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NITROGEN AND PHOSPHORUS RUNOFF LOSSES FROM A NUTRIENT-POOR TROPICAL MOIST FOREST¹

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Abstract. The Caura River of Venezuela drains 47 500 km² of undisturbed tropical moist forest overlying the Guayana Shield within the Orinoco River watershed. Discharge measurements and water samples were taken of the Caura biweekly for 2 yr. Samples were analyzed for total nitrogen, total phosphorus, and various species of these two elements. Losses of nitrogen (9.98 kg·ha⁻¹·yr⁻¹) and of phosphorus (0.46 kg·ha⁻¹·yr⁻¹) were unexpectedly high. Concentrations of total N and total P showed only minor seasonal variations, despite major seasonal changes in discharge. The data are consistent with the hypothesis that mature forested ecosystems have high yields of critical nutrients because they are not accumulating biomass. The data also show, however, that this mature ecosystem strongly buffers seasonal variations in nutrient loss.

Key words: *nitrogen; nitrogen fixation; nutrient cycling; phosphorus; tropical moist forest; Venezuela.*

INTRODUCTION

Watersheds vary widely in the rates at which they lose nitrogen and phosphorus. Such variations are of special interest ecologically in that nitrogen and phosphorus often govern the growth rates of plants. Although it is now clear that disruption of the vegetative cover of an ecosystem leads to large losses of nitrogen, phosphorus, and other elements (Likens et al. 1977, Bormann and Likens 1979, Vitousek et al. 1979), the factors that regulate the loss of critical nutrients from mature, undisturbed ecosystems are not well known. This is especially true of watersheds in the humid tropics, where nutrient mass balance has been studied much less frequently than in the temperate zone (Meybeck 1982).

Several sets of factors influence the retention of nutrients by ecosystems. First, nutrient retention appears to vary with ecosystem maturity. One current theory holds that nutrient retention will be most pronounced during biomass accumulation (Vitousek and Reiners 1975, Gorham et al. 1979). The basic physical conditions of an ecosystem are also important. Large amounts of rainfall may cause such effective leaching that nutrients are lost in considerable quantities despite the vegetative cover. Low temperatures may retard biological activity, and thus reduce biological retention. In addition, certain kinds of ecosystems may have abundant geologic sources of nutrients that would otherwise be in short supply. A third set of mechanisms has to do with differential mobility of nutrient fractions. For example, nitrate, which is often the dominant inorganic nitrogen species in soils, is more mobile in groundwater than ammonium, which is more likely to become attached to charged surfaces (Vitousek et al. 1979). Thus chemical speciation, which may be

biologically controlled, can affect the retention of a nutrient by an ecosystem. A fourth consideration is the degree and type of nutrient deficiency. The organisms in an ecosystem may most effectively immobilize the element for which the ratio of demand to supply is greatest, and nutrient retention mechanisms may be most effective in nutrient-poor systems (Chapin 1980, Jordan and Herrera 1981).

The present study deals with losses of nitrogen and phosphorus in river flow from the watershed of the Caura River, Venezuela, over a 2-yr interval. The Caura watershed occupies a portion of the Guayana Shield, a highly weathered Precambrian formation. The data provide an example of macronutrient export rates from an undisturbed, forested tropical ecosystem.

STUDY SITE AND METHODS

The Caura River, which has a drainage area of 47 500 km², is a major tributary of the Orinoco River (Fig. 1). The watershed area is 29% premontane rain forest (precipitation ≈ 6000 mm/yr), 42% very humid premontane and tropical forest (2500 to 4500 mm/yr), and 29% humid tropical forest (2200 mm/yr) (Ewel et al. 1976). The observed runoff during the 2-yr study was 2423 mm/yr. Runoff from the Caura River drainage increases between April and August, when it reaches a relatively sharp peak. Runoff then decreases from August to April, but the rate of decrease is most rapid between August and October or November. The seasonal pattern is quite consistent among years (Venezuelan government, unpublished gauge data).

The Caura is classified as a "black" water; it has a tea-colored appearance caused by dissolved organic carbon. Analysis has shown, however, that the concentrations of dissolved organic carbon in the Caura River are not exceptionally high (mean = 3.96 mg/L, $n = 51$; Lewis et al. 1986).

