



## Nitrogen yields from undisturbed watersheds in the Americas

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**Abstract.** Yields of total fixed nitrogen and nitrogen fractions are summarized for thirty-one watersheds in which anthropogenic disturbance of the nitrogen cycle, either through land use or atmospheric deposition, is negligible or slight. These yields are taken as representative of background conditions over a broad range of watershed areas, elevations, and vegetation types. The data set focuses on watersheds of the American tropics, but also includes information on the Gambia River (Africa) and some small watersheds in the Sierra Nevada of California. For the tropical watersheds, total nitrogen yield averages  $5.1 \text{ kg ha}^{-1} \text{ y}^{-1}$ . On average, 30% of the total is particulate and 70% is dissolved. Of the dissolved fraction, an average of 50% is organic and 50% is inorganic, of which 20% is ammonium and 80% is nitrate. Yields are substantially lower than previously estimated for background conditions. Yields of all nitrogen fractions are strongly related to runoff, which also explains a large percentage of variance in yield of total nitrogen ( $r^2 = 0.85$ ). For total nitrogen and nitrogen fractions, yield increases at about two-thirds the rate of runoff; concentration decreases as runoff increases. There is a secondary but significant positive relationship between elevation and yield of DIN. Ratios DON/TDN and PN/TN both are related to watershed area rather than runoff; DON/TDN decreases and PN/TN increases toward higher stream orders. The analysis suggests for tropical watersheds the existence of mechanisms promoting strong homeostasis in the yield of N and its fractions for a given moisture regime, as well as predictable downstream change in proportionate representation N fractions. Yields and concentrations for small tropical watersheds are much larger than for the few temperate ones with which comparisons are possible.

### Introduction

The nitrogen cycle has been changed by agriculture, waste disposal, land use, and anthropogenic release of inorganic nitrogen compounds to the atmo-

sphere (Vitousek et al. 1997). While of global scope, these perturbations vary regionally (Howarth et al. 1997). In some regions, anthropogenic perturbation of the nitrogen cycle is still small. For present purposes, we define minimally disturbed regions as those with 80% or more natural vegetative cover, population density below 5 indiv. km<sup>-2</sup> and estimated anthropogenic nitrogen deposition (NO<sub>y</sub>-N) below 2.5 kg ha<sup>-1</sup> y<sup>-1</sup> (from models: Holland et al. 1997). Flux measurements from such regions, which are becoming increasingly scarce, are the only direct source of information on baseline conditions for the nitrogen cycle over a range of physiographic, hydrologic, and ecological conditions. The purpose of this paper is to summarize and analyze information on the yield of nitrogen compounds in runoff from watersheds in which anthropogenic disturbance has not greatly affected the nitrogen cycle.

The objectives of this paper parallel those of Meybeck (1982), who used a synthesis of information on nitrogen and other elements to reach conclusions about background conditions. The present effort differs from Meybeck's in that it focuses specifically on nitrogen and emphasizes yields (mass area<sup>-1</sup> time<sup>-1</sup>) rather than concentrations (mass volume<sup>-1</sup>). We deal here only with background conditions, and not with the full range of perturbed conditions, as Meybeck did. Our analysis benefits from recent accumulation of new information on nitrogen yields from minimally disturbed environments. This enriched data base allows for the first time some statistical analysis of factors influencing the natural nitrogen cycle.

The working hypothesis for this analysis is that watersheds, when unperturbed by human influence, will show nitrogen yields that can be predicted on the basis of general environmental variables such as drainage area or amount of runoff, as explained below. The hypothesis is tested empirically with field estimates of nitrogen yield from watersheds in which the nitrogen cycle has been little perturbed by human activities.

## Methods

The basis for the present analysis is annual yield of total fixed nitrogen, or of any major components of the total fixed nitrogen pool, from watersheds of known area. Raw data underlying the annual yield estimates include information on concentration and discharge, which together can be used in computing discharge-weighted mean concentrations that can be converted into annual yields. Temporally fragmentary data have been excluded; all of the data considered here span at least one annual cycle and include no fewer than six measurements per cycle for both discharge and concentration. For most sites included in the analysis, information is available on multiple years and includes many more than six measurements per year. Some data sets used

in the analysis lack one or more components. Statistical analyses are applied only to data sets for which relevant data are available; thus the number of measurements varies from one statistical test to another.

