Biogeochemistry **45:** 169–195, 1999.

Composition and deposition of throughfall in a flooded forest archipelago (Negro River, Brazil)

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Accepted 24 August 1998

Key words: Amazon, flooded forest, Negro River, rain, solutes, throughfall

Abstract. The sources of spatial and temporal variation and rates of nutrient deposition via throughfall were studied for 9 months in the Anavilhanas archipelago of the Negro River, Brazil. A total of 30 events was sampled individually for rain and throughfall chemistry in a 1-ha plot of flooded forest. Throughfall samples were collected in 40 collectors distributed in five parallel transects in the study plot, while rain was collected in 4 collectors in an adjacent channel. Volume-weighted mean (VWM) concentrations of solutes in rain were consistently lower than in throughfall, except for H^+, NO_3^- and NH_4^+. Ratios of VWM concentrations of rain to throughfall indicated that K^+, followed by Mg^{2+} and PO_4^{3-}, were the most enhanced solutes as rain passed through the forest canopy. The deposition of solutes varied significantly among transects, except for Na^+ and Ca^{2+}, and was significantly correlated with maximum flooding depth, foliar nutrient content, soil fertility and canopy closure for most solutes. The concentrations of PO_4^{3-} and most major ions were higher in throughfall compared to those in rain due to canopy exchange and dry deposition. In contrast, NO_3^-, NH_4^+ and H^+ were retained due to immobilization by leafy canopy and ion exchange processes. Solute inputs via throughfall (not including stemflow) to a floodplain lake (Lake Prato) of the archipelago accounted for 30 to 64% of the total for most solutes in the lake at high water, which indicates that throughfall is an important source of nutrients to the aquatic ecosystem of the Anavilhanas archipelago.

Introduction

The floodplains of the Amazon basin store and cycle large amounts of carbon and nutrients (Forsberg 1984; Junk & Howard-Williams 1984; Lenz et al. 1986; Engle & Melack 1993). About one-third of these floodplains are covered by flooded forests (Sippel et al. 1994), which are seasonally inundated for periods of up to nine months. During this period, throughfall, which is defined as the incident precipitation that passes through the canopy of trees (Parker 1983), can result in large transfers of dissolved nutrients and other solutes to the aquatic system. The processes involved in the interactions between tree canopies and rain include leaching or diffusion of materials from internal plant tissues, uptake of ions in rainfall by leaves or epiflora, and washing-off and dissolution of aerosols and particles that accumulate on the forest canopy during rain-free periods (Lovett & Lindberg 1984; Schaefer & Reiners 1989).

In the Negro River, the largest tributary of the Amazon River, precipitation largely regulates the chemistry of its acidic, electrolyte-poor black waters (Sioli 1968; Gibbs 1970). Nutrient-rich white-water floodplains of the Solimões River receive most nutrients from upland runoff and floodwaters (Lesack & Melack 1995). In contrast, the floodplain habitats of the Negro River, which are mostly located in archipelagoes in the middle of the river channel, depend more on atmospheric sources for nutrients. Previous studies of throughfall for the Brazilian Amazon basin indicate that there are large solute fluxes via throughfall in *terra firme* forests (Franken et al. 1982; Forti & Moreira-Nordemann 1991; Forti & Neal 1992). Hence the transfer of solutes from the flooded forest canopy to the underlying water of Negro River floodplains could be of major importance to the productivity and ecology of the ecosystem.

In this study, we determine the chemical composition and deposition rates of nutrients and major solutes in throughfall of the Anavilhanas archipelago located in the lower Negro River. We examine the factors that regulate solute fluxes by analyzing the spatial and temporal variability of throughfall, and discuss the ecological implications of solute inputs via throughfall to the aquatic environment of the Negro River floodplain.

Study area

The Anavilhanas archipelago occupies an area of 88,500 ha and comprises a large portion of the lower Negro River floodplain (Sippel et al. 1994). The archipelago is an intricate network of channels, lakes and islands (Figure 1) mostly covered by mature forest. The islands are elongated, reaching up to 30 km in length, and commonly contain one or more lakes. The 96 lakes of the archipelago vary in size, shape and depth, and most have a small channel connecting them to the river. Increasing river level causes the lakes to gradually fill and swell, thereby flooding adjacent forests for six to nine months of the year. The primary sources of water supply to these lakes are the river and direct rainfall. At low water, many lakes become isolated from the main channel causing clay and sand beaches to emerge.

The stage of the Negro River changes up to 12 m over the course of the annual hydrological cycle (Williams & Melack 1997). The rainy season in the lower Negro River occurs between December and May, while the period of

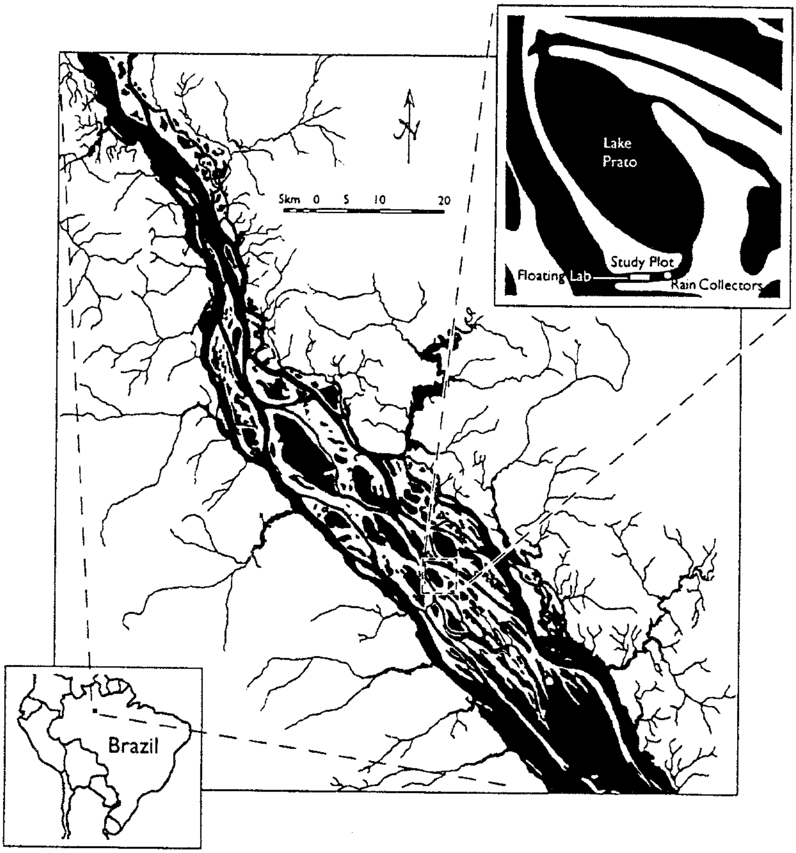

Figure 1. Map of the Anavilhanas archipelago indicating the location of Lake Prato, the study-site plot where throughfall collectors were installed, rain collectors, and the floating laboratory at the entrance of the inlet channel. Black areas represent lake or river water.

high water and its associated flooding occur between March and September. The peak of the high water phase usually occurs in June or July. In addition to the effect of seasonal rainfall, impoundment of the Negro River at the confluence with the Solimões-Amazon River contributes to water level fluctuations of the lower Negro River (Goulding et al. 1988).

