment studies which have been conducted in the Amazon. Comparison of net nutrient balance among sites within the Amazon (Table 3) show that the values obtained during the present study are quite different from previous studies. The values are all low in magnitude relative to the previous studies and are all positive (excluding Na^+ and Cl^-), thereby indicating apparent net accumulation of nutrients with the ecosystem. By contrast, the previous studies show either relatively large net accumulations or relatively large net losses. Given that the results of the present study are based on a single year which was unusually wet, and not typical or average conditions, one could question why these results and comparisons are of general interest. One good answer is that the differences in net balance among

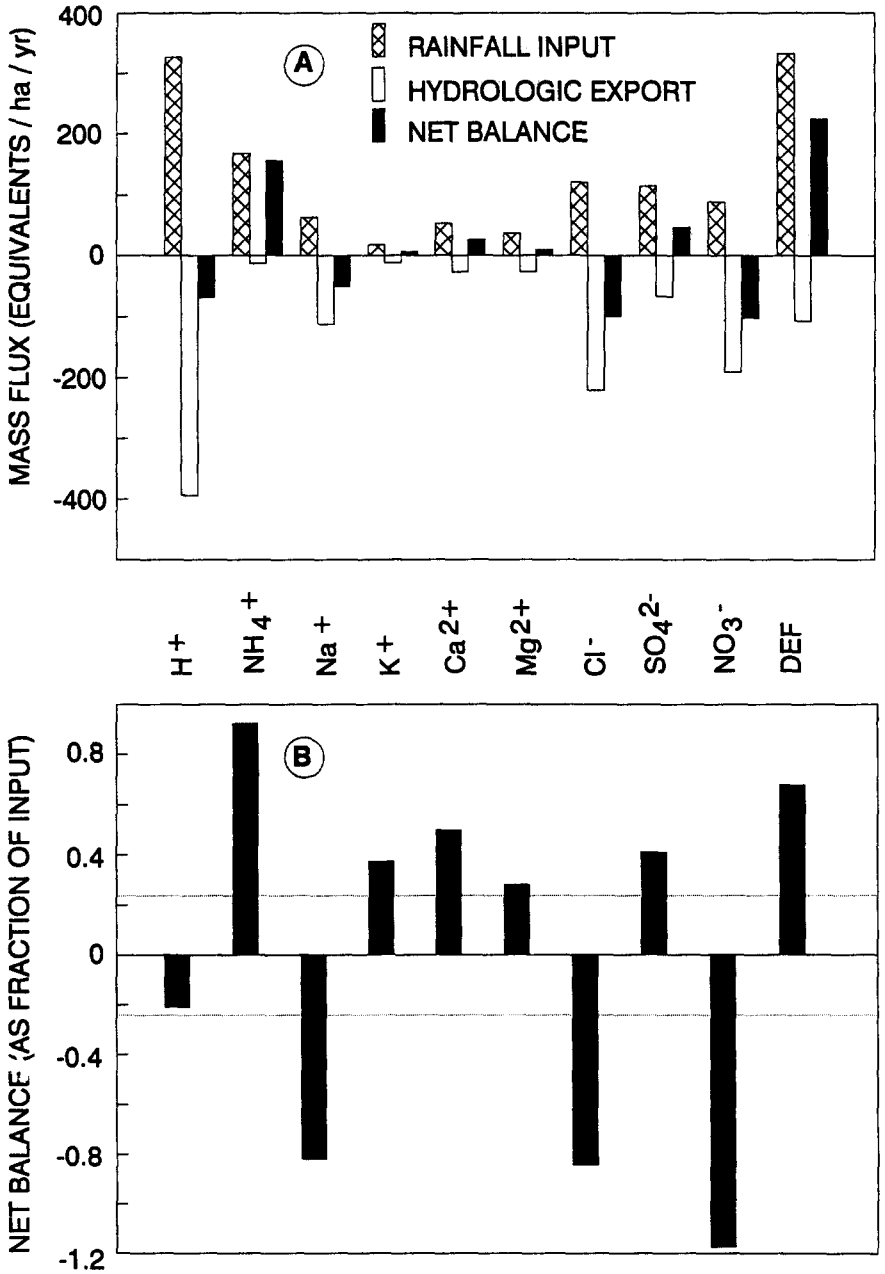

Fig. 1. Comparison of the rainfall input, hydrologic export (via streamflow plus subsurface outflow), and the net balance of major ions within the gauged unit of rainforest ecosystem during the period of study (A). Net balance is also shown expressed as a fraction of the rainfall input to the ecosystem (B). The dotted line in panel B represents a worst-case estimate of the measurement error associated with the net balance values.

