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# Linking soils and streams: Response of soil solution chemistry to simulated hurricane disturbance mirrors stream chemistry following a severe hurricane

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ABSTRACT

Understanding the drivers of forest ecosystem response to major disturbance events is an important topic in forest ecology and ecosystem management. Because of the multiple elements included in most major disturbances such as hurricanes, fires, or landslides, it is often difficult to ascribe a specific driver to the observed response. This is particularly true for the long-term effects of hurricanes on forest ecosystem nutrient cycling. Hurricane disturbance opens the forest canopy by removing leaves and branches or snapping boles, and in so doing turns living biomass into debris that is deposited on the forest floor. At the watershed scale, past work in the Luquillo Mountains of Puerto Rico shows that these changes in forest structure and detrital dynamics result in large increases in stream water nitrate and potassium concentrations in streams draining volcaniclastic terrain. The Canopy Trimming Experiment (CTE) was designed to simulate the major effects of hurricane disturbance, and disentangle the effects of canopy opening and debris addition on forest biology and biogeochemistry following a hurricane. Using the chemistry of soil solution as an integrated indicator of biogeochemical response to hurricane simulation, the experimental manipulations show that the synergistic effects of both canopy opening and debris addition are needed to elicit one of the whole-watershed responses to hurricanes, a large pulse of nitrate ($NO_3$) concentration in stream water that lasted approximately 18 months. Manipulation of either canopy openness or debris addition alone had little effect on soil solution chemistry for $NO_3$, or for any other solute measured (dissolved organic matter, phosphate, ammonium, major cations and anions, and silica). None of the treatments resulted in the increased potassium (K) seen in stream water following hurricane disturbance. For $NO_3$, the time course of response and recovery following combined treatments of canopy opening and debris addition was similar to that observed in stream water after actual hurricanes. The CTE provided further evidence that tree regrowth following hurricane disturbance controls the return of $NO_3$ concentrations to pre-hurricane levels in this tropical forest. The lack of response in K to hurricane simulation suggests that leaching of the added debris, which was not captured in the experimental manipulations, is a major driver of K concentrations following disturbance. Hurricane disturbance, which is significant in many humid tropical forests, results in pulsed outputs of nitrogen in stream water that can be clearly ascribed to interactions between damage and recovery of canopy vegetation, and decomposition of detrital inputs on the forest floor.



## 1. Introduction

Understanding the watershed-scale response to disturbance is a fundamental topic for forest ecology, as it links forest condition and forest management to the environmental health of downstream aquatic ecosystems. Seminal work at the Hubbard Brook Experimental Forest showed that manipulation of forest vegetation through various felling practices can result in large and persistent changes in stream chemistry, which reflect changes in forest nutrient cycling (Bormann and Likens, 1979). Using the whole-watershed approach, various authors have examined the effects of natural disturbance agents such as fire (Spencer et al., 2003), ice (Houlton et al., 2003) and insect outbreaks (Swank et al. 1981) on stream chemistry. Changes in nitrogen (N) dynamics occurred following each of these watershed disturbances, reflecting the sensitivity of watershed N cycles to disturbance, the large pools of N relative to exports in stream water (e.g. Chestnut et al., 1999), and the mobility of nitrate ($NO_3$) ions in soils.

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Tropical forests play a disproportionate role in global carbon and nutrient cycling, due to their large biomass, high rates of carbon fixation and nutrient cycling, and the many areas of high runoff in the humid tropics (Schlesinger and Bernhardt, 2013). Hurricanes represent an important form of disturbance in tropical forests globally (Lugo, 2008), as they have immediate and large effects on forest canopy structure. They also have immediate effects on stream runoff and nutrient export from forested basins, due to the large runoff events that typically accompany the high winds (Tsai et al., 2009). The nature of the long-term biogeochemical responses to hurricanes is less well documented, as most studies of tropical forest response to hurricanes have focused on the hydrologic and biogeochemical characteristics of the actual hurricane runoff rather than longer-term effects (McDowell, 2011). An exceptional opportunity to understand the long-term response of tropical forests to hurricane disturbance is presented by the Luquillo Mountains of Puerto Rico, an area that experiences relatively frequent severe hurricanes (at least each 50–60 years; Scatena and Larsen, 1991). Past work there shows that across similar geologies of volcaniclastic terrain, streams respond in a similar way to hurricane disturbance, such as with sharp increases in stream $NO_3$ concentrations following Hurricane Hugo in 1989 (McDowell et al., 1996; Schaefer et al., 2000). The increase in $NO_3$ persisted for approximately 1.5 y, which was the approximate length of time for canopy closure following disturbance (Fernandez and Fetcher, 1991). Increases in stream potassium (K) concentrations were also observed over the same time frame. Following Hurricane Georges in 1998, both $NO_3$ and K were again elevated for about 18 months in the Sonadora stream (McDowell et al., 2013), and similar patterns were noted for most other streams in the Luquillo Mountains (Schaefer et al., 2000).