Between 1 May 1982 and 30 April 1984, samples

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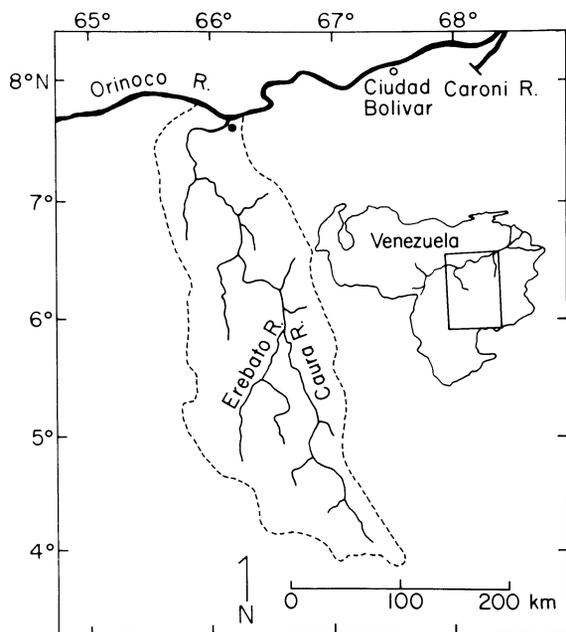


FIG. 1. Map of the Caura River drainage. ● location of the sampling station.

were taken biweekly near the mouth of the Caura River at a point where the seasonal average width of the river is close to 600 m (Fig. 1). On each occasion, the entire river cross section was sampled with a flow-integrating sampler lowered over the entire vertical profile at four points across the river (Stevens et al. 1980). For mass-balance studies on large rivers, this type of sampling is essential in view of the potentially uneven distribution of dissolved and suspended materials (Curtis et al. 1979, Lewis et al. 1984a).

The river samples were stored in a dark cooler pending transport to a field laboratory located on the Orinoco River at Ciudad Bolivar. At the field laboratory, measured amounts of the sample were filtered through dry, preweighed Whatman GF/C glass fiber papers (effective pore size $0.7 \mu\text{m}$; Sheldon 1972), which were then reweighed after they had been dried at 60°C . Concentration of particulate material was calculated from the mass gain of the filters. Particulate materials were combusted in a CHN analyzer for determination of percent carbon and percent nitrogen. These combustions were done in triplicate, and the analyzer was calibrated on each run against National Bureau of Standards orchard leaves or reagent-grade EDTA.

A second portion of the particulate material was analyzed for particulate phosphorus by pyrolysis and subsequent orthophosphate determination by an acid-molybdate method (Solorzano and Sharp 1980a). Long-pathlength spectrophotometry was required because of the low phosphorus concentrations. The analysis was continuously checked for recovery of phosphorus spikes of known concentration. Analyses were also run on field replicates.

The filtered portion of the sample was immediately analyzed for soluble fractions of nitrogen and phosphorus. Nitrate was determined by cadmium-copper reduction and subsequent analysis of nitrite by an azo dye method (Bendschneider and Robinson 1952, Wood et al. 1967). Ammonium analyses were done in triplicate by a modified Solorzano technique (Grasshoff 1976). Total soluble nitrogen was analyzed by a persulfate digestion method leading to determination of total soluble nitrogen as nitrate (slightly modified from Solorzano and Sharp 1980b). Soluble reactive phosphorus was determined by a molybdate method (Solorzano and Sharp 1980a), and total soluble phosphorus was determined by the same method following digestion with persulfate. All of these methods were accompanied by determinations of spike recovery, replicate analyses, and use of appropriate standards.

The Venezuelan Ministerio de Obras Pùblicas takes daily stage-height readings near the mouth of the Caura. The Ministerio and the United States Geological Survey have also made a number of discharge measurements. The relationship between gauge readings and discharges was: $D = 272.27H^{1.424}$, where D = discharge, in cubic metres per second, and H = gauge height, in metres. The fit of this relationship to the data was excellent ($r = 0.97$). This relationship was used in calculating the daily discharge over the 2-yr study interval.

RESULTS

The literature shows that the relationship of discharge to concentration, if significant, is often curvilinear, and may have either positive or negative curvature (e.g., Feller and Kimmins 1979, Lewis and Grant 1979, Lesack et al. 1984). Several curvilinear models are possible. For the Caura data (Figs. 2 and 3) there was only a small degree of curvature in the few instances where significant relationships were found (Table 1). Consequently, it was not possible to distinguish differences in fit between alternative curvilinear models. Table 1 shows the results for a semilogarithmic fit ($C = b \log Q + a$; C = concentration, Q = discharge, a and b fitted constants). The pattern of significant relationships and directions of curvature are the same for a hyperbolic fit, as used by Lesack et al. (1984) following Johnson et al. (1969). The relationships between yield (Y) to the river (=losses in runoff from the watershed) and discharge, as shown in Table 1, were determined from the relationship $Y = aQ^b$. The exponent b indicates the nature of the yield response (cf. Lewis and Grant 1979): $b > 1.0$ indicates that yield increases faster than discharge, and $b < 1.0$ indicates the opposite.

