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Long-term dynamics of organic matter and elements exported as coarse particulates from two Caribbean montane watersheds

T. Heartsill Scalley*,[1], F. N. Scatena*,†, S. Moya* and A. E. Lugo*

* International Institute of Tropical Forestry, USDA Forest Service, Jardín Botánico Sur, 1201 Calle Ceiba, Río Piedras, Puerto Rico 00926-1115
† Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316, USA
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Abstract: In heterotrophic streams the retention and export of coarse particulate organic matter and associated elements are fundamental biogeochemical processes that influence water quality, food webs and the structural complexity of forested headwater streams. Nevertheless, few studies have documented the quantity and quality of exported organic matter over multiple years and under a range of conditions that includes both droughts and hurricanes. This study quantifies the export of coarse particulate organic matter (CPOM, > 12.7 mm), over 18 y in two headwater streams in north-east Puerto Rico. Daily exports ranged from 0 to over 170 g ha^{-1} d^{-1} and averaged 7.39 g ha^{-1} d^{-1}, with similar amounts coming from leaves (3.5 g ha^{-1} d^{-1}) and wood (3.2 g ha^{-1} d^{-1}). Export of coarse particulate organic carbon was 3.0 g ha^{-1} d^{-1} which constitutes only 1.32% of carbon exports. Most litter falling into the streams was processed in place as only 2.3% of the leaf litter falling directly into these perennial channels was exported as CPOM. On average, 6 wk y^{-1} had no exports while events transporting more than 10 g ha^{-1} d^{-1} occurred every 2.8 mo. Instead of a single annual pulse as observed in deciduous systems, there were annual peaks in CPOM exports during May and September and less export during the drier period from December to February. Ratios of C:N in the exported material were highest in the driest month and lowest during rainy months, while leaf fluxes for nitrogen, phosphorus and calcium were highest in rainy months and lowest during February. Although median daily exports and exports during low- and base-flow periods were similar before and after Hugo, after 16 y exports during moderate- and high-flow periods were still less than those in the 2 y prior to the hurricane. Our observations indicate a system with high rates of internal processing that quickly returns to median daily conditions following hurricanes but requires several decades for storm-flow exports to return to pre-disturbance conditions and indicates that the long-term pattern of CPOM export is associated with the level of maturity of watershed vegetation.

Key Words: allochthonous, coarse particulate organic matter (CPOM), elements, export, leaves, litterfall, nutrients, Puerto Rico, streams

INTRODUCTION

The export and retention of coarse particulate organic matter (CPOM) and associated elements are fundamental biogeochemical processes that strongly influence water quality, food webs and the structural complexity of forested headwater streams (Benstead *et al.* 2009, Fisher & Likens 1973, Martinelli *et al.* 1991, Meyer *et al.* 1998, Pyron *et al.* 1999, Tank *et al.* 2010, Wallace *et al.* 1999, Webster *et al.* 1994). The amount of CPOM that is stored or transported from a headwater stream can vary with rainfall, plant phenological patterns, stream flow, channel geomorphology, rates of litter decomposition and biotic processing (Covich & Crowl 1990, Wallace *et al.* 1997). Seasonal pulses of litter into streams and their subsequent transport are major annual biogeochemical events in some deciduous systems (Fisher & Likens 1973). In tropical and subtropical (*sensu* Holdridge 1967) headwater streams, leaf litter is also an important source of energy and structure (Cross *et al.* 2008, Crowl *et al.* 2001, Ortiz Zayas *et al.* 2005, Selva *et al.* 2007) but knowledge about the temporal dynamics of litter export is lacking. Montane tropical forests can have multiple leaf-fall events each year instead of the single dominant pulse of deciduous forests (Zalamea & González 2008, Zou *et al.* 1995). In addition, storms and droughts bring organic matter pulses of different quality into streams (Beard *et al.*

[1] Corresponding author. Email: theartsill@fs.fed.us

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Table 1. Characteristics of the Bisley Experimental Watersheds, Luquillo, Puerto Rico, during the organic matter (CPOM >12.7 mm) export study period, 1987–2005.

Characteristic	Bisley 1	Bisley 2	Combined	Reference
Drainage area (ha)	6.70	6.34	13	Scatena 1989
Altitude at collection point (m asl)	261	267		Scatena 1989
Streambed area (m^2)	991	2249	3240	This study
Stream channel length (m)	918	868	1786	Scatena 1989
Mean annual rainfall 1993–2005 (mm y^{-1})			3596	Heartsill Scalley *et al.* 2007
Mean annual run-off 1993–2005 (mm y^{-1})	1738	1822	1780	This study
Litterfall (g m^{-2} d^{-1})			2.38–3.45	Lodge *et al.* 1991, Beard *et al.* 2005
Hurricane litterfall (g m^{-2} d^{-1})			477–868	Lodge *et al.* 1991, Ostertag *et al.* 2003
Active channel width at collection net (m)	1.08	2.59		This study
Drainage density (m ha^{-1})	142	133	137	Scatena 1989
Mean number of weeks per year without CPOM export	6.6	6.5		This study

2005, Covich *et al.* 2003, Goldsmith *et al.* 2008, Lodge *et al.* 1991, Ostertag *et al.* 2003, Selva *et al.* 2007, Vogt *et al.* 1996).