The specific drivers of these long-term (1–2 years) responses to hurricane disturbance are as yet undetermined. The input of leaves, branches, and boles to the forest floor releases carbon (C), N, and other nutrients during decomposition, and thus could contribute to the delivery of these solutes to stream runoff. At the same time, opening of the forest canopy due to hurricane disturbance probably decreases the uptake of nutrients by trees and understory vegetation. Both groundwater and stream chemistry responded strongly to hurricane disturbance in the Luquillo Mountains following Hurricane Hugo in 1989, with significant increases in $NO_3$ and K concentrations, despite attenuation of N in riparian groundwater (McDowell et al., 1996; McDowell et al., 2013). A long-term experiment in the Luquillo Experimental Forest of Puerto Rico, the Canopy Trimming Experiment, was designed to disentangle the effects of canopy opening and debris inputs on the response of tropical forest ecosystems to the large-scale disturbance associated with major hurricanes (Shiels et al., 2010). As one component of this large factorial experiment, we sampled the soil solution in unmanipulated control plots, as well as plots that received either one or both of the simulated hurricane treatments: canopy trimming and debris addition. In this paper we address the following questions regarding the response to these experimental disturbances: (1) Which treatments affect solute dynamics in soil solution? (2) What are the relationships among solutes in the soil solution? (3) Does the timing and magnitude of the response in soil solution to simulated hurricanes reflect the whole-watershed response evident in historical stream chemistry response to actual hurricanes?

## 2. Methods and materials

### 2.1. Site description

This study was conducted in the Luquillo Experimental Forest, Puerto Rico, near the University of Puerto Rico's El Verde Field Station (EVFS; 18°20′N, 65°49′W), which is a site of past work on soil solution chemistry (McDowell, 1998), groundwater chemistry (McDowell et al., 1992, 1996) and long-term stream chemistry (McDowell and Asbury, 1994; Schaefer et al., 2000; McDowell et al., 2013). The Luquillo Mountains are warm, wet, and show little seasonality in rainfall (McDowell et al., 2012). At the EVFS, annual rainfall averages approximately 3500 mm, and mean annual temperature is 23 °C (McDowell et al., 2012). The study area is located in Tabonuco (*Dacryodes excelsa* Vahl) forest type, with *Prestoea acuminata* (Willdenow), *Manilkara bidentata* (A.DC.)A.Chev.) and *Sloanea berteriana* Choisy as other common species (Shiels et al., 2010). The landscape is steep and rocky and the soils have developed from volcaniclastic sediments. The soils are oxisols in the Zarzal series which have high (>50%) clay content in the top 50 cm and organic matter content ranging from 1% to 6% (Soil Survey Staff, 1995). The exchangeable cation content of the soils is intermediate compared to montane tropical forests worldwide, with somewhat higher exchangeable phosphorus (P) and lower total N content than other sites (Silver et al., 1994).

### 2.2. Experimental design

The Canopy Trimming Experiment (CTE) is a long-term plot-scale manipulation designed to investigate various drivers that could contribute to the response of tropical montane forests to hurricane disturbance. Briefly, the experiment was constructed with two factorial experimental manipulations in blocks, designed to simulate two different aspects of hurricane disturbance. The first manipulation (Trim) involved trimming all boles and branches > 10 cm diameter in the forest canopy and above 3 m height, as well as removing palm leaves that reached at least 3 m height, in 30 × 30 m plots to simulate the canopy openness associated with hurricane damage. All of the debris was removed and weighed. The second manipulation (Debris) involved the deposition of this cut material (debris) onto the forest floor to simulate the debris redistribution caused by hurricane damage. Based on this factorial design, the four possible treatments for a plot within a block were No Trim + No Debris (unmanipulated control), Trim + No Debris, No trim + Debris, and Trim + Debris. These treatments were established in three completely randomized blocks to account for any spatial variation in soils and vegetation for a total a total of 12, 30 × 30 m plots. In the 20 × 20 m interior of each plot, three porous cup ceramic tension lysimeters (Soil Moisture Corporation) were installed at a depth of 40 cm prior to initiation of the experiment for a total of 36 lysimeters. The locations of each lysimeter within the 20 × 20 m interior were chosen at random in available boulder-free areas.

The blocks were manipulated (canopy trimmed and debris weighed and redistributed) in series, with the manipulations occurring between October 2004 and June 2005. The trimming was performed by professional arborists and typically took 1 month to complete. Trimming generated 11 ± 0.4 Mg fresh weight of debris composed of leaves and twigs, branches and palm fronds; after a loss of 17% of the mass during storage, a total of 5.4 ± 0.1 Mg dry weight of material (67% wood, 29% twigs and leaves, and 4% palm fronds) was added to the debris plots (Shiels and González (2014)). The materials were stored on tarpaulins during processing and were exposed to the elements, but mass losses were similar on a percentage basis among plots (Richardson et al. 2010). The nutrient content of the debris was not calculated as part of the experimental setup, but nutrient concentrations were measured on canopy litterfall by Silver et al. (2014). Further details on the experimental manipulations are given by Shiels et al. (2010). A detailed map of the blocks and plots is given by Richardson et al. (2010) and Shiels and González (2014).

### 2.3. Field sampling and chemical analysis

Monthly sampling was conducted from 2003 to 2010 by evacuating the lysimeters to 0.7 MPa 1 week before sampling, and returning the following week to extract the soil water collected. Not all lysimeters contained water sufficient to sample during every monthly sampling event, but some soil solution was obtained from each treatment during almost every month. Samples were filtered at EVFS laboratory with a Whatman GF/F glass fiber filter (0.7 μm nominal pore size), and then frozen and shipped to the Water Quality Analysis Laboratory at the University of New Hampshire for all chemical analyses. Samples were analyzed for anions ($NO_3$, $SO_4$, and Cl) and cations (Na, K, Ca, and Mg) using Dionex micromembrane suppressed ion chromatography. A Westco SmartChem robotic analyzer was used to analyze $NH_4$, $PO_4$, and $SiO_2$. Organic matter was measured as non-purgeable dissolved organic carbon (DOC).