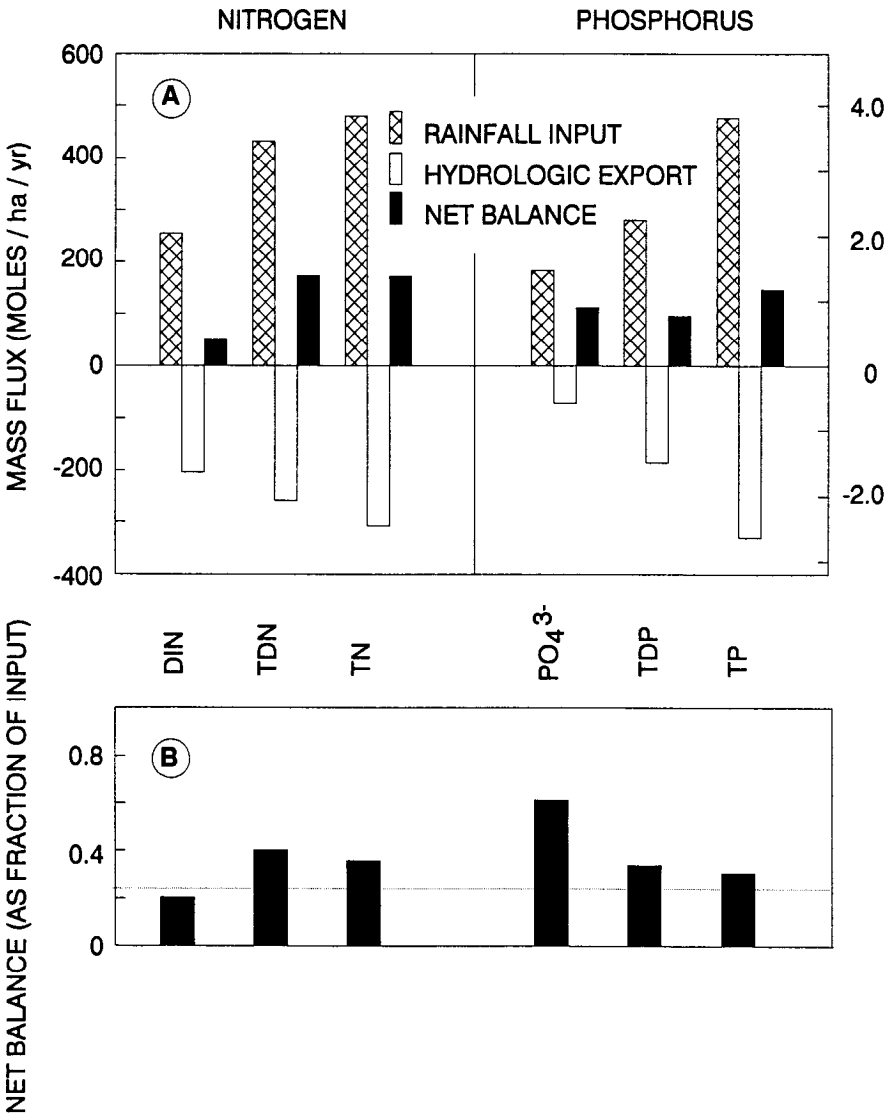

Fig. 2. Comparison of the rainfall input, hydrologic export (via streamflow plus subsurface outflow), and the net balance of nitrogen and phosphorus within the gauged unit of rainforest ecosystem during the period of study (A). Note the different scales of mass flux for nitrogen and phosphorus. Dissolved inorganic nitrogen (DIN) represents the sum of $NH_4^+ + NO_3^-$. Other forms of N and P are as defined in Table 2. Net balance is also shown expressed as a fraction of the rainfall input to the ecosystem (B). The dotted line in panel B represents a worst-case estimate of the measurement error associated with the net balance values.

Table 2. Summary of rainfall input and hydrologic export fluxes, and the net balance of solutes for the small catchment. Shown for comparison is the average annual rate of nutrient accumulation measured in an aggrading stand of forest at Hubbard Brook. DEF represents the deficit of anions relative to ionic balance and represents a measure of organic acids present (Lesack & Melack 1991). PN and PP respectively represent particulate nitrogen and phosphorus. DON and DOP respectively represent dissolved organic nitrogen and phosphorus.

Element	Rainfall input	Hydrologic export	Net balance[a]	Potential accumulation by an aggrading forest[b]
		Equivalents/ha/yr		
H^+	326	395	−69	
NH_4^+	168	13	155	
Na^+	62	113	−51	9
K^+	19	12	7	156
Ca^{2+}	53	27	26	474
Mg^{2+}	37	27	11	74
Cl^-	120	221	−101	
SO_4^{2-}	114	67	47	125
NO_3^-	88	191	−103	
DEF	332	107	225	
		Moles/ha/yr		
TN[c]	480	308	172	1190
TDN[d]	431	258	174	
TP[e]	3.8	2.6	1.2	90
TDF[f]	2.2	1.5	0.8	
PO_4^{3-}	1.5	0.6	0.9	

[a] Based on INPUT–EXPORT
[b] Values from Hubbard Brook (Bormann & Likens 1979)
[c] Sum of $NH_4^+ + NO_3^- +$ DON + PN
[d] Sum of $NH_4^+ + NO_3^-$ + DON
[e] Sum of PO_4^{3-} + DOP + PP
[f] Sum of PO_4^{3-} + DOP

the present and previous studies cannot be readily reconciled by differences in moisture regime during the periods of observation.

The relations between solute concentrations and stream discharge observed by Lesack (1993a) indicate that export rates of most solutes should

Table 3. Comparison of the estimated net balance of elements reported for small catchments within the Amazon rainforest. In the case of the Reserva Ducke measurements from 1968–72, the average runoff value represents only a rough approximation.

Element	Reserva Ducke[a] (1968–72)	Barro Branco[b] (1976–77)	Tonka[c] (Suriname)	San Carlos[d] (Venezuela)	San Carlos[e] (Venezuela)	Present
Annual Rainfall (mm):						
	2475	2070	2143	3565	3565	2870
Annual Runoff (mm):						
	825?	400	514	1595	2100	1692
			Equivalents/ha/yr			
Na^+		413	−465			−51
Cl^-		480	−34			−101
K^+		44	284	205	−2.6	7.0
Ca^{2+}	−32		409	349	−20	26
Mg^{2+}	−26		−156	230	−66	10.5
SO_4^{2-}			306			47
			Moles/ha/yr			
TN	−1710	414	1330	−186	−550	173[f]
TP	3.2	3.1	19.4	−178	9.7	1.2[g]