A 1-ha site located on the edge of Lake Prato in the center of the Anavilhanas archipelago was selected for this study (Figure 1). In the study site, density and crown area of trees and lianas ≥ 7 cm were 600 stems ha^{-1} and 13,750 m^2 ha^{-1}, respectively; the latter due to multiple layers of canopy (Filoso 1996). The upper canopy was mostly above the level of maximum inundation, and tree density, species diversity and crown area were the highest in the areas of less inundation.

In a floristic survey of the 1-ha study plot, 42 species were recorded, with *Luhea cymulosa* and *Astrocaryum jauari* as the most frequent (Filoso 1996). In terms of canopy cover, *L. cymulosa*, *Ocotea fasciculata* and *Sclerolobium hypoleucum* were the dominant species, covering about 10% of the total area. In a combined abundance-cover scale, *L. cymulosa* was the dominant species.

Methods

Field sampling

Throughfall was collected from March to December 1991 in the 1-ha stand of flooded forest. Rainfall was sampled simultaneously with throughfall. One pair of rain collectors was placed on a raft anchored in open water adjacent to the study plot, and another on the top of a 8-m post at the floating laboratory (about 4 m above the lab roof). Most forest was flooded from March until September.

The throughfall of 30 individual events was sampled; events were defined as discrete periods of measurable rainfall $\geq$ 2.5 mm between rain-free intervals of at least 3 hours. The duration of each storm event and of dry periods between storms were recorded manually and with a solid-state data logger connected to a tipping-bucket rain gauge.

The sampling of throughfall was done in 40 collectors distributed in five parallel transects of 200 m adjacent to the margin of Lake Prato (Figure 1). From the margin of the lake to the highest ground of the plot, the slope created a flooding gradient in the study area. At the peak of high water, the maximum inundation depth was 6 m near the open water of the lake and about 1 m on the opposite side of the study plot. The distribution of collectors maximized the number of tree species sampled in the study plot, as the distribution of tree species in Amazon flooded forests is a function of flooding gradient (Revilla 1981, 1991).

The collectors were made of polyethylene funnels 30 cm in diameter, screwed onto 4-L plastic containers. Nylon nets (0.63 mm mesh) pre-leached with deionized water (DIW) were placed between the funnels and the containers to prevent coarse material from falling into the samples. Plastic rings tied by nylon lines to tree trunks held the collectors under the forest canopy. Collectors were maintained at 1.0 to 1.5 m above the water surface, or ground when the forest was not flooded. As the water level changed, the collectors were moved vertically, but no more than about 0.5 m horizontally. Throughfall volume was measured with manually-read rain gauges placed adjacent to the throughfall collectors.

Samples were collected about two hours after daytime rain events because trees remained wet and contributed to throughfall for about 1 hour after a storm. Night events were collected up to 8 hours later, but these accounted for $<10\%$ of all events sampled. After collection, bottles containing samples were capped and immediately taken to the field laboratory for analysis. After use, the bottles were washed with DIW and occasionally acid washed and rinsed with DIW until conductivity of the rinse water was below 0.5 μS cm^{-1}. The nylon screens were replaced and collectors cleaned daily with DIW. When possible, clean funnels and nylon screens were installed immediately prior to an event. Field blanks were occasionally collected for chemical analyses by rinsing rainfall collectors and a subset of throughfall collectors with DIW; rinse water samples had no detectable contamination.

Laboratory analyses

The sampling of all major solutes in throughfall was done on an event basis (n = 30), and samples from each of the 40 collectors were analyzed expediently on site to reduce problems associated with chemical losses or transformations. Subsamples of unfiltered throughfall and rain water were analyzed for pH, acid neutralizing capacity (ANC) and conductivity within 24 hours of collection. The remaining water was filtered through Gelman *AE* glass fiber filters (1 μm nominal pore size), and aliquots stored at 4 °C in pre-washed Nalgene polyethylene bottles for analyses of NO_3^-, PO_4^{3-}, NH_4^+, total dissolved N and P (TDN and TDP), Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, and SO_4^{2-}. For analysis of dissolved organic carbon (DOC), aliquots were filtered through pre-combusted and rinsed glass-fiber filters.

pH was measured at room temperature after a 2 minute equilibration period. ANC was determined by titration with 0.1 N HCl in an open beaker (Gran 1950, 1952). Ammonium was determined on filtered samples within 12 hours of collection by a phenol-hypochlorite technique, and soluble reactive phosphorus (SRP) within 24 hours with a molybdenum blue-ascorbic acid method (Strickland & Parsons 1972). Samples were analyzed for NO_3^- (NO_2^- plus NO_3^-) within 2 days by cadmium-copper reduction (Wood et al. 1967). Total dissolved N and P were analyzed within one week by persulfate digestion (Valderrama 1981) followed by the analyses of SRP and NO_3^- described above.

Aliquots for DOC analysis were wet-oxidized in ampoules using the persulfate oxidation technique of Menzel and Vaccaro (1964) within a few hours after collection. The DOC generated was measured by acidification and headspace equilibration (Stainton 1973) using a gas chromatograph with a thermal conductivity detector.

Concentrations of Cl^- and SO_4^{2-} were determined by ion chromatography with a Dionex model 2010i. Base cation concentrations were determined by atomic absorption spectrophotometry using a Varian SpectrAA with air-acetylene flame for Na^+ and K^+ (no additives) and nitrous oxide flame for Ca^{2+} and Mg^{2+} (KCl added). Quality control and assurance guidelines are discussed elsewhere (Melack et al. 1998).

Vegetation parameters

We hypothesized that canopy closure (CC), foliar nutrient content (FN), soil fertility (SF) and flooding depth (FD) influenced the deposition of throughfall in the study area. Canopy closure, foliar nutrient content, and flooding depths were measured for all the trees above the throughfall collectors, while soil fertility was determined at two evenly spaced points in each transect.

Canopy closure was measured using photographs taken above each throughfall collector at a fixed angle of 45°. Each photograph was overlaid by a paper grid with 20 evenly distributed holes, and the number of holes blocked by the forest canopy in the photograph were used as an indicator of the extent of canopy closure.

Foliage for nutrient content was collected during the high and low water seasons. Samples were collected with a plant trimmer and subsequently labeled and dried at 85 °C for at least 48 hours. Samples were ground with a Wiley mill and redried at 85 °C prior to analysis. Soil cores of 50 cm were collected from two locations in each transect using a bucket type soil augur. Foliar and soil analyses were performed at EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) in Manaus, Brazil. Analyses included the determination of N, P, Na^+, K^+, Ca^{2+} and Mg^{2+}, and P, Na^+, K^+, Ca^{2+}, Mg^{2+}, Al and pH for foliage and soil, respectively. Cation concentrations were determined by atomic absorption spectrophotometry after acid digestion, and N determined with the Kjeldahl method.

