March 2000

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Douglas A. Schaefer
University of Puerto Rico

William H. McDowell
University of New Hampshire

Frederick Scatena
University of Pennsylvania, fns@sas.upenn.edu

Clyde E. Asbury

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Abstract
Stream water chemistry responds substantially to watershed disturbances, but hurricane effects have not been extensively investigated in tropical regions. This study presents a long-term (2.5-11 y) weekly record of stream water chemistry on eight forested watersheds (catchment basins) in the Luquillo Mountains of Puerto Rico. This includes a period before and at least 2 y after the disturbance caused by the 1989 Hurricane Hugo. Nitrate, potassium and ammonium concentrations increased after the hurricane and remained elevated for up to 2 y. Sulphate, chloride, sodium, magnesium and calcium showed smaller relative significant changes. Average stream water exports of potassium, nitrate and ammonium increased by 13.1, 3.6 and 0.54 kg ha $^{-1}$ y $^{-1}$ in the first post-hurricane year across all watersheds. These represent increases of 119, 182 and 102 of record. The increased stream outputs of potassium and nitrogen in the first 2 y post-hurricane are equivalent to 3of the hurricane-derived plant litter. Effects of hurricanes on tropical stream water potassium and nitrogen can be greater than those caused by canopy gaps or limited forest cutting, but less than those following large-scale deforestation or fire.

Comments
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NOTE: At the time of publication, author Fred Scatena was affiliated with the USDA Forest Service. Currently (June 2006), he is a faculty member in the Department of Earth and Environmental Science at the University of Pennsylvania.

Journal of Tropical Ecology (2000) 16:189–207. With 4 figures

Effects of hurricane disturbance on stream water concentrations and fluxes in eight tropical forest watersheds of the Luquillo Experimental Forest, Puerto Rico

DOUGLAS. A. SCHAEFER*[1], WILLIAM H. McDOWELL†, FREDRICK N. SCATENA‡ *and* CLYDE E. ASBURY[2]

**Institute for Tropical Ecosystem Studies, Box 363682, University of Puerto Rico, San Juan, PR 00936*
†Department of Natural Resources, University of New Hampshire, Durham, NH 03824, USA
‡International Institute of Tropical Forestry, USDA Forest Service, Rio Piedras, PR 00928

(Accepted 30th September 1999)

ABSTRACT. Stream water chemistry responds substantially to watershed disturbances, but hurricane effects have not been extensively investigated in tropical regions. This study presents a long-term (2.5–11 y) weekly record of stream water chemistry on eight forested watersheds (catchment basins) in the Luquillo Mountains of Puerto Rico. This includes a period before and at least 2 y after the disturbance caused by the 1989 Hurricane Hugo. Nitrate, potassium and ammonium concentrations increased after the hurricane and remained elevated for up to 2 y. Sulphate, chloride, sodium, magnesium and calcium showed smaller relative significant changes. Average stream water exports of potassium, nitrate and ammonium increased by 13.1, 3.6 and 0.54 kg ha^{-1} y^{-1} in the first post-hurricane year across all watersheds. These represent increases of 119, 182 and 102% respectively, compared to the other years of record. The increased stream outputs of potassium and nitrogen in the first 2 y post-hurricane are equivalent to 3% (potassium) and 1% (nitrogen) of the hurricane-derived plant litter. Effects of hurricanes on tropical stream water potassium and nitrogen can be greater than those caused by canopy gaps or limited forest cutting, but less than those following large-scale deforestation or fire.

KEY WORDS: biogeochemistry, disturbance, long-term records, nutrient export, stream chemistry, tropics

[1] To whom correspondence should be addressed.
[2] Deceased.

INTRODUCTION

Streamwater chemistry integrates a watershed's (catchment basin's) biogeochemical responses to disturbance. Studies in both temperate (e.g. Likens *et al.* 1970, Vitousek *et al.* 1979) and tropical (Anderson & Spencer 1991, Bruijnzeel 1990) regions have clearly demonstrated that disturbances that substantially reduce plant nutrient uptake (over a wide range of soil types) lead to increases in the export of nitrogen and other nutrients in streamwater. Given the variety of vegetation, soil types and biotic disturbances that occurs in the tropics, nutrient exports there have not been thoroughly described.

The effects of disturbances such as canopy gaps and logging in the tropics have been linked to spatial scale and soil type. Canopy gaps smaller than 0.02 ha had little effect on soil water chemistry in Costa Rica (inceptisols) and Venezuela (inceptisols and ultisols; Parker 1985, Uhl *et al.* 1988, Vitousek & Denslow 1986). Cut forest clearings of 0.05 ha or larger led to nitrogen, calcium and magnesium concentration increases of two- to fourfold in soil water for up to 2 y in Costa Rica (inceptisols), but potassium, ammonium and phosphate did not respond to disturbance (Parker 1985). Unlike canopy gaps, logging removes much plant material from the site (Anderson & Spencer 1991), especially wood that may act subsequently to reduce soil nutrient availability by microbial immobilization (Zimmerman *et al.* 1995). A study of selective logging on 13 ha in Malaysia (ultisols) found a two- to threefold increase in nitrate concentrations in streamwater that persisted for 1 y (Zulkifli Yusop 1989 in Bruijnzeel 1990). The longer (5-y) duration of elevated potassium concentrations in streamwater may have been related to enhanced mineral weathering in the soils (L.A. Bruijnzeel, *pers. comm.*). Calcium and magnesium concentrations did not respond to disturbance in that study. Brouwer (1996) compared streamwater concentrations in baseflow and stormflow in a Guyana forest before and after logging (spodosols). This was a highly managed cut where gaps were smaller than 0.05 ha, unlogged buffer strips were left along stream channels and steep slopes were avoided. Potassium concentrations in baseflow increased immediately after logging, and ammonium, nitrate and sodium concentrations increased 1 y later. For these three ions the magnitude of the concentration increases were 150 to 200%. Concentrations of other ions were not significantly altered. In a larger logged gap (0.34 ha) in the same study, soil water concentrations of potassium, calcium, magnesium, sulphate and nitrate all increased, with potassium concentrations decreasing after 34 mo because of renewed vegetation uptake (Brouwer 1996). In a logging project of larger areal extent in Malaysia (spodosols and ultisols), Malmer & Grip (1994) noted that exports of nitrogen, phosphorus and potassium increased for as long as 3 y following the disturbance. Additional studies of logging effects on streamwater chemistry reviewed by Anderson & Spencer (1991) illustrate that the disturbance effect continues until forest becomes re-established.