The analysis includes three independent variables that might be expected to influence nitrogen yield: area, elevation, and annual specific runoff (mm/yr). Area is a surrogate for a cluster of variables, including the time and distance of transport for nitrogen in a drainage network. In this sense, there is a connection between area and the river continuum concept, which postulates changes in organic carbon and nutrients as water passes from one stream order to the next (Allan 1995). Elevation, the second independent variable, is estimated as the mean of the highest and lowest elevations for small watersheds and as the area-weighted mean for large watersheds. Elevation is related to mean gradient and topographic relief, both of which might influence the transit time of nitrogen in soil, and thus the uptake or biologically-induced partitioning of fixed nitrogen. Gradient and relief also are related to erosion, which in turn may influence the transport of particulate nitrogen. Specific runoff (mm/yr), which for convenience is referred to here as runoff, is the third independent variable. It is estimated for years coincident with the water chemistry data used in calculating yields. Specific runoff reflects the flushing rate of the terrestrial system, and by this means may affect nitrogen transport and residence time of fixed nitrogen and nitrogen fractions in the watershed. Because runoff reflects precipitation, soil moisture, and vegetation, it also may be related to a complex of biological factors including potential for biological uptake or processing of nitrogen, and potential for nitrogen fixation.

Few temperate sites and no arctic sites are included here (Table 1). With the exception of studies in the Sierra Nevada of California, data from temperate locations cannot pass the screening criteria because of strong regional enrichment of precipitation in fixed nitrogen, even at relatively long distances from industrial centers. Yield from arctic regions has seldom been measured (but see Meybeck 1982) and presents interpretational difficulties that are difficult to resolve for the present analysis.

Six sites at high elevation in the Sierra Nevada of California are sufficiently free from atmospheric contamination to be part of the data set. The Sierra Nevada data form a distinctive cluster. The reasons for this cannot be resolved because there are too many possibilities, including not only latitude but also elevation (the Sierra Nevada sites are considerably higher than any of the tropical sites included in the data base). Because the Sierra Nevada sites form a distinct population, they have been excluded from the statistical analysis. Therefore, the conclusions of the statistical analysis apply specifically to tropical sites of low to moderate elevation over a wide range of

Table 1. Summary of information on watersheds, sequenced by area, that meet the screening requirements for the data set on nitrogen yields from undisturbed watersheds.

Site	Lat	Long	Elev m asl	Area km <sup>2</sup>	Runoff mm y <sup>-1</sup>	Veg.	Sources <sup>1</sup>
Tropical Watersheds							
Amazon (Óbidos)	5 S	60 W	750	5000000	1200	Forest	i, j
Madeira	8 S	62 W	870	1300000	740	Forest	i, j
Solimões at Içá	3 S	70 W	850	1200000	1200	Forest	i, j
Orinoco	7 N	67 W	800	950000	1300	Mixed	k
Negro	0 S	67 W	200	620000	1600	Forest	i, j
Paraguay River	19 S	57 W	600	363500	123	Savanna	b
Japurá	2 S	68 W	300	300000	2000	Forest	i, j
Juruá	5 S	68 W	200	220000	900	Forest	i, j
Apure	8 N	70 W	550	170000	300	Savanna	k
Guaviare	4 N	69 W	880	150000	1800	Forest	l
Trombetas	0 N	58 W	200	130000	540	Forest	i, j
Meta	6 N	69 W	880	110000	1600	Savanna	l
Caroní	6 N	63 W	800	95000	1700	Forest	k
Caura	6 N	66 W	800	47500	2400	Forest	m
Gambia River	13 N	14 W	500	42000	110	Savanna	c
Ícacos	18 N	66 W	700	3.20	3683	Forest	h
Rio Tempisqueito	10 N	85 W	960	3.19	2900	Forest	g
Rio Tempisqueito Sur	10 N	85 W	915	3.11	4300	Forest	g
Quebrada Kathia	10 N	85 W	1070	2.64	3100	Forest	g
Sonadora	18 N	66 W	700	2.60	2497	Forest	h
Quebrada El Jobo	10 N	85 W	815	0.55	1400	Forest	g
Quebrada Zompopa	10 N	85 W	850	0.37	2800	Forest	g
Quebrada Marilin	10 N	85 W	735	0.36	1600	Forest	g
Braço do Mota	3 S	61 W	100	0.18	1650	Forest	e
Tóronja	18 N	66 W	400	0.16	1750	Forest	h
Temperate Watersheds							
Emerald Lake	36 N	189 W	2800	1.20	854	Alpine	a
Spuller Lake	38 N	119 W	3130	1.00	789	Alpine	a
Log Creek	37 N	119 W	2070	0.50	219	Forest	d
Tharp's Creek	37 N	119 W	2070	0.13	219	Forest	d
Sierra Lake 1	37 N	119 W	2960	0.01	352	Alpine	f
Sierra Lake 2	37 N	119 W	2960	0.00	595	Alpine/ rock	f