Data analyses

Volume-weighted means (VWM) were used to express mean solute concentrations of throughfall and rainfall during the study period. VWM was calculated as

$$VWM = \frac{\sum_{n=1}^{i} C_i V_i}{\sum_{n=1}^{i} V_i} \qquad (1)$$

for all events $i \geq 2.5$ mm sampled, where C_i and V_i are concentration and volume, respectively. VWM was calculated using the total volume of rain or throughfall sampled in 1991. Total rainfall for the Anavilhanas area in 1991 was obtained from the city of Novo Airão (2°37′S, 60°57′W) using the data of DNAEE (Departamento National de Águas e Energia Elétrica).

Annual deposition was calculated as

$$D = (C)(V) \tag{2}$$

where D is deposition, C is the VWM concentration of a solute and V is the total volume of rain or throughfall for the 1991 water year. The product of total rainfall in 1991 (DNAEE) and the ratio of throughfall to rain volume (0.79) from our sampled events was used as an estimate of total throughfall volume for the 1991 water year. Net deposition was calculated as the difference between throughfall and rainfall deposition.

Organic anion concentrations were estimated from DOC concentrations and pH values using a model proposed by Oliver et al. (1983). According to the model, in natural colored waters where most of the organic carbon is humic material, the organic anion concentration that results from the dissociation of humic material ($HA = H^+ + A^-$) can be estimated as:

$$[A^-] = \frac{\bar{K}[C_r]}{\bar{K} + [H^+]} \tag{3}$$

where A^- is the organic anion concentration, C_T is the organic acid concentration (fulvic plus humic acids), and $\bar{K}$ is the mass action quotient estimated from the sample pH using the equation:

$$\text{p}\bar{K} = 0.96 + 0.90\text{p}H - 0.039(\text{p}H)^2. \tag{4}$$

Statistical analyses

The non-parametric Kruskal-Wallis test was used to test the null hypothesis that there were no differences in throughfall deposition among the collectors distributed in the five transects of the study plot. This analysis was performed in SYSTAT using values from each collector from all sampled storms.

Solutes that showed significant differences among transects were tested against flooding gradient, foliar nutrient content, soil fertility, and canopy closure using a Spearman correlation matrix. Since foliar nutrient content and soil fertility were parameters composed of several sub-factors (N, P, Na^+ K^+, Ca^{2+}, Mg^{2+}, Al and pH), Principal Component Analysis (PCA) was used to find indicator variables for each parameter.

Exploratory common factor analysis with varimax rotation (SYSTAT) was performed with VWM concentrations of solutes in throughfall from the sampled storms to help explain the possible common sources of solutes. To predict the contribution of dry deposition and canopy exchange in net throughfall, we used a multiple regression model with data from the dry and rainy seasons. This regression method was proposed by Lovett and Lindberg (1984) based on the assumption that net throughfall flux is a linear function of internal leaching from vegetation and the rate at which ions accumulate on external canopy surfaces. External canopy accumulation, or dry deposition, is proportional to the rain-free period before an event, while internal leaching or canopy exchange is proportional to the event size. Analyses were performed using net throughfall of each solute as the dependent variable against both the rain volume of each storm and the rain-free period (in hours) that preceded them as independent variables. Net solute deposition for each storm was the mean value from all collectors in the study plot. Regressions were performed in SYSTAT without the interception option to be consistent with the model provided by Lovett and Lindberg (1984) and Puckett (1990).

The importance of solute deposition via throughfall to Prato Lake

In order to assess the importance of throughfall inputs to Prato Lake, solute inputs were estimated for throughfall, rain, and the Negro River during the high water period, when most of the forest was flooded. Solute inputs were calculated by multiplying the volume of each source by their solute concentrations.

The volumes of water in Lake Prato at high and low water were calculated from a detailed bathymetric map provided by Garcia (1995). The residual lake water was estimated as the lake volume at low water. The volume of riverine water in the lake at high water was calculated as the difference of the total volume of the lake from the sum of volumes of throughfall, rainfall, and the residual water of the lake at low water.

The validity of the Prato Lake data for extrapolation to other lakes in the Anavilhanas archipelago was assessed using their ratio of open water to flooded forest area. The number of lakes in the archipelago and their area of open water and flooding forest were determined using Side-Looking Airborne Radar (SLAR) imagery from the *Radambrasil* project and computerized planimetry.

It is assumed in this analysis that Lake Prato has only one channel connecting it to the Negro River. Hence, riverine inputs enter Lake Prato through this channel during rising water, and lake water leaves the lake through this channel during falling water. Although this is not true for Lake Prato, which has one permanent inlet, and two permanent outlets (Figure 1),

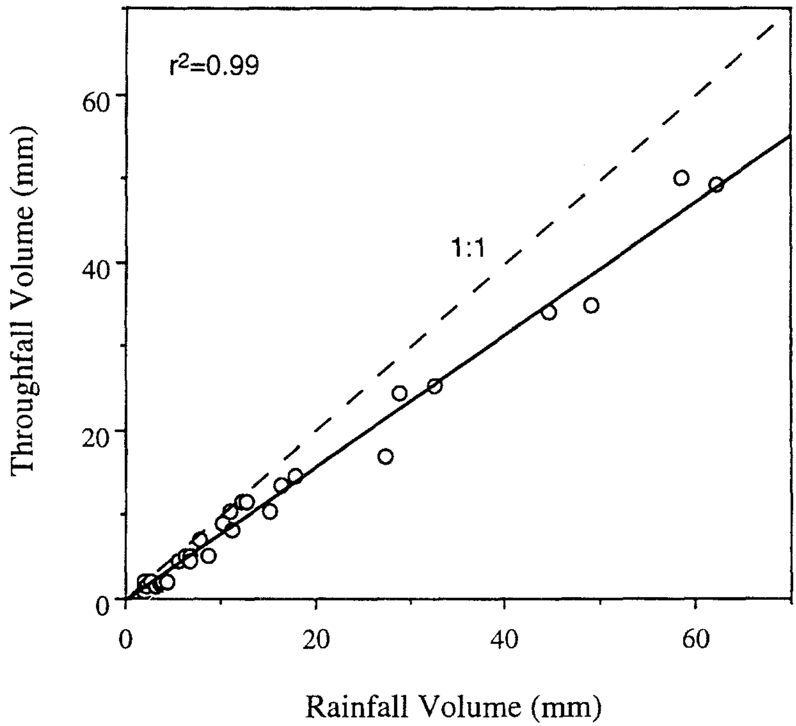

Figure 2. The relationship of rain and throughfall volumes for events sampled during the study period (April–December 1991).

Lake Prato is used as an analog for other lakes (63) in the Anavilhanas archipelago that have only one channel connecting them to the Negro River.