Nitrogen

The relationship of nitrate concentration to discharge was complex (Fig. 2) but showed several distinctive features: (1) at the time of highest discharge,

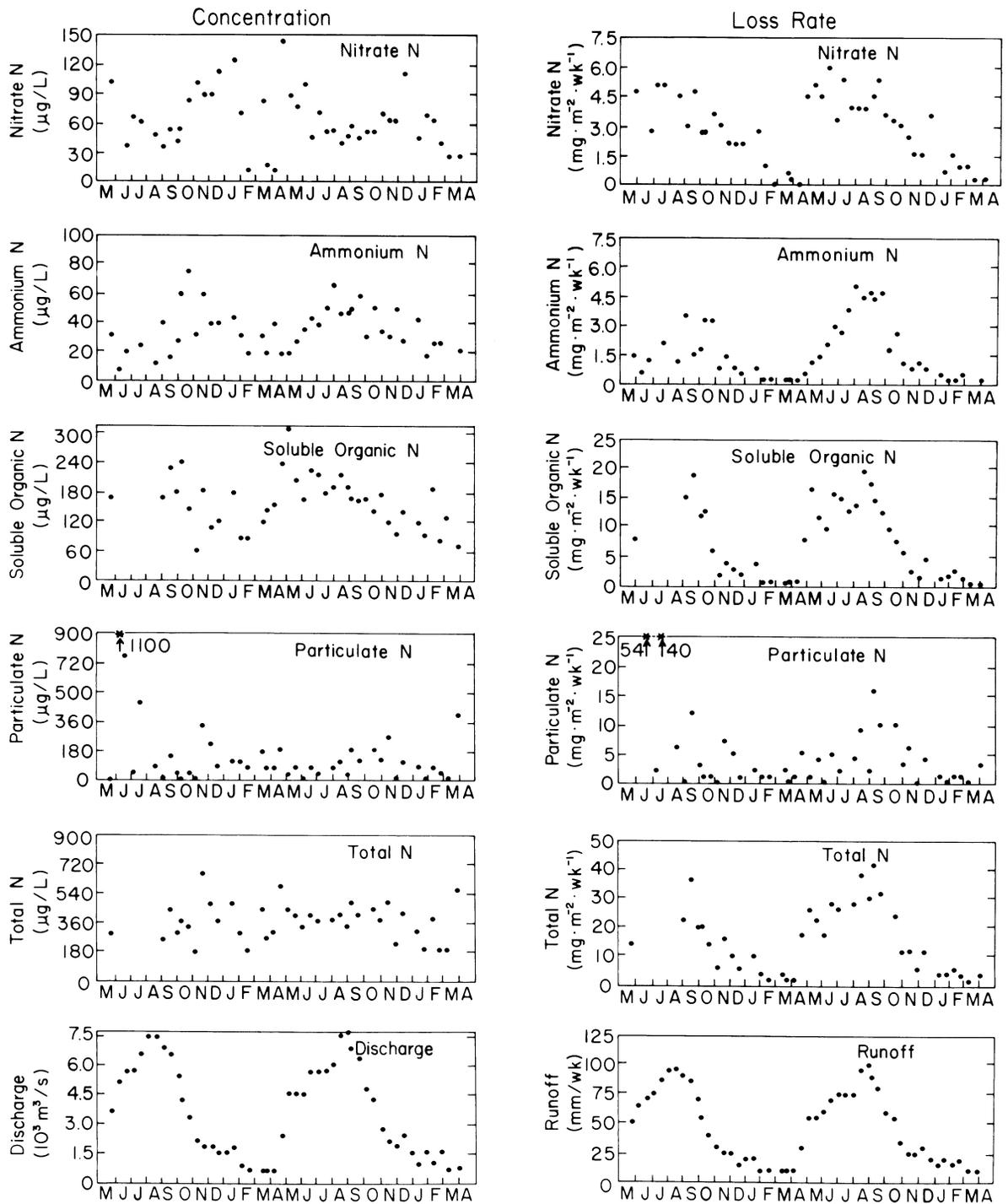


FIG. 2. Concentrations and watershed losses for nitrogen and nitrogen fractions in runoff over the course of the study.

dilution produced an inverse relationship between nitrate concentration and discharge; (2) during the period of lowest flow, the concentration of nitrate was exceptionally low; and (3) for a brief period coincident with the first few days of rising water, nitrate concentration was unusually high. Watershed nitrate yields, which are the products of discharges and concentrations,

showed a correspondence of peak nitrogen yield with peak discharge and a steep decline in nitrogen yield up to the 1st wk of rising water. Just as the water began to rise, however, nitrate yield briefly increased to a level near the annual maximum.