<sup>1</sup> Sources: a: Melack et al. 1997; b: Hamilton et al. 1997; c: Lesack et al. 1984; d: Williams and Melack 1997a, b; e: Lesack 1993, Williams et al. 1997; f: Williams 1997; g: Newbold et al. 1995; h: McDowell and Asbury 1994; i: Richey unpublished; j: Lewis et al. 1995; k: Lewis and Saunders 1990; l: Weibezahn 1990; m: Lewis et al. 1986

watershed sizes, moisture regimes, and vegetation types. The Sierra Nevada data are tabulated as a means of providing perspective on the data for tropical locations.

## Results

Table 2 summarizes the annual yields of nitrogen and nitrogen fractions for watersheds in this analysis. Fewer than half of the studies that meet the criteria for the analysis include all major fractions of total fixed nitrogen. Measurements of nitrate are most common, whereas measurements of ammonium, dissolved organic nitrogen, and particulate nitrogen are less common. Estimates of total nitrogen yield are available for 17 of the 31 watersheds shown in Table 2.

The three independent variables for this analysis (elevation, area, runoff) were tested for statistical relationships to each other (log-log transformation followed by regression analysis). Elevation is unrelated to runoff or to area ( $p > 0.05$ ); area is significantly but weakly ( $r^2 = 0.26$ ) related to runoff:  $\log(\text{runoff, mm y}^{-1}) = 3.34 - 0.071 \log(\text{area, km}^2)$ . In this data set, large watersheds tend to have less runoff per unit area than small watersheds.

A multiple regression analysis following log-log transformation of all variables shows that, for total nitrogen and each of the nitrogen fractions shown in Table 2: (1) significant variance can be explained ( $p < 0.05$ ) by the three independent variables, (2) runoff is consistently the dominant variable explaining variance, and (3) when runoff is used first in multiple regression analysis, area explains no significant added variance and elevation explains significant added variance only for dissolved inorganic nitrogen and its components. For these reasons, the remainder of the analysis can be simplified by focus on relationships between yield and runoff, except in the case of dissolved inorganic nitrogen and its components, for which elevation is also important (Table 3).

### *Inorganic nitrogen*

Inorganic nitrogen consists primarily of ammonium and nitrate. Although the ammonium ion will be in equilibrium with ammonium hydroxide and ammonia, ammonium predominates at the pH of most surface waters (Erickson 1985). For present purposes, the composite of all forms will be designated as ammonium. In principle, nitrite and gaseous nitrogen oxides also could be present. Broad experience with the analysis of nitrite in surface waters has shown that nitrite is a negligible contributor to inorganic nitrogen in flowing waters in the absence of wastewater or anaerobic water sources

Table 2. Nitrogen yields for the watersheds listed in Table 1 (sources as in Table 1). Totals for DIN, TDN, and TN may not equal the sum of fractions if totals were analyzed separately from fractions.