This study examines the export of leaves, wood and miscellaneous plant material in two adjacent headwater streams in north-eastern Puerto Rico over an 18-y period that includes droughts, storms, hurricanes and rainfall events of varying intensity. The primary objectives of the study were to: (1) quantify long-term coarse particulate organic matter and elements (N, P, K, Ca, Mg, Al, Fe and Mn) exported in these headwater systems; and (2) evaluate how seasonal and successional dynamics affect the quantity and quality of this export. In particular our hypotheses were: (1) CPOM export follows the seasonal pattern of rainfall and streamflow, (2) exported CPOM is a very small percentage relative to litterfall entering these streams, (3) there is seasonal variation in CPOM quality, (4) CPOM export recovers at the same time scale as does litterfall following hurricane defoliation. The duration of this continuous record of CPOM dynamics (mass and chemical elements) provides a unique data resource to address these hypotheses and characterize temporal variability in this resource of headwater-stream foodwebs.

METHODS

Study site

This study was conducted in two of the Bisley Experimental Watersheds (18°20′N, 65°50′W) of the Luquillo Experimental Forest in north-east Puerto Rico (Table 1). The two adjacent drainages, Bisley 1 and 2 are located in the 'subtropical wet forest life zone' *sensu* Holdridge (Ewel & Whitmore 1973) and are covered with mature tabonuco forest dominated by *Dacryodes excelsa* Vahl. The geomorphology, soils, above-ground biomass and disturbance history of the drainages are described in detail elsewhere (Heartsill Scalley *et al.* 2010, Royo *et al.* 2011, Scatena 1989, Scatena & Lugo 1995). Mean annual rainfall and throughfall are 3482 mm and 2131 mm respectively (Heartsill Scalley *et al.* 2007). Rainfall and stream run-off occur in every month but are lowest from January to March. Hurricanes, tropical storms, landslides and tree falls are common disturbances and Saharan dust and Caribbean volcanic activity can influence precipitation quantity and quality.

The perennial channels that drain each watershed are underlain by volcanoclastic bedrock and are steep gradient, boulder-lined streams that are fed by a dense network of intermittent channels and 1–2-m-wide leaf-filled swales (Scatena 1989). Both of these forested watersheds have closed canopies above the main channels. The riparian vegetation along the main channels tends to have lower biomass and higher stem densities than upland vegetation but a greater number of tree species and higher cover by ferns and climbers (Heartsill Scalley 2005, Heartsill Scalley *et al.* 2009, Scatena & Lugo 1995). While there are no distinct riparian tree species (Heartsill Scalley 2005) in this forest type, understorey vegetation and soil characteristics define a riparian zone that has an average width of 22 m for perennial channels and 10 m for intermittent channels (Scatena 1990). The introduction of bamboo in the 1930s has led to present-day bamboo stands along some streams reaches, like the sample collection point in Bisley 1 (O'Connor *et al.* 2000). The vegetation adjacent to the collection point of Bisley 2 does not contain bamboo, but a mixture of introduced mahogany and native hardwoods.

On 18 September 1989 hurricane Hugo passed over the study areas and resulted in widespread defoliation, crown damage and uprooting. This was the largest storm to affect the area in 60 y (Scatena & Larsen 1991) and it reduced the watershed's above-ground biomass by 50% (Scatena & Lugo 1995). Vegetation in riparian valleys and slopes suffered the greatest effects, as measured by per cent of stem breaks and uprooted stems per plot. Overall, 1 kg m^{-2} or 455 times the mean daily litterfall fell during the storm (Lodge *et al.* 1991). After 5 y, average

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Table 2. Coarse particulate organic matter (CPOM), coarse particulate organic carbon (CPOC) export (≥12.7 mm) components (g ha^{-1} d^{-1}) and ash % from Bisley Experimental Watersheds, 1987–2005, Luquillo, Puerto Rico. Values are mean ± 1 standard error, * refers to estimated weighted mean.