Ammonium concentrations followed a pattern whose form was similar to that of discharge, but the peak of

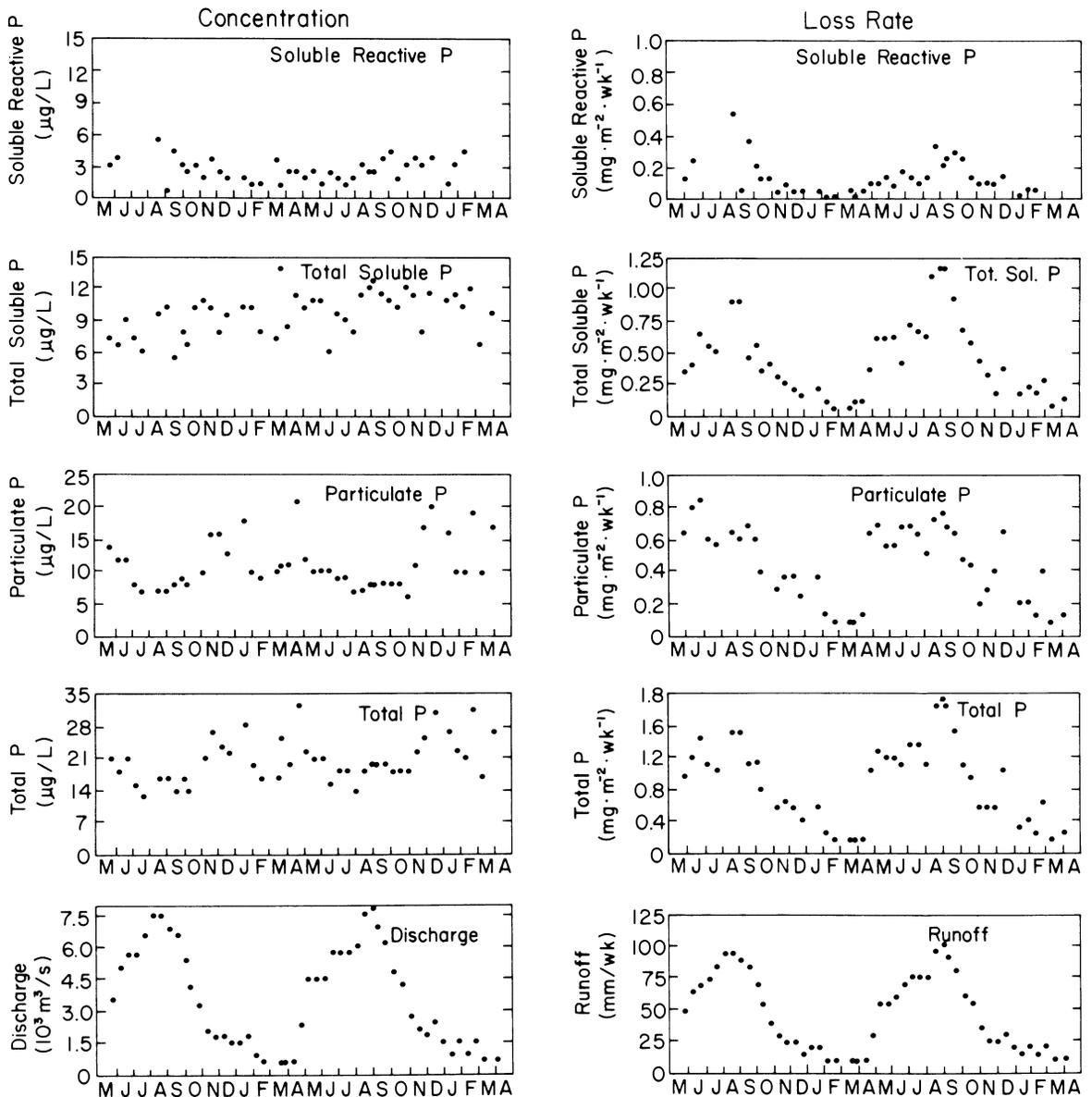


FIG. 3. Concentrations and watershed losses for phosphorus and phosphorus fractions in runoff over the course of the study.

ammonium concentrations was significantly offset from the peak of discharge. The relative variance in ammonium concentrations was about the same as for nitrate (Table 1), but the absolute concentrations of ammonium were considerably lower. The pattern of yield for ammonium was strongly dominated by the pattern of discharge, and there was no significant relationship of concentration to discharge.