Results

Comparison of throughfall and rain

The 30 storms sampled for throughfall and rain had a frequency distribution of volume representative of all the events that occurred during the study period (Filoso 1996). Total depth of rain collected during the study period was 468 mm, or 22.5% of the 2,083 mm recorded for 1991 (DNAEE). The relationship of the total volume of rain versus that of throughfall for the 30 events sampled shows that losses of rain volume occurred as rain passed through the forest canopy (Figure 2). The average throughfall depth was 78.5% ± 3.2% of total rainfall, or 1,635 mm in 1991, indicating that approximately 21% of rainfall volume was lost due to canopy interception. The percent

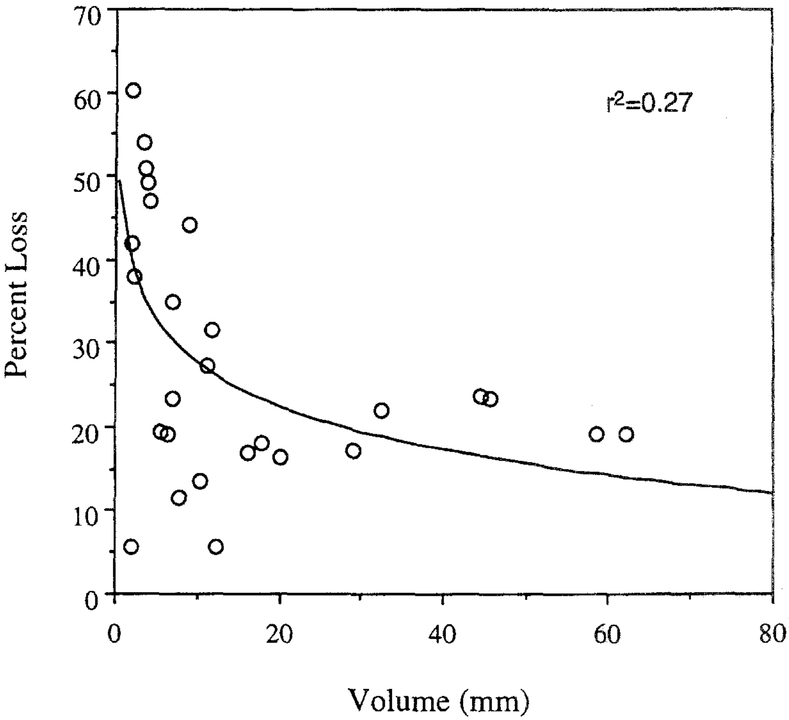

Figure 3. The relationship of rainfall volume and percent loss of rain by the forest canopy (n = 27 events).

interception loss of rain volume decreased logarithmically with increasing event size (Figure 3).

The VWM concentrations of most solutes in rain were consistently lower than in throughfall, indicating that there were net gains in these solutes as rain passed through the forest canopy (Table 1). In contrast, there was a net loss of NO_3^- in the rainy season, NH_4^+ in the dry season, and H^+ in both seasons. Similar to the seasonal differences observed in the solute concentrations of rain (Lesack & Melack 1991; Williams et al. 1997a), the VWM concentrations of most throughfall solutes in the dry season were higher than those in the rainy season. Ratios of VWM concentrations of rain to throughfall showed that K^+, followed by Mg^{2+} and PO_4^{3-} were the most enhanced solutes in throughfall in both seasons (Table 2). By charge balance, only 50% and 30% of the anions were measured in rain and throughfall, respectively, but the deficits were proportional to the concentrations of DOC (Table 1).

Table 1. Volume-weighted mean concentrations of sampled rain and throughfall events during the entire study period, and the rainy and dry seasons.

Solute	Annual		Rainy season		Dry season		Sample
	Rain	Throughfall	Rain	Throughfall	Rain	Throughfall	size
Events	30	30	12	12	18	18	
Volume (mm)	468	369	195	156	273	213	
Cl^-	2.1	9.3	1.2	4.3	4.1	19.8	754
NO_3^-	2.7	2.7	1.1	0.5	6.0	7.4	711
SO_4^{2-}	3.1	6.5	1.6	3.5	6.5	13.0	760
PO_4^{3-}	0.19	1.64	0.17	0.80	0.24	3.31	701
ANC	−3.6	31.9	−2.8	21.4	−23.5	48.5	633
NH_4^+	2.2	2.2	0.5	1.1	5.8	4.6	704
Na^+	5.1	10.2	3.6	7.1	8.4	16.5	752
K^+	0.9	43.4	0.6	24.9	1.6	80.5	744
Ca^{2+}	5.9	16.9	3.5	9.6	11.1	31.5	749
Mg^{2+}	1.5	13.6	0.8	7.0	2.8	26.8	750
H^+	9.8	3.2	6.5	2.1	16.2	5.1	633
TDN	6.4	34.5	3.3	23.4	12.5	49.6	601
TDP	0.18	1.20	0.11	0.48	0.31	2.20	596
Σ anions	8.1	52.0	4.1	30.5	16.8	92.0	
Σ cations	25.4	89.5	15.5	51.8	45.9	165.0	
Deficit	17.3	37.5	11.4	21.3	29.1	73.0	
DOC	0.11	0.81	0.12	0.72	0.11	0.94	360

All concentrations are expressed in μeq L^{-1}, except for TDN, TDP (μM), and DOC (mM). The number of events for DOC is 3 and 7 for the rainy and dry seasons, respectively. Negative ANC in rain is assumed to be zero in the Σ anions calculation. The anions required to balance the Σ anions with the Σ cations are designated in the Deficit category.

Spatial variability and sources of solutes in Anavilhanas throughfall

Throughfall deposition of all solutes varied significantly among transects, except for Na^+ and Ca^{2+} (Figure 4). The spatial variation of the solute deposition was significantly correlated with the measured parameters of CC, FD, SF and FN; all these parameters were intercorrelated. Measured concentrations of TDP in throughfall were lower than those of PO_4^{3-} (Table 3). We attribute the low values of TDP to a smaller sample size representing larger volume events commonly lower in TDP than smaller volume events. We therefore calculated the ratio of PO_4^{3-} to TDP in 568 throughfall samples for which

Table 2. The ratios in rain to throughfall for annual and seasonal VWM concentrations of solutes.

Solute	Annual	Rainy season	Dry season
Cl^-	0.23	0.26	0.21
NO_3^-	0.99	2.42	0.81
SO_4^{2-}	0.48	0.45	0.50
PO_4^{3-}	0.12	0.35	0.07
NH_4^+	0.98	0.45	1.25
Na^+	0.51	0.51	0.51
K^+	0.02	0.02	0.02
Ca^{2+}	0.35	0.36	0.35
Mg^{2+}	0.11	0.11	0.11
H^+	3.09	3.02	3.16

there were matching data. Phosphate was about 48% of TDP in these samples, and *TDP was determined using this ratio (Table 3). Similarly, *TDN in Table 3 was calculated using 568 samples where there were matching data for NH_4^+ and NO_3^-, and the ratio of inorganic N to TDN in these samples was 13%.

