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Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico

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Summary Nutrient fluxes in rainfall and throughfall were measured weekly in a mature subtropical wet forest in NE Puerto Rico over a 15-year period that included the effects of 10 named tropical storms, several prolonged dry periods, and volcanic activity in the region. Mean annual rainfall and throughfall were 3482 and 2131 mm yr^{-1}, respectively. Average annual rainfall and throughfall fluxes of K, Ca, Mg, Cl, Na, and SO_4—S were similar but somewhat larger than those reported for most tropical forests. Rainfall inputs of nitrogen were comparatively low and reflect the relative isolation of the airshed. More constituents had seasonal differences in rainfall fluxes (6 out of 12) than throughfall fluxes (4 out of 12) and all volume weighted throughfall enrichment ratios calculated for the 15-year period were greater than one. However, median weekly enrichment ratios were less than 1 for sea salts and dissolved organic carbon, between 1 and 2 for Mg, Ca, SiO_2 and SO_4—S, and greater than 10 for NH_4—N, PO_4—P, and K. Droughts tended to reduce enrichment ratios of cations and sea-salts, but increased enrichment ratios of NH_4—N, PO_4—P, and K. In the weeks following hurricanes and tropical storms, relative throughfall tended to be higher and enrichment ratios tended to be lower. Saharan dust and the activity of Caribbean volcanoes can also be detected in the time series. Nevertheless, the impacts of particular events are variable and modified by the magnitude of the event, the pre- and post-event rainfall, and the time since the previous event. Rainfall, throughfall, rainfall pH, and rainfall fluxes of seven constituents had decreasing trends over the 15-year period. However, these decreases were small, less than inter-annual and annual varia-

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tions, and not considered to be ecologically significant. These long-term observations indicate that physical and biological processes associated with water passing through the canopy act to buffer internal nutrient cycles from inter-annual and seasonal variations in rainfall inputs.

Introduction

Rainfall and throughfall are major sources of nutrients in tropical forests (Proctor, 2005). Although throughfall is notorious for being spatially and temporally variable (Holwerda et al., 2006), throughfall studies that have more than 10 years of record and records that include multiple disturbances are lacking in the tropics and elsewhere. Tropically based studies have demonstrated the short-term impacts of reduced throughfall (Nepstad et al., 2002) and quantified annual nutrient fluxes associated with rainfall and throughfall (McDowell et al., 1990; Bruijnzeel, 1989; Veneklaas, 1990; Burghouts et al., 1998; Brouwer, 1996; Cavelier et al., 1997; Eklund et al., 1997; McDowell, 1998; Waterloo et al., 1999; McDonald and Healey, 2000; Loescher et al., 2002; Hölscher et al., 2003; Liu et al., 2003). Nevertheless, inter-annual variations in climate and the impacts of specific tropical storms and droughts can affect nutrient fluxes and ecological processes in different ways (Beard et al., 2005). This paper analyzes a 15-year time series of rainfall and throughfall constituent fluxes in a mature subtropical wet forest in Northeastern Puerto Rico. Two general questions are addressed: (1) what are the seasonal and inter-annual variations in rainfall and throughfall constituent fluxes in this forest; and (2) how do rainfall and throughfall constituent fluxes respond to named tropical storms, droughts, Saharan dust, and regional volcanic activity.

Methods

Site description

This study was conducted in the Bisley watersheds of the Luquillo Experimental Forest in Northwest Puerto Rico (18°20′N, 65°50′W). The site is located in the subtropical wet forest life zone and has been described in detail elsewhere (Scatena, 1989). The watersheds range in elevation from 265 to 456 m above sea level and are covered by mature secondary tabonuco (*Dacryodes excelsa*) type forests. The site is located 12 km to the east of the extensively studied El Verde Field Station (Fig. 1; Odum and Pigeon, 1970; McDowell et al., 1990). Both sites are on the windward side of the island, are at similar elevations, and are covered with similar mature secondary tabonuco type forests.

The Bisley study area is directly exposed to the northeasterly trade winds and has a maritime Köppen A2m type tropical climate (Schellekens et al., 1999). Rainfall and runoff occur in every month of the year in this relatively aseasonal environment. Convective storms, northeasterly trade winds, Saharan dust, winter cold fronts, tropical storms, depressions, and hurricanes all influence the site (Odum and Pigeon, 1970; Prospero and Nees, 1986; Scatena, 1989; McDowell et al., 1990; Larsen, 2000). Measured and simulated annual evapotranspiration of the Bisley watersheds and the surrounding tabonuco forest range from 2.0 to 3.0 mm day^{-1} (Wu et al., 2006). Rainfall events are gen-

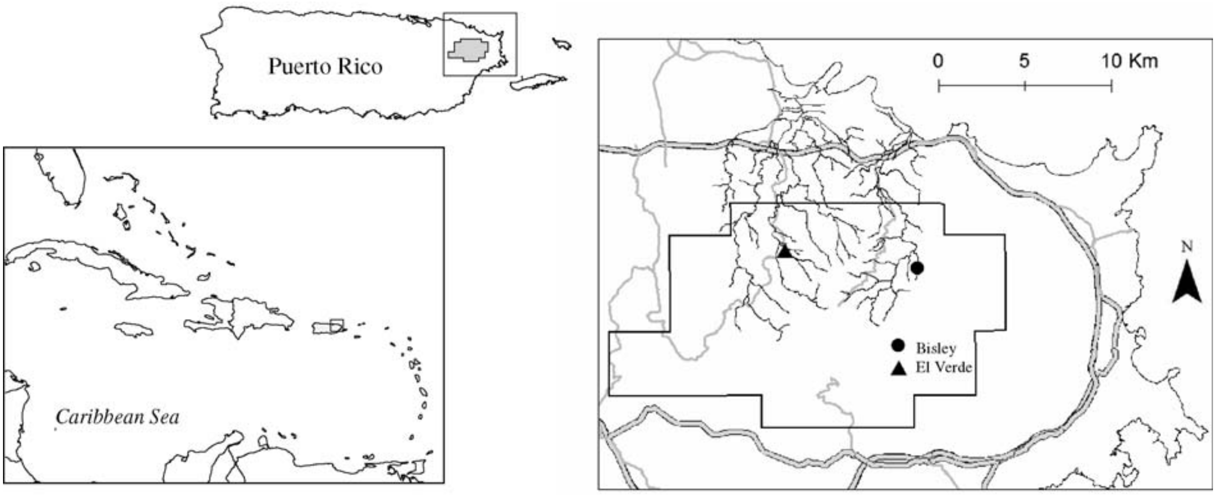

Figure 1 View of the Caribbean with the location of the Bisley watersheds, within the Luquillo Experimental Forest in northeast Puerto Rico.

erally small (median daily rainfall of 3 mm) but numerous (267 rain days per year) (Schellekens et al., 1999).

Although a decade-long time series of throughfall has never been presented for this or any other tropical forest, throughfall has been extensively studied in this forest (Odum and Pigeon, 1970; Clements and Colon, 1975; Scatena, 1990; Schellekens et al., 1999; Schellekens et al., 2000; Holwerda et al., 2006). Canopy interception of rainfall at Bisley is relatively high (~40%) and relative throughfall ranks among the lowest recorded for tropical lowland forests (Bruijnzeel, 1989). Nevertheless, the interception values at Bisley are similar to those measured in other maritime tropical forests and confirm the notion that rainfall interception is relatively high in tropical forests that receive more than 3000 mm yr^{-1} of rainfall and are located on islands or continental edges (Schellekens et al., 1999). The site's relative high annual interception and evaporation are attributed to the high frequency of low intensity short-duration rainfalls, net upward transport of evaporated moisture associated with the heat from condensation, advected energy, and a relatively low aerodynamic resistance of the canopy (Scatena, 1990; Schellekens et al., 2000).

During the study period, the forest was influenced by a series of tropical storms, hurricanes, and droughts of ranging magnitudes (Fig. 2). Hurricane Hugo, September 18, 1989, was the largest hurricane of the sequence reported here and is the largest storm to impact the area in the past 70 years (Scatena and Larsen, 1991). The hurricane defoliated the entire area, reduced the aboveground biomass by 50%, and toppled the above-canopy walk-up tower used for meteorological measurements. Nevertheless, weekly throughfall measurements were not interrupted and the meteorological tower was re-established after seven months. Within one year, both hydrologic cycles and nutrient exports in stream flow approached pre-hurricane levels (Scatena et al., 1996; Schaefer et al., 2000). Within five years, aboveground biomass was 86% of the pre-hurricane levels and leaf area and litter fall had returned to pre-hurricane levels (Scatena et al., 1996).

During the study period the site was also impacted by hurricanes Bertha (July 6, 1996), Hortense (September 10, 1996), Marilyn (September 15, 1996), and Georges (September 22, 1998). Of these hurricanes, Georges was the largest and resulted in localized defoliation and uprooting (Ostertag et al., 2003). Although Bertha, Hortense, and Marilyn occurred during the same year and brought heavy rainfall, they passed far enough away to only cause minor crown damage and relatively small increases in litter fall. Both rainfall and throughfall were measured for all of these storms.