Site	kg ha <sup>-1</sup> y <sup>-1</sup>						
	NH <sub>4</sub> -N	NO <sub>3</sub> -N	DIN	DON	TDN	PN	TN
Tropical Watersheds							
Amazon (Óbidos)	0.24	1.68	1.92	1.94	3.86	2.42	6.06
Madeira		1.30	1.30	1.30	2.60	2.03	4.63
Solimões at Içá		2.40	2.40	1.36	3.76	3.90	7.66
Orinoco	0.33	1.04	1.50	2.08	3.58	2.41	5.98
Negro		0.67	0.67	2.48	3.15	0.02	1.47
Paraguay River					0.57	0.16	0.73
Japurá		2.04	2.04	1.84	3.88	2.44	8.60
Juruá		1.82	1.82	1.21	3.02	1.44	4.45
Apure	0.13	0.41	0.53	0.80	1.33	1.54	2.87
Guaviare	0.31	0.94	1.24				
Trombetas			0.53				3.01
Meta	0.37	1.78	2.14				
Caroní	0.61	1.46	2.07	2.35	4.42	0.75	5.17
Caura	0.89	1.49	2.38	4.00	6.38	3.64	9.98
Gambia River					1.11	0.15	1.26
Icacos	0.68	2.54	3.22	4.79	8.01	1.80	9.80
Rio Tempisquito		6.10	6.10	3.00	9.10		
Rio Tempisquito Sur		4.90	4.90	2.10	7.00		
Quebrada Kathia		5.60	5.60	1.50	7.10		
Sonadora	0.30	1.39	1.69	3.74	5.43	0.47	5.90
Quebrada El Jobo		4.30	4.30	2.00	6.30		
Quebrada Zompopa		6.00	6.00	3.40	9.40		
Quebrada Marilin		4.00	4.00	1.90	5.90		
Braço do Mota	0.14	0.60	0.74	2.87	3.61	0.70	4.31
Tóronja	0.26	0.90	1.16	2.80	3.96	0.48	4.40
Temperate Watersheds*							
Emerald Lake	0.04	0.56	0.60				
Spuller Lake	0.01	0.45	0.45				
Log Creek	0.01	0.00	0.02				
Tharp's Creek	0.01	0.01	0.01				
Sierra Lake 1	0.01	0.03	0.04				
Sierra Lake 2	0.04	0.07	0.11				
Mean (tropical only)	0.39	2.43	2.53	2.37	4.70	1.52	5.08
Number of sites	11	22	23	20	22	16	17
Standard error	0.23	1.80	1.73	1.00	2.40	1.18	2.71

\* Excluded from statistical summaries.

Table 3. Summary of the relationship between total nitrogen and various nitrogen fractions and amount of runoff (log-log). All relationships are statistically significant at  $p < 0.05$ . The table also shows, based on the statistical relationships, the expected yields and volume-weighted mean concentrations of the nitrogen fractions at low runoff (e.g., Gambia), at the savanna-forest transition (400 mm), in the mid-range of forest runoff (2000 mm), and at highest runoff (4000 mm).

Fraction or Ratio	Const	Slope	Std. err. slope	$r^2$	N (kg ha <sup>-1</sup> y <sup>-1</sup> ) at runoff (mm y <sup>-1</sup> )				N (μg l <sup>-1</sup> ) at runoff (mm y <sup>-1</sup> )			
					100	400	2000	4000	100	400	2000	4000
Ammonium-N*	-2.57	0.65	0.23	0.46	0.05	0.13	0.38	0.59	54	33	19	15
Nitrate-N*	-2.33	0.80	0.24	0.36	0.19	0.56	2.05	3.56	186	141	102	89
Dissolved inorg. N*	-2.41	0.84	0.19	0.49	0.19	0.60	2.31	4.13	186	149	115	103
Dissolved org. N	-1.44	0.55	0.11	0.57	0.46	0.98	2.37	3.48	457	245	119	87
Total diss. N	-1.50	0.67	0.05	0.89	0.69	1.75	5.15	8.19	692	438	257	205
Particulate N**	-1.68	0.58	0.22	0.34	0.30	0.67	1.72	2.57	302	169	86	64
Total N**	-1.24	0.63	0.07	0.85	1.05	2.51	6.91	9.45	1047	627	376	267

\* Significant added variance for elevation (see text).

\*\* Excludes R. Negro.

(Meybeck 1982; Stumm & Morgan 1996). The reactive oxides of nitrogen (primarily NO and NO<sub>2</sub>) cannot long persist in water. N<sub>2</sub>O, which is much less reactive, is of interest as a greenhouse gas but occurs at very low concentrations and thus does not contribute much to the mass transport of fixed nitrogen. Therefore, we treat the sum of ammonium and nitrate as dissolved inorganic nitrogen (DIN).

Table 2 shows the mean yield of ammonium (0.39 kg ha<sup>-1</sup> y<sup>-1</sup>; 23% of DIN) at the 11 sites for which information on ammonium is available. Some studies excluded ammonium after initial analyses showed it to be present only at very low concentrations. In this sense, the mean in Table 2 may be biased toward locations that have easily measurable concentrations of ammonium. If missing values for ammonium are treated as zeros, ammonium accounts for about 15% of total inorganic nitrogen. Thus the true mean is probably between 15% and 23%; we assign it a nominal value of 20%.