Depending on extent and severity, fire can have even larger effects by volatilizing biomass N, immediately increasing soil available pools of other nutrients and removing wood and so its microbial immobilization potential. Fires in tropical forests have also led to streamwater concentration increases as reported by Nakane *et al.* (1983) and Malmer & Grip (1994). Forest plots of 0.5 ha in Venezuela were experimentally burned by Uhl *et al.* (1982) and Uhl & Jordan (1984). In those studies, soil water concentrations of magnesium, nitrate, calcium and potassium increased for 1 to 2 y.

In addition to dissolved ions, increased erosional losses accompany all these types of forest disturbance (Anderson & Spencer 1991). Effects of hurricanes and floods (these are in essence high stream flows with and without forest canopy damage, respectively) in this forest will be compared in a separate manuscript.

Hurricanes transfer live foliage and wood to the forest floor, and permit rapid regeneration by those trees not killed outright. Although hurricanes are important large-scale disturbances in many tropical areas, their effects on streamwater chemistry have rarely been reported. Waterloo (1994) measured stream chemistry in a pine plantation in Fiji before and after the passage of a tropical cyclone. In that disturbance, 10% of the boles were damaged and 15 months' equivalent of pine needle litter fell. Compared to pre-disturbance conditions, streamwater concentrations of sodium, potassium, magnesium, calcium and chloride increased significantly, sulphate decreased and ammonium and nitrate were unchanged in that study.

As both the spatial scale of disturbances and the disposition of biomass have been shown to affect forest biogeochemical responses, it was hypothesized in this study that the large-scale forest damage by hurricanes would change streamwater chemistry more than does canopy gap formation, but less than other large-scale forest disturbances that remove biomass, fire and logging. To test that hypothesis, long-term (1983–1994) weekly streamwater chemistry data were analysed from eight watersheds in northeastern Puerto Rico that were substantially damaged by the September 1989 Hurricane Hugo.

METHODS

Study sites

The watersheds (catchment basins) studied are all located in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18°15′N, 65°50′W, Figure 1). Four of the watersheds (Quebrada Sonadora (QS), Quebrada Toronja (QT), Quebrada Prieta A (QPA) and Quebrada Prieta B (QPB)) are within the Espiritu Santo drainage basin and the El Verde Research area of the LEF. The other four watersheds (Puente Roto Mameyes (PRM) and Bisley

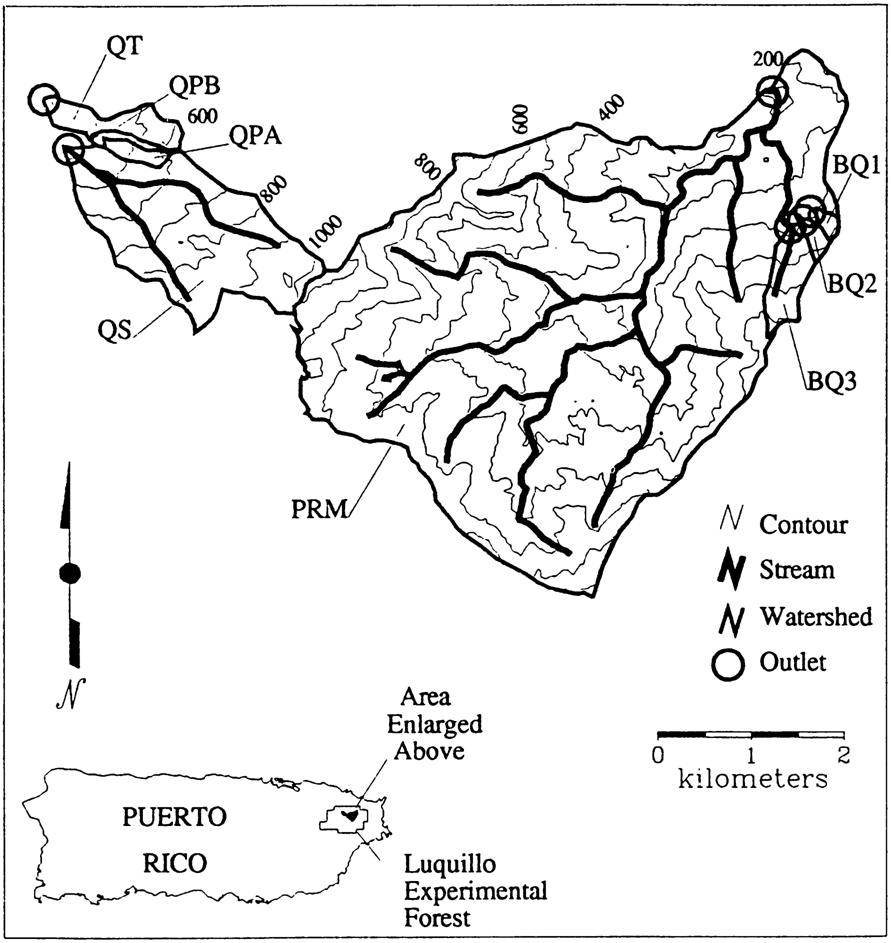

Figure 1. Map of the El Verde (QS, QT, QPA and QPB) and Bisley (PRM, BQ1, BQ2, BQ3) watersheds in the Luquillo Experimental Forest, northeastern Puerto Rico, showing 100-m elevation contours and stream channels in each watershed. Watershed abbreviations are given in Table 1.

Quebradas 1, 2 and 3 (BQ1, BQ2 and BQ3)) are within the Rio Mameyes drainage basin and the Bisley Research area of the LEF. Annual average temperatures at 400 m (streamwater samples from all eight watersheds are collected near this elevation) are *c.* 22 °C with little seasonality. Watershed areas range from 6 to 1752 ha (Table 1) and based on the precipitation vs. elevation regression derived for the Luquillo Mountains in Garcia *et al.* (1996), the catchment mean annual rainfall ranges from 3400 to 4240 mm. These perennial streams have steep-gradient, boulder-lined channels that are fed by a dense network of variable source areas, intermittent channels and leaf-filled swales (Ahmad *et al.* 1993, Scatena & Lugo 1995).

The study watersheds are all underlain by Cretaceous volcanoclastic andesitic sandstones (Scatena 1989), deposited on the sea floor and subsequently

Table 1. Elevation range, area and forest types of the eight Luquillo Experimental Forest, Puerto Rico watersheds compared in this study.