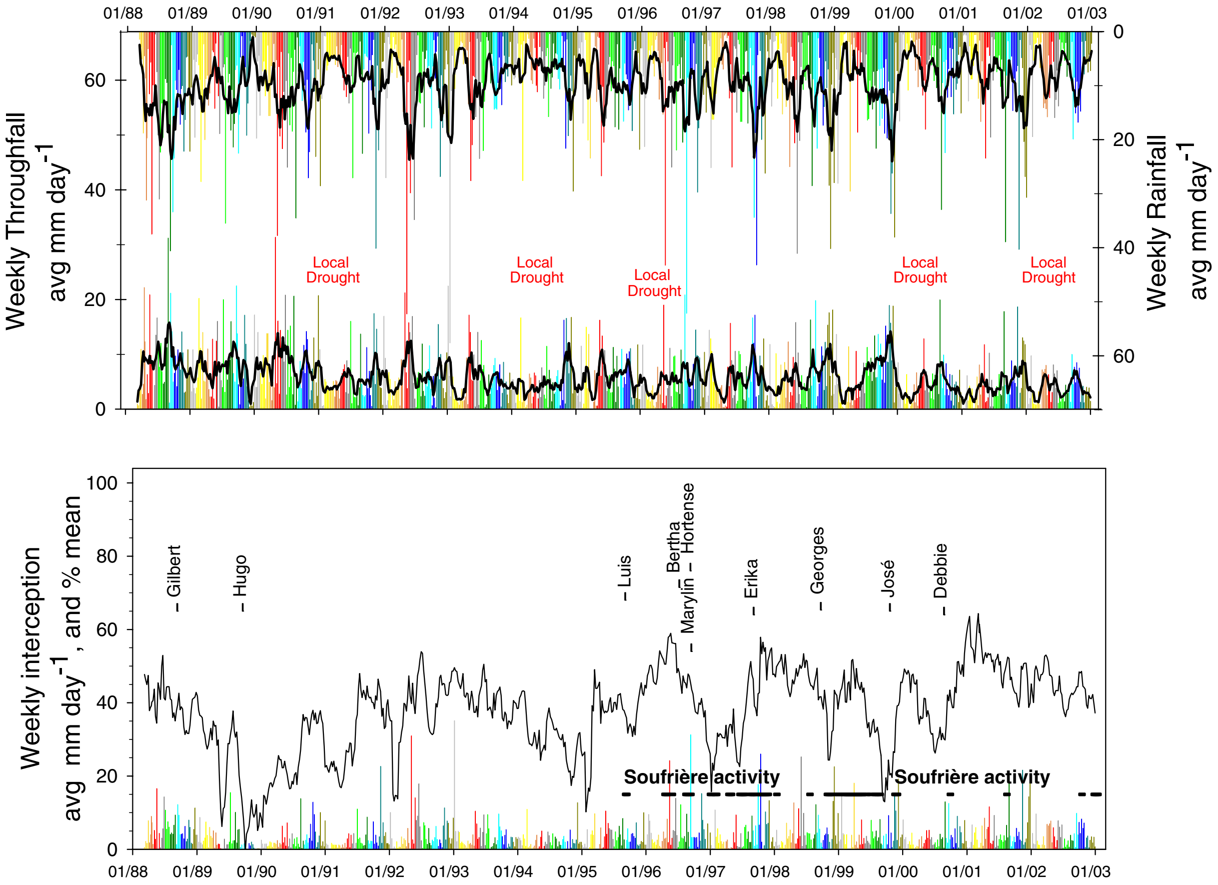

Figure 2 Meteorological events, volcanic activity and weekly throughfall, rainfall, and interception as weekly mean mm per day. Black line represents running average. Bar colors represent January in grey, February in yellow, March in dark yellow, April in orange, May in red, June in dark grey, July in light green, August in dark green, September in light blue, October in dark blue, November in cyan and December in olive.

Several meteorological droughts also occurred during the study period. Like other Puerto Rican droughts (Larsen, 2000; Covich et al., 2003), the intensity and effects of these drought periods was spatially and temporally variable. Pronounced droughts were observed in both the region and study area following Hurricane Hugo and in 1991, 1994, and 1996. Localized drought conditions were also observed in the study area in 2000 and 2002 (see methods and results for detailed descriptions).

In July 18, 1995, Soufrière Hills volcano on the island of Montserrat (16°45′N, 62°12′W) had its first complete eruption in over 100 years (www.mvo.ms). This andesitic stratovolcano is located 500 km to the south of the Bisley study area and has had over five distinct eruptive phases and over 25 eruptive stages since 1995. Phase 1 occurred between July 1995 and early 1998 when the dome grew and collapsed several times. Phase 2 occurred between early 1998 and late 1999. There were no lava extrusions but several dome collapses and small to moderate explosions during this period. The third phase was defined by the dome building and collapses that occurred between November 1999 and July 2003. During this phase, Puerto Rico experienced several noticeable volcanic ash falls in late July and early August 2001. The fifth and current phase began in August 2005 with dome growth and extrusive activity.

Methods

Rainfall and throughfall collection

The rainfall and throughfall measured in this study were collected and measured in the same manner for the duration of the study, and in accordance with our previous publications (Scatena, 1990; Schellekens et al., 1999; Holwerda et al., 2006). Bulk rainfall and throughfall were collected weekly (i.e. every Tuesday morning) and occasionally before and after major storms. Total rainfall was collected in a 25 m above canopy walk-up tower that is located on the divide between the two catchments and at an elevation of 361 m above sea level. Throughfall was measured in the 3 ha area that surrounds the walk-up tower using randomly placed but fixed gauges that were located on ridges, hill-slopes, gaps, and stream channels (Scatena, 1990). The rainfall collector and each throughfall collector had identical 143 cm^2 funnel collectors. Throughfall collectors were 30 cm above ground level surface. As many as 35 collectors were operated at any given time for the time series presented here. However, during one study on the influence of the spatial arrangement of collectors, 90 collectors were operating (Holwerda et al., 2006).

During the course of this long-term data collection, several companion studies were conducted to compare the performance of different arrangements of throughfall collectors. These arrangements include steel gutters fitted with tipping buckets, and networks of fixed and roving gauges (Schellekens et al., 1999; Holwerda et al., 2006). While the roving gauges had the smallest standard error of all the configurations, there was no statistical difference in the mean collection volumes of the roving and fixed collectors (Holwerda et al., 2006). Moreover, an analysis of variance (ANOVA) comparison of 60 fixed gauges, 30 roving gauges, and the 30 fixed gauges used in this study indicated that the relative throughfall measured by the different arrangements were not significantly different at the 0.05 significance level (Holwerda et al., 2006). Therefore, only the results from the weekly time series of fixed collectors are presented here.

During Hurricane Hugo in 1989, the canopy tower that held the climate station and rainfall collector was toppled. Although the forest's canopy was completely defoliated, most of the throughfall collectors remained intact. Those eight collectors that were destroyed were randomly re-located within 10 m of their original location and throughfall was collected without interruptions. The meteorological tower was also replaced seven months after the event. In the meantime we collected rainfall in a clearing adjacent to the tower that was created by the Hurricane. During this period, the canopy remained defoliated and rainfall and throughfall volumes were essentially identical.

Chemistry

During every collection, bulk rainfall and throughfall were collected for chemical analysis. Water for the rainfall analysis was collected from the above-canopy rainfall collector. The throughfall sample was a composite of water collected in six collectors. These six throughfall collectors were selected at the beginning of the study because their mean and median throughfall volumes and conductivities were similar to the mean and medians of all the 31 collection bottles and therefore they are considered representative of the site. These collection bottles were cleaned or replaced on a weekly basis and contained filters to prevent frogs and litter from entering the bottles.

Water samples were delivered to the laboratory on the same day they were collected. Chemical analysis was conducted in the same manner as previous studies of the LEF (McDowell et al., 1990; McDowell and Asbury, 1994; McDowell, 1998). Protocols and the original data are available on the Luquillo LTER web-page (http://luq.lternet.edu/data/lterdb20/metadata/lterdb20.htm). In the laboratory, pH and conductivity were measured following the procedures specified by NADP (1984) and McDowell et al., 1990). Samples were filtered using pre-combusted glass fiber filters (Whatman GF/F). Until 1997, samples were held refrigerated for analysis, with a sub-sample for ammonium analysis preserved by acidification with sulfuric acid (McDowell et al., 1990). After 1997, samples were stored frozen until analysis for all constituents except silica, which was analyzed on a refrigerated subsample. During the first nine years of the study, most samples were analyzed at the University of Puerto Rico. After 1997, all samples were analyzed at the University of New Hampshire. Silica (phosphomolybdate), phosphorus (ammonium molybdate), and ammonium (phenol-hypochlorite) were analyzed throughout the study period using spectrophotometric methods using a Technicon AA II or Lachat Quickchem. Cations were analyzed with atomic absorption spectrophotometry from 1988–1994, and with ion chromatography from 1994 on. Anions were measured with ion chromatography. Dissolved organic carbon and nitrogen were measured using persulfate digestion (McDowell et al., 1987; Solorzano and Sharp,

1980) prior to 1997, and with high temperature Pt-catalyzed combustion after 1997 (Merriam et al., 1996). Cross lab comparisons and analysis of samples using the different techniques indicated that comparable results were obtained with different laboratories and methods (e.g. McDowell et al., 1990; Merriam et al., 1996).

Data manipulation and statistical analysis

Rainfall and throughfall fluxes (kg ha^{-1} day^{-1}) were calculated from weekly concentration values multiplied by the corresponding amount of weekly rainfall or throughfall. Enrichment ratios were defined as the ratio of throughfall constituent flux over the corresponding rainfall constituent flux. Local meteorological drought conditions were defined as those weeks when throughfall volumes were within the lowest 5% of those observed during the 15-year study period.