### 2.4. Data analysis

The first question was assessed using a separate ANOVA for each solute. First, a mixed model ANOVA was tested in SAS 9.3 with proc mixed with block as a random effect, the two experimental manipulations (trim and debris) as fixed effects and year also as a fixed effect. We used individual lysimeters within blocks as the replicates as a repeated effect in the model. This model included all of the interactions among fixed effects. To simplify the effects of time, we lumped the data into three time periods based on the response of stream chemistry to hurricane disturbance observed in past work: measurements prior to experimental manipulation (pretreatment), months 0–24 after manipulation started (early treatment), and months 25–48 after manipulation started (late treatment). Because the treatments took almost 8 months to accomplish, the early treatment period began sometime between October 2004 and March 2005. Significant effects were further investigated with the lsmeans command in proc mixed with a Tukey adjustment on all the interaction terms for the fixed effects in the model. Because there were complex interactions between time period and the treatment effects for solutes, separate mixed model ANOVAs were run for each of the three time periods in order to interpret the main effects of the treatments. One lysimeter was removed from the analysis because the ammonium concentrations became consistently two orders of magnitude higher than the other lysimeters.

The second question was addressed by testing correlations among the variables. In addition, the relationships among variables were examined visually to detect non-linear associations among variables.

The third question was evaluated qualitatively. The 7-year record of monthly means from the lysimeter dataset was compared to a 7-year record of monthly mean stream chemistry data. Stream water values are the average of three streams (Quebrada Sonadora, Quebrada Prieta, and Quebrada Toronja) that drain the area near the EVFS in response to Hurricane Hugo, which occurred in September 1989 (data from Schaefer et al., 2000).

## 3. Results

### 3.1. Response of soil solution chemistry to hurricane simulation

Of all the solutes measured, only $NO_3$ showed a significant response to the full hurricane simulation (Trim + Debris), and the response occurred only during the early pretreatment period (Table 1). The lysimeters in this treatment had significantly higher $NO_3$ than the other three treatments. In a lysimeter in the Trim + Debris treatment, for example, $NO_3$-N concentrations increased from a background of 0.010–0.030 mg $L^{-1}$ prior to treatment to almost 7.5 mg $L^{-1}$ within 10 months after the manipulation (Fig. 1). Across all blocks, lysimeters in the Trim + Debris treatment showed a similar pattern of response and return to baseline within approximately 18 months of manipulation. Peak $NO_3$–N concentrations reached or exceeded 2 mg $L^{-1}$ in five of the nine lysimeters in the Trim + Debris treatment. Neither of the two other experimental treatments produced $NO_3$ concentrations that differed from pre-treatment concentrations (Table 1, Fig. 2). Although the Trim + No Debris treatment produced $NO_3$–N concentrations that were elevated over No Trim + Debris and No Trim + No Debris, across all blocks and lysimeters, monthly average concentrations only exceeded 0.5 mg/L on one pre-treatment date, and one post-treatment date. In contrast, in the Trim + Debris plots, average $NO_3$–N reached 2.3 mg $L^{-1}$, and exceeded 0.5 mg $L^{-1}$ for 8 months in a row (Fig. 2). In these experimental plots, $NO_3$–N averaged 0.05 mg $L^{-1}$ in the 2 years prior to treatment, and 20-fold higher (0.83 mg $L^{-1}$) in the 2 years following treatment (Table 1).

Unlike $NO_3$, none of the other solutes measured showed a significant increase in the early treatment time period and recovery to pretreatment levels in the late treatment time period in response to either manipulation or their interaction (Table 1). One other response to the manipulations was a significant trim effect on Cl with lower concentrations in the trimmed plots in both the early and late treatment time periods. Similarly, Na was significantly lower in the trimmed plots during the late treatment time period. The only solute other than $NO_3$ that showed a strong pattern over the entire course of the experiment was K. Rather than responding to experimental manipulation, however, the concentrations of K in lysimeters declined in all treatments from the outset of the experiment. In the unmanipulated control lysimeters, for example, the concentrations of K declined by 65%, from 0.57 to 0.20 mg $L^{-1}$ in the pre-treatment vs early treatment periods. A similar response was observed in all the other treatments, including the Trim + Debris hurricane simulation (Table 1). This change in pre- and post-treatment K concentrations was associated with a sharp decline from the onset of lysimeter sampling, suggesting a strong disturbance effect associated with lysimeter installation, but no effects of the actual experimental manipulations themselves (Fig. 3). Finally, throughout the entire study, the Ca concentrations were consistently higher in the Trim + Debris treatments, significantly so in the pretreatment and late treatment periods. Because this effect was not affected by the experiment, these differences are likely due to random variation among the plots.