		Elevation range (m)	Area (ha)	Forest types
El Verde watersheds				
QS	Quebrada Sonadora	350–1050	265	Tabonuco, Colorado, Palm and Elfin
QT	Quebrada Toronja	267–635	51	Tabonuco and Palm
QPA	Quebrada Prieta A	395–635	17	Tabonuco and Palm
QPB	Quebrada Prieta B	410–635	10	Tabonuco and Palm
Bisley watersheds				
PRM	Puente Roto Mameyes	100–1050	1752	Tabonuco, Colorado, Palm and Elfin
BQ1	Bisley Quebrada 1	260–415	6.7	Tabonuco
BQ2	Bisley Quebrada 2	267–465	6.34	Tabonuco
BQ3	Bisley Quebrada 3	265–665	35	Tabonuco and Palm

uplifted. Soils are dominated by the Zarzal-Cristal complex, clayey, isohyperthermic, epiaquic pedons that classified as Aquic Haplohumults and Typic Kandiudox on the ridges and slopes, and Typic Tropaquepts and Fluvaquents in valley bottoms (Soil Survey Staff 1995). Compared to soils from over 30 other tropical montane forests, concentrations of exchangeable Ca, Mg and K are intermediate at Bisley and El Verde (Silver *et al.* 1994). Exchangeable phosphorus is slightly higher, and total soil nitrogen is slightly lower than in those other tropical montane forests (Silver *et al.* 1994).

The history of hydrologic studies in the LEF includes continuous stream flow monitoring by the U.S. Geological Survey since 1969. Rainfall at El Verde has been monitored continuously since 1975 and at Bisley since 1987. Intermittent rainfall records at other stations in the LEF are available from 1896, with several stations reporting annual totals since the 1920s (Brown *et al.* 1983). Bimonthly streamwater chemistry for several LEF watersheds has been reported since 1969 (U.S. Geological Survey, 1969–1994). Regular chemical sampling of a high-elevation (750–1000 m) stream in the LEF in 1981 and 1982 was reported by Frangi & Lugo (1985).

Vegetation types of the LEF include Tabonuco, Colorado and Elfin forests at progressively higher elevations, with Sierra Palm forests concentrated along streams (Brown *et al.* 1983). The study watersheds are completely covered with primary or mature secondary forests. During the first half of this century parts of these watersheds were used for shade coffee, timber harvesting, charcoal production and subsistence agriculture. Since the mid-1940s, the forest has been allowed to redevelop naturally without human intervention (Garcia-Montiel & Scatena 1994).

Hurricanes, landslides and treefall gaps are common disturbances in these watersheds (Waide & Lugo 1992). On 18–19 September 1989 Hurricane Hugo crossed northeastern Puerto Rico and affected these study watersheds with category-3 hurricane force (Scatena & Larsen 1991). Hurricanes of this magnitude or greater are estimated to pass over the LEF once every 50 to 60 y, causing landslides, widespread defoliation and the uprooting of trees

(Weaver 1986). Hurricane Hugo caused greater damage to the Bisley watersheds than the more sheltered El Verde watersheds (Boose *et al.* 1994). In Bisley, standing aboveground biomass and nutrient contents were reduced by *c.* 50% by the hurricane (Scatena *et al.* 1993). By 2 y after the hurricane, the re-establishment of pre-disturbance values of throughfall and litterfall indicated a recovery of those forest canopy characteristics (Scatena *et al.* 1996). Soil nitrate and exchangeable potassium pools also increased in Bisley following the hurricane and returned to pre-hurricane values within 9 mo (Silver *et al.* 1996). Additional information on the ecology of the study area and on effects of Hurricane Hugo can be found elsewhere (Brown *et al.* 1983, Lodge & McDowell 1991, Odum & Pigeon 1970, Reagan & Waide 1996, Scatena *et al.* 1996, Walker *et al.* 1991).

Sample collection and analysis

Weekly water sampling began on QS and QT in 1983 (McDowell & Asbury 1994), BQ1, BQ2 and BQ3 in 1988, and PRM, QPA and QPB in 1989, thus this study includes a period prior to Hurricane Hugo and 5 y after (Table 2). Streamwater sampling at QT was discontinued in November 1987 and reinitiated immediately after the September 1989 hurricane.

The streamwater samples were filtered (pre-combusted Whatman glass-fibre filters) within 4 h of collection. Ammonium and nitrate samples were refrigerated prior to analysis, and ammonium samples were also preserved by acidification. Ammonium was analysed colorimetrically by phenol hypochlorite flow-injection analysis (Lachat). Chloride and nitrate samples were analysed

Table 2. Starting and ending dates of the sampling and analysis (period in months) for the streamwater chemistry data presented in this study for eight Luquillo Experimental Forest, Puerto Rico watersheds compared in this study.

	Watersheds							
Ions	QS	QT	QPA	QPB	PRM	BQ1	BQ2	BQ3
Sulphate	6/83	6/83	6/89	6/89	5/89	10/88	10/88	10/88
(65–137 mo)	11/94	11/94	11/94	11/94	11/94	11/94	11/94	11/94
Chloride	6/83	6/83	10/89	10/89	10/89	10/88	10/88	10/88
(61–137 mo)	11/94	11/94	11/94	11/94	11/94	11/94	11/94	11/94
Nitrate	6/83	6/83	6/89	6/89	5/89	10/88	10/88	10/88
(61–133 mo)	7/94	7/94	7/94	7/94	7/94	7/94	7/94	7/94
Ammonium	6/83	6/83	6/89	6/89	6/89	10/88	10/88	10/88
(36–108 mo)	6/92	6/92	6/92	6/92	6/92	6/92	6/92	6/92
Sodium	6/83	6/83	6/89	6/89	5/89	10/88	10/88	10/88
(35–107 mo)	5/92	5/92	5/92	5/92	5/92	5/92	5/92	5/92
Potassium	6/83	6/83	6/89	6/89	5/89	10/88	10/88	10/88
(34–106 mo)	4/92	4/92	4/92	4/92	4/92	4/92	4/92	4/92
Magnesium	6/83	6/83	6/89	6/89	5/89	10/88	10/88	10/88
(34–106 mo)	4/92	4/92	4/92	4/92	4/92	4/92	4/92	4/92
Calcium	6/83	6/83	6/896/89	5/89	10/88	10/88	10/88	10/88
(29–100 mo)	10/91	10/91	10/91	10/91	10/91	10/91	10/91	10/91

colorimetrically until September 1989 (Lachat), and then by high-pressure liquid chromatography (Waters), following an intercalibration period. Cations were analysed by atomic absorption spectroscopy (Perkin Elmer). For quality assurance purposes the analytical laboratory participates in U.S. Environmental Protection Agency and U.S. Geological Survey inter-laboratory comparison programmes and splits rain water samples with the National Atmospheric Deposition Program Central Analytical Laboratory. Sampling periods used in this study for each site and ion are given in Table 2.