All statistics were considered significant with an alpha of 0.05 and computed using SAS software (Version 9, SAS Institute 2003). Flux data for rainfall and throughfall constituents were transformed with a natural logarithm when appropriate to meet the assumptions of parametric statistical analysis. Correlations and regressions were used to describe general trends and relationships. General linear model (GLM) and repeated measures analysis of variance (ANOVA) were used to compare the amount of rainfall and throughfall among the 15 years of the study period. Post-hoc univariate tests of mean differences within the GLM ANOVA models were used to assess differences among study years. General linear model (GLM), repeated measures analysis of variance (ANOVA), and *post hoc* univariate tests of mean differences were used to compare the concentrations and fluxes between years and months for all the constituents (NH_4–N, NO_3–N, TDN, PO_4–P, K, Ca, Mg, DOC, Cl, Na, SO_4–S, SiO_2, and pH). The influence of named storms, droughts, Saharan dust, and the Montserrat volcano on constituent fluxes and enrichment ratios were compared using descriptive statistics, repeated measures analysis of variance by event, and Wilcoxon's sign rank tests.

The duration of continuous sampling needed to obtain reliable estimates of constituent fluxes will vary with the type and density of collectors, the frequency of collection, and the actual rainfall sequence being analyzed. To estimate the time series length needed to obtain stable daily mean flux values with this time series, the coefficient of variation (CV) and standard deviation (SD) of the means of successive sampling periods of different lengths were compared. This was done using the averages, SD and CV of the estimated daily means calculated using the series of continuous and successive sampling intervals that ranged from 10 to 500 weeks.

Results

General patterns of rainfall and throughfall

Over the 15-year study period, mean annual rainfall and throughfall were 3482 and 2131 mm yr^{-1}, respectively. During the study period there was only one week where there was no measurable rainfall or throughfall (May 23, 1989). Mean daily rainfall was 9.54 mm day^{-1} and mean daily throughfall was 5.84 mm day^{-1}. The lowest mean daily throughfall values (4.34 ± 0.48 and 3.84 ± 0.37 mm day^{-1}) were observed in 2000 and 2002. The highest mean daily throughfall (8.79 ± 0.98 and 8.50 ± 0.87 mm day^{-1}) occurred in 1988 and 1990 (Fig. 2, *post hoc* analysis of means, $F_{14,758} = 4.14$, $p < 0.0001$).

March had the lowest average monthly rainfall and throughfall (Fig. 3). The months of January through April had lower monthly rainfall (*post hoc* analysis $F_{11,761} = 3.35$, $p = 0.0002$) and throughfall (*post hoc* analysis

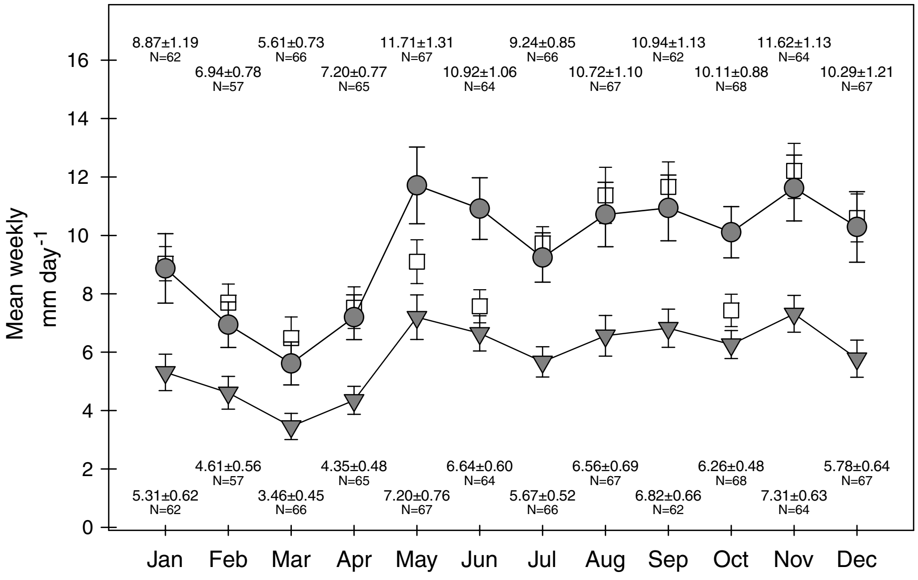

Figure 3 Per month mean weekly rainfall in mm/day for Bisley (gray circles), for El Verde (white squares), and mean weekly throughfall in mm/day for Bisley (gray inverted triangles). Error bars represent one standard error of the mean. Mean, one standard deviation and number of weeks for Bisley rainfall are at top of figure, while Bisley throughfall values are at bottom of figure.

$F_{11,761} = 3.90$, $p < 0.0001$) than the rest of the year. Rainfall at the nearby El Verde field station during the same period had similar monthly trends and statistically similar average annual value; 9.18 ± 15.77 mm day^{-1} for El Verde compared to 9.54 ± 8.45 mm yr^{-1} for Bisley. However, over the 15-year period average rainfall in the months of May, June, and October were significantly lower at El Verde (Fig. 3). These seasonal differences are apparently related to the greater exposure of Bisley to the northeast trade winds and the presence of the afternoon adiabatic winds that are more pronounced at El Verde than Bisley (see Odum and Pigeon, 1970).

In spite of the occurrence of two above average wet years towards the end of the study period (1998 and 1999), both annual mean weekly rainfall (Pearson Correlation $r = -0.096$, $p = 0.007$, $n = 775$) and throughfall (Pearson Correlation $r = -0.199$, $p < 0.0001$, $n = 775$) had weak but significant decreases over the entire study period. Moreover, regression slopes of the entire weekly time series indicate that rainfall and throughfall decreased at an average rate of 0.20 and 0.23 mm yr^{-1}, respectively. These average decreases are much less than the variation between years (Fig. 4) and are less than average daily rainfall and throughfall.

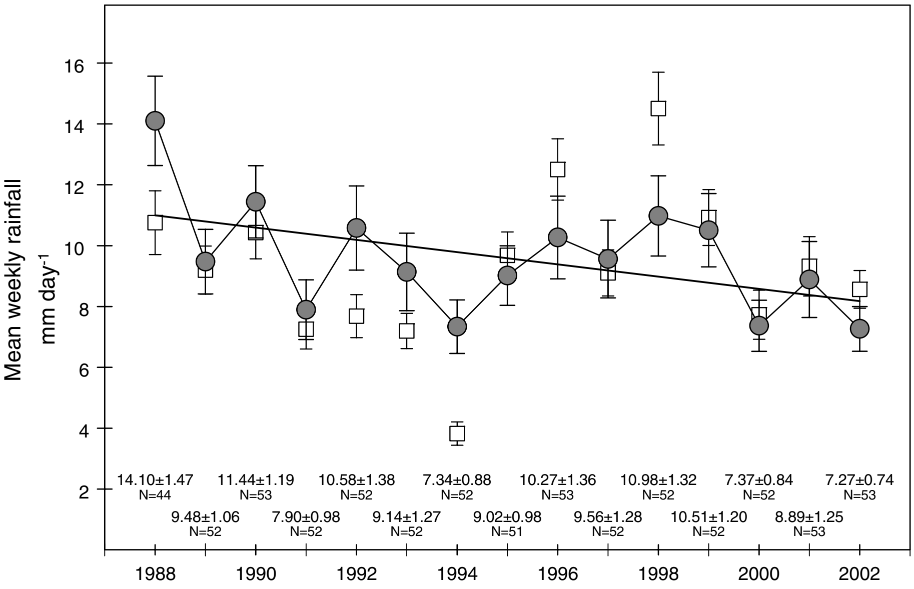

Figure 4 Per year mean weekly rainfall in mm/day for Bisley (gray circles) and for El Verde (white squares) with regression line for Bisley data. Error bars represent one standard error of the mean. Mean, one standard deviation and number of weeks for Bisley rainfall are at bottom of figure.

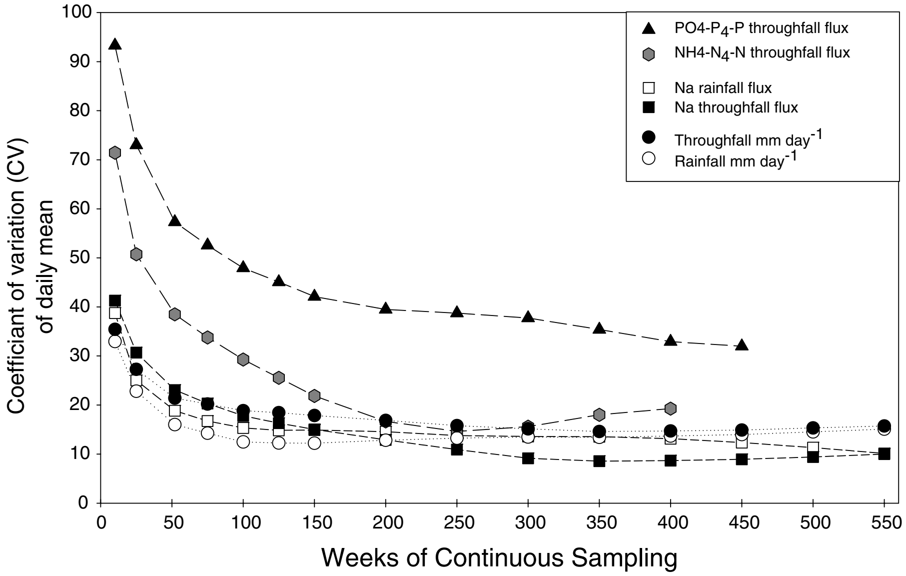

Figure 5 Standard deviations based on running average for successive weekly samples. Rainfall and throughfall, Rainfall flux of Na and throughfall flux of Na. White circles represent rainfall and grey circles represent throughfall.