[a] Brinkmann (1983, 1985)
[b] Franken & Leopoldo (1984)
[c] Poels (1987)
[d] Based on soil water lysimetry (not a catchment budget) from Jordan (1982), Jordan et al. (1982), Jordan & Heuveldop (1981)
[e] Modified estimate from San Carlos data by Bruijnzeel (1991)
[f] Sum of $NH_4^+ + NO_3^- +$ DON + PN
[g] Sum of $PO_4^{3-} +$ DOP + PP

be higher during wetter than normal years. In cases where differences in soil mineralogy and degree of leaching between sites are negligible, the highest export rates should be observed at the site experiencing the highest runoff and lowest rates at the driest site. In a comparison of nutrient export rates among the same studies listed in Table 3, but excluding the San Carlos site, Lesack (1993a) showed that the gross export rates in the present study are generally as low or substantially lower than the lowest rates reported in the other

studies, despite the fact that runoff rates in the present study were 2–4 times higher than in the other studies. The Tonka site may have different soils or nutrient inputs via rainfall than the present study, but this is not the case for the Reserva Ducke/Barro Branco region (Lesack 1993a). Because of differences in methodology and problems establishing the amount of runoff (Bruijnzeel 1991), the San Carlos site was excluded from that comparison. A second issue is that Lesack & Melack (1991) recently demonstrated the average annual deposition fluxes of nutrients via rainfall in the present study are significantly lower than previously reported among mass balance studies conducted in the Amazon (this includes the studies in Table 3, except the Tonka site) and have argued that interannual variation in deposition may be relatively small (within $\pm 30\%$) in the absence of unusual long-range atmospheric advection events. The above findings have two important consequences. First, differences in atmospheric deposition are unlikely to reconcile the differences in net balance between our study and the previous studies. Second, we should expect our catchment to show a net loss of nutrients during an unusually wet year instead of net gain (will be fully addressed in sections that follow).

The credibility of the present study has previously been established by substantial evaluations of atmospheric deposition estimates (Lesack & Melack 1991), water balance characteristics (Lesack 1993b), and estimates of gross nutrient export for the region (Lesack 1993a), while major uncertainties associated with the other studies have been reported in other independent evaluations (*cf.* Keene & Galloway 1984; Bruijnzeel 1990; Bruijnzeel 1991). Methodological problems with water sampling and chemical analysis, and overestimation of atmospheric deposition among previous studies appear to be the best supported among hypotheses identified by Bruijnzeel (1991) and Lesack (1993a) that could potentially reconcile the rather large differences in net nutrient balance reported among studies in the Amazon.

Reconciliation of mass balance measurements

Although the values of net nutrient accumulation obtained during the present study are low compared to previously reported values, the quantities are large relative to the input fluxes via rainfall. According to the nutrient retention hypothesis of Vitousek & Reiners (1975), if an ecosystem such as ours is neither aggrading nor senescing ($\delta S \approx 0$), the biota should be taking up and releasing nutrients at roughly balanced rates. There is no visible evidence, based on 1:30,000 aerial photography taken 30 years prior to this study and based on Landsat imagery from the 1970's, that our study site has been significantly disturbed during recent times or is now aggrading, and the study site has been classified by A. Gentry (Missouri Botanical Garden; details provided by Lesack 1993b) as mature rainforest. Moreover, the rates of nutri-

ent accumulation are substantially lower than has been reported for actively aggrading forest ecosystems, such as Hubbard Brook (Table 2). However, given that climatic conditions during the present study were representative of a one in 10 wet year, we expected the ecosystem to show a net loss of nutrients rather than net gain. Instead, all of the elements measured in the present study, except for Na^+ and Cl^-, appear to be accumulating in quantities ranging from 0.30 to 0.50 of the input flux via rainfall. We have identified several hypotheses that could provide an explanation.

Interannual variation in water available for runoff

First, the ecosystem may be in balance, when averaged over several years, but may show imbalances from year to year, driven by alternating wet, dry, or normal years of rainfall (*hypothesis one*). The period of measurement in the present study was indeed wetter than the year prior to the study. While the amount by which stored groundwater increased is too small, and typical groundwater concentrations are too low to account for the apparent imbalances in net ecosystem storage measured during this study (Lesack 1993a, 1993b), the potential for interannual variability in flushing of solutes through the catchment soils is considerable. Analysis of an 18 year rainfall record from Reserva Ducke (Fig. 3) combined with improved recent estimates of actual evapotranspiration (Shuttleworth 1988) demonstrates that while rainfall varies from about 2000 mm to 2800 mm (±20%) during 1 in 10 dry or wet years, the amount of water available for runoff should range from about 700 to 1400 mm (factor of 2) between dry and wet years. Moreover, previous work has shown that despite variation in rainfall rate by threefold within a given year, solute deposition fluxes remain comparable throughout the year (Lesack & Melack 1991; Andreae et al. 1990a) because of the dynamic relations between solute concentrations versus the size and frequency of storms. For example, as the frequency and magnitude of rainfall events increased during wetter portions of the year (wet season) relative to the dryer portions (dry season), the solute concentrations in the rainwater decreased by a comparable amount resulting in similar deposition flux rates. Because solute deposition fluxes are not proportional to intraannual variation in rainfall, there is no reason to expect, in the absence of unusual events such as long-range advection of dust plumes from Africa (*cf.* Harriss et al. 1990), that interannual variation in solute deposition fluxes should be greater than interannual variation in rainfall.

In contrast, the relations between solute concentration and stream discharge for most of the solutes measured in the present study indicate that materials annually exported should be in proportion to annual runoff (Lesack 1993a). Consequently, because the variability in rainfall inputs is small com-