According to the factor analysis, four factors were required to explain 93.5% of the systematic variance in the solute deposition of throughfall events during the study period. Loading of variables on factors, communalities, and percents of variance are grouped by size (Table 5). All factors were well defined by the variables. Factor 1 grouped most of the solutes, but none of the variables were complex (i.e. loaded heavily on more than a single factor). Sodium, Ca^{2+}, Mg^{2+}, K^+, ANC and TDN had high loadings on factor 1, although ANC and TDN also had moderate loadings on factors 4 and 3, respectively. Factor 2 grouped SO_4^{2-}, Cl^- and H^+, while factor 3 grouped NO_3^- and NH_4^+, and factor 4 grouped PO_4^{3-} and TDP.

The multiple regression model was used to determine the relative importance of dry deposition and canopy exchange to net throughfall deposition. The results of the model were significant ($p < 0.05$) for all the solutes in both seasons, except for Na^+ in the rainy season (Table 6), meaning that net throughfall deposition in our study site can be predicted from rain volume and the rain-free period that preceded a storm. The contribution of canopy exchange to net throughfall in the rainy season was significant for all ions (except Na^+), while dry deposition was significant for Cl^- only. In contrast, all solutes made significant contributions to net deposition in the dry season,

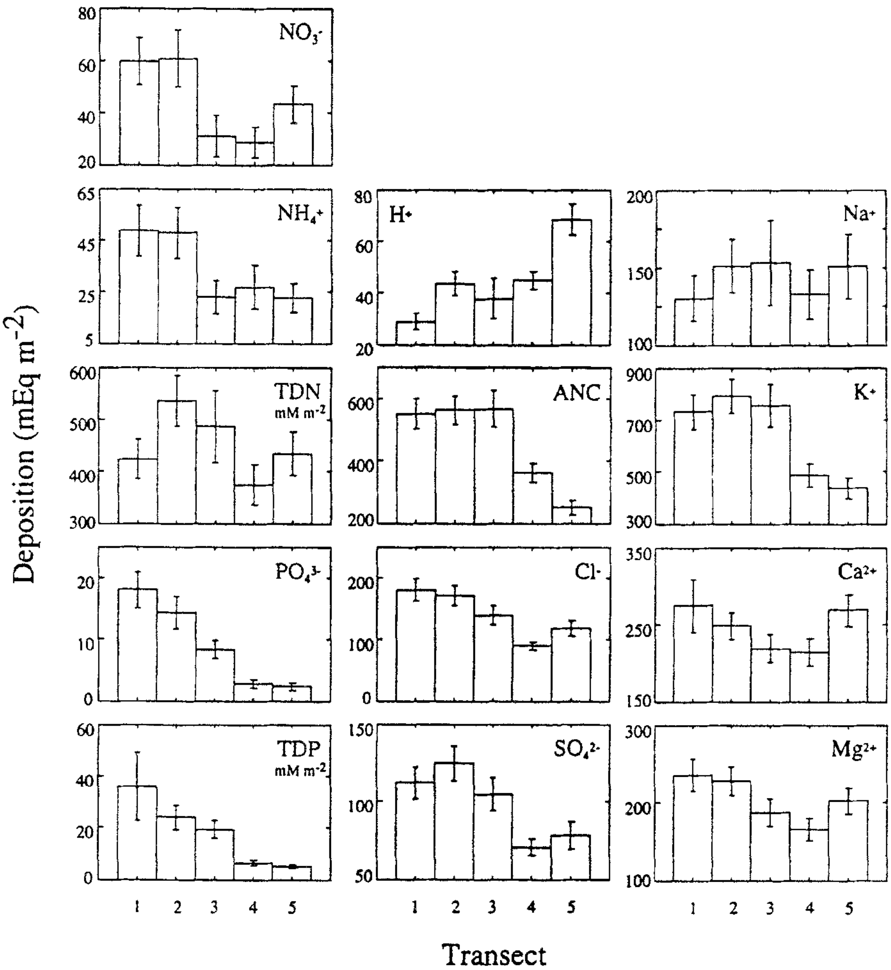

Figure 4. Throughfall solute deposition in each transect of the study plot. The average maximum flooding depths for each transect (from 1 to 5, the latter boardering Lake Prato) were 1, 2, 3, 5, and 6 meters, respectively.

except Cl^-, PO_4^{3-} and H^+ via dry deposition, and Ca^{2+} and NH_4^+ via canopy exchange.

Importance of throughfall fluxes to Prato Lake

From the radar imagery (SLAR), it was determined that the Anavilhanas archipelago has a total of 96 lakes, of which only 21% had an open water area larger than 3 km^2. Also, the average ratio of area of flooded forest to open water was estimated to be 2 on average, which was close to the ratio of 1.9 observed for the Prato Lake. Therefore, roughly two-thirds of the total

Table 3. Deposition rates of soluts from rain and throughfall.

	Rainfall	Throughfall	Net throughfall
Cl^-	1.56	5.38	3.82
NO_3^-	3.45	2.74	−0.71
SO_4^{2-}	3.13	5.13	2.00
PO_4^{3-}	0.31	2.12	1.81
ANC	0.00	31.80	31.8
NH_4^+	0.82	0.66	−0.16
Na^+	2.44	3.83	1.39
K^+	0.73	27.7	27.0
Ca^{2+}	2.46	5.54	3.08
Mg^{2+}	0.37	2.70	2.33
H^+	0.21	0.05	−0.16
TDN	8.30	35.0	26.7
*TDN	8.30	26.5	18.2
TDP	0.30	1.55	1.25
*TDP	0.31	4.45	4.14

Net throughfall is calculated as throughfall minus rainfall deposition, and is expressed in kg ha^{-1} yr^{-1}. Asterisks indicate that TDN and TDP were estimated by the ratio of inorganic N to TDN and PO_4^{3-} to TDP, respectively, for 568 events with matching data.

volume of rain that falls onto the surface of floodplain lakes in Anavilhanas is intercepted by forest canopy during inundation.

The water volume of Prato Lake with and without the area of flooded forest was 41×10^6 m^3 and 17×10^6 m^3, respectively. The volume of rain that fell onto the open surface of the lake, from the beginning of the rising water to the peak of high water in 1991, was approximately 8.6×10^6 m^3, and the volume of throughfall that fell onto the average area of flooded forest (flooded mostly from March to July) was 8.4×10^6 m^3.

Discussion

Throughfall volume

It has been reported in other studies of throughfall in forested areas (Lloyd et al. 1988; Pucket 1991; Whelan & Anderson 1996) that the volume of water measured in throughfall and rain for the same events tend to decrease due to

Table 4. Spearman correlation matrix of solute deposition variables versus vegetation parameters of the study plot.