Comparison of the averages, CV and STD of continuous sampling intervals of varying length indicates that the CV of daily rainfall and daily throughfall stabilizes at 15–20% after 2 years of sampling (Fig. 5). Daily rainfall constituent fluxes stabilized after 2–3 years while most throughfall constituent fluxes need 4–6 years of continuous sampling before their CV and STD stabilized. More than 8 years of continuous weekly throughfall sampling are needed for the CV and STD of PO_4–P and NH_4–N to stabilize. When they do stabilize they can still have CV of 40% (Fig. 5).

Rainfall concentrations through time

Rainfall concentrations were different among years for 11 of the 13 constituents: NH_4–N ($F_{12,346} = 11.67$, $p < 0.0001$), NO_3–N ($F_{13,486} = 7.24$, $p < 0.0001$), TDN ($F_{10,256} = 6.61$, $p < 0.0001$), PO_4–P ($F_{13,421} = 4.10$, $p < 0.0001$), K ($F_{14,554} = 1.74$, $p = 0.0451$), Ca ($F_{14,553} = 2.64$, $p = 0.001$), DOC ($F_{7,198} = 5.86$, $p < 0.0001$), Cl ($F_{13,521} = 2.48$, $p = 0.0028$), Na ($F_{14,553} = 2.16$, $p = 0.0004$), SO_4–S ($F_{14,538} = 10.75$, $p < 0.0001$), and pH ($F_{13,551} = 11.79$, $p = 0.0001$). Only Mg ($F_{14,554} = 1.29$, $p = 0.2080$) and SiO_2 ($F_{12,462} = 1.32$, $p = 0.2048$) did not have differences in their rainfall concentrations among years (Table 1).

Mean rainfall concentrations were different among months for 7 of the 13 constituents: Ca ($F_{11,556} = 3.13$, $p = 0.0004$), Mg ($F_{11,557} = 7.22$, $p < 0.0001$), DOC ($F_{7,198} = 9.54$, $p = 0.0033$), K ($F_{11,557} = 2.31$, $p = 0.0088$), Cl ($F_{11,523} = 11.10$, $p < 0.0001$), Na ($F_{11,556} = 14.79$, $p < 0.0001$), and SO_4–S ($F_{11,541} = 1.79$, $p = 0.0525$). There were no differences in concentration among months for NH_4–N, NO_3–N, TDN, PO_4–P, SiO_2, and pH (Table 1).

Rainfall flux through time

There were differences in rainfall flux values among years for 8 of the 12 nutrients: NH_4–N ($F_{12,325} = 6.00$, $p < 0.0001$), NO_3–N($F_{13,392} = 3.06$, $p = 0.0003$), TDN ($F_{10,251} = 98.20$, $p < 0.0001$), PO_4–P ($F_{12,398} = 1.93$, $p < 0.0291$), DOC ($F_{7,198} = 9.54$, $p < 0.0001$), Cl ($F_{13,518} = 2.58$, $p = 0.0018$), SiO_2 ($F_{12,244} = 4.27$, $p < 0.0001$), and SO_4–S ($F_{14,536} = 589$, $p < 0.0001$). There were no differences among years for rainfall fluxes of K, Ca, Mg, and Na (Fig. 7). Over the 15-year study period, trends in weekly rainfall fluxes were apparent for 7 of the 12 nutrients; NH_4 (Pearson Corr $r = -0.350$, $p < 0.000$, $n = 338$), NO_3–N (Pearson Corr $r = -0.265$, $p < 0.000$, $n = 406$), TDN (Pearson Corr $r = -0.174$, $p = 0.004$, $n = 261$), PO_4–P (Pearson Corr $r = -0.159$, $p = 0.001$, $n = 413$), DOC (Pearson Corr $r = -0.370$, $p < 0.0001$, $n = 206$), SO_4–S (Pearson Corr $r = -0.209$, $p < 0.0001$, $n = 550$) and SiO_2 (Pearson Corr $r = -0.132$, $p < 0.0343$, $n = 257$). These constituents had a tendency to decrease throughout the study period. Rainfall pH also tended to decrease throughout the study period (Pearson Corr $r = -0.243$, $p < 0.000$, $n = 565$). All rainfall nutrient fluxes were positively correlated with the amount of rainfall. However, rainfall volume only explained between 3% (PO_4–P) and 40% (Cl) of the variance in weekly nutrient fluxes.

Within years, there were differences among months in the mean rainfall flux of 6 of the 12 nutrients: NH_4–N

Table 1 Mean weekly fluxes and volume weighted concentrations during the 15-year study period, 1988–2002, for rainfall and throughfall

	Rainfall					Throughfall					Enrichment ratio			
	yr	mn	*n*	Average flux (kg ha^{-1} d^{-1})	Volume weighted [] (mg L^{-1})	yr	mn	*n*	Average flux (kg ha^{-1} d^{-1})	Volume weighted [] (mg L^{-1})	*n*	Median	SD	Volume weighted [] (mg L^{-1})
NH_4–N	*	*	339	0.002	0.025	*		422	0.018	0.302	307	12.4	492	12.08
NO_3–N	*	*	406	0.004	0.0451	*		553	0.006	0.1085	372	1.79	271	2.41
TDN	*		262	0.013	0.135	*	*	276	0.048	0.758	223	4.39	40.2	5.62
PO_4–P	*		411	0.0003	0.004	*	*	418	0.003	0.055	340	13.2	133	13.75
K			559	0.022	0.219	*	*	666	0.170	2.815	539	10.0	17.6	12.85
Ca		*	561	0.044	0.439	*		664	0.057	0.942	541	1.50	2.8	2.15
Mg			563	0.037	0.367	*		666	0.036	0.604	543	1.12	1.5	1.65
DOC	*	*	207	0.332	3.569	*		232	0.361	6.301	188	.80	2.4	1.77
Cl	*	*	551	0.386	4.022	*		579	0.331	5.785	505	.80	2.4	1.44
Na		*	569	0.243	2.430	*	*	666	0.181	3.009	548	.80	1.6	1.24
SO_4–S	*		551	0.126	1.300	*		613	0.149	2.576	511	1.49	10.3	1.98
SiO_2	*		257	0.101	1.130	*		436	0.102	1.778	220	1.37	30.0	1.57
pH	*		565	5.17		*		629	6.14		553	1.17	0.14	

Asterisks represent significant differences in flux among years (yr) and/or months (mn) for each constituent. Enrichment ratio is throughfall flux over rainfall flux, SD is the standard deviation of sample, and [] is concentration. Median values for pH.

($F_{11,326} = 2.07$, $p = 0.0218$), NO_3—N ($F_{11,394} = 1.82$, $p = 0.0485$), Ca ($F_{11,548} = 2.30$, $p = 0.0092$), DOC ($F_{11,194} = 2.37$, $p = 0.0091$), Cl ($F_{11,250} = 2.71$, $p = 0.002$), and Na ($F_{11,556} = 2.70$, $p = 0.0022$). There were no differences among months in the rainfall fluxes of TDN, PO_4—P, K, Mg, SO_4—S, and SiO_2 (Table 1). There was a positive correlation between the rainfall fluxes of NO_3—N and SO_4—S (Pearson Corr $r = 0.448$, $p < 0.0001$, $n = 343$).

Throughfall concentrations through time

There were differences among years for all throughfall nutrients concentrations ($F > 2.87$, $p < 0.0042$) and pH ($F_{13,615} = 15.18$, $p < 0.0001$). Among months there were differences in the mean throughfall concentrations of 9 of 13 constituents: PO_4—P ($F_{11,416} = 1.88$, $p = 0.0401$), K ($F_{11,5655} = 2.69$, $p = 0.0021$), Ca ($F_{11,656} = 2.38$, $p = 0.0069$), Mg ($F_{11,656} = 4.82$, $p < 0.0001$), Cl ($F_{11,568} = 8.86$, $p < 0.0001$), DOC ($F_{11,220} = 2.90$, $p = 0.0014$), Na ($F_{11,655} = 14.47$, $p < 0.0001$), SO_4—S ($F_{11,604} = 2.44$, $p = 0.0055$), and SiO_2 ($F_{11,258} = 2.39$, $p = 0.0067$). There were no differences in throughfall concentrations among months for NH_4—N, NO_3—N, TDN and pH.

Throughfall flux through time

There were differences in all throughfall nutrient fluxes among years ($F > 2.41$, $p < 0.0051$, Table 1). Among months there were differences in throughfall fluxes for 4 of 12 nutrients: TDN ($F_{11,264} = 2.23$, $p = 0.0135$), PO_4—P ($F_{11,406} = 2.10$, $p = 0.0193$), K ($F_{11,655} = 3.94$, $p < 0.0001$), and Na ($F_{11,655} = 1.98$, $p = 0.0281$). Throughfall nutrient fluxes were also correlated to the amount of throughfall, which explained from 3% (PO_4—P) to 32% (Cl) of the variance of weekly values. The only exception was the throughfall flux of NH_4—N which was not related to the amount of throughfall ($r = 0.066$, $p = 0.173$, $n = 422$). There were no differences in fluxes among months for NH_4—N, NO_3—N, Ca, Mg, DOC, Cl, SO_4—S, and SiO_2 ($F < 1.70$, $p > 0.0698$). Over the 15-year study period, trends in weekly throughfall fluxes were only apparent for 2 of the 12 flux nutrients; PO_4—P tended to increase (Pearson Corr $r = 0.231$, $p < 0.000$, $n = 418$) while SiO_2 (Pearson Corr $r = -0.160$, $p = 0.001$, $n = 436$) had weak tendencies to decrease throughout the study period. There was also a weak positive correlation for throughfall fluxes of NO_3—N and SO_4—S (Pearson Corr $r = 0.290$, $p < 0.0001$, $n = 475$).