	Leaves	Wood	Miscellaneous	Total
Bisley 1	3.0 ± 0.5	3.3 ± 0.5	0.5 ± 0.2	6.8 ± 0.9
Bisley 2	4.0 ± 0.5	3.2 ± 0.4	0.7 ± 0.2	8.0 ± 0.9
Combined 1 and 2				
CPOM	3.5 ± 0.3	3.2 ± 0.3	0.6 ± 0.1	7.4 ± 0.6
CPOC	1.3 ± 0.1	1.5 ± 0.1	0.2 ± 0.2	3.0*
Ash %	22.4 ± 1.1	6.6 ± 0.4	46.5 ± 2.0	17.3*

daily litterfall rates and seasonal patterns in litterfall had returned to background levels (Scatena *et al.* 1996). In mid-1990, a series of large storms passed near the watersheds and caused localized effects but much less change than Hugo (Ostertag *et al.* 2003). Differences in species composition among geomorphic settings (i.e. ridges, slopes, valleys) that were apparent before Hugo had not returned after 15 y but differences in stem densities and structure between riparian and upland areas were beginning to emerge (Heartsill Scalley *et al.* 2010). Nevertheless, after 15 y the watershed's basal area and above-ground biomass had returned to pre-hurricane levels while species richness, diversity indices and stem densities exceeded pre-hurricane levels.

Measurement of organic matter and element exports from headwater streams

In both streams, a 12.7 × 12.7-mm metal mesh was placed across the channel and anchored to the entrance structures of culverts that divert all the stream flow beneath a small road. These meshes extend from low-flow stream levels to high flow levels and effectively trap all the CPOM that is transported from the watersheds to the culverts. From 1987 to 2005, collections of all the CPOM that was trapped in the nets were made every other Tuesday and following large storm events. Several mesh sizes and trap designs were tested between 1987 and 1989, as they would unfortunately break during high discharge events. Thus the export values reported for the dates of 1987 to 1989 (Table 2) are considered underestimates because of gaps caused by the failure of the nets. Since 1989, the trapping mesh has withstood the highest discharges and is considered to accurately reflect the total quantity and temporal dynamics of CPOM exported from the drainages. Nevertheless, this 12.7-mm mesh size is larger than the 4 mm used by Wallace *et al.* (1995) in their long-term study of Appalachian mountain streams, than the 2 mm used by Selva *et al.* (2007) in southern Amazon headwater streams and larger than the > 1 mm used in many temperate stream studies of fine particulate matter dynamics (Allan 1995).

Export was calculated from the material collected in the nets over the sampling periods and is reported as mass per area of watershed per day (g ha^{-1} d^{-1}). Samples were dried at 65 °C for a minimum of 2 wk and then sorted. Mass and elements were determined for the sorted categories of leaves, small wood <2.5 cm diameter, large wood ≥2.5 cm diameter and miscellaneous parts (flowers, fruits and other plant parts). A subsample for each of the sorted CPOM categories was analysed for per cent ash (Table 2). The ash content and moisture correction factor were determined utilizing the Leco Thermogravimetric Analyser, model TGA 701 (LECO Corp. 2000, St. Joseph, MI, USA). Ash content calculations are done by the instrument software and reported as a percentage.

Starting in 1993 chemical analyses of C, N, P, K, Ca, Mg, Al, Fe and Mn were conducted on monthly aggregated samples (i.e. two collection periods). Processing of all samples was done at the Analytical Laboratory of the International Institute of Tropical Forestry (USDA-Forest Service, Río Piedras, Puerto Rico). Between January 1993 and January 1995, the macro-Kjeldahl nitrogen method was used (Chapman & Pratt 1979). After February 1995, nitrogen was determined using the macro Dry Combustion method by means of the Leco CNS-2000 Analyser (LECO Corp. 2000, St. Joseph, MI, USA). Prior to January 2003, the samples were mineralized by concentrated nitric acid and 30% hydrogen peroxide. The analytical determination of P, Ca, K, Mg, Mn, Fe and Al were performed by a Beckmann DCP-AES model Spectraspan V (Chao-Yong & Schulte 1985). After January 2003, the digestion procedure changed to a mixture of concentrated nitric acid, concentrated hydrochloric acid and 30% hydrogen peroxide. The same elements were analysed by means of a Spectro Plasma Emission Spectrometer model Spectra Ciros CCD – ICP. This method is a modified version of the procedure that appears in Chao-Yong & Schulte (1985). Before changing analytical methods or instruments, the new method was always validated using certified reference materials and by reanalysing a number of archived samples. This processing maintains the quality and continuity of validity of the long-term datasets.

Organic matter values are reported relative to the size of the entire drainage (g ha^{-1} d^{-1}) above the collection point. Elemental concentrations are reported as mass-weighted (mg g^{-1}) and element flux as (mg ha^{-1} d^{-1}). Values reported as Bisley watersheds combined, are the area-based weighted average of values from Bisley 1 and Bisley 2. Organic matter and element export dynamics were explored by comparing event and monthly values of organic matter, elements and molar carbon to nitrogen (C:N) ratios for all the sorted components (leaves, small wood <2.5 cm diameter, large wood