VPAR	H^+	ANC	Cl^-	NO_3^-	SO_4^{2-}	PO_4^{3-}	TDN	TPN	NH_4^+	Na^+	K^+	Ca^{2+}	Mg^{2+}	CC	FD	SF
CC	**−0.46***	**0.35***	**0.35***	**0.39***	**0.47***	**0.36***	**0.35***	**0.40***	**0.35***	−0.03	**0.35***	**0.42***	**0.36***	**1.00***		
FD	**−0.51***	**0.54***	**0.52***	**0.46***	**0.54***	**0.35***	**0.47***	**0.44***	**0.33***	−0.05	**0.39***	0.19	**0.40***	**−0.46***	**1.00***	
SF	**0.52***	**0.61***	**0.53***	**0.41***	**0.53***	**0.33***	**0.46***	**0.44***	**0.34***	−0.01	**0.44***	0.21	**0.40***	**0.46***	**0.97***	**1.00***
FN	**−0.39***	**0.47***	**0.47***	**0.44***	**0.44***	**0.24***	**0.70***	**0.42***	**0.45***	0.02	**0.55***	**0.34***	**0.39***	**0.52***	**0.55***	**0.50***

Significant coefficients are marked with an asterisk ($p < 0.05$; $n = 40$). Vegetation parameters (VPAR) are designated as CC (canopy cover), FD (flooding depth), SF (soil fertility), and FN (foliar nutrient content).

Table 5. Loadings on factors, communalities, eigenvalues, and percent variances of variables from all storms sampled for throughfall ($n = 30$).

Variables	Factor 1	Factor 2	Factor 3	Factor 4	Communalities
Na^+	0.84	0.41	0.22	0.21	0.993
K^+	0.70	0.38	0.36	0.42	0.985
Ca^{2+}	0.82	0.40	0.30	0.27	0.997
Mg^{2+}	0.75	0.21	0.46	0.35	0.992
ANC	0.68	0.34	0.27	0.50	0.940
TDN	0.61	0.49	0.44	0.34	0.975
SO_4^{2-}	0.26	0.84	0.24	0.42	0.979
H^+	0.34	0.82	0.20	0.06	0.896
Cl^-	0.37	0.76	0.23	0.39	0.975
NO_3^-	0.27	0.22	0.92	0.21	0.938
NH_4^+	0.40	0.30	0.68	0.30	0.936
PO_4^{3-}	0.43	0.40	0.32	0.72	0.976
TDP	0.49	0.29	0.41	0.69	0.982
Eigenvalues	10.21	0.90	0.63	0.42	
% Variance explained	37.48	24.69	19.11	17.20	

the interception of rain by the forest canopy. In the Anavilhanas archipelago, about 21% of the rain volume measured during the study period was lost via interception. Similar interception losses were reported in studies of *terra firma* forests in the central Amazon, which varied from approximately 20% (Franken et al. 1982) to 11% (Lloyd et al. 1988) and 9% (Lloyd & Marques 1988).

Interception losses occur as a combination of water evaporated from the canopy during a storm, water that runs down trunks and branches as stemflow, and water held in the canopy after a storm (Lloyd et al. 1988). Evaporation and stemflow were not determined for the Anavilhanas forest, but the water held in the canopy, or canopy capacity, could be calculated using a simple regression model proposed by Lloyd et al. (1988). The model predicted a throughfall depth of zero for a rainfall depth of 2.4 ± 1.05 mm, which gives an estimate of canopy capacity that is three times higher than that determined for the upland forest studied by Lloyd et al. (1988). The higher canopy capacity estimated for the Anavilhanas flooded forest may be due to unaccounted

Table 6. Regression estimates of dry deposition (mg m^{-2} hr^{-1}) and canopy exchange (mg m^{-2} cm^{-1} of rain) in net throughfall (TF) of the rainy (n = 12 events) and dry seasons (n = 18 events).

Solute	Dry deposition	Canopy exchange	r^2	Net throughfall deposition
Rainy season				
Cl^-	6.36 ± 2.0*	10.6 ± 1.6***	0.94***	25.5
NO_3^-	2.27 ± 2.2	−12.6 ± 2.6**	0.84**	−14.7
SO_4^{2-}	4.1 ± 2.7	4.80 ± 2.0*	0.71*	18.6
PO_4^{3-}	0.38 ± 0.2	0.43 ± 0.1*	0.88*	1.06
ANC	41.1 ± 61	195 ± 46**	0.84**	334
NH_4^+	0.45 ± 0.5	−1.56 ± 0.4*	0.74*	−1.65
Na^+	3.86 ± 4.5	2.73 ± 4.0	0.06	15.2
K^+	3.86 ± 4.5	174 ± 45**	0.71**	241
Ca^{2+}	4.31 ± 4.5	13.0 ± 3.6**	0.78**	26.1
Mg^{2+}	2.95 ± 2.3	8.60 ± 2.8*	0.70*	21.4
H^+	0 ± 0	−0.76 ± 0.2**	0.83**	−1.73
Dry season				
Cl^-	0.92 ± 0.9	64.9 ± 11***	0.76***	62.2
NO_3^-	14.7 ± 3.6**	−10.8 ± 7.1**	0.84**	−2.73
SO_4^{2-}	−9.2 ± 4.5*	39.5 ± 9.2***	0.60**	−18.0
PO_4^{3-}	0.3 ± 0.3	2.65 ± 0.5**	0.72***	3.93
ANC	54.2 ± 18.3**	315 ± 36***	0.92**	352
NH_4^+	−6.43 ± 1.8**	−1.95 ± 2.5	0.57**	−5.91
Na^+	6.43 ± 2.7**	10.7 ± 4.5*	0.61**	15.8
K^+	58.8 ± 18.4*	294 ± 44***	0.85***	366
Ca^{2+}	14.7 ± 5.5*	11.0 ± 9.0	0.55**	41.0
Mg^{2+}	8.3 ± 2.7**	21.0 ± 5.4**	0.75*	33.9
H^+	0 ± 0	−1.59 ± 0.4 **	0.49*	−1.85
TDN	118.3 ± 20***	159.2 ± 44**	0.83***	247
TDP	7.0 ± 1.4**	22.4 ± 2.1**	0.75***	70.3

Estimates are followed by their standard error and level of significance, the latter indicated by either '*' ($p < 0.05$), '**' ($p < 0.01$), or '***' ($p < 0.001$). Units for net throughfall deposition are in mg m^{-2}.

Table 7. Comparison of estimated annual solute loads from throughfall, rainfall, and Negro River water to Lake Prato. The combined estimated loads, including the residual left in the lake at its lowest water level, are compared with the values measured in the lake at high water (Filoso 1996).

Solute	Throughfall	Rainfall	Riverine	Residual	Σ of sources	Lake Prato
Cl^-	2.76	0.69	4.22	0.05	7.72	9.84
NO_3^-	1.42	1.47	3.76	0.02	6.67	8.47
SO_4^{2-}	2.59	1.29	3.31	0.04	7.23	4.38
PO_4^{3-}	0.20	0.05	0.31	0.01	0.57	0.004
NH_4^+	0.33	0.34	0.02	0.00	0.69	0.12
Na^+	2.01	1.03	11.2	0.13	14.4	21.4
K^+	10.2	0.35	9.49	0.07	20.1	18.6
Ca^{2+}	6.81	1.04	9.92	0.07	17.8	17.6
Mg^{2+}	1.42	0.16	3.39	0.02	5.00	5.89
H^+	0.03	0.08	0.33	0.00	0.44	0.31
DOC	81.3	11.4	157	0.9	251	368

Values are expressed in Tons yr^{-1}; DOC is in Tons C yr^{-1}.

evaporation and stemflow losses, or differences in forest structure, such as the high occurrence of lianas in our study plot.