Yield of ammonium increases with yield of nitrate ( $\log \text{NH}_4\text{-N kg ha}^{-1} \text{ y}^{-1} = 0.91 \log \text{NO}_3\text{-N kg ha}^{-1} \text{ y}^{-1} - 0.54$ ;  $r^2 = 0.62$ ). The coefficient of the log-log relationship is not significantly different from 1.0, i.e., the ratio of ammonium to DIN is essentially constant over a broad range of DIN concentrations. Yield of ammonium is positively related to amount of runoff; it increases about 50% when runoff doubles (Table 3). Secondarily, it is also positively related to elevation ( $R^2 = 0.73$  for runoff plus elevation; for runoff alone,  $r^2 = 0.46$ ).

As shown by Table 2, the yield of nitrate averages 2.4 kg ha<sup>-1</sup> y<sup>-1</sup>, and is strongly and positively related to runoff (Table 3, Figure 1). When both runoff and elevation are included as independent variables in a multiple regression analysis (log-log),  $R^2 = 0.49$ , while runoff alone gives  $r^2 = 0.36$ .

Because the trends in yield of ammonium and nitrate are similar, both are reflected in yields of DIN, which shows a strong positive relationship with amount of runoff, and a weaker relationship with elevation ( $R^2 = 0.65$  for runoff and elevation together,  $r^2 = 0.55$  for runoff alone).

Yields of dissolved inorganic nitrogen passing from the Sierra Nevada watersheds, which are excluded from the statistical analysis of Table 3, are extraordinarily low (all  $\leq 0.6$  kg ha<sup>-1</sup> y<sup>-1</sup>; Table 2). These watersheds are uniformly small, but they overlap in size with small tropical watersheds that have much higher yields. Although the runoff for these watersheds is among the lowest for the data set, the inorganic nitrogen yields are far lower than would be expected from the rest of the data set on the basis of runoff (Figure 1).