Time-series plots of rain inputs and streamwater concentrations are presented as 9-wk moving averages. This approach minimized rapid fluctuations caused by concentration-discharge interactions, made longer-term patterns more apparent, and permitted data from several streams and ions to be presented together. Stream concentration data are presented in two groups, the El Verde streams (QS, QT, QPA, QPB), and the Bisley streams (PRM, BQ1, BQ2, BQ3). Moving averages were not plotted where there were gaps in sampling or in particular chemical analyses.

Annual watershed chemical outputs for the six streams where daily streamflow measures were available (i.e. all except QPA and QPB) were determined in the following manner. Linear regressions were developed between the logarithm of sampling-day streamflow and the chemical concentrations for each stream, ion and year. Where these regressions were statistically significant ($P < 0.05$), they were used to estimate chemical concentrations on the days not sampled, based on streamflows for those days. The resulting daily concentrations were multiplied by daily streamflow, summed over the entire year, and expressed as kg ha^{-1} y^{-1}. Where these regressions were not significant, average concentrations were multiplied by daily streamflows for the appropriate year and stream. The annual chemical fluxes so calculated for QS for calendar years 1984 through 1986 differed by 10% or less from those calculated by McDowell & Asbury (1994), who used instantaneous discharge instead of daily discharge for the same watershed and period. For our flux calculations, years were defined by the date of Hurricane Hugo; for example 1990 began on 19 September 1989 and ended on 18 September 1990.

All streamflow and stream chemistry data collected for this study are available on the Luquillo LTER World-wide Web home page (http://SUNCEER.UPR.CLU.EDU/) or by mail from the senior author.

RESULTS

Average streamwater concentrations before and after hurricane disturbance

Streamwater concentrations were previously reported for QS and QT (McDowell & Asbury 1994) and are compared in Table 3 to the six additional LEF streams in this study. That table compares streamwater concentrations averaged over the first year after hurricane disturbance (September

Table 3. Average ionic concentrations in Luquillo Experimental Forest, Puerto Rico streams (ug l^{-1} for nitrate-N and ammonium-N; mg l^{-1} for all others) for all years except the first post-hurricane year (first row), and during the first year after (second row) Hurricane Hugo (19 September 1989 to 18 September 1990), followed by the percentage change in concentrations (third row). Each ion is followed by the average change across streams in parentheses. Not all streams were sampled for chloride before 1989.

	El Verde streams				Bisley streams			
Ion	QS	QT	QPA	QPB	PRM	BQ1	BQ2	BQ3
Nitrate-N	86	56	53	46	73	91	122	104
(+207%)	226	170	232	142	238	191	370	312
	163	204	338	211	226	110	203	200
Potassium	0.26	0.31	0.4	0.4	0.77	1.01	1.02	0.81
(+77%)	0.70	0.64	0.7	0.6	1.09	1.37	1.40	1.33
	169	106	83	78	42	36	37	64
Ammonium-N	26	24	20	22	28	41	25	20
(+62%)	23	25	27	29	44	92	57	50
	−12	4	35	9	57	124	128	150
Calcium	1.84	5.19	3.5	3.0	9.50	4.42	5.25	4.11
(+6%)	2.19	5.37	4.5	3.5	7.51	4.34	5.78	3.80
	19	3	29	17	−21	−2	10	−8
Magnesium	1.12	3.56	2.9	2.7	4.07	2.70	2.73	2.98
(+0.4%)	1.38	3.59	3.6	3.1	1.88	2.67	2.76	2.81
	23	1	24	15	−54	−1	1	6
Sodium	3.97	6.58	5.7	5.5	6.80	6.94	6.35	6.49
(+5%)	4.90	6.43	6.3	5.8	6.15	7.15	6.66	6.77
	23	−2	11	5	−10	3	5	4
Chloride	7.33	8.58			8.57	8.51	8.18	8.74
(+5%)	8.45	8.50	9.3	9.2	10.02	8.26	8.78	10.00
	15	−1			17	−3	7	14
Sulphate	2.39	2.30	4.3	3.6	4.14	3.65	3.42	2.35
(−20%)	2.06	2.03	2.0	1.9	3.08	3.48	3.16	2.41
	−12	−12	−53	−47	−26	−5	−8	3

1989–September 1990) with concentrations averaged over all other years of record.

Concentration differences among streams outside the first post-hurricane year are considered first. Nitrate concentrations were lower in the El Verde streams than in the Bisley streams (Table 3). Watersheds QS and QT had the lowest potassium concentrations. Watershed QPA had lower ammonium concentrations than QS or QT. Calcium concentrations were higher for PRM than those previously reported for QT, and the other five watersheds had higher concentrations than did QS (Table 3). Magnesium was lower at QS than the other watersheds, and sodium concentrations were higher at Bisley than El Verde watersheds. Chloride and sulphate concentrations were each similar across watersheds.

After the hurricane, potassium showed larger absolute increases at the Bisley watersheds, and larger percentage increases at the El Verde watersheds. Nitrate concentrations increased by 110 to 338% across all watersheds (Table 3). Ammonium increased by 57 to 154% at the Bisley watersheds during the first post-hurricane year (1990), but at QS and QT, peak concentrations occurred 1 y later (1991). Calcium and magnesium concentrations showed either relatively a small response, or a response delayed until 1991. Sodium increased during the first post-hurricane year only at QS, and sulphate and chloride concentrations decreased or were unchanged (Table 3).

Streamwater concentrations through time

Time-series plots of 9-wk moving-average streamwater concentrations before and after hurricane disturbance offer additional contrasts among watersheds and ions (Figures 2 and 3).

For both El Verde and Bisley, the stream water ionic concentrations most affected by disturbance included potassium (Figures 2a and 3a), nitrate (Figures 2b and 3b) and ammonium (Figures 2e and 3e). The post-hurricane nitrate peak was of unprecedented magnitude and duration with respect to our long-term sampling, and was observed in all eight watersheds. Nitrate concentrations returned to their pre-hurricane values by June 1990 in Bisley BQ1, BQ2 and BQ3 (the most disturbed watersheds), but not until March 1991 in the other five watersheds (Figures 2b and 3b).

The post-hurricane potassium concentration peak (Figures 2a and 3a) was of similar relative magnitude to the nitrate peak (i.e. both approximately tripled their pre-hurricane concentrations). For all watersheds except QS, potassium concentrations declined to pre-hurricane levels by October 1990. The post-hurricane potassium peak was higher in all Bisley watersheds than in El Verde watersheds.