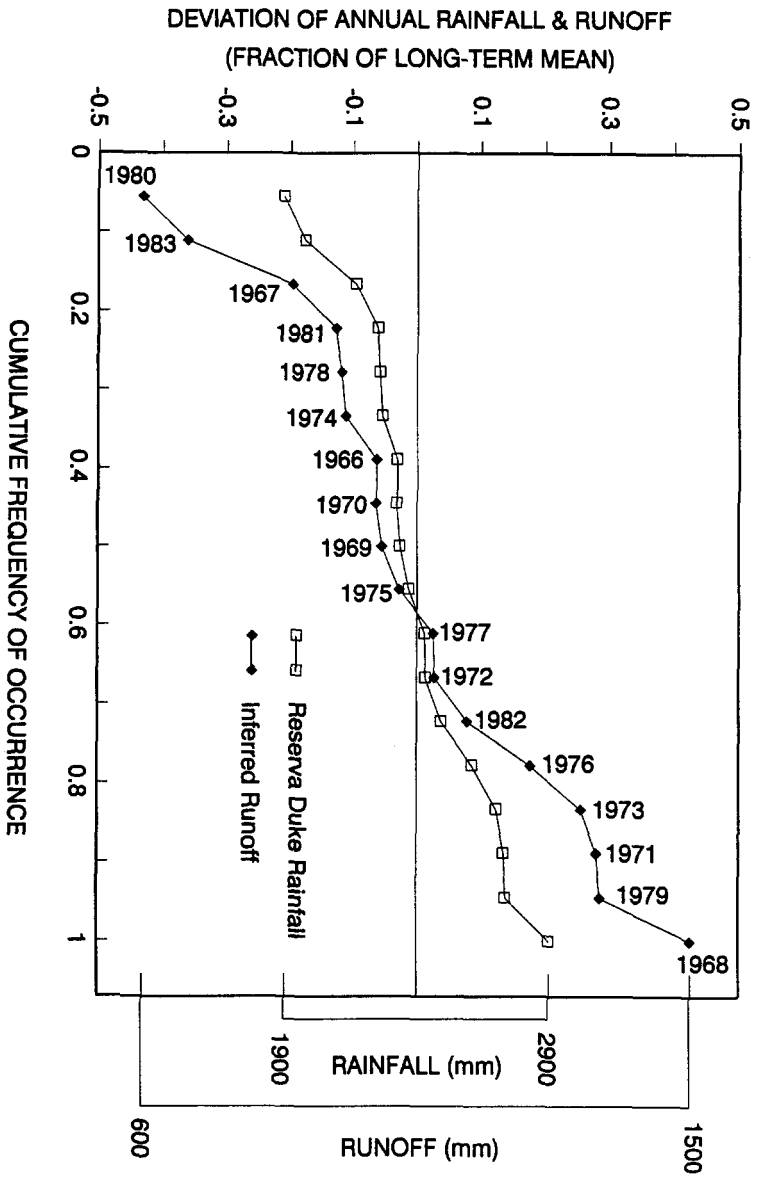

Fig. 3. Comparison of the interannual variability of rainfall versus runoff in the central Amazon. The amounts of water (mm of rainfall and runoff) and the deviation of the annual amounts (expressed as a fraction of the long-term mean) are both plotted as functions of the cumulative frequency of increasingly wet years. Rainfall is based on an 18 yr record from Reserva Ducke (courtesy of the Instituto Nacional de Pesquisas da Amazonia), a forest reserve with rainfall characteristics comparable to the present study site (Lesack 1993b; Lesack & Melack 1991). Inferred runoff amounts are obtained by subtracting estimates of actual evapotranspiration (*ET*) from the rainfall values. Assuming that *ET* varies from 1300 mm to 1400 mm in respective correspondence with the driest and wettest years in the record (Lesack 1993b; Bruijnzeel 1990; Shuttleworth 1988), *ET* for each given year was obtained by direct interpolation.

pared to variability in gross export fluxes, the "apparent" net ecosystem balance may appear to vary considerably from year to year as a function of variable solute flushing rates through the catchment driven by the amount of water available for runoff. However, if the above mechanism is of prime importance in generating stochastic variations in apparent ecosystem storage during alternating wet or dry years, it is somewhat surprizing that Na^+ and Cl^- are the only two elements which show a net loss from the ecosystem during a 1 in 10 wet year.

Unmeasured losses of particles and gases to the atmosphere

Alternatively, the ecosystem may be in balance, but all of the losses have not been measured. Two potential pathways by which difficult to measure losses could occur include subsurface groundwater outflow through the deep tropical soils of the basin and atmospheric entrainment of gases and aerosols emitted from the terrestrial ecosystem. The fluxes of solutes exported by groundwater outflow represented only a small portion of the gross annual export of solutes from the catchment (Lesack 1993a, 1993b). By contrast, losses to the atmosphere represent a plausible possibility (*hypothesis two*). During the Amazon boundary layer experiment (Harriss et al. 1988, 1990), conducted in the central Amazon during July-August 1985 (ABLE-2A: dry season) and during April–May 1987 (ABLE-2B: wet season), low-altitude aerosol gradients measured during aircraft flights indicated that the forest canopy was a source of a broad range of materials, including particles of vegetation and leaf cuticle, to the atmospheric boundary layer and to the free troposphere. The particulates can be leached by atmospheric water vapor, thereby providing a mechanism for transporting elements that do not have a gas phase, such as Na^+, K^+, Ca^{2+}, or P from the forest to the atmosphere.

Ground-based studies conducted concurrently during the ABLE missions demonstrated substantial emission rates of a variety of aerosols and important trace gases. For example, Artaxo et al. (1988, 1990) established from ground-based measurements that emission of biogenic particles by the forest was the dominant source of aerosol in the central Amazon during the dry season and was the majority source of aerosol during the wet season. Subsequent longer-term monitoring by Artaxo et al. (1994) of three stations in varied states of disturbance along a north-south gradient across the Amazon has shown that biogenic particles and biomass burning particles, on average, have dominated the fine mode mass concentration of aerosols relative to other sources such as soil dust particles and marine aerosols. Given the atmospheric circulation characteristics of the region, Artaxo et al. (1994) have concluded that large amounts of essential plant nutrients are mobilized into the atmosphere and are possibly lost from the Amazon basin via long-range transport.

For an example of the potential importance of trace gas emissions, Andreae et al. (1990b) estimated a mean annual emission of reduced sulfur-gases (sum of dimethyl-sulfide (DMS), methyl-mercaptan (MeSH), and H_2S) from rainforest ecosystems in the central Amazon of about 2 ± 1 nmol/m^2/min. Although it is questionable whether these short-term measurements can be extrapolated to an annual scale, this could represent a mass flux in the range of 5 to 16 mol/ha/yr. The upper end of this range overlaps our estimate of 23.5 ± 14 mol/ha/yr for the net apparent accumulation of sulfur in the ecosystem.