Enrichment ratios and correlations among nutrients

All constituents had positive correlations between their weekly rainfall and throughfall fluxes. In particular, there were strong positive correlations among rainfall and throughfall fluxes of Ca, Mg, K, and Na ($r > 0.59$, $p < 0.001$). Enrichment ratios calculated for the entire 15-year period were all greater than one. However, median weekly enrichment ratios were less than one for sea salts and dissolved organic carbon and between 1 and 2 for Mg, Ca, SiO_2 and SO_4—S (Table 1). In contrast, median weekly enrichment ratios for NH_4—N, PO_4—P, and K were greater than 10. Only K had significant differences in monthly enrichment ratios ($F_{11,528} = 2.97$, $p < 0.0001$). *Post hoc* analyses indicated that monthly differences in K enrichment ratios coincided with the month with the highest (October) and the lowest (January) fluxes. While there were no detectable seasonal differences in the enrichment ratios of other nutrients, the enrichment ratios of cations (Ca, Mg, K, Na) tended to be highest from September through November (Fig. 6).

Changes in response to specific atmospheric events

Tropical storms and hurricanes

Over the course of the 15-year study, 10 named tropical storms passed close enough to the site to cause noticeable increases in rainfall and throughfall. The individual events varied in intensity of wind and rain, crown damage and litterfall, pre- and post-event rainfall, and in the length of time since the previous event. When the seven weeks before the event were compared to the seven weeks after the event for all named storms combined, there was a tendency for increased throughfall and increased throughfall fluxes for all constituents. In general, events that had maximum daily gusts less than 15 m^{-1} s^{-1}, average daily wind speeds less than 12 m^{-1} s^{-1}, and litter inputs less than 15 g m^2 day^{-1} did not have any clear or prolonged post-event changes in throughfall chemistry quality or quantity. Larger events (e.g. Hugo, Luis, Bertha, and Georges) that had maximum daily gusts greater than 25 m^{-1} s^{-1}, average daily winds greater than 15 m^{-1} s^{-1}, and litter fall inputs greater than 20 g m^2 day^{-1}, did have changes in the quality and quantity of throughfall.

Hurricane Hugo passed directly over the study area on September 18, 1989 and was the largest natural disturbance in the 15-year study period and the largest hurricane to impact the area in over 70 years (Scatena and Larsen, 1991; Scatena et al., 1996). Because the forest's canopy was almost completely defoliated by the storm, many of the throughfall sampling bottles had no canopy overhead and were effectively collecting rainfall for several months until an understory and overstory canopy developed. Mean weekly throughfall constituent fluxes during the seven weeks after Hugo were lower than the 7 weeks before the storm for K ($F_{1,10} = 34.92$, $p < 0.0001$), Ca ($F_{1,10} = 40.84$, $p < 0.0001$), Mg ($F_{1,10} = 12.27$, $p = 0.0057$), and Na ($F_{1,10} = 14.03$, $p = 0.0038$). The throughfall flux of SiO_2 increased ($F_{1,10} = 748$, $p = 0.0291$) and there were no significant differences in mean weekly throughfall pH or NO_3—N for the seven weeks before and after Hugo.

In 1996, seven years after Hurricane Hugo, the forest's leaf area index, above ground biomass, and rates of litter fall were similar to pre-hurricane values (Scatena et al., 1996) and the forest was impacted by a series of smaller tropical storms that occurred over a 2-month period (Fig. 2; Bertha, Hortense, Marilyn). None of these events completely defoliated the canopy like Hugo nor was a regional post-hurricane drought observed. Both the relative and absolute values of throughfall had a tendency to be higher in the seven weeks following the first of these storms, Bertha July 6, 1996. Nevertheless, there was a significant dif-

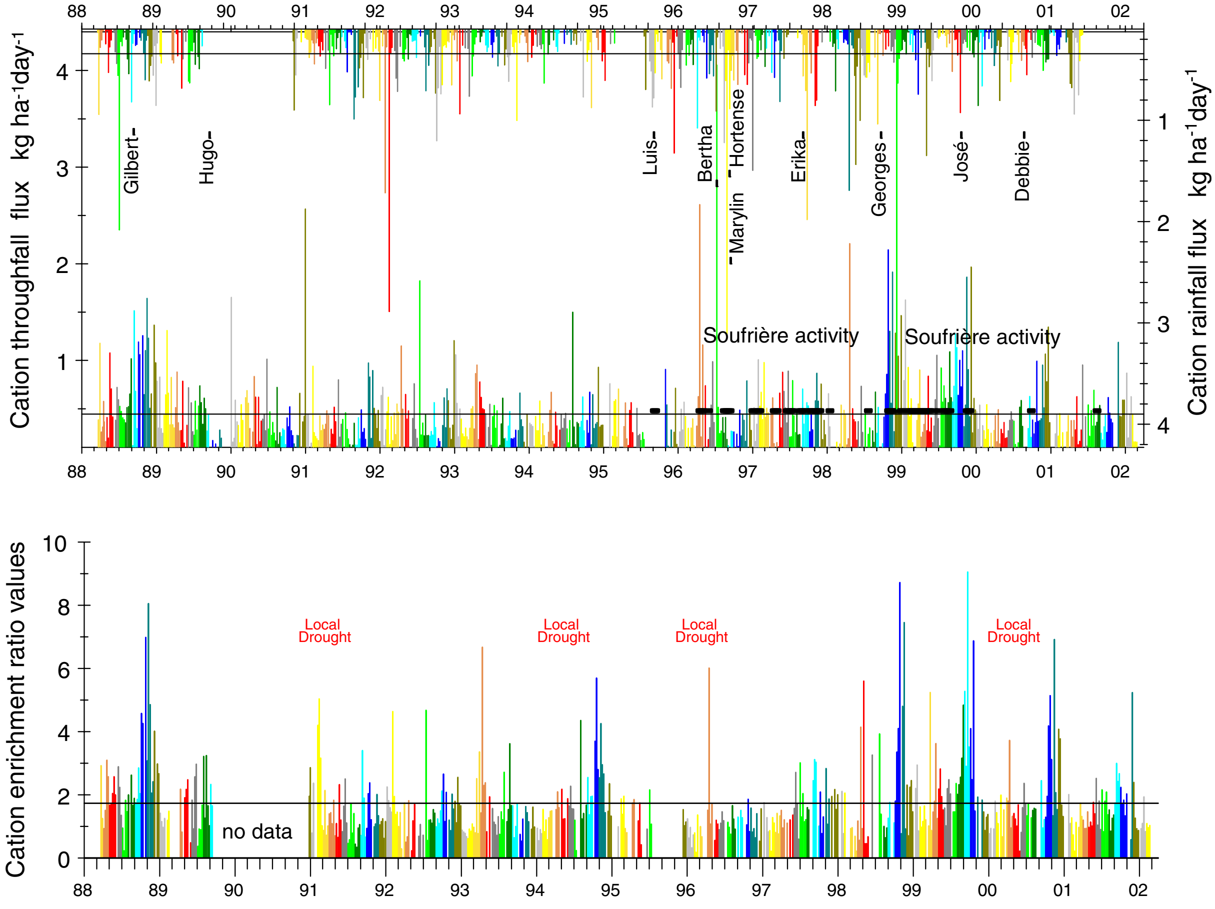

Figure 6 Top panel has throughfall and rainfall flux over the study period for the sum of cations (Ca, Mg, K and Na). Bottom panel has enrichment ratio values for the sum of cations. Meteorological events and volcanic activity are identified. Black lines represent the mean value. Bar color legend same as in Fig. 2.

ference in average throughfall pH, it decreased the post-event, ($F_{1,12} = 6.86$, $p = 0.0224$), but there were no differences in the average fluxes of PO_4—P, K, Ca, Mg, Cl, Na, and SO_4—S between the seven weeks before and after the passage of Bertha. Enrichment ratios for K, Ca, Mg, Cl, and Na did have a tendency to be lower over the seven weeks after the hurricane compared to the previous seven weeks. In contrast, the enrichment ratio of PO_4—P had a tendency to be higher after the hurricane.

Hurricane Georges was the second largest storm in the time series and passed through the site on September 22, 1998, two years after the swarm of storms in summer of 1996. Litter fall on the day of this event was 55% of annual litterfall (Ostertag et al., 2003). Both the relative and the absolute value of mean weekly throughfall were slightly higher during the seven weeks after Georges, compared to the seven previous weeks. All throughfall constituents (NH_4—N, NO_3—N, TDN, PO_4—P, K, Ca, Mg, DOC, Cl, Na, SO_4—S, and SiO_2) had higher mean weekly fluxes in the seven weeks period after the hurricane. However only the throughfall fluxes of NH_4—N ($F_{1,11} = 6.73$, $p = 0.0249$) and PO_4—P ($F_{1,11} = 6.30$, $p = 0.0290$) had significantly higher values in the period after the storm. The mean weekly enrichment ratio for PO_4—P also tended to be higher after the hurricane, but there were no differences in the enrichment ratios for K, Ca, Mg, Cl and Na.