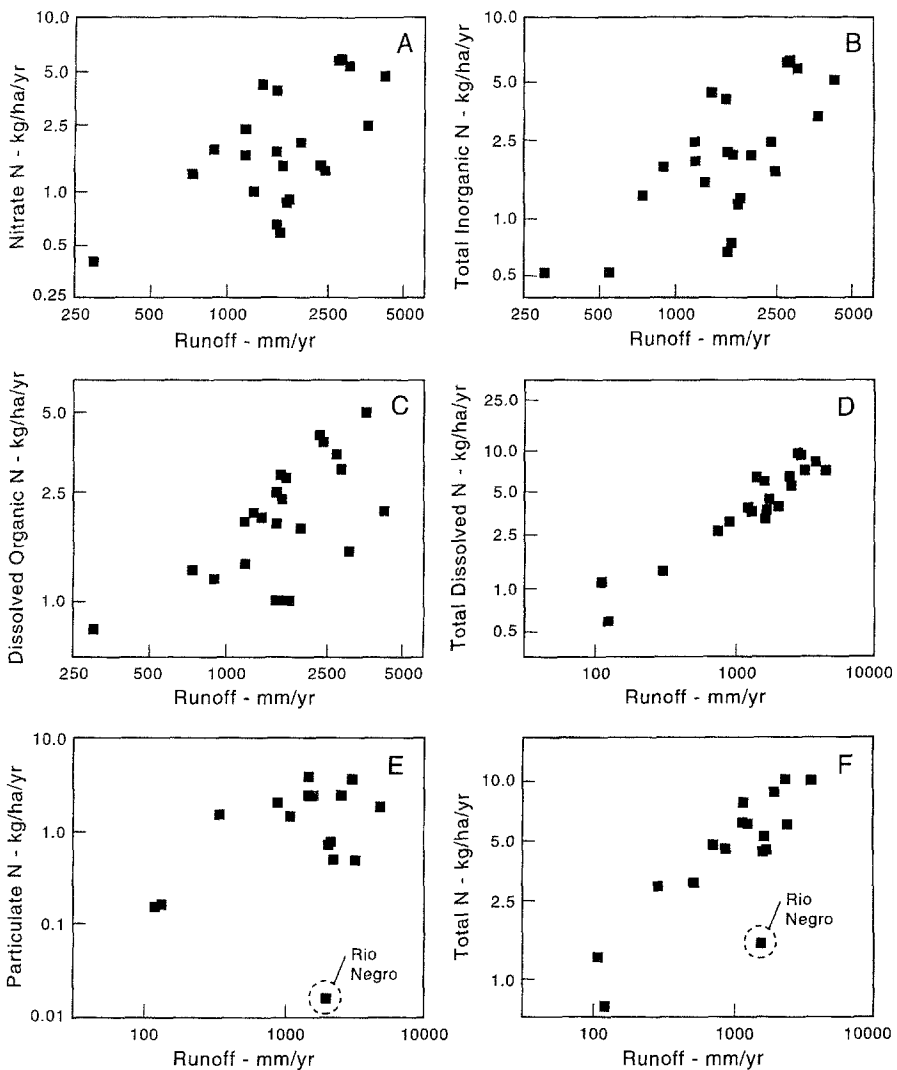


Figure 1. Relationship of annual runoff to annual yields of nitrogen fractions and total nitrogen in minimally disturbed tropical watersheds.

### *Dissolved organic and total dissolved nitrogen*

The mean yield of dissolved organic nitrogen (DON) from the 20 watersheds in which it was measured is  $2.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ , i.e., the same as the yield of DIN. Yield of DON is positively related to amount of runoff (Table 3). Yield of total dissolved nitrogen (TDN) also shows a strong positive relationship to runoff (Table 3, Figure 1). The exponent for the log-log relationship is

significantly ( $p < 0.05$ ) below 1: yield of dissolved nitrogen increases about two-thirds as fast as runoff.

### *Particulate nitrogen*

Yield of particulate nitrogen (PN) averages  $1.5 \text{ kg ha}^{-1} \text{ y}^{-1}$  across the 16 watersheds for which it was measured. A plot of the relationship between yield of particulate nitrogen and runoff shows that the Rio Negro has an anomalously low yield of particulate nitrogen (Figure 1), which reflects its extraordinarily low load of suspended solids. If the Rio Negro is removed as a special case, there is a significant positive relationship between particulate nitrogen and amount of runoff (Table 3).

### *Total nitrogen*

Yield of total nitrogen (TN) is closely and positively related to the amount of runoff (Figure 1), but increases at only about two-thirds the rate of runoff (Table 2). The Rio Negro is anomalous because of its exceptionally low yield of particulate nitrogen, as mentioned above.

### *Ratios*

The ratios DON/TDN and PN/TN were analyzed statistically. Conclusions about complementary ratios (DIN/TDN and TDN/TN) follow directly from the two ratios that were analyzed.

The ratios DON/TDN and PN/TN are, as shown by multiple regression analysis (ratios untransformed, independent variables log transformed), significantly related to area but not to elevation or runoff after area is taken into account. The mean of the ratio DON/TDN is 0.50 (std deviation, 0.17); larger watersheds have proportionately less DON in the TDN fraction (Figure 2, Table 4). The mean of the ratio PN/TN is 0.30 (standard deviation, 0.16); larger watersheds have proportionately more PN (Table 4).

## **Discussion**

Yields of total nitrogen and all nitrogen fractions show a strong and positive relationship to amount of runoff. Yields increase less rapidly than runoff, however, and this accounts for a decline in discharge-weighted mean concentrations of total nitrogen and nitrogen fractions with increasing annual runoff (Table 3). Because runoff is correlated with vegetation, the relationship between nitrogen yield and runoff corresponds to a relationship between

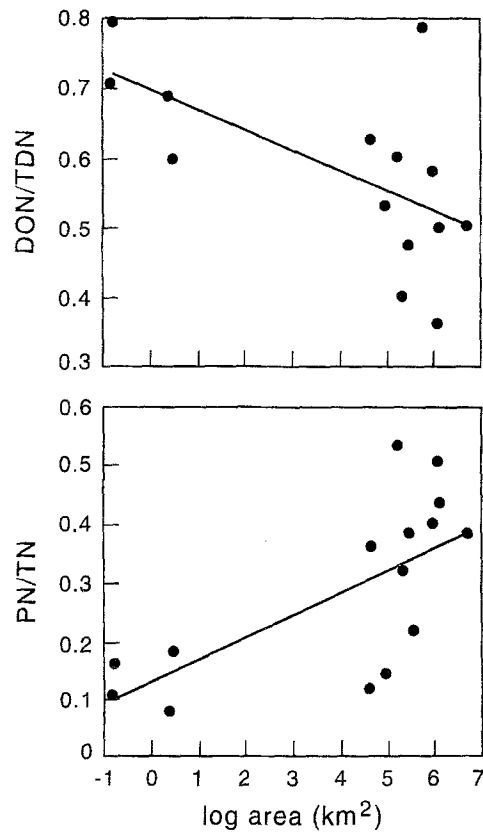


Figure 2. Relationship of watershed area to ratios DON/TDN and PN/TN for minimally disturbed tropical watersheds.