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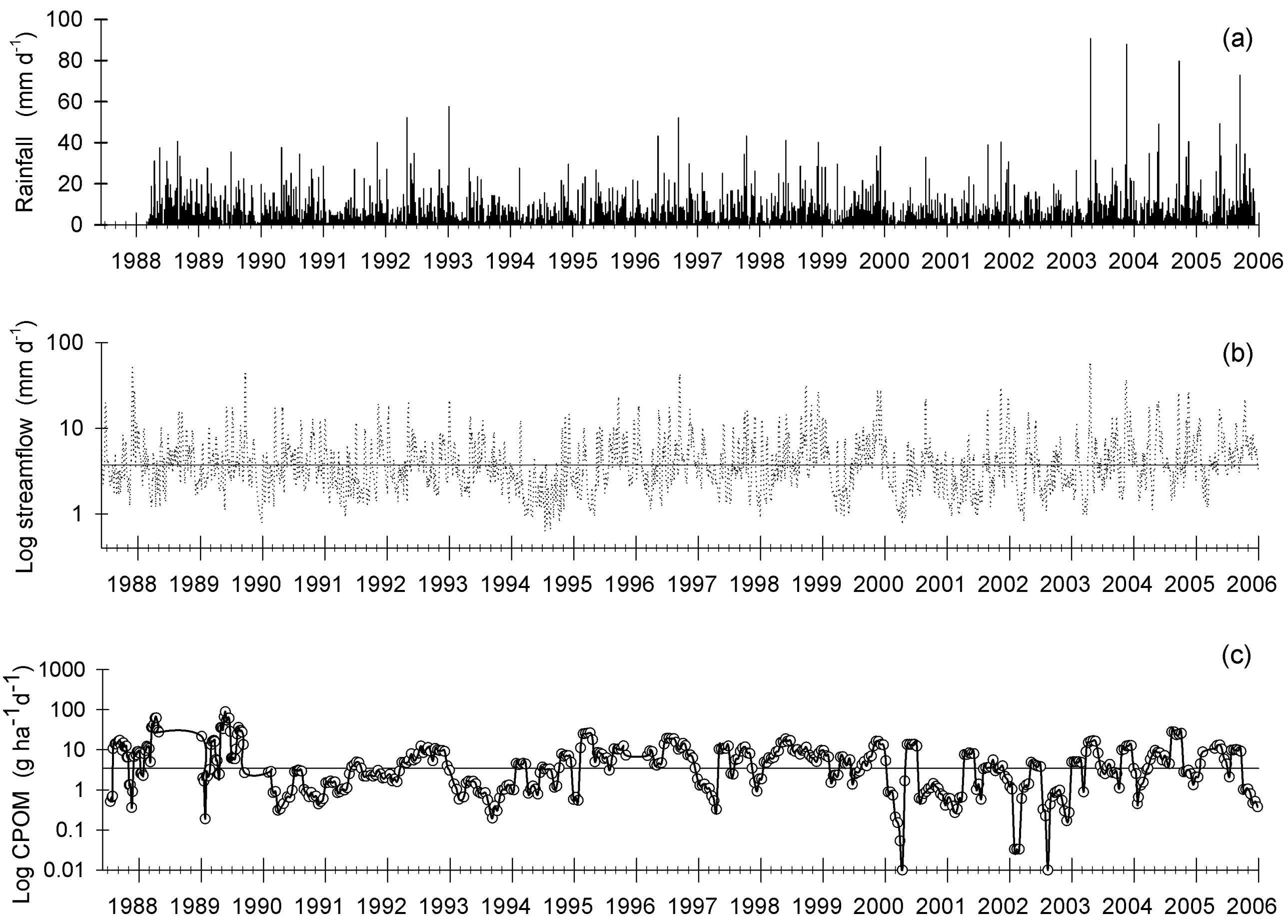

Figure 1. Time series of rainfall, stream flow and exported coarse particulate organic matter (CPOM ≥12.7 mm) from the Bisley Experimental Watersheds 1 and 2 combined, Luquillo, Puerto Rico. Total weekly rainfall (mm d^{-1}) (a), log of weekly average stream flow (mm d^{-1}) (b) and log of 4-wk average CPOM export (g ha^{-1} d^{-1}) (c). Reference line through plot indicates mean value for complete time series.

≥2.5 cm diameter and miscellaneous plant parts). The effects of storms and droughts on organic matter and element exports were assessed by comparing the values of samples taken following an event with the average values of non-event periods and values from other events. Drought periods assessed were those previously identified by Heartsill Scalley *et al.* (2007). The named storms and hurricanes that were compared were Luis: 5 September 1995, Marilyn: 16 September 1995; Bertha: 9 July 1996; Hortense: 10 September 1996; Erika: 5 September 1997; Georges: 22 September 1998; Jose: 20 October 1999; Debbie: 23 August 2000; and Jeanne: 15 September 2004. Recovery of export dynamics was analysed through comparisons of four previously defined periods of distinct forest structure and composition (as presented in Heartsill Scalley *et al.* 2010). The exports for the period pre-hurricane, 5, 10 and 15 y post-hurricane Hugo were compared by subsampling exports from 14-mo periods relative to four time periods: 1988–1989, 1994, 1999 and 2004.