Approximately 60% of total soluble nitrogen was accounted for by organic nitrogen, and 40% by the inorganic ions. Soluble organic nitrogen reached its peak concentration just as the water began to rise, and declined steadily thereafter. The yield of soluble organic nitrogen was strongly influenced by discharge and

by high concentrations of soluble organic N at the start of the runoff season; the result was a broad peak of yield between May and September. There was a significant but weak positive relationship between concentration and discharge for soluble organic N, and this was reflected in a significant positive relationship between discharge and total soluble nitrogen. These relationships are evident in exponents >1.0 for the yield equations (Table 1).

Particulate nitrogen accounted for approximately one-third of total nitrogen. Patterns in the concentration data for particulate N were weak; the yield pattern for particulate N was determined mainly by discharge. Concentrations of total nitrogen showed no discernible

TABLE 1. Summary of time-weighted annual mean concentrations and watershed losses by runoff (=annual yields to the river) for the Caura River, Venezuela, based on biweekly sampling over a 2-yr interval. Discharge (Q) and nutrient concentration (C) are related on a semilogarithmic basis: $C = b \log Q + a$, where a and b are fitted constants; concentrations of particulates and of specific nutrient fractions are related on a log-log basis; and discharge and loss (Y) are related on a log-log basis: $Y = aQ^b$.

	Nutrient concentration†					Nutrient loss‡			
	Mean ($\mu\text{g/L}$)	CV (%)	Compared with discharge		Compared with particulates: $r§$	Mean ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	CV (%)	Compared with discharge	
			r	$b\ddagger$				r	b
Nitrate N	65	46	0.03	...	0.30*	1.49	59	0.87*	1.15
Ammonium N	35	46	0.17	...	-0.22	0.89	86	0.85*	1.18
Soluble organic N	159	34	0.60*	0.00330	-0.24	4.00	82	0.96*	1.27
Total soluble N	262	26	0.52*	0.00229	-0.04	6.34	74	0.97*	1.23
Particulate N	139	151	0.03	...	0.14	3.64	207	0.52*	0.99
Total N	401	31	0.21	...	0.08	9.98	75	0.94*	1.11
Soluble reactive P	2.48	44	0.11	...	-0.00	0.063	89	0.87*	1.11
Total soluble P	9.47	22	-0.11	...	0.08	0.240	69	0.96*	0.98
Particulate P	11.02	36	-0.62*	-0.00296	0.83*	0.234	51	0.92*	0.79
Total P	20.47	23	-0.54*	-0.00171	0.70*	0.461	57	0.96*	0.88

† Minor inconsistencies in totals are due to slightly different numbers of analyses for fractions.

‡ Exponents were computed only for relationships that are statistically significant.

§ Correlation coefficients were calculated after log transformation of both variables to improve normality.

* Correlation significant at $P = .05$.

|| To minimize influence of missing values, the total was calculated as the sum of fraction averages rather than as the average of the sum of fractions.

pattern. The yield of total nitrogen thus reflected discharge almost exclusively.

Phosphorus

Concentrations of soluble reactive phosphorus, which includes both orthophosphate and certain proportions of soluble organic phosphorus (Rigler 1968, Levine and Schindler 1980), lacked pronounced seasonal variation and accounted for a relatively small proportion of total phosphorus (Table 1). Total soluble phosphorus concentrations also lacked a seasonal pattern, and were almost four times as high as concentrations of soluble reactive phosphorus (Table 1). Because of the lack of relationship between concentration and discharge, the yield was determined by discharge.

Concentrations of particulate phosphorus had a surprisingly small amplitude of variation, but showed a weak pattern that was close to being the inverse of discharge. A high positive correlation of particulate P with total particulate matter (Table 1) shows that the inverse relationship between particulate P and discharge was caused by a slight dilution of total particulate matter by high discharges. However, a brief flushing effect just as the discharge began to rise was evident for particulate phosphorus, as it was for nitrate.