If the accumulation values in our budget actually represent losses to the atmosphere, this would imply that a minimum of about 41% (23.5 of 57 mol/ha/yr; derived from Table 2) of the sulfur input via rainfall is sulfur that has been recycled from the rainforest through the atmosphere. Analogously, the portion of the rainfall input for other elements (K^+, Ca^{2+}, Mg^{2+}, N, and P) contributed by recycling through the atmosphere would range from about 30% to 50%. Modelling calculations of Andreae et al. (1990b) indicate only a relatively small portion of the reduced sulfur-gas emissions from the rainforest may be available to support local production of SO_4^{2-} aerosols and wet deposition. Nevertheless, given the considerable interannual range of soil flushing that occurs in the central Amazon as a function of the amount of water available for runoff in wet years versus dry years, and the important role of soil wetness in controlling gas emission rates (Andreae et al. 1990b; Bakwin et al. 1990; Andreae & Andreae 1988), the long-term representativeness of the ABLE results remains a question and gaseous emissions may indeed contribute significantly to elemental recycling.

Other potential hypotheses

There are at least two other hypotheses that could potentially reconcile the mass balance results of the present study, but these are more difficult to evaluate. First, the region could be experiencing a higher input flux of nutrients now than in the past, as a result of recent increases in biomass burning that may have enhanced the nutrient content of precipitation (*hypothesis three*). The additional input of nutrients could be fueling an increase in net primary productivity which is resulting in the accumulation of new plant biomass. Although this cannot be fully evaluated from the information presently available, there is some evidence that this explanation may be unlikely given the particular circumstances of the present study. While there is evidence that significant increases in forest burning have occurred over the last decade, the field work for the present study was conducted during 1984. If this hypothesis is correct, the forest would have to be responding to a fertilization effect that

began before 1984. The extent to which biomass burning may have affected the rates of atmospheric deposition at that point in time is not clear.

Firstly, biomass-burning plumes and haze layers were observed via aircraft (Andreae et al. 1988) during the 1985 dry season (ABLE-2A). However, the results of Talbot et al. (1988) and Artaxo et al. (1988) obtained over the same period demonstrated that the background aerosol was remarkably uniform in distribution and composition and apparently dominated by biogenic emissions. Although natural biogenic emissions appeared to dominate over pyrogenic emissions at that point in time, Andreae et al. (1988) demonstrated that it is difficult to precisely distinguish the relative importance of each because the chemical composition of the haze layer aerosols are quite similar to the background aerosol in the boundary layer.

A second issue is that if the nutrient content of rainfall had become enhanced during the period of our study because of anthropogenic activities, we expect that atmospheric deposition rates during the dry season (when most of the burning occurs) should be more enhanced than during the wet season. During our study, the average rates of N and P deposition varied less than 20% among the wet and dry seasons despite a threefold variation in average rainfall rate among the seasons (Lesack & Melack 1991). Similarly, during the two ABLE missions (1985 dry season and 1987 wet season) Andreae et al. (1990a) observed similar rates of deposition among each of the wet and dry seasons despite a five-fold variation in rainfall rate among the two observation periods (each about 6 weeks in length). However, it remains unresolved whether the dry season deposition rates were similar to wet season deposition during this period because anthropogenic burning (during the dry season) had already elevated the dry season deposition rates or whether dry season deposition rates could be expected to significantly exceed wet season deposition if anthropogenic burning had significantly enhanced the nutrient content of rainfall in the region. An additional complication is that the relative amounts of atmospheric deposition which occur during each of the wet and dry seasons may be influenced by interannual variations in large-scale atmospheric circulation and long-range transport of chemical species. Evidence obtained during ABLE-2B (Swap et al. 1992; Andreae et al. 1990a; Talbot et al. 1990; Artaxo et al. 1990) indicates that significant amounts of dust and pyrogenic species from Africa were transported into the Amazon during the 1987 wet season but that the amounts are dependent on atmospheric circulation during a given year.

Another hypothesis that could potentially reconcile the results of this study is that the forest (even though mature) may be in a shifting-mosaic state with a gap regime that results in patches of relatively young forest imbedded in the mosaic of mature forest (*cf.* Hubbell & Foster 1986). Patches of young

forest within the mostly mature forest could be a sink for the apparent nutrient retention observed in this study (*hypothesis four*). Because there have not been many direct tests of Vitousek & Reiners (1975) nutrient retention hypothesis (Hedin et al. 1995), it may not necessarily be the best model on which to base an interpretation of mass balance data for forested catchments under all circumstances. Its applicability should be dependent on the size scale of the mosaic regime within a given area of forest, relative to the size of the catchment being studied. A number of years of study would be necessary to evaluate the potential importance of this explanation, including data on rates of plant production, nutrient inputs via precipitation, and the extent that nutrient availability limits plant production, as well as year to year variation in each. Although beyond the scope of this study, a full complement of such ecological data would be required to establish a fully explored explanation for the apparent nutrient retention observed during this study.

Implications for nutrient budgets in tropical rainforests

Although each of the above hypotheses could simultaneously contribute to the apparent net accumulation of nutrients observed during this study, we believe that the information presently available establishes a reasonable degree of plausibility for *hypothesis one* (ecosystem is in balance on average but interannual variation in water available for runoff drives year to year imbalances) and *hypothesis two* (ecosystem is in balance but losses of particles and gases to the atmosphere were not measured). The other hypotheses may still be important to a more complete understanding of the biogeochemical dynamics of the Amazon rainforest, but we are not able to fully evaluate the plausibility of these hypotheses in our particular study from the information and data presently available. Nevertheless, because *hypotheses one* and *two* are plausible, there are at least two important implications for the interpretation of mass balance data from tropical rainforest catchments.