A repeated-measures analysis of variance (ANOVA) with a generalized linear model (GLM) procedure was used in the analyses of mean differences of organic matter and element exports. The post hoc Ryan–Einot–Gabriel–Welsch multiple range (REGWQ) test was used to compare means among months, years and between watersheds. When appropriate, data were $\log_e$-transformed, although $\log_{10}$ is presented. All statistics were done with the program SAS, version 9.1 and were considered significant at an alpha level of 0.05.

RESULTS

Exported coarse particulate organic matter during 1987–2005

Over the 18-y study period, the mean export of CPOM from both watersheds was 7.39 g ha^{-1} d^{-1}. The highest measured exports occurred before and during hurricane Hugo. Periods of consistently low exports occurred during 1990–1991, 1993–1994 and 2000–2002, while relatively high exports occurred between 1995 and 2000 (Figure 1). In 1996, when numerous storms and hurricanes passed the island, both watersheds

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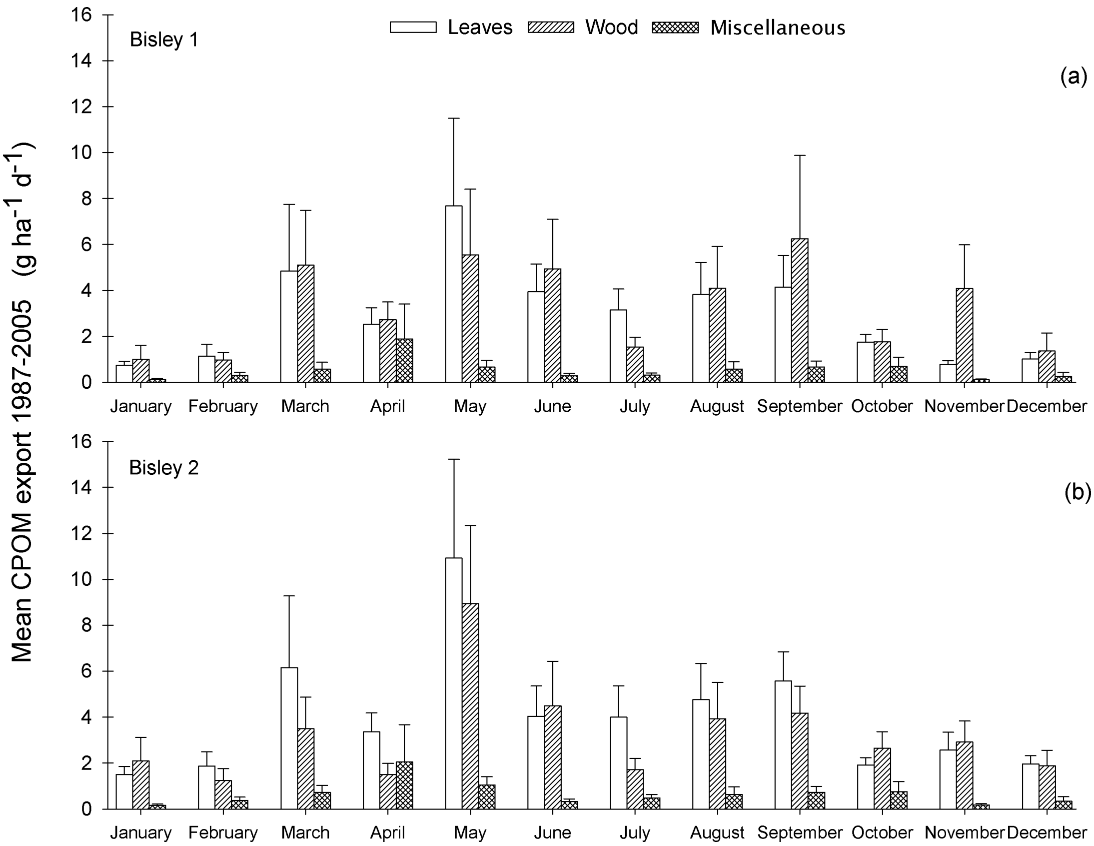

Figure 2. Leaves, wood and miscellaneous plant parts exported (CPOM ≥12.7 mm). Mean monthly values and 1 SE in Bisley Experimental Watershed 1 (a) and 2 (b).

had collections every sampling period. In contrast, during the dry year of 2002 there were 24 non-consecutive weeks without exports. Considering the study period overall, the temporal distribution of CPOM export is highly log-normal. Over the entire period there were, on average, 6 wk y^{-1} where there was no CPOM export and over 72% of the weeks transported less than 2.5 g ha^{-1} d^{-1} of leaves.