### 3.2. Relationships among solutes

There were a number of statistically significant relationships among solutes in soil solution. Among all solute pairs, the strongest relationship was between Na and Cl ($r = 0.82$; $p < 0.001$). Similar relationships were observed between Mg and Cl ($r = 0.48$), but Cl was a poor predictor of Ca. Because of the large number of observations in the entire dataset (over 2,100 individual samples), most correlations between solute pairs were statistically significant, but weak, with absolute values of the correlation coefficients less than 0.15.

The relationship between $NO_3$ and DOC was strongly hyperbolic, with high concentrations of DOC never associated with high $NO_3$, and conversely, high concentrations of $NO_3$ were never associated with high DOC (Fig. 4). Nitrate also showed a similar, hyperbolic relationship with Ca (Fig. 4). The concentrations of the other nutrients, PO4 and $NH_4$, did not show similar relationships as $NO_3$ with DOC.

**Table 1**
Average lysimeter soil solution chemistry for samples collected during the pretreatment period, approximately 2 years before treatment began; the early treatment period, 0–24 months after treatment began; and the late treatment period, 25–48 months after treatment began. Values shown are arithmetic mean (±1 standard error); for each treatment, $n$ = 8 or 9 lysimeters. Units are mg $L^{-1}$ except for $NH_4$ and $PO_4$, which are both in µg $L^{-1}$. DOC is dissolved organic carbon. Significant effects (Trim, Debris, or Trim × Debris) are based on the mixed model ANOVA results for each time period. Small letters indicate significant differences among the four treatments (Trim + Debris, Trim + No Debris, No Trim + Debris, No Trim + No Debris).

| | Pre-treatment | | | | | Early treatment | | | | | Late treatment | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No Trim + No Debris | No Trim + Debris | Trim + No Debris | Debris + Trim | Treatment effects | No Trim + No Debris | No Trim + Debris | Trim + No Debris | Debris + Trim | Treatment effects | No Trim + No Debris | No Trim + Debris | Trim + No Debris | Debris + Trim | Treatment effects |
| $NH_4$–N | 18.5 (1.53) | 18.4 (1.47) | 44.9 (20.06) | 23.1 (5.76) | | 17.1 (2.15) | 17.5 (1.91) | 15.0 (2.33) | 12.3 (1.59) | | 11.9 (1.16) | 10.0 (0.92) | 11.9 (1.28) | 8.4 (0.73) | |
| $NO_3$–N | 0.07 (0.03) | 0.05 (0.03) | 0.05 (0.02) | 0.05 (0.02) | | 0.03[b] (0.01) | 0.06[b] (0.02) | 0.29[b] (0.07) | 0.83[a] (0.23) | D, T, D × T | 0.04 (0.02) | 0.09 (0.03) | 0.04 (0.01) | 0.08 (0.03) | |
| DOC | 2.8 (0.55) | 2.0 (0.41) | 4.1 (1.70) | 2.7 (0.87) | | 2.7 (0.46) | 2.6 (0.40) | 3.0 (1.10) | 1.8 (0.39) | | 2.5 (0.39) | 2.4 (0.71) | 2.1 (0.67) | 1.6 (0.23) | |
| $PO_4$–P | 4.5 (0.74) | 3.3 (0.26) | 39.0 (31.01) | 3.5 (0.26) | | 3.4 (0.21) | 2.9 (0.14) | 6.3 (3.19) | 3.1 (0.15) | | 3.7 (0.67) | 2.5 (0.05) | 3.1 (0.31) | 7.3 (4.26) | |
| Na | 6.4 (0.94) | 5.9 (0.61) | 7.1 (0.73) | 6.1 (0.32) | | 5.0 (0.66) | 6.3 (0.61) | 5.3 (0.26) | 5.2 (0.42) | | 6.1[ab] (0.88) | 7.0[a] (1.01) | 4.8[ab] (0.69) | 3.3[b] (0.26) | T |
| K | 0.58 (0.10) | 0.43 (0.03) | 1.42 (0.83) | 0.72 (0.17) | | 0.20 (0.01) | 0.47 (0.11) | 0.62 (0.36) | 0.28 (0.03) | | 0.18 (0.02) | 0.21 (0.05) | 0.39 (0.22) | 0.17 (0.01) | |
| Ca | 0.96[ab] (0.12) | 0.64[b] (0.09) | 1.32[a] (0.32) | 0.86[ab] (0.14) | D | 0.80 (0.13) | 0.43 (0.12) | 0.65 (0.16) | 0.52 (0.12) | | 0.87 (0.15) | 0.34 (0.10) | 0.83 (0.29) | 0.50 (0.09) | D |
| Mg | 1.1 (0.24) | 0.9 (0.13) | 1.3 (0.23) | 1.0 (0.05) | | 1.0 (0.21) | 1.0 (0.07) | 1.0 (0.08) | 0.9 (0.08) | | 1.4 (0.27) | 1.3 (0.13) | 1.3 (0.20) | 0.9 (0.05) | |
| Cl | 11.0 (1.37) | 9.8 (1.22) | 13.8 (1.77) | 11.1 (0.98) | | 8.9 (1.56) | 10.1 (0.94) | 7.6 (0.66) | 7.0 (0.82) | T | 11.7 (2.16) | 11.4 (1.65) | 8.9 (1.99) | 5.7 (0.58) | T |
| $SO_4$–S | 0.82 (0.21) | 0.53 (0.08) | 0.66 (0.17) | 0.71 (0.17) | | 0.53 (0.12) | 0.65 (0.11) | 0.55 (0.11) | 0.55 (0.07) | | 0.52 (0.12) | 0.43 (0.06) | 0.41 (0.11) | 0.43 (0.04) | |
| $SiO_2$ | 3.5 (0.46) | 3.6 (0.60) | 5.5 (2.64) | 3.0 (0.44) | | 1.8 (0.27) | 1.7 (0.27) | 4.3 (2.30) | 2.0 (0.37) | | 1.7 (0.28) | 2.3 (0.69) | 4.2 (2.75) | 1.9 (0.38) | |