First, given that the amount of water available for runoff during wetter or dryer than normal years may vary by a factor of 2 and that the gross flux of solutes exported from the catchment is proportional to the amount of water available for runoff, the potential interannual variability in the flushing of elements through rainforest ecosystems appears to be considerable, and may represent a critical control on the apparent change in ecosystem storage detected by annual-scale nutrient budgets in small catchments. We also expect that variability in detectable ecosystem storage will decline as the spatial-scale of the investigation increases above that of small catchments, though the data required to test this is not yet available. Of particular concern is that most of the information thus far available on rainforest ecosystems has been based on short-term (often one year) measurements subsequently pre-

sented as case studies. Although we do not have multiyear data on the mass balance of our particular system, we were able to obtain long-term climatic records which were used to place the study year into proper context. We were also able to predict how the mass balance of the system should respond during wet and dry years, based on detailed analysis of how atmospheric deposition and hydrologic export of solutes changed as a function of storm size, storm frequency, and stream discharge. Consequently, we are able to conclude that our mass balance results are not in agreement with results previously published for small catchments in the central Amazon and the differences are not likely to be reconciled by differences in soils or differences in climatic regime during the period of measurement. Prior to the present study, the critical data apparently has not been available to place the results from small catchment studies in the Amazon (and elsewhere) into more appropriate context by evaluating the degree of interannual variability that might be expected. Our understanding of how well the results of previous studies are representative of ecosystems at time scales longer than one year is very poor, and we believe that this may be an important reason why recent reviews of the mass balance data available for tropical forests (*cf.* Vitousek & Sanford 1986; Proctor 1987; Bruijnzeel 1991) yielded few generalizations. Our ability to detect less than catastrophic changes to these ecosystems will remain poor until our knowledge of longer-term dynamics, spatial dynamics, and representativeness have been improved.

Second, the idea that exchanges of materials between terrestrial ecosystems and the atmosphere can be an important component of ecosystem-scale elemental budgets is not new (e.g. Gorham et al. 1979; Haines 1983; Delmas & Servant 1983; Mooney et al. 1987). What does require rethinking, however, is that losses of aerosols and particulates containing elements which do not exist as gases may be critical for the interpretation of nutrient budgets in rainforests located on deeply-weathered or nutrient-poor soils. For example, K should be entirely depleted and profoundly limiting to forest growth, relative to P, in old tropical soils (P. Vitousek, Stanford University, Pers. Comm.) because of its higher soil mobility, yet the available evidence does not support this. Atmospheric mobility of K could explain this observation. We postulate that the atmospheric deposition term for a representative subunit of a regional rainforest ecosystem might be conceptually partitioned as:

$$I_P = I_{PN} + I_{PR} - E_{CR} + I_{PL} - E_{RL} \quad (2)$$

where I_{PN} represents new input of nutrients to the regional ecosystem and is derived either from fixation processes in the atmosphere or as the balance between materials advected out and into the region from adjacent regional ecosystems (e.g. savannas, oceans) by large-scale atmospheric circulation; where E_{CR} and I_{PR} represent a balance respectively between materials

entrained into the atmosphere as particulates, aerosols, and reduced gases from a given ecosystem subunit by atmospheric convection and the amount of that material which is redeposited back into a comparable ecosystem subunit before the atmospheric circulation removes the material from the region; and where E_{RL} and I_{PL} represent a balance respectively between localized resuspensions of particulate material from a given ecosystem subunit and the amount of that material which re-settles before it can leave the subunit via entrainment through the forest boundary layer. If we postulate that samples of bulk precipitation measure the sum of I_{PN}, I_{PR}, and I_{PL}, while samples of precipitation events measure the sum of I_{PN} and I_{PR}, we can explain why our measurements of atmospheric deposition at Lake Calado, based on event samples versus bulk samples, were not different from each other. Because the bulk samples were collected in the middle of a lake, the collector presumably was sufficiently far from the terrestrial ecosystem that capture of the I_{PL} flux did not occur.

A schematic representation of this model (Fig. 4) illustrates how atmospheric deposition associated with refuge islands of rainforest contained within large deforested areas potentially could be altered relative to undisturbed areas. True inputs via rainfall (I_{PN}) that would replenish nutrients to a completely deforested landscape include material advected into the ecosystem as a result of large-scale atmospheric circulation. Alternatively, the amount of recycled nutrients contributed by rainfall (I_{PR}) may play an important role in sustaining tracts of rainforest larger than some threshold area or in replenishing nutrients to deforested patches which are small. If areas of undisturbed forest are reduced to relatively small refuge islands located within large deforested areas, two scenarios are possible. Conversion of forest to pasture or cropland could result in less material entrained into the atmosphere by convection which would then reduce the flux of recycled nutrients (I_{PR}) to the forest refuges (*scenario one*, depicted in Fig. 4). This scenario, in fact, is consistent with recent work by Shukla et al. (1990). Employing a general circulation model with a sophisticated land-surface parameterization, they were able to demonstrate that conversion of forest to grassland could reduce atmospheric moisture convergence and associated convection within the Amazon region, and thereby reduce rainfall by an amount considerably larger than would be predicted from plant physiology and known evapotranspiration rates alone.