Throughfall composition and deposition

Increases in the solute concentrations of rain due to interactions with forest canopy have been reported in throughfall studies world wide (Parker 1983; Johnson & Lindberg 1992; Pedersen et al. 1995; Lin et al. 1997). The common mechanisms that regulate the chemical composition and deposition of throughfall are dry deposition and canopy exchange (Lovett & Lindberg 1984, Lovett et al. 1996; Lin et al. 1997). Dry deposition involves the wash-off of particles and dissolution of aerosols that have accumulated on canopy surfaces between events, while canopy exchange includes the leaching of internal material from plant tissues and leaf surfaces, and the active uptake of ions in rainfall by leaves or epiflora (Parker 1983; Schaefer et al. 1988).

Both dry deposition and canopy exchange can vary in space and time, as these processes are related to biological characteristics of the forest, such as stand age, soil fertility, plant nutrient status, the presence of insects, leaf area, and epiphyte activity (Lawrence & Fernandez 1993; Lovett et al. 1996). In Amazon flooded forests, many of these characteristics are associated with flooding regime (Revilla 1981, 1991). In our study site, throughfall deposition of solutes varied spatially among transects probably because of the association with the parameters of FN, SF, and CC, which were also correlated with flooding gradient (Table 6). Thus, flooding gradient can be considered an indicator of the spatial variability of throughfall fluxes in the Anavilhanas archipelago. Flooding gradient can potentially be estimated on a larger spatial scale using synthetic aperture radar (SAR) images and classification techniques (Hess et al. 1995).

The deposition of most solutes varied significantly among transects, except for Ca^{2+} and Na^{+} (Figure 4). Calcium was not correlated with any of the measured vegetation parameters, and similar spatial variability for Ca^{2+} was observed in a subtropical forest in Taiwan (Lin et al. 1997).

The temporal variation in the concentration and deposition of solutes in throughfall in the archipelago during the wet and dry seasons should be, in large part, related to the large seasonal variation of rainfall depth that is characteristic in the central Amazon (Lesack & Melack 1991). A ratio of rainfall depth of about 2:1 for the wet and dry seasons may cause variations of internal processes of the forest which are associated with canopy exchange. Similarly, external processes such as dry deposition associated with natural and anthropogenic factors probably change seasonally, such as the extensive biomass burning that occurs in the dry season compared to the rainy season.

We determined the relative importance of internal versus external processes on throughfall composition and deposition using the regression model proposed by Lovett and Lindberg (1984), and the the common sources of solutes in throughfall using the results from our exploratory factor analysis. For base cations, which were grouped together in the factor analysis results, canopy exchange appears to be the dominant source of solutes to net throughfall, while dry deposition contributes only in the dry season, especially for Na^{+}. Dry deposition was less important than foliar leaching as a source of base cations probably because none of them have a gaseous phase, and the dry deposition of base cations associated with the aeolean transport of soil dust and particles is low in remote areas of continuous forest (Lawson & Winchester 1979). At the end of the dry season, when most burning and associated haze occurs, dry deposition can potentially contribute more to throughfall fluxes. However, the negligible influence of biomass burning on the rain chemistry of the central Amazon (Williams et al. 1997a) suggests that dry deposition of base cations is not important for throughfall in the Anavilhanas forest.

The fluxes of base cations via throughfall in other forests have been reported to be controlled by the exchange of ions in forest canopy for those in precipitation, especially for H^{+} and K^{+} (Schaefer & Reiners 1989; Hambuckers & Remacle 1993). Sodium and Mg^{2+} commonly have low foliar concentrations that result in less leaching than K^+ (Parker 1983), while the magnitude of Ca^{2+} leaching will depend in large part on the nutrient status of the forest (Schaefer & Reiners 1989).

For SO_4^{2-} and Cl^-, dry deposition is often the main contributing source of throughfall deposition (Lawson & Winchester 1979; Andreae 1985; Lindberg et al. 1986). However, in the absence of any major anthropogenic or oceanic sources nearby, canopy exchange should be the dominant factor controlling the fluxes of these ions in throughfall, as indicated by our results of the regression model.

The relatively high contribution of dry deposition to throughfall during the rainy season compared to that in the dry season could be evidence of increased biogenic emissions from plants, soils and wetlands (Talbot et al. 1988) and/or marine sources (Williams et al. 1997a) during the rainy season. The possibility that limited canopy pools might be leached to depletion during the more frequent and larger storms of the rainy season should be considered also. However, regardless of what controls the deposition of SO_4^{2-} and Cl^- in the flooded forest of Anavilhanas, the grouping of these anions in our factor analysis (Table 5) suggests that the controlling mechanism(s) is similar for both solutes.

Hydrogen ion deposition also seems to be derived mainly by canopy exchange. However, immobilization rather than leaching should be the dominant process responsible for H^+ fluxes in throughfall (Schaefer & Reiners 1989, Pedersen et al. 1995). The retention of H^+ is probably due to ion exchange with base cations and NH_4^+ in leafy canopy, which would decrease the free acidity of rain and result in a larger relative contribution of organic acids to the total acidity of throughfall (Schaefer & Reiners 1989; Draaijers & Erisman 1995).

The association of NO_3^- and NH_4^+ in the factor analyses agrees with the data reviewed by Parker (1983), which show that these ions act similarly in throughfall. Nitrate and NH_4^+ can be either leached from or retained by the forest canopy depending on concentration gradients between the canopy and rainfall. Active uptake may occur, especially for oxidized nitrogen compounds (Draaijers & Erisman 1995), although ionic exchange processes are probably the dominant mechanisms (Lindberg et al. 1986; Garten & Hanson 1990). Extended periods of contact between rain and forest canopy usually increases retention of both ions, while increasing rainfall acidity increases the permeability of leafy canopy and the cation exchange between the canopy and solutes in rain (Schaefer & Reiners 1989).

Throughfall deposition of both NO_3^- and NH_4^+ in Anavilhanas during the rainy season was apparently controlled by their retention via canopy exchange, while during the dry season, dry deposition was the controlling factor for NO_3^-. Regional forest burning in the dry season is likely to increase emissions of NO and NO_2 to the atmosphere and, consequently, dry deposition rates of NO_3^- onto the forest canopy (Crutzen et al. 1985; Matson & Vitousek 1990). Biomass burning and emissions of NH_3 by soil and vegetation also control concentrations of NH_4^+ (Galbally 1985; Andreae et al. 1988; Talbot et al. 1988). Although we believe that biomass burning had a negligible influence on the throughfall chemistry in this study, alternatively, dry and wet deposition of NO_3^- in remote areas can be regulated by the oxidation of NO and NO_2 produced in the atmosphere by lightning (Lindberg et al. 1986; Warneck 1988). Burning as a source of NO_x to the global atmosphere is of the same order of magnitude as production by lightning (Andreae et al. 1988).