Table 4. Relationships between watershed area and the ratios of nitrogen fractions (area is log transformed, ratio is not transformed).

Ratio	Constant	Slope	SE Slope	$r^2$	Ratios by Stream Order**					
					2	4	6	8	10	12
					Ratios by Area (km <sup>2</sup> )					
					10	10 <sup>2</sup>	10 <sup>3</sup>	10 <sup>4</sup>	10 <sup>5</sup>	10 <sup>6</sup>
DON/TDN	0.70	-0.029	0.011	0.38	0.67	0.64	0.61	0.58	0.55	0.52
PN/TN*	0.13	0.034	0.014	0.49	0.17	0.21	0.25	0.29	0.33	0.37

\* R. Negro omitted.

\*\* As determined approximately from area.

nitrogen yield and vegetation type: savanna yields far less total nitrogen and individual nitrogen fractions than forest (Table 3). Amount of precipitation, which affects runoff, probably influences both the deposition and fixation rates for nitrogen, as well as the rate at which nitrogen is released through decomposition. Also of likely importance is a relationship between amount of water moving through soil and the probability that individual molecules or ions will be entrained in the flow. Quantitative separation of these factors is not possible at present.

The relative influence of biotic factors may explain a secondary relationship between DIN and elevation. In headwaters, inorganic N delivered by precipitation or released by decomposition and nitrification may have lower probability of uptake than it would at lower elevation where the terrain is flatter and thus more conducive to long residence times for shallow groundwater. This possibility seems contradicted by low DIN yields from the Sierra Nevada watersheds (Table 2) as well as some in Chile (Hedin et al. 1995). Comparisons may be misleading, however, because the tropical watersheds of the present analysis reach only moderate elevations (Table 1).

Nitrogen fractionation is surprisingly well constrained, but does show trends with watershed area, and thus with stream order. The river continuum concept suggests that progression from headwaters to large rivers will be accompanied by increased processing of carbon or nutrients (Allan 1995). This very general prediction is consistent with the data in that the particulate-bound form of nitrogen (PN) becomes proportionately more important at high stream orders. Decrease in proportion of DON at higher stream orders could signify progressive DON mineralization with increasing stream orders, but other explanations cannot be ruled out.

The present analysis validates a number of Meybeck's (1982) conclusions, but also suggests some refinements. Meybeck estimated average  $\text{NO}_3^-$ -N concentrations as 100  $\mu\text{g/L}$  for all climate zones combined and 75  $\mu\text{g/L}$  for the tropics. Our data indicate a higher number (close to 120  $\mu\text{g/L}$  for tropical runoff of 1000 mm). Our data also demonstrate the high importance of runoff in relation to both yields and concentrations of nitrate and all other nitrogen fractions (e.g., a 10-fold difference in yield of nitrate between dry savanna and very wet forest). Our data generally support Meybeck's conclusion about the proportion of ammonium in DIN under natural conditions: his estimate of the mean is 15%, whereas ours is 15–23%.

Because of scarce measurements, Meybeck estimated DON from DOC (mean DON = 260  $\mu\text{g/L}$ ). Our direct estimates indicate a lower mean, at least for the tropics (162  $\mu\text{g/L}$  @ 1000 mm), and also a very strong relationship to amount of runoff. His estimate of particulate N (550  $\mu\text{g/L}$  N), also based on ratios, is much higher than ours (115  $\mu\text{g/L}$  @ 1000 mm). As a result

primarily of differences in estimates for DON and PN, our estimates for TN (4.5 kg/ha/yr or 450  $\mu\text{g/L}$  at 1000 mm) are about half as high as Meybeck's (935  $\mu\text{g/L}$ ). The close relationship of runoff to DON ( $r^2 = 0.89$ ) and total N ( $r^2 = 0.85$ ) in our data is remarkable.

For the American tropics, the present analysis provides a means of estimating nitrogen yields and concentrations over a broad range of natural conditions. Background yields and concentrations give in turn a basis for evaluating growing anthropogenic perturbation of the nitrogen cycle.