Total and individual components of exported CPOM were not statistically different between the two watersheds (Figure 2). However, there was a tendency for more leaf export from Bisley 2 than Bisley 1 (Table 2). Within each watershed there were significant differences in exports among mean yearly and monthly values found for leaves (Bisley 1: $F_{29,455} = 2.72$, $P < 0.001$, Bisley 2: $F_{29,446} = 2.60$, $P < 0.001$), wood (Bisley 2: $F_{29,446} = 1.84$, $P = 0.005$), and total CPOM (Bisley 1: $F_{29,455} = 2.31$, $P < 0.001$, Bisley 2: $F_{29,446} = 2.83$, $P < 0.001$). Mean export of wood in Bisley 1 was not significantly different among months or years (Figure 3). When exports from the two watersheds are combined, the year before (1988) and the year of hurricane Hugo (1989) had the highest values for leaf CPOM (12.7, 11.4 g ha^{-1} d^{-1}) ($F_{29,931} = 5.14$, $P < 0.001$) and total CPOM (22.5, 20.4 g ha^{-1} d^{-1}) ($F_{29,931} = 4.88$, $P < 0.001$) exports (Figure 4). Mean wood exports were lowest (<1 g ha^{-1} d^{-1}) in 1993 and 2002 ($F_{29,933} = 2.42$, $P < 0.001$) and in some years as many as 12 collection periods (21% of the time) did not have measurable wood exports (Figure 4).

Seasonal or monthly CPOM exports varied following the general pattern of rainfall and stream discharge (Figure 5). The greatest amounts of leaf ($F_{11,949} = 3.80$, $P < 0.001$), wood ($F_{11,949} = 2.64$, $P = 0.002$), and total litter ($F_{11,949} = 3.76$, $P < 0.001$) were exported during May, while the lowest amounts were exported during December, January and February. However, there were also relatively high exports observed during March and this may be due to high litter fall from trees and lianas during the dry season.

Exported elements in CPOM during 1993–2005

Concentrations. Mass-weighted concentrations of total elements exported were different between the watersheds. Bisley 1 had higher values for K (ANOVA $F_{1,1058} = 4.40$, $P = 0.036$) while Bisley 2 had higher values for Ca (ANOVA $F_{1,1058} = 79.6$, $P < 0.001$), Mg (ANOVA $F_{1,1058} = 69.6$, $P < 0.001$), Al (ANOVA $F_{1,1058} = 8.56$, $P = 0.035$) and Fe (ANOVA $F_{1,1058} = 5.79$, $P < 0.0163$)

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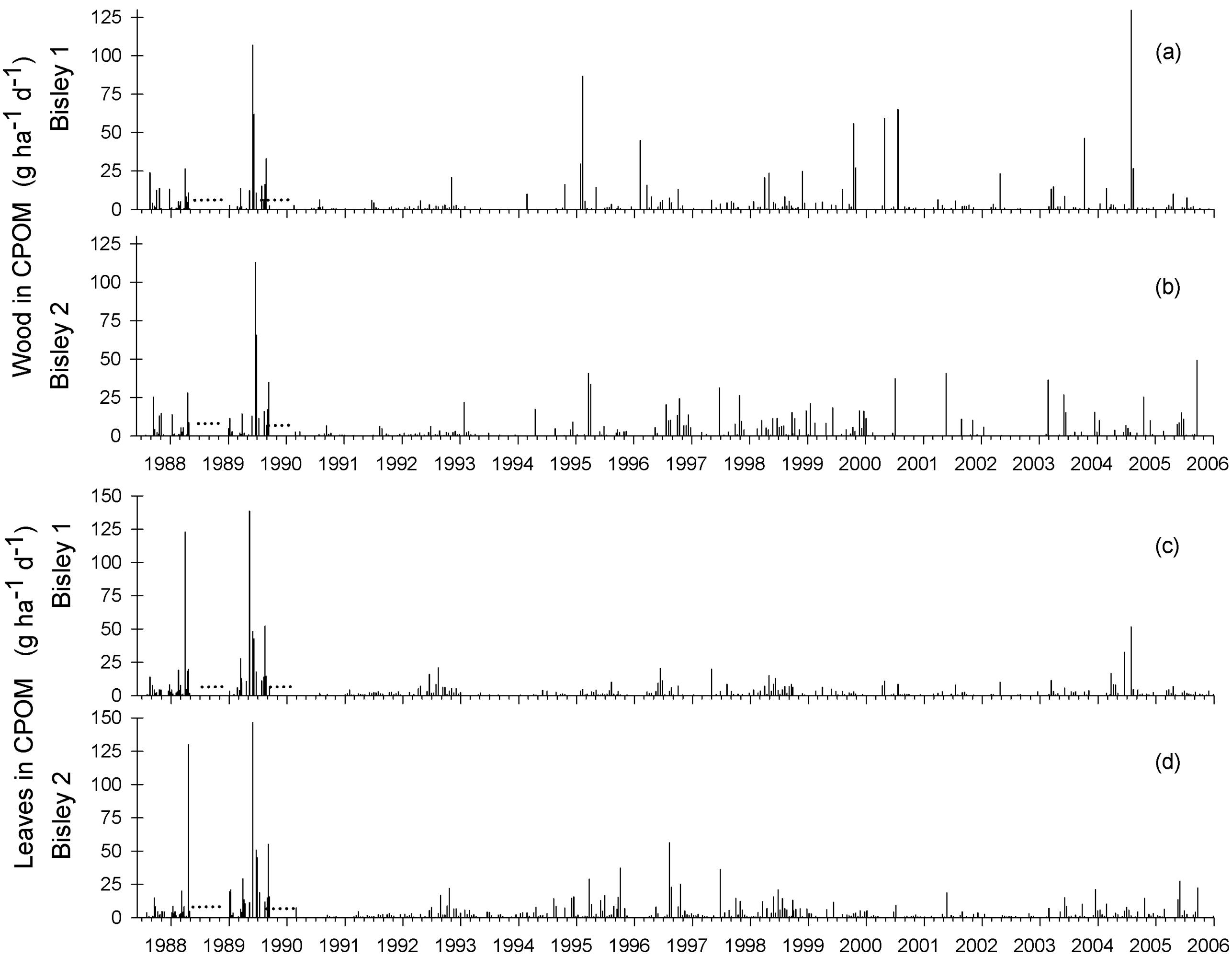