Hurricane disturbance appeared to have only a minor effect on magnesium (Figures 2c and 3c) and calcium (Figures 2d and 3d) concentrations. For these ions, the annual periodicity in concentrations result from inverse concentration/discharge relationships, and seasonality in streamflow. This periodicity was essentially unchanged by hurricane disturbance. Sodium, sulphate and chloride concentrations were the least affected by hurricane disturbance, and are not shown in Figures 2 and 3.

Streamwater output fluxes

For the six watersheds where streamwater chemical fluxes were calculated, the year immediately following hurricane disturbance (1990) to all other years of record was compared (Figure 4). Mean fluxes (kg ha^{-1} y^{-1}) across catchments in 1990 increased significantly ($P < 0.05$, t-test) for potassium (24.1 vs. 11.0), nitrate-N (5.6 vs. 2.0) and ammonium-N (1.1 vs. 0.5), but not for chloride (198 vs. 166), sodium (138 vs. 114), calcium (107 vs. 74), magnesium (53 vs. 45) or sulphate (60 vs. 59). The three ions with significant differences are considered in detail; for the other ionic fluxes only average annual values for the entire period of record will be discussed.

Nitrate-N fluxes ranged from 1.0 to 2.3 kg ha^{-1} y^{-1} across watersheds for all except the first post-hurricane year, during which they increased to 2.6 to 8.4

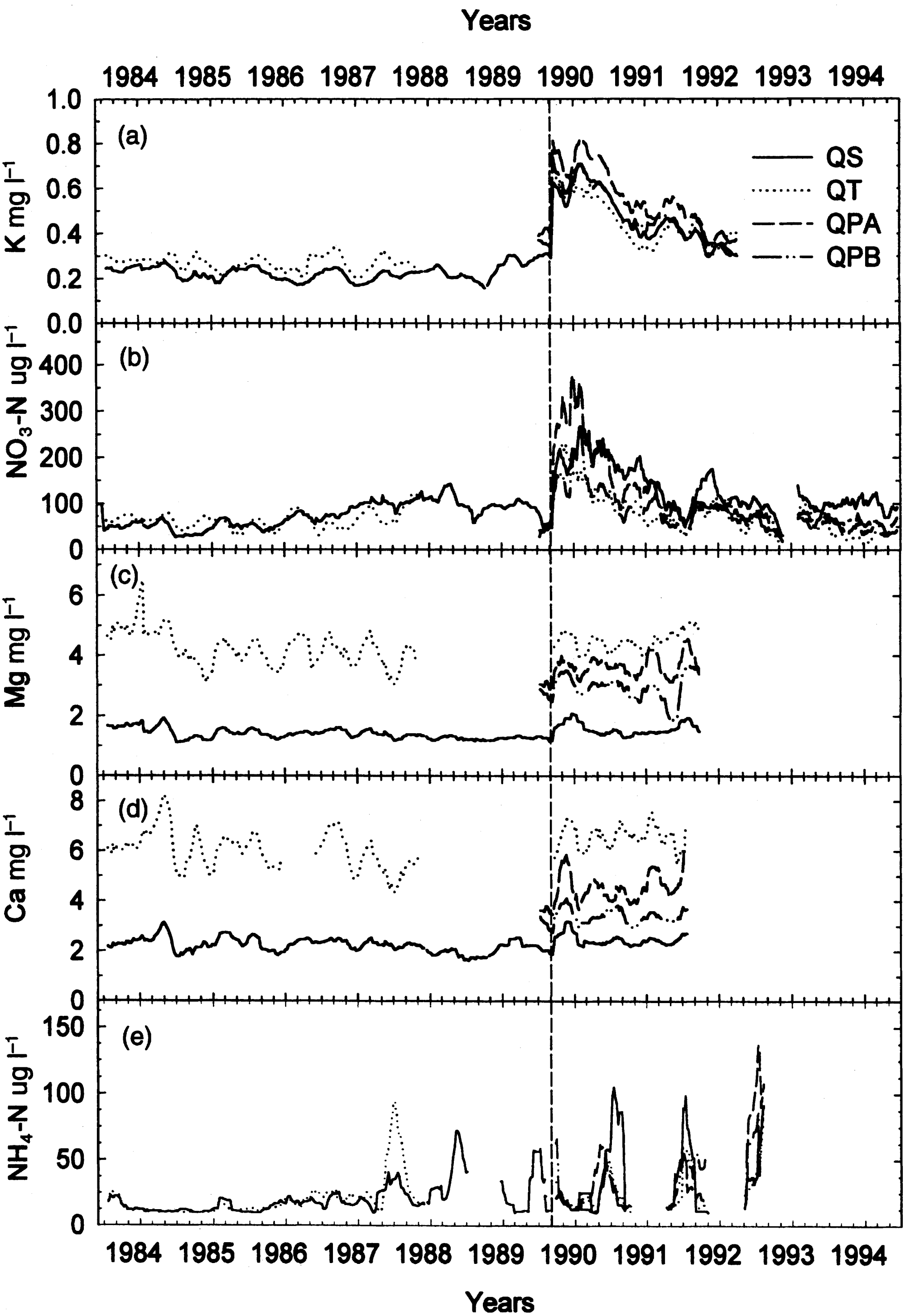

Figure 2. Concentrations in El Verde, Puerto Rico streams before and after Hurricane Hugo, 9-wk moving averages. (a) potassium, (b) nitrate-N, (c) magnesium, (d) calcium and (e) ammonium-N. The vertical lines mark the time of hurricane disturbance.