It may also be possible that conversion of forest to pasture or cropland would result in an increase in dust in the atmosphere, with more material entrained into the atmosphere than from the former forest (*scenario two*). Because repeated burning may also be used to control secondary vegetation after conversion, emissions of many chemical species could be further

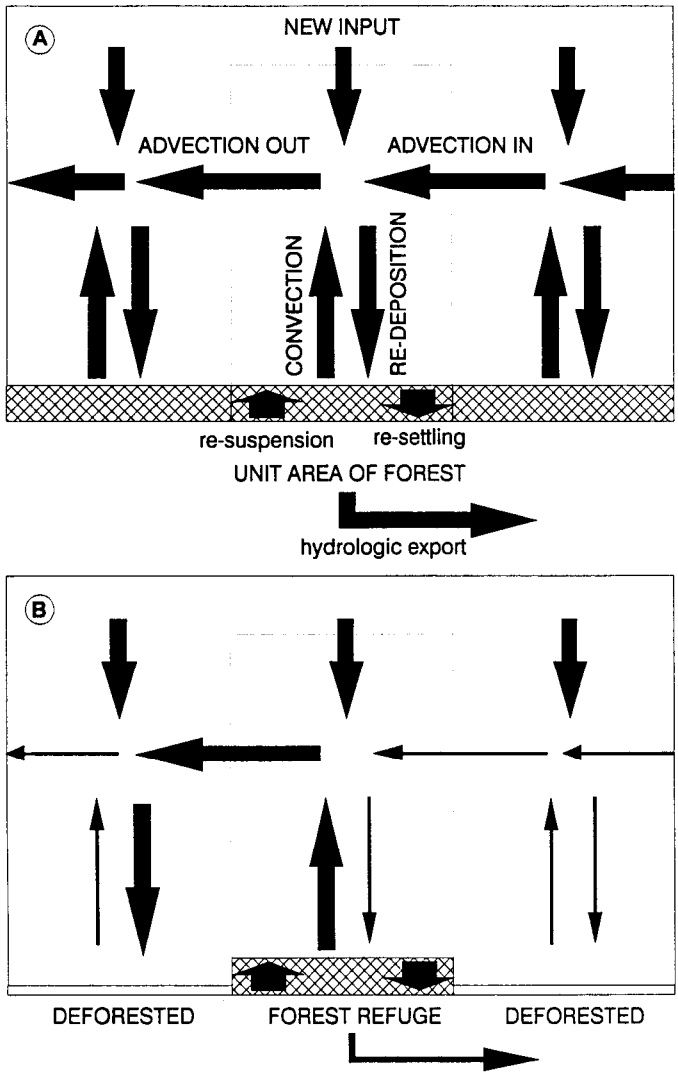

Fig. 4. Schematic representation of the potential cycling of nutrients between a regional-scale rainforest ecosystem and the atmosphere (A), and how the cycling pathways are postulated to change if regional-scale tracts of forest are reduced to relatively small refuge islands within large deforested areas (B). Though not drawn to a precise scale, arrow widths reflect relative magnitudes of flux pathways. New input (I_{PN} from equation 2) reflects true inputs to the ecosystem derived from fixation processes in the atmosphere or advected from adjacent regional-ecosystems by large-scale atmospheric circulation. Advective exchanges represent materials entrained into the atmosphere from the terrestrial ecosystem by atmospheric convection (E_{CR}), but which are redeposited back into the ecosystem (I_{PR}) before the large-scale atmospheric circulation removes the material from the region. Localized resuspensions (E_{RL}) of particulate material that resettle (I_{PL}) before they can be entrained from the forest boundary layer are also represented. The scenario in Panel B assumes that conversion of forest would result in less material entrained into the atmosphere by convection which would then reduce the flux of recycled nutrients (I_{PR}) to the forest refuges.

enhanced relative to the forested condition. Under this scenario one could argue that the flux of recycled nutrients (I_{PR}) to forest refuges might increase as the surrounding landscape was "converted". We are not yet convinced which of the above scenarios is more plausible, but expect that it is important to find out. While a non-forested landscape might represent a more "erodible substrate", it might also result in decreased atmospheric convection within the region and therefore less potential to "erode it". We also expect that dust derived from surface soils in the central Amazon would be severely depleted in most nutrients (especially P and K) relative to particulates and aerosols derived from forest biomass.

The long-term effect on the cycling of nitrogen-based gases and aerosols through the atmosphere, which could potentially replenish N to forest fragments is somewhat uncertain. In a relatively recent evaluation of the effects of tropical deforestation on the emissions of trace gases, Keller et al. (1991) reasoned that release of NO_x from soils could strongly increase following removal of the forest canopy. The major reason is that forest cutting stimulates decomposer activity (including nitrifiers and denitrifiers) by providing a large influx of detritus substrate and by causing elevated soil temperatures as the shading effect of the canopy is removed. Given that Keller et al. were not aware of any long-term studies which have tracked NO_x emissions from the conditions of initial deforestation to older pasture in the wet tropics, it is possible that enhanced NO_x emissions could be a transient phenomenon which lasts only a few years (until the influx of new substrate is exhausted). On the other hand, if N-fertilizers are used extensively for agricultural crops, enhanced NO_x emissions could be sustained by denitrifier activity.

A last issue relevant to our conceptual partitioning of atmospheric deposition as in equation 2 and Fig. 4 is the relative importance of the inputs of "new" nutrients (I_{PN}) versus nutrients recycled through the atmosphere (I_{PR}) in sustaining the productivity of the Amazon rainforest. Swap et al. (1992) have recently proposed that some portion of the productivity of the Amazonian forests may be dependent upon critical trace elements contained in soil dust originating in the Sahara/Sahel of Africa. Based mostly on measurements obtained during ABLE-2B, they were able to derive estimates of the annual deposition fluxes of various chemical species associated with intrusions of Saharan dust into the central Amazon during the wet season. Given that these flux estimates actually exceeded (except for K^+) the average wet deposition fluxes (Na^+, NH_4^+, Cl^-, NO_3^-, SO_4^{2-}, PO_4^{3-}) obtained by Andreae et al. (1990a) over six weeks during ABLE-2B, Swap et al. concluded that the major ionic composition of precipitation in the central Amazon may be strongly influenced by inputs of material from Africa. Although the range of potential interannual variation in dust transport is not known, this result

Table 4. Comparison of measured fluxes of annual atmospheric deposition via rainfall in the central Amazon versus estimates of potential annual deposition via intrusions of Saharan dust into the central Amazon during the wet season. PN and PP respectively represent particulate nitrogen and phosphorus. DON and DOP respectively represent dissolved organic nitrogen and phosphorus.