Figure 3. Export of wood and leaves ($\geq$ 12.7 mm) 1987–2005 from Bisley Experimental Watershed (BEW). Wood for BEW1 (a), BEW 2 (b), leaves for BEW 1 (c) and BEW 2 (d). Dates with no data are marked with dots.

exports. There were no differences in total concentrations of N, P and Mn between the watersheds. Leaves and miscellaneous litter components (including flowers and fruits) had higher element concentration values of N, P, K, Ca, Mg, Al, Fe and Mn compared with wood (Table 3).

In Bisley 1, there were monthly differences in concentration of elements exported in leaves for N ($F_{11,152} = 2.45$, $P = 0.008$), P ($F_{11,152} = 2.48$, $P = 0.007$) and Ca ($F_{11,152} = 2.73$, $P = 0.003$). Exports of N and P were highest in September, and Ca was highest in December. Bisley 2 had no differences in the concentrations of monthly element exports. For the combined watersheds, differences among months in total CPOM element exports were weak and followed the same patterns as those observed in Bisley 1 for N, P and Ca. There were differences among years for combined watersheds ($F_{12,1047} = 2.24$, $P < 0.008$) in total CPOM element concentrations of all elements (N, P, K, Ca, Mg, Al, Fe, Mn).

Monthly C:N ratios fluctuated for leaves, wood, miscellaneous and total organic matter. C:N ratios (mean $\pm$ 1 SD) were highest for large wood (110 $\pm$ 51.1), followed by small wood (76.8 $\pm$ 33.7), and were lowest (24.2 $\pm$7.9) for miscellaneous plant parts (Table 3). The highest leaf C:N ratios of exported leaf CPOM occurred in March while the lowest were observed during the rainy months of May and September (Figure 5).

Element fluxes. Leaf element flux accounted for more than 70% of all CPOM element exports (Table 4). Element fluxes from leaf exports were greater in Bisley 2 than in Bisley 1 over the entire study period for N, P, K, Ca and Mg. Leaf flux exports for Al, Fe and Mn were the same for both watersheds. When combining values from the two watersheds, monthly differences in leaf element fluxes were observed for N ($F_{11,268} = 4.06$, $P < 0.0001$), P ($F_{11,270} = 3.49$, $P < 0.0001$) and Ca ($F_{11,270} = 3.58$, $P < 0.0001$). The highest fluxes occurred in May and September, while the lowest were in February (Figure 5). Fluxes of K, Mg, Al, Fe and Mn also followed