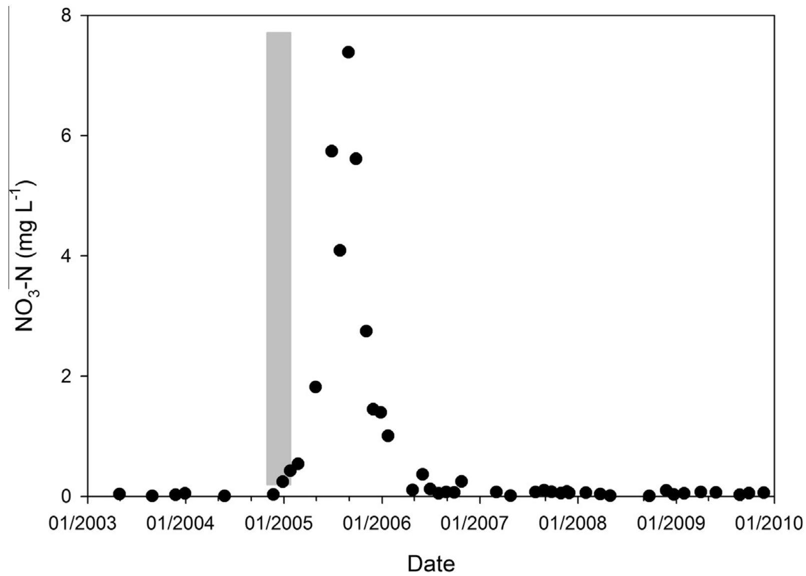


**Fig. 1.** Response of soil solution $NO_3$–N concentration (mg $L^{-1}$) to experimental hurricane simulation (Trim + Debris) in the individual lysimeter (Lysimeter 18) with the largest response to the experimental manipulation. The gray bay indicates the time period when the experimental manipulations occurred for this block.

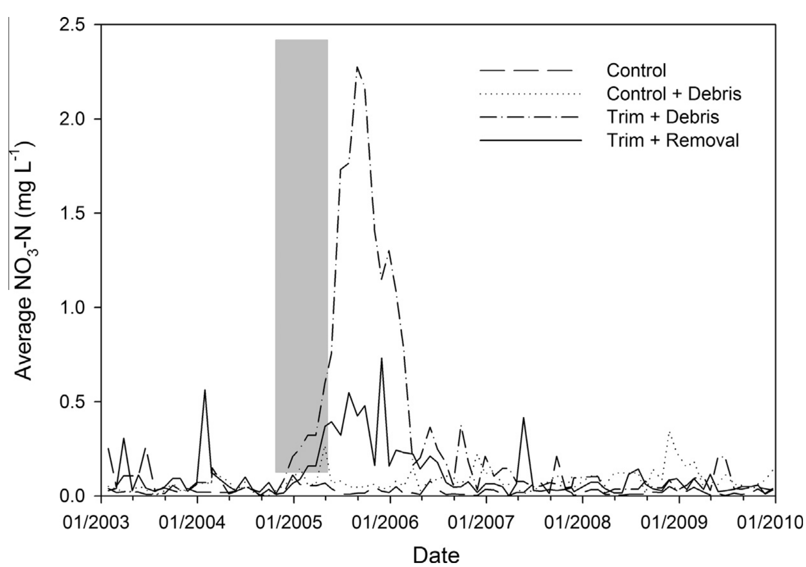


**Fig. 2.** Soil solution $NO_3$–N concentration (mg $L^{-1}$) over time as a function of experimental treatment (Trim + Debris, Trim + No Debris, No Trim + Debris, No Trim + No Debris). Data shown are monthly average concentrations by treatment. The experimental treatments were conducted by blocks, with manipulations occurring from October 2004 to June 2005 depending on the block; the gray bar indicates the manipulation periods for all four blocks.

## 4. Discussion

### *4.1. Response to hurricane simulation*

Experimental manipulations provide a mechanistic link between driver and response that is not possible with an uncontrolled observational study of a natural disturbance such as a hurricane. In this experimental manipulation of the two primary drivers (canopy opening and debris addition to the forest floor) associated with whole-ecosystem response to hurricanes, it is clear that both drivers are necessary to obtain the whole-ecosystem response to hurricane disturbance. Hurricane Hugo caused large alterations in canopy structure, as well as large inputs of organic debris to the forest floor (Lodge and McDowell, 1991; Scatena et al., 1996). The response of groundwater and stream water to Hurricane Hugo was a sharp and consistent increase in $NO_3$ within a few months of the hurricane, as well as a less consistent increase in K concentrations and no obvious changes in other solutes (McDowell et al., 1996; Schaefer et al., 2000; McDowell et al., 2013). The response of soil solution to experimental hurricane simulation largely mirrored the response of stream chemistry (Fig. 5), with large increases in $NO_3$ concentrations within a few months of disturbance, and a return to background levels within 2 years. The experimental hurricane simulation (trim + debris) captured the timing of this response remarkably well (Fig. 5), suggesting that the experiment was particularly appropriate for understanding the alterations in N cycling that result from hurricane disturbance.