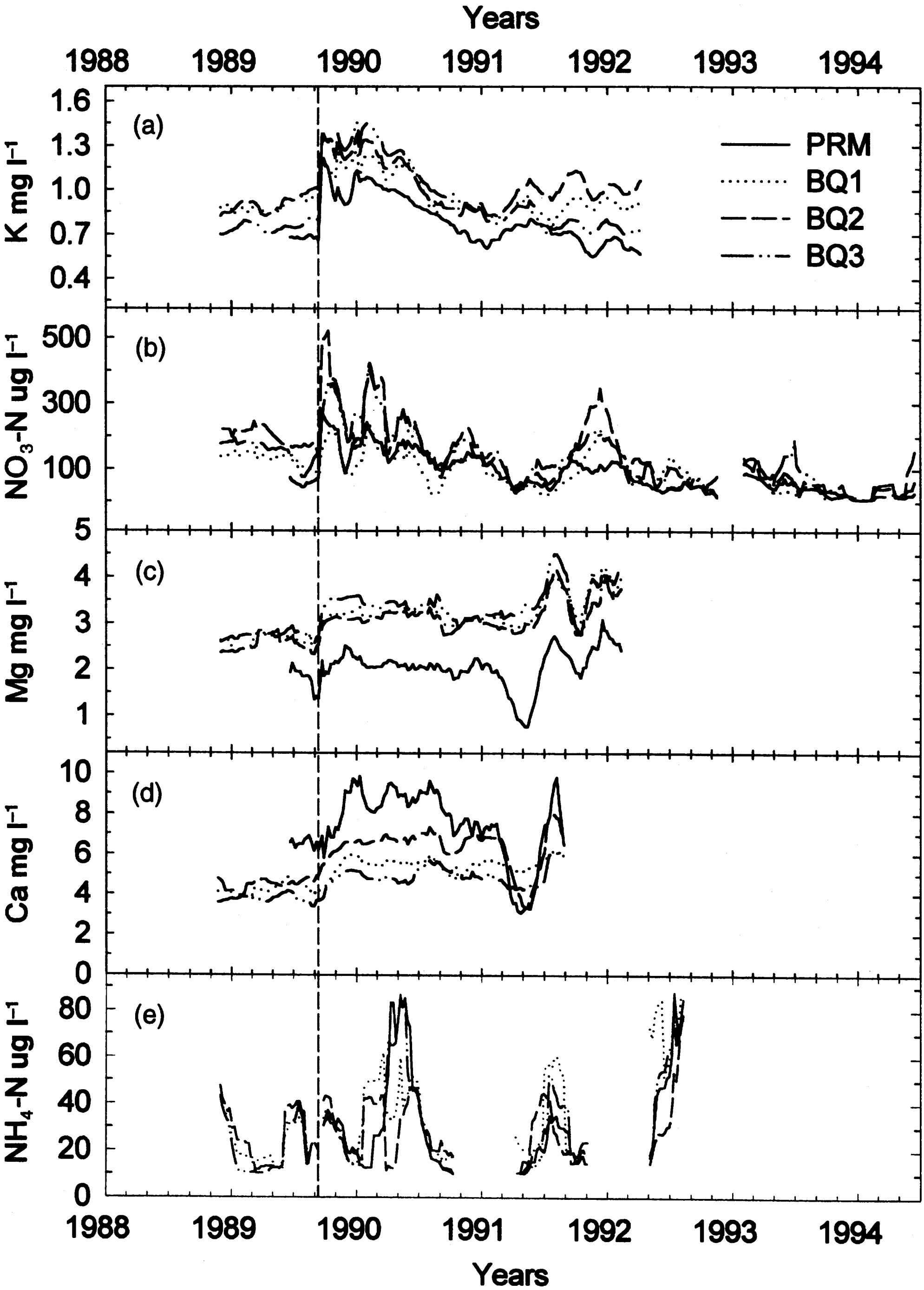

Figure 3. Concentrations in Bisley, Puerto Rico streams before and after Hurricane Hugo, 9-wk moving averages. (a) potassium, (b) nitrate-N, (c) magnesium, (d) calcium and (e) ammonium-N. The vertical lines mark the time of hurricane disturbance.

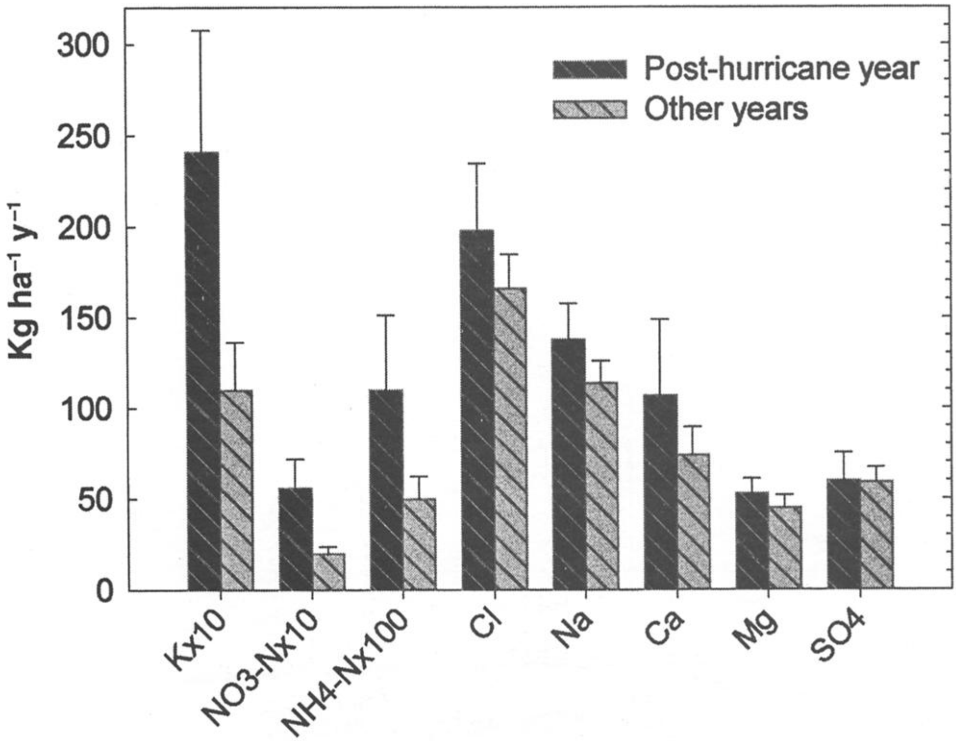

Figure 4. Comparison of stream chemical fluxes in the first year after Hurricane Hugo (1989) in the Luquillo Experimental Forest, Puerto Rico, with to those averaged over all other years of record (see text). Bars show mean values across watersheds ± 95% confidence intervals (n=6).

kg ha^{-1} y^{-1}. Potassium fluxes averaged 24.1 kg ha^{-1} y^{-1} in 1990 and 11.0 kg ha^{-1} y^{-1} in all other years. The Bisley watersheds had larger potassium fluxes than did the El Verde watersheds, both in the first post-hurricane year and in all other years (Table 4). Fluxes of ammonium-N increased in 1990 from the Bisley but not the El Verde watersheds.