Droughts

During the 1990's below average annual rainfalls were observed in the Lesser and Greater Antilles (Diaz, 1996) and across Puerto Rico (Larsen, 2000). Several meteorological droughts were also recognized during the study period. Some of these droughts were recognized regionally (1989, 1991, 1994, 1996), while some (2000 and 2002) were only recognized in Bisley (Figs. 2 and 4). These low rainfall periods were never observed in the month of September and were most frequent in March (Fig. 3). During these low rainfall conditions, the concentrations of nutrients in throughfall were higher than during non-drought periods (Table 2). However, there was a tendency for lower enrichment ratios for cations (K, Ca, Mg,), sea-salts (Cl, Na) and DOC during these dry periods. In contrast, the enrichment ratios of NH_4—N, NO_3—N, TDN and PO_4—P tended to increase during these dry conditions (Table 2).

Saharan dust

Saharan dust is common in the Caribbean atmosphere between April and September (Prospero and Nees, 1986) and most pronounced in Puerto Rico between May and August (McDowell et al., 1990). Of all the constituents, only Ca fluxes and concentrations showed significant differences be-

Table 2 Weekly median enrichment ratios, throughfall fluxes, and throughfall concentrations for all constituents during local drought and non-drought conditions in the Bisley watersheds

	Enrichment ratio				Throughfall flux kg ha^{-1} d^{-1}				Throughfall []mg L^{-1}	
	n	Local Drought	*n*	Non drought	*n*	Local drought	*n*	Non drought	Local drought	Non drought
*NH$_4$–N	8	85.18	301	11.65	17	3.82	407	10.21	1939.53	187.22
*NO$_3$–N	13	2.78	361	1.76	21	0.93	535	2.80	190.26	60.52
TDN	6	10.53	220	4.36	9	0.01	269	0.03	4.23	0.71
*PO$_4$–P	11	46.23	331	13.06	14	0.60	406	1.75	236.49	36.34
K	12	8.07	529	10.17	23	0.03	645	0.13	9.57	2.70
Ca	12	0.87	528	1.50	23	0.01	643	0.04	2.43	0.91
Mg	12	0.84	533	1.12	23	0.01	645	0.03	1.77	0.59
DOC	7	0.50	183	0.84	10	0.04	225	0.24	15.17	6.44
Cl	12	0.73	495	0.84	21	0.05	560	0.27	17.77	6.33
Na	12	0.52	538	0.81	23	0.02	645	0.15	8.13	3.17
SO$_4$–S	14	1.83	499	1.49	21	0.02	594	0.12	7.14	2.57
SiO$_2$	5	0.43	217	1.43	17	0.00	421	0.02	1.04	0.41

Local drought conditions were defined as the lowest 5% of throughfall values in the study area during the 15-year study period. Throughfall flux for *NH$_4$–N, *NO$_3$–N, and *PO$_4$–P is g ha^{-1} d^{-1}, and concentration is μeq L^{-1}.

tween ''Saharan Dust Months'' and the rest of the year. However, even though these differences are detectable, they were not large. Moreover, the six-month (April–September) ''Saharan Dust'' period contributes approximately 60% of the total annual inputs of Ca in rainfall, but only 50% of the total Ca in throughfall. Likewise, slightly more Ca enters the forest from throughfall during the four wettest months (September–December), a period when Saharan dust contributions are considered to be relatively minor, than during the four months (May–August) when Saharan dust is most common.

Montserrat volcano

During the 15-year period, there were 76 weeks when the Soufrière Hills volcano produced ash clouds of 1800 m (6000 ft) or more (Allen et al., 2000; Robertson et al., 2000, www.mvo.ms, www.volcano.und.edu). All of these ''eruptive weeks'' occurred between 1995 and 2002 and altered Bisley throughfall fluxes more than rainfall fluxes. Mean cation enrichment ratios were 2.0 vs 1.7($F_{1,529} = 4.19$, $p = 0.0412$) and cation throughfall fluxes were 0.60 vs 0.43 kg ha^{-1} day^{-1} ($F_{1,659} = 13.20$, $p = 0.0003$) and these were both significantly larger during these eruptive weeks. Mean and median rainfall flux of TDN was also greater during eruptive weeks ($F_{1,260} = 9.04$, $p = 0.0029$). Mean throughfall PO$_4$–P flux was 5.9 vs 2.8 g ha^{-1} day^{-1} and mean throughfall NH$_4$–N flux was 32.0 vs 16.9 g ha^{-1} day^{-1} and these were noticeable larger during weeks of eruptive volcanic activity. There were significant differences in 10 out of 13 throughfall constituent fluxes (NH$_4$–N, TDN, PO$_4$–P, K, Ca, Mg, DOC, Na, SO$_4$–S) with greater values occurring during volcanic activity ($F > 4.21$, $p < 0.0405$, Table 3). There were no differences in the throughfall fluxes of NO$_3$–N, Cl and SiO$_2$ when comparing eruptive weeks to non-eruptive weeks (Table 3).

Estimates of the nutrient contributions of the Soufrière Hills volcano to the Bisley study area can be made from difference in throughfall fluxes between eruptive and non-eruptive weeks and the number of eruptive weeks during the 15-year period (Table 3). In general, 3–5% of the throughfall cation flux can be attributed to volcanic activity. Approximately 17% of the total PO$_4$–P throughfall flux was transported during eruptive weeks and volcanic activity can be considered to have contributed 4.3% of the total. Likewise, 12.5% of the SO$_4$–S entered the forest during eruptive weeks and the volcanic activity can be considered to have contributed 3.6% of the total. Volcanic contributions may also account for 9.6% of the total TDN throughfall flux and appears to have influenced throughfall DOC but not rainfall DOC fluxes.

Discussion

Over the course of the 15-year study, water that passed through the Bisley canopy was enriched such that the total flux of nutrients to the forest floor from throughfall was greater than the rainfall inputs into the canopy. Relative to the storage of nutrients in the leaf compartment of the forest's full canopy annual throughfall flux are equal to 16%, 20%, 120%, 67%, and 93% of the leaf compartment for N, P, K, Ca, Mg, respectively (Scatena et al., 1993). Throughout this 15-year period there were consistent differences in the behavior of certain constituents (Ca, Mg, Cl, Na, SiO$_2$, SO$_4$–S) compared to others (NH$_4$–N, NO$_3$–N, TDN, PO$_4$–P and K). The annual rainfall fluxes of the former group are relatively abundant in Bisley compared to other tropical sites (Fig. 7). They also have relatively low median weekly enrichment ratios (Table 1), are common in seawater and dust (McDowell et al., 1990), and had stable CV and STD after 4–6 years of continuous sampling. In contrast, the rainfall inputs of the later group were relatively low in Bisley compared to other tropical sites (Fig. 7) and 6–8 years of continuous sampling is needed before their CV and STD stabilize. They also had higher median weekly enrichment ratios (Table 1) and enrichment ratios that increased during droughts (Table 2). These differences reflect the importance of canopy-level biological processes that

Table 3 Rainfall and throughfall fluxes kg ha^{-1} d^{-1} during volcanic activity in Soufrière Hills

	Volcanic activity			Non-volcanic activity			
	n	Median	SD	*n*	Median	SD	
Rainfall							
NH_4—N_*	30	0.654	0.926	308	0.754	5.390	
NO_3—N_*	47	0.905	3.551	359	1.495	9.402	
TDN	32	0.017	0.014	230	0.007	0.013	√
PO_4—P_*	64	0.133	0.325	349	0.119	1.130	
K	62	0.017	0.043	496	0.013	0.033	
Ca	63	0.039	0.037	497	0.027	0.061	
Mg	64	0.025	0.039	499	0.024	0.053	
DOC	32	0.310	0.198	174	0.276	0.277	
Cl	67	0.318	0.395	465	0.291	0.331	
Na	63	0.184	0.241	505	0.181	0.265	
SO_4—S	58	0.063	0.190	493	0.075	0.196	
SiO_2	23	0.014	0.453	234	0.015	0.387	
pH	43	5.180	0.675	522	5.165	0.662	
Throughfall							
NH_4—N	32	11.999	43.791	391	9.050	24.601	√
NO_3—N	59	2.803	6.346	496	2.643	23.885	
TDN	30	0.063	0.086	246	0.031	0.042	√
PO_4—P	56	2.026	8.888	362	1.519	3.905	√
K	67	0.183	0.282	600	0.117	0.162	√
Ca	67	0.057	0.069	598	0.039	0.074	√
Mg	67	0.038	0.035	600	0.026	0.046	√
DOC	31	0.396	0.584	201	0.220	0.414	√
Cl	70	0.301	0.241	510	0.254	0.293	
Na	67	0.178	0.180	600	0.138	0.161	√
SO_4—S	57	0.154	0.216	556	0.110	0.137	√
SiO_2	50	0.022	0.032	386	0.024	0.507	
pH	42	6.035	0.345	587	6.170	0.508	√

Fluxes for $^*NH_4$—N, $^*NO_3$—N, and $^*PO_4$—P are g ha^{-1} d^{-1}. Significant differences in flux between periods of volcanic and non-volcanic activity are represented by √. SD is standard deviation.

enrich throughfall in K, NH_4—N, NO_3—N, TDN and PO_4—P. Canopy-level biological processes that enrich throughfall were most pronounced for NH_4—N, whose weekly throughfall fluxes were not even correlated to the amount of weekly rainfall or throughfall. This lack of correlation between rainfall and throughfall fluxes of NH_4—N has also been observed in other tropical forests (McDowell et al., 1990; Veneklaas, 1990).