About half of the total phosphorus was attributable to particulate phosphorus and half to soluble phosphorus. Because of the lack of strong concentration patterns for total soluble phosphorus, the weak pattern for particulate phosphorus was also detectable in total phosphorus (Table 1).

The correlations of discharge with concentration were significant and positive for soluble organic N and total soluble N, and were significant and negative for par-

ticulate P and total P. However, the coefficients are not high and the corresponding yield exponents (b) do not differ greatly from 1.0.

DISCUSSION

The runoff yield of total nitrogen from the Caura River watershed is very high relative to yields from other minimally disturbed watersheds (Table 2). Because geologic sources of nitrogen are small, the nitrogen yields in runoff from the Caura River drainage set a lower bound for the amount of nitrogen fixation in the watershed. Although fixed (nonmolecular) nitrogen is deposited within the watershed from the atmosphere, significant net gain by this mechanism for a watershed as large as that of the Caura River is unlikely in view of the relatively short atmospheric residence time for gaseous fixed nitrogen other than N_2O (a few days in the entire troposphere; Sonderlund and Svensson 1976). Furthermore, the similarity of adjacent watersheds to that of the Caura suggests that the amounts of atmospheric nitrogen derived from surrounding watersheds would be similar to the atmospheric export to those watersheds. Lightning over or very near the watershed is a net source of atmospheric fixed nitrogen, but nitrogen budgets consistently show that this source accounts for <10% of atmospheric nitrogen deposition (Rosswall 1981). Thus it seems unlikely that net atmospheric transport to the Caura watershed exceeds $1\text{--}2 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of fixed nitrogen.

In view of the maturity of the forests in the Caura watershed, major aggradation seems unlikely. In a system near steady state with small net atmospheric transport, total nitrogen loss in runoff is essentially the rate of nitrogen fixation minus the rate of denitrification.

TABLE 2. Comparative data on N and P concentrations and watershed losses by runoff (=yields to the river) for minimally disturbed watersheds.

Watershed	Runoff (mm/yr)	Concentration ($\mu\text{g/L}$)		Loss ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)		Source
		Total N	Total P	Total N	Total P	
Caura River drainage	2423	401	20	9.98	0.46	this study
Gambia River	110	1145	70	1.26	0.077	Lesack et al. 1984
Canadian Shield, Ontario	277	339	18	0.94	0.05	Schindler et al. 1976
Andrews Forest, Oregon*	1427	83	46	1.18	0.65	Fredricksen 1976
Hubbard Brook, New Hampshire†	833	481	2	4.01	0.019	Likens et al. 1977†
Summit County, Colorado‡	418	201	8	0.84	0.035	Lewis et al. 1984b†
Global average	370	840	500§	3.10	1.85	Meybeck 1982

* Average of watersheds HJA 9 and 10; 1972, 1973.

† From Likens et al. 1977: Table 9.

‡ Average for four watersheds, 1982.

§ Average strongly affected by a few rivers with high particulate P.

The nitrogen fixation rate in the watershed must therefore exceed denitrification losses by $\approx 10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Dense stands of legumes often have fixation rates between 50 and $100 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Gordon and Wheeler 1983), but among mature undisturbed ecosystems, fixation rates $> 10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ are unusually high. Although it has long been suspected that nitrogen fixation rates in tropical forests are high, field confirmation from large watersheds such as that of the Caura have previously been unavailable.

The patterns of nitrogen concentration and nitrogen yield give some information about factors that control the retention of nitrogen in the Caura River drainage. Minima for nitrate concentrations that coincide with very low flows in the growing season are familiar from studies of small watersheds in the temperate zone (e.g., Likens et al. 1977, Martin 1979, Lewis et al. 1984b). These minima appear to represent the effect of biological demand, which is strong enough to account for reductions in nitrate concentration when the rate of water flow through the system is relatively low. At high discharge, there is a dilution effect. Because of the contrasting effects of biological uptake and dilution, the maximum nitrate concentrations occur at intermediate discharges. The brief peak of nitrate concentrations just at the time of first rising water probably represents a purging phenomenon whose explanation is nitrate accumulation in seasonally dry soil layers (Viner 1975, Vitousek and Melillo 1979).

Although Sonderlund and Svensson (1976) have stated that organic N and nitrate are the only important forms of nitrogen in river discharge, the data for the Caura River demonstrate that ammonium can be a significant component of inorganic nitrogen in rivers draining tropical moist forest. Meybeck (1982) has shown that the relative importance of ammonium in uncontaminated rivers is a declining function of total soluble inorganic N. However, as pointed out by Meybeck, the amount of information on ammonium concentrations in rivers draining natural watersheds is small. The Caura River has ammonium concentrations well above those expected from Meybeck's trend line.