Considering the entire record, average annual calcium fluxes were lowest at QS (47 kg ha^{-1} y^{-1}), highest at PRM (199 kg ha^{-1} y^{-1}) with the others ranging from 77–108 kg ha^{-1} y^{-1} (Table 4). Similarly, QS fluxes of magnesium (29 kg ha^{-1} y^{-1}) were lower than at other streams (those ranging from 5– 66 kg ha^{-1} y^{-1}). Sodium fluxes were essentially equal at QS and QT (101 and 99 kg ha^{-1} y^{-1}), and higher at all Bisley streams (ranging from 129–161 kg ha^{-1} y^{-1}). Sulphate and chloride fluxes were higher at PRM (89 kg ha^{-1} y^{-1} and 200 kg ha^{-1} y^{-1}, respectively) than at any other stream.

Annual streamwater fluxes were calculated using concentration vs. log (discharge) regressions for each ion, stream and year. For calcium, magnesium and sodium these models typically had negative slopes because streamwater concentrations decreased at high streamflows. Potassium and nitrate concentrations also were diluted at high streamflows, but this pattern reversed (with

Table 4. Annual stream ionic fluxes (kg ha^{-1} y^{-1}) for the six catchments with stream flow measurements in the Luquillo Experimental Forest of Puerto Rico. Years begin on the previous 19 September, the date of Hurricane Hugo. The final two rows show increases during the first post-hurricane year (1990) compared to all other years, in absolute (Abs.; kg ha^{-1} y^{-1} change) and relative (Rel.; percent change) terms, with values averaged across all catchments presented in italics in the Years columns.

(a) Potassium, nitrate and ammonium, the ionic fluxes most sensitive to hurricane disturbance (average change more than 90%).

	Potassium							Nitrate							Ammonium						
	Years	QS	QT	PRM	BQ1	BQ2	BQ3	Years	QS	QT	PRM	BQ1	BQ2	BQ3	Years	QS	QT	PRM	BQ1	BQ2	BQ3
	1984	5.1	2.6					1984	0.74	0.52					1984	0.26	0.11				
	1985	7.8	5.3					1985	1.38	1.07					1985	0.38	0.24				
	1986	5.2	5.2					1986	1.87	0.70					1986	0.38	0.40				
	1987	5.8	4.9					1987	2.88	1.26					1987	0.60	0.53				
	1988	7.2						1988	3.70						1988	1.38					
	1989	6.2			19.1	20.0	16.1	1989	1.95			3.09	4.32	3.85	1989	0.60			0.49	0.60	0.41
	1990	16.4	9.7	30.3	28.4	31.6	28.4	1990	5.29	2.60	6.61	3.96	8.35	6.69	1990	0.54	0.39	1.22	1.91	1.30	1.07
	1991	6.1	3.2	16.9	20.5	15.9	14.2	1991	2.15	0.57	2.41	2.56	2.11	1.96	1991	0.78	0.33	0.49	1.43	0.45	0.37
	1992	6.4	5.6	17.9	20.5	22.5	15.2	1992	2.70	0.97	2.27	1.97	3.48	2.47	1992	0.52	0.41	0.82	0.51	0.38	0.33
	1993							1993	0.96	2.53	1.48	0.82	1.43	1.31							
	1994							1994	1.33	0.36	0.41	0.23	0.17	0.18							
Abs.	*10.4*	10.2	5.3	13.0	8.4	12.1	13.2	*3.4*	3.3	1.6	5.0	2.2	6.0	2.4	*0.53*	−0.07	0.05	0.56	1.10	0.82	0.70
Rel.	*90*	164	112	75	42	62	87	*191*	169	161	302	128	262	122	*98*	−11	14	86	136	172	191

Table 4. *(cont.)*

(b) Magnesium and calcium, the ionic fluxes with smaller relative increases in the first post-hurricane year.

Magnesium

	Years	QS	QT	PRM	BQ1	BQ2	BQ3
	1984	27	40				
	1985	31	62				
	1986	29	62				
	1987	32	58				
	1988	36					
	1989	25			59	52	55
	1990	32	55	52	55	62	60
	1991	18	35	81	51	50	53
Abs.	*8*	7	12		0	12	6
Rel.	*19*	30	28		1	23	11

Calcium

	Years	QS	QT	PRM	BQ1	BQ2	BQ3
	1984	41	56				
	1985	53	97				
	1986	45	101				
	1987	53	82				
	1988	57					
	1989	43			92	99	77
	1990	51	82	209	90	131	81
	1991	33	48	188	87	96	73
Abs.	*14*	11	18		0	33	7
Rel.	*19*	27	27		0	34	9

(c) Sulphate, Chloride and sodium, the ionic fluxes with variable responses to hurricane disturbance.

Sulphate

	Years	QS	QT	PRM	BQ1	BQ2	BQ3
	1984	50	22				
	1985	75	44				
	1986	63	51				
	1987	55	32				
	1988						
	1989	34			64	84	37
	1990	48	31	86	72	71	52
	1991	40	23	97	73	55	42
	1992	64	37	95	76	70	51
	1993	62	93	109	74	57	47
	1994	33	17	56	28	21	17
Abs.	*3*	–5	–9	–4	9	14	13
Rel.	*6*	–8	–22	–4	14	24	33

Chloride

	Years	QS	QT	PRM	BQ1	BQ2	BQ3
	1984	149	79				
	1985	189	172				
	1986	166	172				
	1987	176	162				
	1988	239					
	1989	171			176	171	174
	1990	198	130	279	171	198	214
	1991	107	70	168	144	110	129
	1992	192	104	164	147	132	157
	1993	185	370	232	175	163	191
	1994	112	87	155	77	73	69
Abs.	*45*	29	–22	99	28	69	70
Rel.	*30*	17	–14	55	19	53	49

Sodium

	Years	QS	QT	PRM	BQ1	BQ2	BQ3
	1984	95	63				
	1985	115	131				
	1986	99	128				
	1987	113	127				
	1988	134					
	1989	93			173	148	143
	1990	115	98	171	148	150	145
	1991	61	54	135	120	100	104
	1992	87	87	178	123	119	123
Abs.	*15*	15	–0	14	10	28	21
Rel.	*12*	15	–0	9	7	23	17

significant positive regression slopes) for 1 to 3 y after the hurricane. Shallow soil water at Bisley was also shown to have increased concentrations of potassium and nitrate for 1 to 3 y after the hurricane (McDowell *et al.* 1996).

DISCUSSION

Potassium, nitrate and ammonium concentrations and fluxes showed dramatic responses to hurricane disturbance. Since vegetation damage caused by Hurricane Hugo was more severe at Bisley than at El Verde watersheds (Boose *et al.* 1994, Scatena & Larsen 1991), our results suggest that greater disturbance leads to larger potassium and nitrogen losses. The subsequent decrease in nitrate and potassium concentrations occurred over the same period as recovery of canopy leaves (as measured by leaf litter collections, Scatena *et al.* 1996), which suggests biological control on the cycling of these ions.