The average annual fluxes of most constituents in Bisley throughfall are within the range reported for most tropical and subtropical sites (Fig. 7). In contrast, the annual rainfall inputs of NH_4—N, NO_3—N, TDN and PO_4—P tend to be slightly lower while Mg, Cl, Na, and SO_4—S are higher than reported for other tropical and subtropical sites (Fig. 7). Nevertheless, the concentrations of these constituents in rainfall are similar to those observed at the nearby El Verde site and at other marine influenced tropical forests (Asbury et al., 1994; Cavelier et al., 1997; Eklund et al., 1997; Waterloo et al., 1999; McDonald and Healey, 2000). Therefore, differences in annual rainfall inputs apparently reflect high annual rainfall rather than large differences in rainfall chemistry (McDowell et al., 1990).

In contrast to base cations and sea salts, the annual rainfall inputs of nitrogen (NH_4—N, NO_3—N, TDN) and PO_4—P tend to be slightly lower in Bisley than those reported for other tropical and subtropical sites (Fig. 7). Correlations between rainfall fluxes and concentrations of NO_3—N and SO_4—S in both Bisley and El Verde (McDowell et al., 1990) indicate the area does receive some anthropogenic loading. However, the relatively low levels of nitrogen and pollution-associated rainfall inputs in Bisley compared to other tropical sites (Fig. 7) is apparently due to the lack of fires in the adjoining landscape, and because the study site's airshed is dominated by relatively unpolluted trade winds that originate in the Atlantic Ocean. Nevertheless, the annual fluxes of nitrogen in Bisley throughfall are similar to other tropical forests (Fig. 7) and the forest ecosystem as a whole is considered to be relatively nitrogen rich (Chestnut et al., 1999).

Comparisons of concentrations, fluxes, and enrichment ratios in the seven weeks before and after named tropical storms indicate that the relative amount of throughfall increases in general after large storms. Each named storm also had elevated concentrations and fluxes during at least one week following the storm. However, other post-storm differences in throughfall chemistry were obscured by differences in rainfall inputs, the magnitude of canopy damage, and the sequence of the storms. The largest

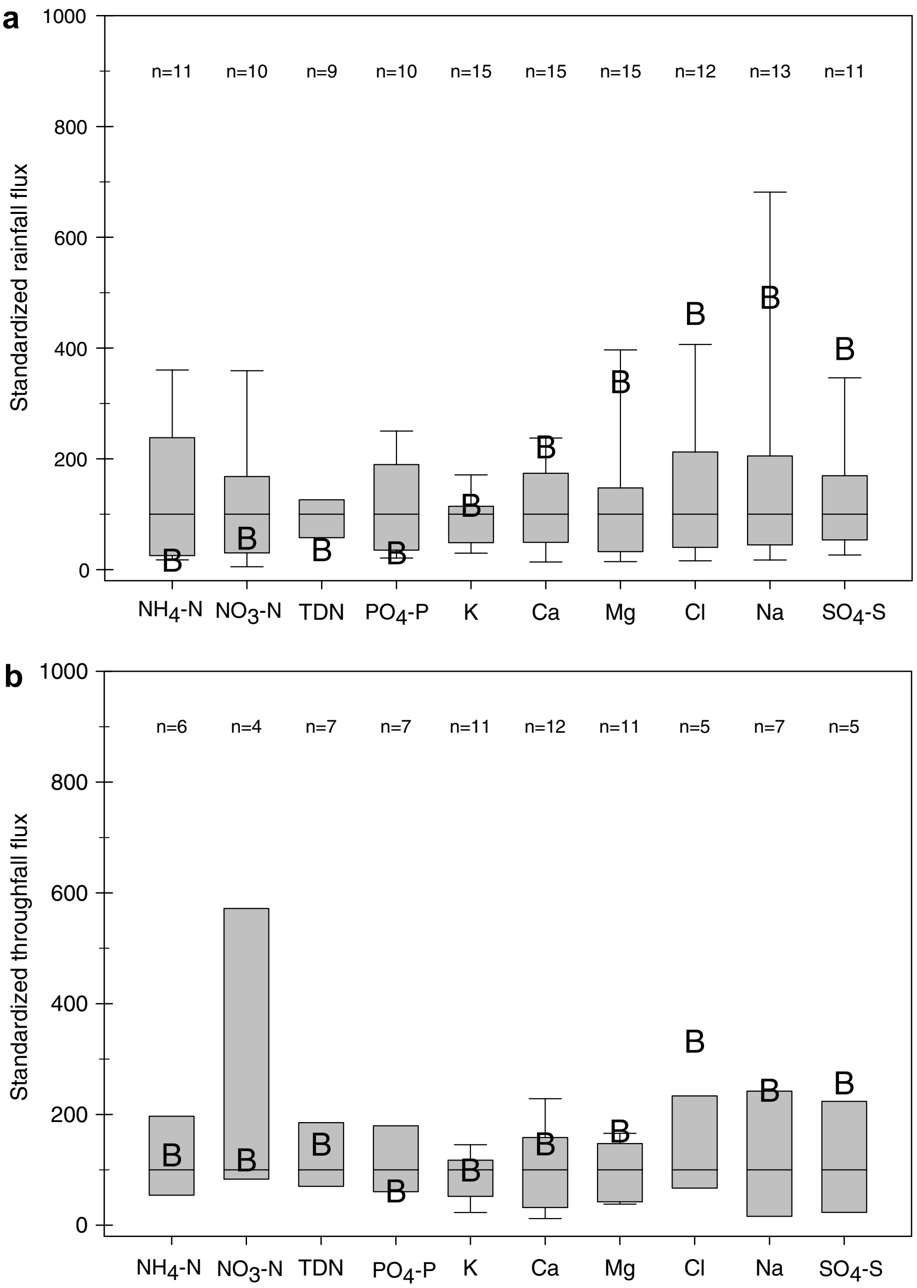

Figure 7 Box plots of standardized values of constituents of: (a) rainfall flux and (b) throughfall flux for wet tropical and subtropical forests. Each box encompasses the 25th through 75th percentile, and the horizontal lines mark the 10th and 90th percentiles. The letter B represents where the value for Bisley is relative to other sites. The values are standardized by dividing the value from a particular site by the median value of all sites and multiplying by 100. Data used were Brouwer (1996), Burghouts (1993) and those compiled by Bruijnzeel (1989), McDowell (1998), Veneklaas (1990) and Liu et al., 2003).

differences occurred after the two hurricanes that had litter-fall increases of more than 50%. However, even these differences only lasted for a few months at most.

During drought conditions rainfall, throughfall, and their associated nutrient fluxes are less, by definition. The lack of water percolating through the canopy also increased the concentrations of throughfall but reduced the enrichment ratios of base cations and sea-salts. These constituents had median weekly enrichment ratios less than 2 and are primarily derived from external inputs. In contrast, droughts increased the enrichment ratios of constituents associated with N, P, and S. These constituents also had median weekly enrichment ratios greater than 10 and are strongly linked to the canopy-level biological processes. These observations suggest that droughts reduce the canopy's ability to retain N and P and support similar conclusions made in studies of other tropical forests (Edwards, 1982; Richardson et al., 2000; Tobón et al., 2004).

Although the Island of Montserrat is approximately 500 km south of the Bisley study site, the easterly prevailing winds typically disperse ash clouds to the south of Puerto Rico (Vogt et al., 1998) and reduce the direct influence of the Soufrière Hill volcano on the island. Nevertheless, constituent throughfall fluxes and enrichment ratios observed in Bisley throughfall are linked to the post 1995 eruptions of Soufrière Hills volcano. In general, the volcanic activity tended to have a larger impact on throughfall than rainfall fluxes which reflects the importance of dry deposition during these periods (Table 3). Over the entire 15-year period, volcanic activity may have contributed 3–5% of the PO_4–P, SO_4–S and cations in throughfall and over 9% of the throughfall TDN and DOC. The mechanisms responsible for the increase in throughfall DOC during eruptive weeks is unclear but maybe related to canopy level interactions of TDN, PO_4–P and DOC.

Over the entire 15 year period, there were small, but statistically significant decreases in weekly rainfall, throughfall, rainfall pH, and in seven out of 12 rainfall flux nutrients. There were no significant trends in throughfall pH and only in two of the throughfall nutrient fluxes PO_4–P, with a tendency to increase and SiO_2 with a tendency to decrease.

Although the species composition and structure of the forest is known to have changed dramatically after Hurricane Hugo (Scatena et al., 1996), these changes were not strongly reflected in changes in weekly throughfall chemistry or fluxes. This lack of relationships with the successional status of the forest, and the similarity between annual average throughfall fluxes in Bisley and other tropical sites (Fig. 7) suggests that biological processes that occur within the canopy and phyllosphere are more important than canopy species composition in influencing throughfall nutrient fluxes in these diverse forests. Furthermore, over this 15-year period of named tropical storms, droughts and successional change, the throughfall nutrient fluxes and patterns were relatively stable and resilient. These observations indicate that the physical and biological processes associated with water passing through the canopy buffer the forest's internal nutrient cycles from external variations in rainfall inputs.

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References

Allen, A.G., Baxter, P.J., Ottley, C.J., 2000. Gas emissions from Soufrière Hills, Montserrat, West Indies: characterization and health hazard assessment. Bulletin of Volcanology 62, 8–19.

Asbury, C.E., McDowell, W.H., Trinidad-Pizarro, R., Berrios, S., 1994. Solute deposition from cloud-water to the canopy of a Puerto-Rican montane forest. Atmospheric Environment 28 (10), 1773–1780.