The muted response in $NO_3$ concentrations to single treatments of either canopy trimming or debris deposition (Trim + No Debris; No Trim + Debris; Fig. 3) shows that the full impacts of hurricane

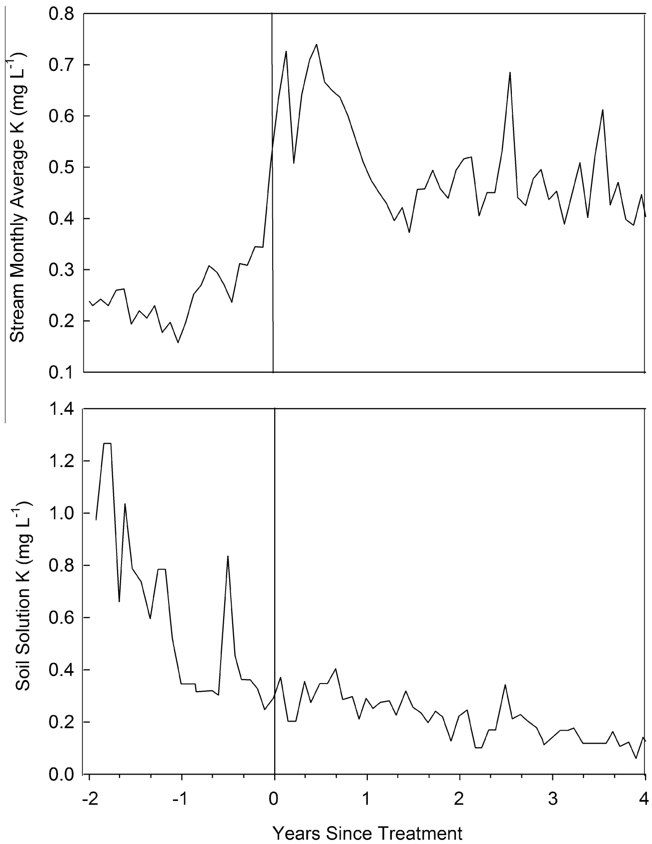


**Fig. 3.** Effects of experimental canopy manipulation and Hurricane Hugo on K concentrations. The experimental treatment that most closely resembles a hurricane (Trim + Debris) is shown. The manipulations associated with the treatments occurred between October 2004 and June 2005, depending on the block. Time zero for the lysimeter data is the month after the treatment manipulations began for each block. Stream water values are the average of three streams (Quebrada Sonadora, Quebrada Prieta, and Quebrada Toronja) in response to Hurricane Hugo, which occurred on September 18, 1989 (data from Schaefer et al., 2000). For the stream dataset, the October monthly mean was considered time zero. All values are monthly mean K concentrations in soil solution (mg $L^{-1}$) or stream water (μg $L^{-1}$).

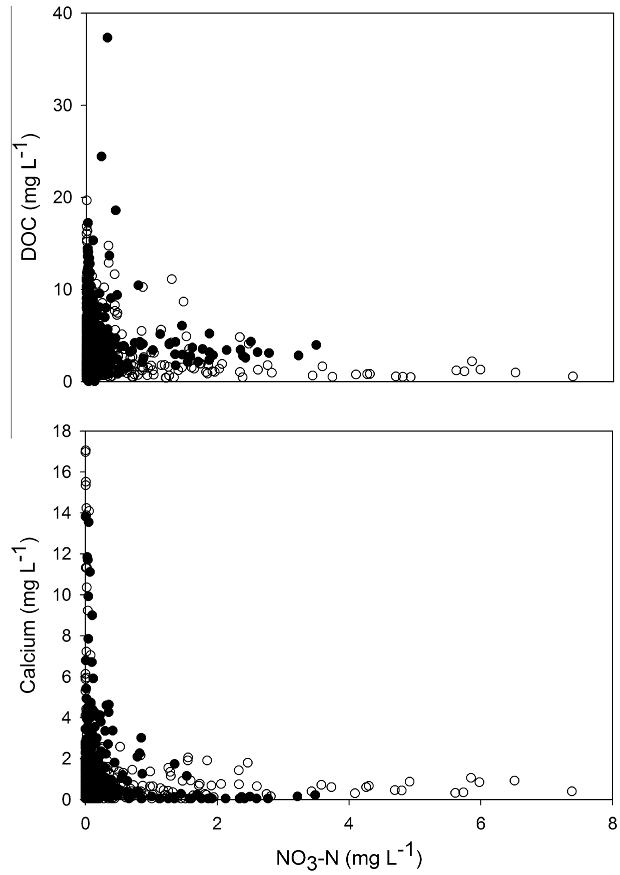


**Fig. 4.** Relationship between DOC and $NO_3$–N (upper panel), and between Ca and $NO_3$–N (lower panel) in individual tension lysimeter samples collected from all experimental treatments throughout the entire study period. Concentrations in mg $L^{-1}$. Open symbols are used for the early treatment period and closed symbols are used for both the pretreatment and late treatment time periods.