The observed patterns in potassium and nitrate concentrations could be caused by reduced plant uptake and/or by microbial release from hurricane-derived litter. Because the duration of both of these post-hurricane peaks is longer than would be expected from the decomposition of leaf litter in terrestrial (months; Zou *et al.* 1995) or aquatic (weeks; Covich & McDowell 1996) environments, such decomposition cannot be the primary source of those peaks. Patterns of soil water chemistry at the Bisley watersheds shown by McDowell *et al.* (1992, 1996) also suggest that the streamwater nitrate peak passed through soil water, as opposed to the decomposition of hurricane-derived litter falling directly into streams.

Scatena *et al.* (1996) showed that aboveground vegetation pools of potassium and nitrogen in Bisley decreased by about 290 and 370 kg ha^{-1} respectively as a result of the hurricane. These pools recovered rapidly over the next 24 mo. Based on the Bisley stream chemical outputs estimated in this study, only about 3% of that potassium and 1% of that nitrogen were lost in streamwater. Silver *et al.* (1996) showed that soil exchangeable pools of potassium and nitrogen increased by about 35 and 12 kg ha^{-1} respectively, and remained elevated for the duration of their monitoring at Bisley (about 250 d post-hurricane). Therefore, we conclude that for 1 to 2 y, both reduced nutrient uptake and litter decomposition left more potassium and nitrate available for the soil exchange sites, transport and for stream export. Subsequent plant uptake into relatively nutrient rich, rapidly growing tissues (Scatena *et al.* 1996) reduced losses to the streams. In addition, the patchy nature of hurricane damage (Boose *et al.* 1994) means that some areas received much less damage. Overall, the loss of biotic control over these ions was temporary and of relatively small magnitude compared to disturbances that involve biomass removal from the site (i.e. fire and logging).

The streamwater concentrations of the ions reported in this study vary inversely with flow on all watersheds, except that potassium, ammonium and nitrate concentrations varied directly with flow in some streams and years.

Water from shallow soil horizons makes a larger contribution to streamwater at high streamflows (e.g. McDowell *et al.* 1992), and after the hurricane when that water became more concentrated in potassium and nitrate, streamwater concentrations increased at high stream flows. The inverse relationship has been reported by McDowell & Asbury (1994) for QS and QT, and by Newbold *et al.* (1995) for mountain streams in Costa Rica. The positive relationships between post-hurricane concentrations and streamflow have not been reported before in tropical montane streams. Lesack (1993) presents examples of other cations with positive concentration vs. flow relationships in the Amazon River.

In the Luquillo Mountains, calcium and magnesium fluxes in streamwater are largely derived from weathering (McDowell & Asbury 1994) and also affected by seasonal hydrological patterns (Figures 2 and 3). McDowell & Asbury (1994) concluded that calcium concentrations were controlled by mineralogical differences among QS, QT and Rio Icacos (an LEF watershed not considered in this study). This study supports McDowell & Asbury's ranking of calcium release from QS and QT, and indicates that the other watersheds in the Bisley area (PRM, BQ1 and BQ2) also release relatively large amounts of calcium. In a larger context, in watersheds where primary minerals became more exposed by hurricane-related soil disturbance, or if nitrification generated sufficient acidity, subsequent cation releases could be even larger.

Several of the chemical fluxes from particular watersheds reported in this study for years other than 1990 were lower than those reported in another study of Caribbean island streams (McDowell *et al.* 1995), including nitrate-N, sodium, potassium, calcium and magnesium. On the other hand, only the highest of the 'undisturbed' magnesium fluxes fell outside the range reported by McDowell *et al.* (1995). In the year after hurricane disturbance PRM exceeded McDowell *et al.*'s (1995) maximum values for calcium and chloride fluxes (195 and 263 kg ha^{-1} y^{-1}, respectively), and PRM, QS, BQ2 and BQ3 all exceeded their maximum values for nitrate-N fluxes (4.8 kg ha^{-1} y^{-1}). Until the hurricane disturbance, LEF stream exports were relatively low compared to other Caribbean streams.

Previous studies of biogeochemical consequences of tropical forest disturbances (fire, logging and cyclone damage) have shown that for small spatial scales, potassium, nitrate and ammonium are temporarily (1 to 3 y) released to soil and streamwater. With disturbance over larger spatial scales (0.05 ha or more), calcium, magnesium and sulphate can also be released. The LEF watersheds (ranging in size from 6 to 1752 ha) showed no distinct patterns in terms of stream export nor disturbance effect with respect to size.

While McDowell *et al.* (1996) found soil water concentration increases of all these ions in response to the 1989 Hurricane Hugo in the LEF, the streamwater changes were generally limited to potassium, nitrate and ammonium. Why might this be so? Hurricane disturbance (unlike fire and to some extent logging) leaves biomass nutrients on-site (McDowell *et al.* 1996), wood debris that can immobilize nutrients through microbial growth (Zimmerman *et al.* 1995), an intact soil seed bank (Guzman-Grajales & Walker 1991) and many surviving plants that respond rapidly to the increased light availability (Fernandez & Fetcher 1991). Apparently these factors combine to limit both the chemicals that respond to hurricane disturbance, and the duration of that response. When biomass is removed from the site (by fire or especially logging), and forest recovery is delayed, effects on streamwater chemistry may be greater and of longer duration.

In summary, massive disturbance to the LEF forest canopy caused by Hurricane Hugo in 1989 caused the largest changes in streamwater concentrations and fluxes observed in the 11-y record. These changes were observed for potassium and nitrate because reduced plant uptake temporarily diminished biological control over those ions. Recovery of the plant canopy within 2 y re-established that biological control. Chemical changes resulting from this hurricane damage were greater than those caused by canopy gaps or limited forest cutting, but smaller than those after large-scale deforestation or fire that have been studied in the tropics. The partial survival of the forest led to a rapid recovery of pre-disturbance stream chemistry.

ACKNOWLEDGEMENTS

Over more than a decade of stream chemistry research in the LEF, many individuals have contributed to sample collection, analysis and data management. We acknowledge this entire group together, because that is the manner in which they have made this project possible. Financial support throughout this study was provided by the U.S. Department of Energy contract DE-AC05-760R 01833, the National Science Foundation grants BSR 8718396, BSR-8811902 and DEB-9411973 for long-term ecological research, the University of Puerto Rico and the USDA Forest Service. We also thank Claire McSwiney and several anonymous reviewers for patiently improving this manuscript, which is dedicated to our deceased coauthor Dr Clyde Asbury.

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