While there were some seasonal losses of both NO_3^- and NH_4^+ as rain passed through the forest canopy, there was a concomitant flux of much larger amounts of dissolved organic nitrogen (DON = TDN – NO_3^- + NH_4^+) in throughfall (Table 3). The large flux of DON observed in throughfall suggests that some N is retained on canopy surfaces by epiphytic algae and is subsequently washed off during later events.

Although dry deposition of PO_4^{3-} occurs in the central Amazon (Lesack & Melack 1991), the results of our analyses indicate that the largest portion of the PO_4^{3-} flux in throughfall was derived from canopy exchange, especially in the wet season. Moreover, canopy exchange is the main factor regulating TDP deposition (Table 6). The relatively large net deposition of PO_4^{3-} in throughfall suggests that there is a net loss of phosphates from the forest canopy, which may be replenished by seasonal flooding (Filoso 1996).

Organic acids are important constituents of precipitation in polluted and remote areas (Galloway et al. 1982; Keene et al. 1983; Likens et al. 1987). Over vegetated areas, the major sources of organic acids can be the oxidation of isoprene or direct emission from vegetation, as organic acids are known to be present in plant tissues (Andreae et al. 1986). In our study, the positive net-throughfall flux of DOC is likely to be a product of foliar leaching of organic acids from the canopy, and the washoff of aerosols and particulates from dry deposition (Keene et al. 1983).

We calculated the concentration of organic acids in rain using the model of Oliver et al. (1983) and 23 samples for which we had measured DOC concentrations. The VWM concentration of organic acids using this model was 15 μeq L^{-1} (n = 23), which is 86% of our annual anion deficit for rain (n = 30 ; Table 1). This finding agrees with that of Williams et al. (1997a), who observed that the sum of cations in Amazon rain is well balanced with that of anions when including the contribution of measured formic and acetic acids. In contrast, the contribution of organic acids in throughfall using the same model was over a factor of 5 times higher (i.e. 110 μeq L^{-1}, n = 300) than our annual anion deficit in Table 1, not including the contribution from ANC. However, our annual anion deficit included over 250 samples for which we could not apply the model of Oliver et al. (1983), since these samples were not analyzed for DOC. We reduced the discrepancy in sample sizes by using only throughfall samples for which there were sets of DOC data (n = 349), and the VWM anion deficit calculated for this data set was 97.3 μeq L^{-1}, or about 90% of our estimate of organic acids calculated above. This model is bound to be imperfect since it uses a value for the carboxyl content of humic substances from rivers and soil water in the Temperate Zone, which should be different than that from throughfall of the central Amazon. That we are aware, the carboxyl content of humic substances in throughfall of the central Amazon has never been measured. However, our estimates of organic acids using this model are only about ±10% different than our anion deficits for both rain and throughfall, and are good evidence that the charge imbalance of our samples is due to the presence of organic acids.

Concentrations of dissolved organic carbon (DIC) < 2 μm were observed in Amazon rain, groundwater and stream water by Williams et al. (1997b) at nearby Lake Calado, and negligible concentrations in several throughfall samples were recorded (unpublished data). Hence, we assume that the ANC measured in the throughfall of our study is due to the presence of organic acid ions, and not HCO_3^-.

Canopy exchange was the dominant source of solutes to net throughfall for the Anavilhanas forest, in contrast to temperate zone forests which commonly have a larger source of dry deposition (Puckett 1990). Dry deposition in our study was a relatively important component of net throughfall only in the dry season. During this period, lower precipitation volumes and a longer dry periods between rain events probably result in the accumulation of biogenic aerosols and particulates in the atmosphere, which eventually settle on the surfaces of vegetation as dry deposition.

The total deposition of solutes via throughfall was higher in Anavilhanas compared to Temperate Zone forests due to higher levels of rainfall in the central Amazon. Solute losses via throughfall may be replenished by flood-waters, since forests flooded with nutrient rich waters have the capacity to remove specific elements directly from the water (Mitsch et al. 1979), or from soils enriched by sediment-rich flooding waters (Brinson et al. 1980). In the nutrient deficient Negro River, nutrient supplies in the Anavilhanas archipelago are partially sustained by fluvial sources from the Branco River, which is a nutrient-rich white water tributary of the Negro River that regulates much of the hydrochemistry of this system (Filoso et al. 1997).

Importance of throughfall fluxes to the Anavilhanas archipelago ecosystem

Since about two thirds of the surface area of floodplain lakes in the Anavilhanas archipelago is covered by flooded forests, throughfall may contribute significant amounts of solutes to the aquatic environment and be of major ecological importance. For instance, the deposition of dissolved P, an essential nutrient for phytoplankton growth often limiting in tropical lakes such as those of the Negro River floodplain (Forsberg 1984), increases about 7 times after rain is intercepted by the forest canopy. More than 45% of the dissolved P in throughfall of Anavilhanas is readily available to phytoplankton as SRP. The N:P ratios of dissolved inorganic nutrients from flood waters and throughfall are commonly 20:1 and 3:1, respectively, which suggest that substantial throughfall inputs would decrease the N:P ratio of surface waters. It is therefore possible that throughfall inputs periodically decrease the N:P ratios to levels below the generally accepted composition of microalgae (Redfield 1966), thereby shifting the nutrient status of these floodplain lakes from P to N limited.

We estimated that solute inputs via throughfall (not including stemflow) to Lake Prato accounted for 30 to 64% of the total for most solutes in the lake at high water, which indicates that throughfall is an important source of nutrients to the aquatic ecosystem of the Anavilhanas archipelago. The large chemical fluxes in throughfall to the floodplain lakes of the Anavilhanas archipelago suggest that lakes which become temporarily isolated from the Negro River are most affected. We estimated that about 70% (63) of floodplain lakes in Anavilhanas become isolated from the Negro River during falling water (i.e. they do not receive riverine inputs, albeit they may be connected to the Negro River by an outlet channel). Consequently, the enrichment of surface waters via throughfall probably plays an important role in the biogeochemical cycling of nutrients and other solutes in many of these floodplains lakes. Increased light penetration in isolated lakes due to siltation and the lack of river turbulence can accentuate primary productivity when associated with increased nutrient concentrations in surface waters. Since throughfall is potentially the largest source of nutrients to these lakes during falling water, these inputs conceivably regulate the primary production of floodplain lakes of the Anavilhanas archipelago during periods of isolation from the Negro River.

Acknowledgements

We thank IBAMA – Manaus for logistical support and EMBRAPA – Manaus for analyses of soil and foliar materials. The contents of this manuscript benefited from the comments of two anonymous reviewers. Financial support was provided by the NASA SIRC/X-SAR program under JPL contract 95E469, NASA grant NAGW-5115, HIRIS – NASA contract NAS5-31713, and a CNPq doctoral fellowship.

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