Beard, K.H., Vogt, K.A., Vogt, D.J., Scatena, F.N., Covich, A.P., Ragnhildur, S., Siccama, T.G., Crowl, T.A., 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. Ecological Monographs 75 (3), 345–361.

Brouwer, L.C., 1996. Nutrient Cycling in Pristine and Logged Tropical Rain Forest, A Study in Guyana. University of Utrecht, pp. 224.

Bruijnzeel, L.A., 1989. Nutrient content of bulk precipitation in south-central Java, Indonesia. Journal of Tropical Ecology 5, 187–202.

Burghouts, T.B.A., 1993. Spatial Heterogeneity of Nutrient Cycling in Bornean Rainforest, Vrije University, pp. 47–79.

Burghouts, T.B.A., Van Stralen, N.M., Bruijnzeel, L.A., 1998. Spatial heterogeneity of element and litter turnover in a Bornean rainforest. Journal of Tropical Ecology 14, 477–506.

Cavelier, J., Jaramillo, M., Solis, D., de Leon, D., 1997. Water balance and nutrient inputs in bulk precipitation in tropical montane cloud forest in Panama. Journal of Hydrology 193 (1–4), 83–96.

Chestnut, T.J., Zarin, D.J., McDowell, W.H., Keller, M., 1999. A nitrogen budget for late-successional hillslope tabonuco forest, Puerto Rico. Biogeochemistry 46 (1–3), 85–108.

Clements, R.G., Colon, J.A., 1975. The rainfall interception process and mineral cycling in a montane rainforest in eastern Puerto Rico. In: Howell, F., Gentry, J., Smith, M. (Eds.), Mineral Cycling in Southeastern Ecosystems. US Energy Research and development Administration, Washington, DC, pp. 812–823.

Covich, A.P., Crowl, T.A., Scatena, F.N., 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. Freshwater Biology 48, 1199–1206.

Diaz, H.F., 1996. Precipitation monitoring for climate change detection. Meteorology and Atmospheric Physics 60, 179–190.

Edwards, P.J., 1982. Studies of mineral cycling in a montane rain forest in New Guinea V. Rates of cycling in throughfall and litter fall. Journal of Ecology 70, 807–827.

Eklund, T.J., McDowell, W.H., Pringle, C.M., 1997. Seasonal variation of tropical precipitation chemistry: La Selva, Costa Rica. Atmospheric Environment 31 (23), 3903–3910.

Hölscher, D., Köhler, L., Leuschner, C., Kappelle, M., 2003. Nutrient fluxes in stemflow and throughfall in three successional stages of an upper montane rain forest in Costa Rica. Journal of Tropical Ecology 19, 557–565.

Holwerda, F., Scatena, F.N., Bruijnzeel, L.A., 2006. Throughfall in a Puerto Rican lower montane rain forest: A comparison of sampling strategies. Journal of Hydrology 327, 592–602.

Larsen, M.C., 2000. Analysis of 20th century rainfall and streamflow to characterize drought and water resources in Puerto Rico. Physical Geography 21 (6), 494–521.

Liu, W.Y., Fox, J.E.D., Xu, Z.F., 2003. Nutrient budget of a montane evergreen broad-leaved forest at Ailao Mountain National Nature Reserve, Yunnan, southwest China. Hydrological Processes 17 (6), 1119–1134.

Loescher, H.W., Powers, J.S., Oberbauer, S.F., 2002. Spatial variation of throughfall volume in an old-growth tropical wet forest, Costa Rica. Journal of Tropical Ecology 18, 397–407.

McDonald, M.A., Healey, J.R., 2000. Nutrient cycling in secondary forests in the Blue Mountains of Jamaica. Forest Ecology and Management 139 (1-3), 257–278.

McDowell, W.H., 1998. Internal nutrient fluxes in a Puerto Rican rain forest. Journal of Tropical Ecology 14, 521–536.

McDowell, W.H., Asbury, C.E., 1994. Export of carbon, nitrogen, and major ions from three tropical Montane watersheds. Limnology and Oceanography 39 (1), 111–125.

McDowell, W.H., Cole, J.J., Driscoll, C.T., 1987. Simplified version of the ampoule-persulfate method for determination of dissolved organic-carbon. Canadian Journal of Fisheries and Aquatic Sciences 44 (1), 214–218.

McDowell, W.H., Gines-Sánchez, C., Asbury, C.E., Ramos Perez, C.R., 1990. Influence of sea salt aerosols and long range transport on precipitation chemistry at El Verde, Puerto Rico. Atmospheric Environment 24 (A), 2813—2821.

Merriam, J., McDowell, W.H., Currie, W.S., 1996. A high-temperature catalytic oxidation technique for determining total dissolved nitrogen. Soil Science Society of America Journal 60 (4), 1050—1055.

NADP,1984. Instruction manual. NAPD/NTP site selection and installation. National Atmospheric Deposition Program, Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, Colorado, USA.

Nepstad, D.C., Moutinho, P., Dias, M.B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D., Guerreiros, J.B., Lefebvre, P., Sternberg, L., Moreira, M., Barros, L., Ishida, F.Y., Tohlver, I., Belk, E., Kalif, K., Schwalbe, K., 2002. The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. Journal of Geophysical Research-Atmospheres 107 (D20), 8085.

Odum, H.T., Pigeon, R.F. (Eds.), 1970. A Tropical Rain Forest. US Atomic Energy Commission, Washington, DC.

Ostertag, R., Scatena, F.N., Silver, W.L., 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. Ecosystems 6 (3), 261—273.

Proctor, J., 2005. Rainforest mineral nutrition: the 'black box' and a glimpse inside it. In: Bonell, M., Bruijnzeel, L.A. (Eds.), Forests Water and People in the Humid Tropics. Cambridge University Press, pp. 422—446.

Prospero, J.M., Nees, R.T., 1986. Impact of the North African drought and El Niño on mineral dust in the Barbados trade winds. Nature 320, 735—738.

Richardson, B.A., Richardson, M.J., Scatena, F.N., McDowell, W.H., 2000. Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. Journal of Tropical Ecology 16 (2), 167—188.

Robertson, R.E.A., Aspinall, W.P., Herd, R.A., Norton, G.E., Sparks, R.S.J., Young, S.R., 2000. The 1995—1998 eruption of the Soufrière Hills volcano, Montserrat, WI. Philosophical Transaction of the Royal Society of London A 358, 1619—1637.

SAS Version 9, SAS Institute 2003, Cary, North Carolina, USA.

Scatena, F.N., 1989. An Introduction to the Physiography and History of the Bisley Experimental Watersheds in the Luquillo Mountains of Puerto Rico. New Orleans, Louisiana, USDA Forest Service, Southern Forest Experiment Station.

Scatena, F.N., 1990. Watershed scale rainfall interception on two forested watersheds in the Luquillo Mountains of Puerto Rico. Journal of Hydrology 113, 89—102.

Scatena, F.N., Larsen, M.C., 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23 (4), 317—323.

Scatena, F.N., Moya, S., Estrada, C., Chinea, J.D., 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley experimental watersheds, Luquillo experimental forest, Puerto Rico. Biotropica 28 (4), 424—440.

Scatena, F.N., Silver, W., Siccama, T., Johnson, A., Sánchez, M.J., 1993. Biomass and nutrient content of the Bisley watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricana Hugo, 1989. Biotropica 25 (1), 15—27.

Schaefer, D.A., McDowell, W.H., Scatena, F.N., Asbury, C.E., 2000. Effects of hurricane disturbance on stream water concentrations and fluxes in eight watersheds of the Luquillo Experimental Forest, Puerto Rico. Journal of Tropical Ecology 16, 189—207.

Schellekens, J., Bruijnzeel, L.A., Scatena, F.N., Bink, N.J., Holwerda, F., 2000. Evaporation from a tropical rain forest, Luquillo Experimental Forest, eastern Puerto Rico. Water Resources Research 36 (8), 2183—2196.

Schellekens, J., Scatena, F.N., Bruijnzeel, L.A., Wickel, A.J., 1999. Modeling rainfall interception by a lowland tropical rain forest in northeastern Puerto Rico. Journal of Hydrology 225, 168—184.

Solorzano, L., Sharp, J.H., 1980. Determination of total dissolved nitrogen in natural waters. Limnology and Oceanography 25 (4), 751—754.

Tobón, C., Sevink, J., Verstraten, J.M., 2004. Solute fluxes in throughfall and stemflow in four forest ecosystems in northwest Amazonia. Biogeochemistry 70, 1—25.

Veneklaas, E.J., 1990. Nutrient fluxes in bulk precipitation and throughfall in two Montane tropical rain forests, Colombia. Journal of Ecology 78 (4), 974—992.

Vogt, P.J., Ellis, J.S., Voight, B., Lefevre, R.J., 1998. ARAC Simulations of the Ash Plume from the December 1997 Eruption of Soufrière Hills Volcano, Montserrat. Eighth Conference on Aviation, Range and Aerospace Meteorology, 79th AMS Annual Meeting. Dallas, Texas, 1999.

Waterloo, M.J., Bruijnzeel, L.A., Vugts, H.F., Rawaqa, T.T., 1999. Evaporation from Pinus caribaea plantations on former grassland soils under maritime tropical conditions. Water Resources Research 35 (7), 2133—2144.

Wu, W., Hall, C.A.S., Scatena, F., Quackenbush, L., 2006. Spatial modeling of evapotranspiration in the Luquillo Experimental Forest of Puerto Rico using remotely-sensed data. Journal of Hydrology 38 (3-4), 733—752.