The positive relationship between discharge and concentration of soluble organic nitrogen does not apply to all soluble organic matter; organic carbon concentration explains no significant amount of the variation in organic nitrogen concentration ($P > .05$). The lack of relationship must be explained by seasonal changes in the nitrogen content of dissolved organic matter.

The phosphorus concentrations of the Caura River are higher than might have been expected. Although it is not unusual to find P concentrations $> 20 \mu\text{g/L}$ in disturbed or naturally erosive watersheds, or in watersheds with nutrient-rich soils, concentrations in the vicinity of $20 \mu\text{g/L}$ could be considered high for watersheds that are undisturbed, heavily vegetated, and poor in nutrients (Table 2). Moderately high phosphorus concentrations combined with high runoff result in a high phosphorus yield for the Caura River drainage. The high phosphorus loss rates may indicate unexpectedly high weathering rates, unexpectedly high net atmospheric transport of phosphorus from points outside the watershed, or disequilibrium of mass balance. The latter two possibilities seem less likely, but cannot yet be ruled out. Although the flux from the Caura watershed is high, low temporal variation in concentrations demonstrates strong buffering, even at the highest rate of runoff.

The Canadian Shield provides an interesting comparison with the watershed of the Caura River. Large portions of the Canadian Shield, like the Guayana Shield, support an undisturbed ecosystem lying on thoroughly weathered, flat substrate that is poor in nutrients (Table 2). The nutrient concentrations in runoff from minimally disturbed portions of the Canadian Shield are almost identical to those in runoff from the Caura watershed; the differences in yields, which are very great, are entirely explained by differences in amount of runoff.

The molar ratio of C:N:P for combined dissolved and particulate materials of the Caura River, weighted for discharge, is 689:14:1. By comparison with the Redfield ratio, which characterizes protoplasm (106:

16:1, Redfield 1958), the runoff yield is enriched in carbon. With respect to woody plants (2040:17:1; Likens et al. 1981) or tropical forest litterfall (Vitousek 1984), the yield is enriched in N and P. Ratios obtained by similar methods for the Gambia River, which drains a much drier watershed (Table 2), indicate lower amounts of carbon and higher amounts of nitrogen with respect to phosphorus (Lesack et al. 1984).

The data for N and P in runoff are consistent with the hypothesis that mature ecosystems have high average nutrient yields because they are no longer aggrading. In addition, the low sensitivity of concentrations to differences in the amount of runoff between seasons shows strong short-term homeostasis.