disturbance are due to the synergistic effects of canopy damage and mineralization of organic debris on the forest floor. Both elements of the hurricane simulation are needed to produce the large and sustained flush of $NO_3$ in soil solution, and thus to mimic the whole-ecosystem response to an actual hurricane. Canopy trimming presumably reduces vegetative demand for N until foliage regrows, and decomposition of debris results in increased N availability as organic N is mineralized. Together, this reduced demand and increased supply of N appear to be responsible for the large increase in soil solution $NO_3$ after hurricane simulation. In support of this conclusion, past work shows that root mortality was high following Hurricane Hugo (and presumably was associated with reductions in N uptake) (Parrotta and Lodge, 1991; Silver and Vogt, 1993), and that the material deposited on the forest floor was rapidly decomposed (Sullivan et al., 1999; Ostertag et al., 2003). In the CTE, decomposition of litter experimentally placed on the forest floor was also rapid (González et al., 2014; Lodge et al., 2014). Decomposition of litter deposited on the CTE plots results in mineralization of organic N to $NH_4$, and subsequent rapid nitrification, as no increase in $NH_4$ was measured in soil solution following experimental treatments (Table 1). This lack of $NH_4$ accumulation in soil solution following experimental manipulation differs from the results obtained by McDowell et al. (1996), who found an initial $NH_4$ accumulation and then a subsequent $NO_3$ accumulation in shallow groundwater sampled in volcaniclastic terrain following Hurricane Hugo. Differences in redox status (patchy oxygen availability along riparian flow paths, and more consistent oxygen availability in upland soils; McDowell et al., 1992 and Silver et al., 1999) are probably responsible for the lack of $NH_4$ accumulation in soil solution.

Experimental simulation of hurricane damage resulted in a much larger change in soil solution $NO_3$ concentrations than those that occurred in stream water after Hurricane Hugo, suggesting the likely importance of riparian N removal in regulating the watershed-scale response to disturbance. Following Hugo, stream water concentrations of $NO_3$–N reached levels several times background, with a peak of 0.30 mg $L^{-1}$ following hurricane disturbance (Fig. 5). In contrast to the stream water response, shallow groundwater reached concentrations of almost 1 mg $L^{-1}$ $NO_3$–N in the Bisley Experimental Watersheds, located a few km from the El Verde site (McDowell et al., 1996). Following Hurricane Hugo, McDowell et al. (1996) also observed declines in $NO_3$ concentration as water moved through the riparian zone. Taken together, these observations suggest that in volcaniclastic terrain, the timing and duration of elevated $NO_3$ in streams following hurricanes is due to canopy damage and regrowth, but that the magnitude of watershed N loss is a function of riparian processes, as suggested by earlier research (McDowell et al., 1996; McDowell, 2001).

The lack of response in K concentrations to the experimental manipulations described here is puzzling, given past observations that K increases in stream water and groundwater following hurricanes (McDowell et al., 1996; Schaefer et al., 2000; McDowell et al.,

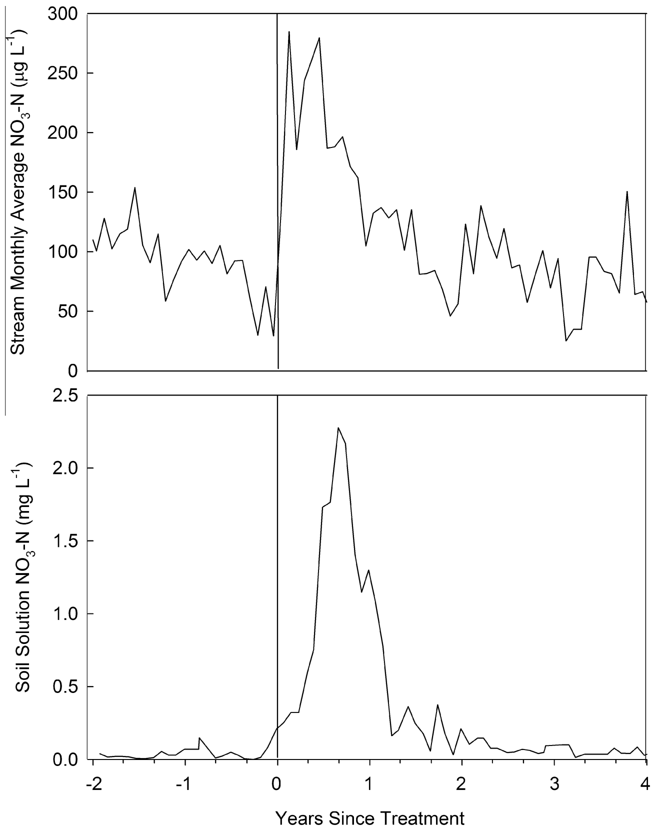


**Fig. 5.** Effects of experimental canopy manipulation and Hurricane Hugo on $NO_3$–N concentrations. The experimental treatment that most closely resembles a hurricane (Trim + Debris) is shown. The manipulations associated with the treatments occurred between October 2004 and June 2005, depending on the block. Time zero for the lysimeter data is the month after the treatment manipulations began for each block. Stream water response is the average of three streams (Quebrada Sonadora, Quebrada Prieta, and Quebrada Toronja) in response to Hurricane Hugo, September 18, 1989. All values are monthly mean $NO_3$–N concentrations in stream water (μg $L^{-1}$) or soil solution (mg $L^{-1}$).