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## References

- Allan JD (1995) *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall, London
- Erickson RJ (1985) An evaluation of mathematical models for the effects of pH and temperature on ammonia toxicity to aquatic organisms. *Water Research* 19: 1047–1050
- Hamilton SK, Sippel SJ, Calheiros D & Melack J (1997) An anoxic event and other biogeochemical effects of the Pantanal wetland on the Paraguay River. *Limnology and Oceanography* 42: 252–272
- Hedin LO, Armesto JJ & Johnson AH (1995) Patterns of nutrient loss from unpolluted, old-growth temperate forests: Evaluation of biogeochemical theory. *Ecology* 76: 493–509
- Holland EA, Braswell BH, Lamarque JF, Townsend A, Sulzman J, Muller JF, Dentener F, Brasseur G, Levy H II, Penner JE & Roelofs GJ (1997) Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *J. Geophys. Res.* 102: 15,849–15,866
- Howarth RW, Billen G, Swaney D, Townsend A, Jaworski N, Lajtha K, Downing JA, Elmgren R, Caraco N, Jordan T, Berendse F, Freney J, Kudeyarov V, Murdoch P & Ahao-Liang S (1996) Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences. *Biogeochemistry* 38: 1–96
- Lesack LFW (1993) Export of nutrients and major ionic solutes from a rainforest catchment in the central Amazon basin. *Water Resources Research* 29: 743–758
- Lesack LFW, Hecky RE & Melack JM (1984) Transport of carbon, nitrogen, phosphorus and major solutes in the Gambia River, West Africa. *Limnology and Oceanography* 29: 816–830
- Lewis WM Jr & Saunders JF III (1989) Concentration and transport of dissolved and suspended substances in the Orinoco River. *Biogeochemistry* 7: 203–240
- Lewis WM Jr, Saunders JF III, Levine SN & Weibezahn FH (1986) Organic carbon in the Caura River, Venezuela. *Limnology and Oceanography* 31: 653–656

- Lewis WM. Jr, Hamilton SR & Saunders JF III (1995) Rivers of Northern South America. In: Cushing C & Cummins K (Eds) *Ecosystems of the World: Rivers* (pp 219–256). Elsevier, Dordrecht, The Netherlands
- McDowell WH & Asbury CE (1994). Export of carbon, nitrogen, and major ions from three tropical montane watersheds. *Limnology and Oceanography* 39: 111–125
- Melack JM, Sickmen JO, Leydecker A & Marrett D (1997) Comparative analysis of high-altitude lakes and catchments in the Sierra Nevada; Susceptibility to acidification. Final Report Contract A032-188. California Air Resources Board
- Meybeck M (1982) Carbon, nitrogen, and phosphorus transport by world rivers. *American J. Science* 282: 401–450
- Newbold JD, Sweeney B, Jackson J & Kaplan L (1995) Concentrations and export of solutes from six mountain streams in northwestern Costa Rica. *J. North American Benthological Society* 14: 21–37
- Stumm W & Morgan JJ (1996) *Aquatic Chemistry*. 3rd edn. Wiley, NY, U.S.A.
- Vitousek P, Aber J, Bayley S, Howarth R, Likens G, Matson P, Schindler D, Schlesinger W & Tilman D (1997) Human alteration of the global nitrogen cycle: Causes and consequences. *Ecological Issues* 1: 1–15
- Weibezahn FH (1990) Hidroquímica y sólidos suspendidos en el alto y medio Orinoco. In: Weibezahn FH, Alvarez H & Lewis WM Jr (Eds) *The Orinoco River as an Ecosystem* (pp. 151–210). Impresos Rubel, Caracas
- Williams MR & Melack JM (1997a) Atmospheric deposition, mass balances and processes regulating streamwater solute concentrations in mixed conifer catchments of the Sierra Nevada, California. *Biogeochemistry* 37: 111–144
- Williams MR & Melack JM (1997b) Effects of prescribed burning and drought on the solute chemistry of mixed-conifer forest streams of the Sierra Nevada, California. *Biogeochemistry* 39: 225–253
- Williams MR & Melack JM (1997c) Solute export from forested and partially deforested catchments in the central Amazon. *Biogeochemistry* 38: 67–102
- Williams MR (1997) Sources of Solutes in Precipitation and Surface Runoff of Mixed-conifer and Alpine Catchments in the Sierra Nevada, California. PhD Thesis. University of California, Santa Barbara, CA