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LITERATURE CITED

- Bendschneider, K., and R. J. Robinson. 1952. A new spectrophotometric method for the determination of nitrate in sea water. *Journal of Marine Research* **11**:87-96.
- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer, New York, New York, USA.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**:233-260.
- Curtis, W. F., R. H. Meade, C. F. Nordin, Jr., N. B. Price, and E. R. Sholkovitz. 1979. Non-uniform vertical distribution of fine sediment in the Amazon River. *Nature* **280**:381-383.
- Ewel, J. J., A. Madriz, and J. A. Tosi, Jr. 1976. Zonas de vida de Venezuela. Sucre, Caracas, Venezuela.
- Feller, M. C., and J. P. Kimmins. 1979. Chemical characteristics of small streams near Haney in South British Columbia. *Water Resources Research* **15**:247-258.
- Fredriksen, R. L. 1976. Nitrogen, phosphorus, and particulate matter budgets of five coniferous forest ecosystems in the Western Cascades Range, Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Gordon, J. C., and C. T. Wheeler. 1983. Biological nitrogen fixation in forest ecosystems: foundations and applications. Dr. W. Junk, The Hague, The Netherlands.
- Gorham, E., P. M. Vitousek, and W. A. Reiners. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annual Review of Ecology and Systematics* **10**:53-84.
- Grasshoff, K. 1976. Methods of sea water analysis. Verlag Chemie, Weinheim, Germany.
- Johnson, N. M., G. E. Likens, F. H. Bormann, D. W. Fisher, and R. S. Pierce. 1969. A working model for the variation in streamwater chemistry at the Hubbard Brook Experimental Forest, New Hampshire. *Water Resources Research* **5**:1353-1363.
- Jordan, C. F., and R. Herrera. 1981. Tropical rain forests: are nutrients really critical? *American Naturalist* **117**:167-180.
- Lesack, L. F., R. E. Hecky, and J. M. Melack. 1984. Transport of carbon, nitrogen, phosphorus, and major solutes in the Gambia River, West Africa. *Limnology and Oceanography* **29**:816-830.
- Levine, S. N., and D. W. Schindler. 1980. Radiochemical analysis of orthophosphate concentration and seasonal changes in the flux of orthophosphate to seston in Canadian shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:479-487.
- Lewis, W. M., Jr., and M. C. Grant. 1979. Relationships between stream discharge and yield of dissolved substances from a mountain watershed. *Soil Science* **128**:353-363.
- Lewis, W. M., Jr., J. F. Saunders III, D. W. Crumpacker, Sr., and C. Bredecke. 1984b. Eutrophication and land use: Lake Dillon, Colorado. Springer, New York, New York, USA.
- Lewis, W. M., Jr., J. F. Saunders III, and F. H. Weibezahn. 1984a. Cross-sectional variation in the chemistry and suspended sediment load of the Orinoco River at Ciudad Bolivar. *Acta Cientifica Venezolana* **35**:382-385.
- Lewis, W. M., Jr., J. F. Saunders III, F. H. Weibezahn, and S. N. Levine. 1986. Organic carbon in the Caura River, Venezuela. *Limnology and Oceanography* **31**:653-656.
- Likens, G. E., F. H. Bormann, and N. M. Johnson. 1981. Interactions between major biogeochemical cycles in terrestrial ecosystems. Pages 93-112 in G. E. Likens, editor. *Some perspectives of the major biogeochemical cycles*. SCOPE Report 17. Wiley, New York, New York, USA.
- Likens, G. E., F. H. Bormann, R. S. Pierce, J. S. Eaton, and N. M. Johnson. 1977. Biogeochemistry of a forested ecosystem. Springer, New York, New York, USA.
- Martin, C. W. 1979. Precipitation and streamwater chemistry in an undisturbed forested watershed in New Hampshire. *Ecology* **60**:36-42.
- Meybeck, M. 1982. Carbon, nitrogen, and phosphorus transport by world rivers. *American Journal of Science* **282**:401-450.
- Redfield, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* **46**:205-221.
- Rigler, F. H. 1968. Further observations inconsistent with the hypothesis that molybdenum blue method measures orthophosphate in lake water. *Limnology and Oceanography* **13**:7-13.
- Rosswall, T. 1981. The biogeochemical nitrogen cycle. Pages 25-50 in G. E. Likens, editor. *Some perspectives of the major biochemical cycles*. SCOPE Report 17. Wiley, New York, New York, USA.
- Schindler, D. W., R. W. Newbury, K. G. Beatty, and P. Campbell. 1976. Natural water and chemical budgets for a small Precambrian lake basin in central Canada. *Journal of the Fisheries Research Board of Canada* **33**:2526-2543.
- Sheldon, R. W. 1972. Size separations of marine seston by membrane and glass fibre filters. *Limnology and Oceanography* **17**:494-498.
- Solorzano, L., and J. Sharp. 1980a. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. *Limnology and Oceanography* **25**:754-758.
- Solorzano, L., and J. Sharp. 1980b. Determination of total dissolved nitrogen in natural waters. *Limnology and Oceanography* **25**:751-754.
- Sonderlund, R., and B. H. Svensson. 1976. The global nitrogen cycle. In B. H. Svensson and R. Sonderlund, editors. *Nitrogen, phosphorus, and sulfur-global cycles*. SCOPE Report 7. Ecological Bulletins-NFR **22**:23-73.
- Stevens, H. H., Jr., G. A. Lutz, and D. W. Hubbell. 1980. Collapsible-bag suspended-sediment sampler. *American Society of Civil Engineers Proceedings* **106**:611-616.
- Viner, A. B. 1975. The supply of minerals to tropical rivers and lakes (Uganda). Pages 227-261 in G. Olson, editor. *An introduction to land-water relationships*. Springer, New York, New York, USA.
- Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* **65**:285-298.
- Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, W. A. Reiners, and R. L. Todd. 1979. Nitrate losses from disturbed ecosystems. *Science* **204**:469-474.

- Vitousek, P., and J. M. Melillo. 1979. Nitrate losses from disturbed forests: patterns and mechanisms. *Forest Science* **25**:605-619.
- Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* **25**:376-381.
- Wood, E. D., F. A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in sea water by cadmium copper reduction to nitrite. *Journal of the Marine Biological Association of the United Kingdom* **47**:23-31.