2013). Only a few individual lysimeters had any samples with elevated K concentrations following manipulations, and no treatment resulted in any persistent elevation of K concentrations such as those that were observed in stream water after Hurricane Hugo (Fig. 3). The most likely explanation for these observations is that K is very labile in leaf debris. It has been known for decades that K is easily leached from fallen leaves (Nykvist, 1959), and most K is stored in vegetation, rather than soils, in this forest type (McDowell, 1998). Given the experimental design of the CTE, in which branches and boles were first trimmed and moved off-site, weighed, and then redistributed to the appropriate experimental treatment several weeks after trimming, K might have been preferentially lost. The leaching of K from leaves is likely to have occurred prior to placement of debris on the plots and thus to have minimized the production of K after the litter debris was returned to the experimental plots.

### 4.2. Biogeochemical linkages among $NO_3$ and other solutes

The use of experimental manipulations provides an opportunity to address fundamental biogeochemical relationships across a scale that would otherwise be difficult to achieve. In the CTE, for example, the large increase in soil solution $NO_3$ concentrations following the trim + debris treatment resulted in a very wide range of $NO_3$–N concentrations, with background levels as lows as 10 or 20 μg $L^{-1}$ in unmanipulated plots, and concentrations in experimental treatments reaching 7 mg $L^{-1}$. Within the context of this study, it is thus possible to assess broad patterns in the biogeochemistry of C and N such as the inverse relationship between DOC and $NO_3$ observed by Taylor and Townsend (2010) in a synthesis of data from various biomes. The results reported here for the CTE clearly fit this global pattern (Fig. 4), and suggest that the lack of available carbon (low DOC concentrations) may limit the microbial uptake or denitrification of $NO_3$ produced by mineralization of the canopy debris that was added to the forest floor plots as part of the hurricane simulation. Although the low DOC/high nitrate samples are almost all from the early treatment period, the relationship holds across all treatments and time periods.

In addition to the $NO_3$–DOC relationship reported in earlier studies, the data presented here also show a novel pattern with respect to Ca and $NO_3$, with a strong inverse relationship between the two solutes (Fig. 4). The basis for this relationship is uncertain. The production of $H^+$ ions during nitrification might make Ca more available in soil solution, but that mechanism should result in higher $NO_3$ being associated with higher Ca, rather than the inverse relationship observed in this study. Calcium might also be released from organic debris that is decomposing, but again that should result in higher $NO_3$ associated with higher Ca, rather than the inverse relationship that was actually observed. Further study is needed to evaluate if there is a similar mechanism to explain this pattern and to determine if this is a widespread phenomenon.

### 4.3. Implications for understanding drivers of watershed-scale disturbance

The results of the Canopy Trimming Experiment suggest that the long-term response of stream chemistry to catastrophic hurricanes is due largely to forest canopy and forest floor processes rather than in-stream processes. Past experimental work at the site shows that decomposition of leaf litter in the stream channel can affect stream chemistry at base flow (Crowl et al., 2001) for periods of a few weeks, and earlier work suggested that leaf litter inputs might indeed have affected stream chemistry in the first few weeks after Hurricane Hugo (Schaefer et al., 2000). Because leaf litter decomposes rapidly in the stream channel and is converted to fine particles by shrimp and other shredding organisms in a few months (Wright and Covich, 2005), in-stream processes are not likely to be responsible for the peak in stream $NO_3$ observed about 6 months following the hurricane. Thus, although stream chemistry can undergo immediate changes in tropical forests following a hurricane (Zhang et al., 2007; Tsai et al., 2009), the largest impacts appear to occur months after hurricane passage, and to be driven largely by terrestrial processes. Similar results have been obtained in temperate forests following major disturbances such as an ice storm at the Hubbard Brook Experimental Forest, which caused elevated $NO_3$ concentrations for approximately 18 months (Houlton et al., 2003).

The time course of response and return to pre-manipulation conditions suggests that recovery of leaf area in the canopy is a key driver of the response to manipulative disturbance. By 2007, 2 years after the Trim + Debris treatment, light levels had declined in the plots to pre-treatment levels (Richardson et al., 2010; Shiels and González, 2014), seedling density had declined to near pre-treatment levels, and leaf litter cover on the forest floor had returned to pre-treatment levels (Shiels et al., 2010). This time course for canopy closure matches the return to background levels in soil solution chemistry, as well as the return to background in stream chemistry of the El Verde area.

Decomposition of the large pulse of organic debris resulting from hurricane passage or our experimental hurricane simulation results in mineralization of organic C, N, and P, but only the $NO_3$ is mobile through the soil profile, and transported to the depth (40 cm) at which soil solution is collected. Past work at the study site shows that soils are highly retentive of DOC (McDowell, 1998), and soils from the El Verde site were among the most retentive of C among a broad range of tropical soils (Neff and Asner, 2001). Soils at El Verde are also highly retentive of $NH_4$ and $PO_4$ (McDowell, unpublished), as are many tropical soils (Matson et al., 1999). Solutes released from decomposition are thus subject to both abiotic retention through adsorption by clay-rich mineral soils, as well as uptake by plants or assimilation by microbes prior to reaching the depth at which soil solution is collected, and thus have little opportunity to enter the hydrologic flow paths that deliver solutes to the stream.

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