Element	Dust input (Swap et al. 1992)	Rainfall input (Present study)
	Equivalents/ha/yr	
NH_4^+	46	168
Na^+	91	62
K^+	14	19
Cl^-	101	120
SO_4^{2-}	95	114
NO_3^-	48	88
	Moles/ha/yr	
TN[a]		480
TDN[b]		431
TIN[c]	95	256
TP[d]		3.8
TDP[e]		2.2
PO_4^{3-}	0.7	1.5

[a] Sum of $NH_4^+ + NO_3^- +$ DON + PN
[b] Sum of $NH_4^+ + NO_3^-$ + DON
[c] Sum of $NH_4^+ + NO_3^-$
[d] Sum of PO_4^{3-} + DOP + PP
[e] Sum of PO_4^{3-} + DOP

potentially suggests that long-range transport (I_{PN}) is a dominant source of nutrients in rainfall of the central Amazon with atmospheric recycling (I_{PR}) contributing a smaller amount. However, this result is not well reconciled with three other observations.

First, although seasonal changes in atmospheric circulation shut down the transport of African dust to the Amazon during the dry season (Swap et al. 1992), direct observations have shown (Lesack & Melack 1991; Andreae et al. 1990a) this has been accompanied by only a minimal to minor decrease in wet

deposition rates during the dry season (i.e. wet deposition rates have remained comparable among the wet and dry seasons). Second, the aerosol studies of Talbot et al. (1988, 1990) and Artaxo et al. (1988, 1990) have indicated that local biogenic emissions on average (during combined wet and dry seasons) represent the dominant aerosol in the central Amazon. Third, if the estimates of dust deposition are directly compared with our measurements of annual wet deposition (Table 4), the potential contribution of Saharan dust is reduced, in particular, ranging from 27% to 55% of total wet deposition for N and P species. Furthermore, if the sum of NH_4^+ and NO_3^- in dust deposition is compared to our estimates of total-N (sum of $NH_4^+ + NO_3^- + DON + PN$) or PO_4^{3-} is compared to our measurement of total-P (sum of $PO_4 + DOP + PP$) the potential contributions are reduced to only 20% and 18% of total annual N and P deposition respectively. This particular example, where dissolved-organic and particulate-organic forms of N and P are included, suggests that the dominant source of N and P in atmospheric deposition is recycling of biogenic emissions through the atmosphere (I_{PR}), though further research is clearly needed to resolve this.

Numerous investigators have argued that atmospheric deposition is a major mechanism of nutrient replenishment in rainforests. Because the nutrients contained in atmospheric deposition "have to come from somewhere", we believe the conceptual model and subtle details of this premise should be carefully reevaluated. The possibility that African dust may be a long-term fertility control on the Amazon rainforest (Swap et al. 1992) is an important finding. However, release of nutrients to the atmosphere and subsequent redeposition in rainfall may represent an unanticipated recycling process of Amazonian rainforests which contributes to their ability to retain and efficiently utilize small amounts of nutrients imported into the ecosystem, and thereby enable high biomass forests to grow in nutrient depleted soils (*cf.* Whittaker 1975). The spatial scale at which the cycling of elements occurs between the terrestrial ecosystem and the atmosphere (the balance between E_{CR} and I_{PR}) may also represent an unanticipated determinant of the minimum critical size of rainforest fragments that are potentially sustainable in areas of deforestation, in contrast to the habitat requirements and mobility of faunal organisms (*cf.* Simberloff 1988; Wilcox & Murphy 1985; Harris 1984; Lovejoy 1982) on which investigations have thus far focussed.

Conclusion

We conclude that our mass balance results are not in agreement with results previously published for small catchments in the central Amazon basin and the differences are not likely to be reconciled by differences in soils or

differences in climatic regime during the period of measurement. Among several mechanisms that could potentially explain the substantial excess of nutrient inputs via rainfall over exports via hydrologic outflows from the ecosystem measured during a wetter than normal year, two are supported by the information presently available while two others cannot be evaluated without further research.

Interannual variability in the flushing of nutrients through rainforest catchments driven by the amount of water available for runoff during wetter or dryer than normal years may be a critical control on the apparent changes in ecosystem storage detected by annual scale nutrient budgets. There remains considerable gaps in our understanding of how well the results of studies previously conducted are representative of ecosystems at time scales longer than one year. We are convinced that our ability to reliably detect changes in these ecosystems which are less than catastrophic will not be possible until our knowledge of longer-term ecosystem dynamics and representativeness have been improved.

Entrainment of materials from the terrestrial ecosystem to the atmosphere, including particulates containing elements which do not exist as gases, may be a particularly important loss pathway in rainforest ecosystems existing on deeply weathered and nutrient poor soils. Release of nutrients to the atmosphere and subsequent redeposition in rainfall may represent an unanticipated recycling process of tropical rainforests which contributes to their ability to retain and efficiently utilize a relatively small amount of nutrients imported into the ecosystem, and thereby enable high biomass trees to grow in nutrient deplete soils.

Acknowledgements

We thank E. Salati, F. Bergamin, and H.O.R. Schubart, directors of the Instituto Nacional de Pesquisas da Amazônia (INPA), and O. Fonseca, G. Vazzoler, A. dos Santos, B. Robertson, and J. Salomão Ribeiro for support and encouragement in Brazil. We appreciate the field assistance provided by Antonio Adalberto da Silva and Lesley Smith, and the laboratory measurements performed by F. Setaro, J. Sickman, and D. Lucero-Sickman. Our analysis benefitted from discussions with R. Harriss, P. Marsh, and D. Moore. The manuscript was improved by the valuable suggestions of M.O. Andreae and an anonymous reviewer. Financial support was received from NSF grants DEB81-11398 and BSR-8706643 to T.R. Fisher and J.M. Melack.

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