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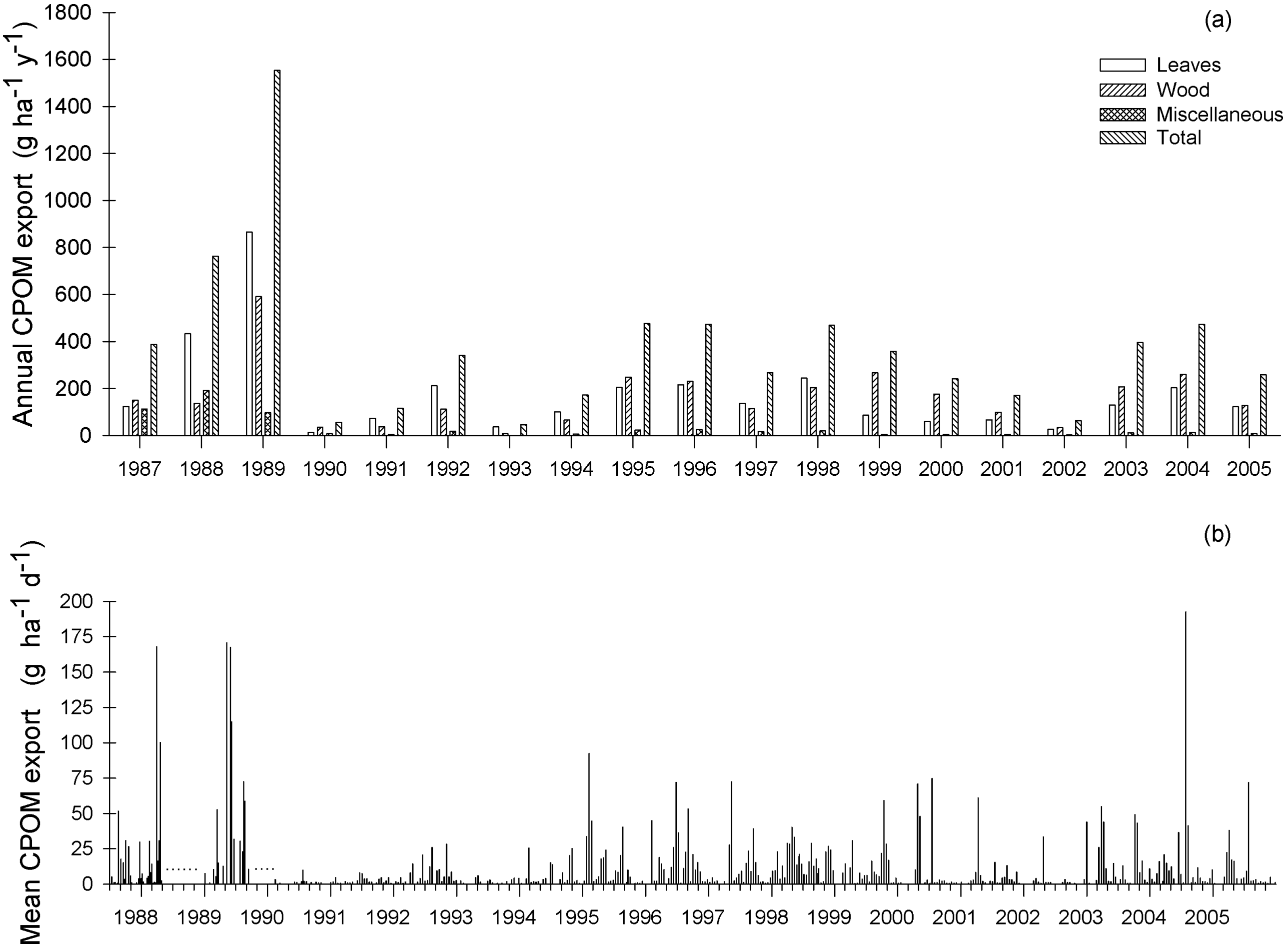

Figure 4. Export (CPOM ≥12.7 mm) from the combined Bisley Experimental Watersheds, annual total export and components (a), and 2-wk values for total export 1987–2005 (b). Dates with no data are marked with dots.

this pattern, although these differences in fluxes were not statistically significant. Annual leaf element exports from the combined watersheds were highest in the wet years of 1996, 1998 and 2004, and lowest in the dry years 1993 and 2002. Wood and total element fluxes followed the same monthly and yearly patterns as leaf fluxes, but only had monthly differences for N, P and Ca. Consistently, we observed higher values of N and Ca during rainy May, and higher values of P in September, a windy month when most hurricanes and low-pressure systems pass the island. The lowest element fluxes occurred during February and December.

Leaf CPOM exports and element fluxes during meteorological events

The highest leaf exports and element fluxes occurred during large storms and hurricanes. The lowest exports occurred during droughts. The exceptions were exports associated with the relatively small storms/hurricanes José and Debbie, which had values close to those observed during droughts. Relative to other storms, the highest leaf fluxes of N, P, Ca, Mg, Al and Fe were observed following storm Bertha.

Comparisons of daily exports during the sampling prior to hurricane Hugo with exports from 5, 10 and 15 y after (1994, 1999, 2004) indicate that while median daily exports were similar, exports associated with moderate flow events were greater prior to Hugo than after (Figures 4 and 6). Export of leaves was greater in the pre-Hugo period, with a mean of 9.1 g ha^{-1}d^{-1}, compared with mean values of 3.1, 1.5, 3.1 g ha^{-1} d^{-1} respectively 5, 10 and 15 y after ($F_{3,455} = 7.53$, $P < 0.0001$). Moreover, comparisons by month of mean daily exports in these four periods also showed consistently higher values in the pre-hurricane period.

DISCUSSION

During our 18-y study period, the CPOM (≥12.7 mm) export time series was an excellent indicator of hillslope and stream interactions at the watershed scale.

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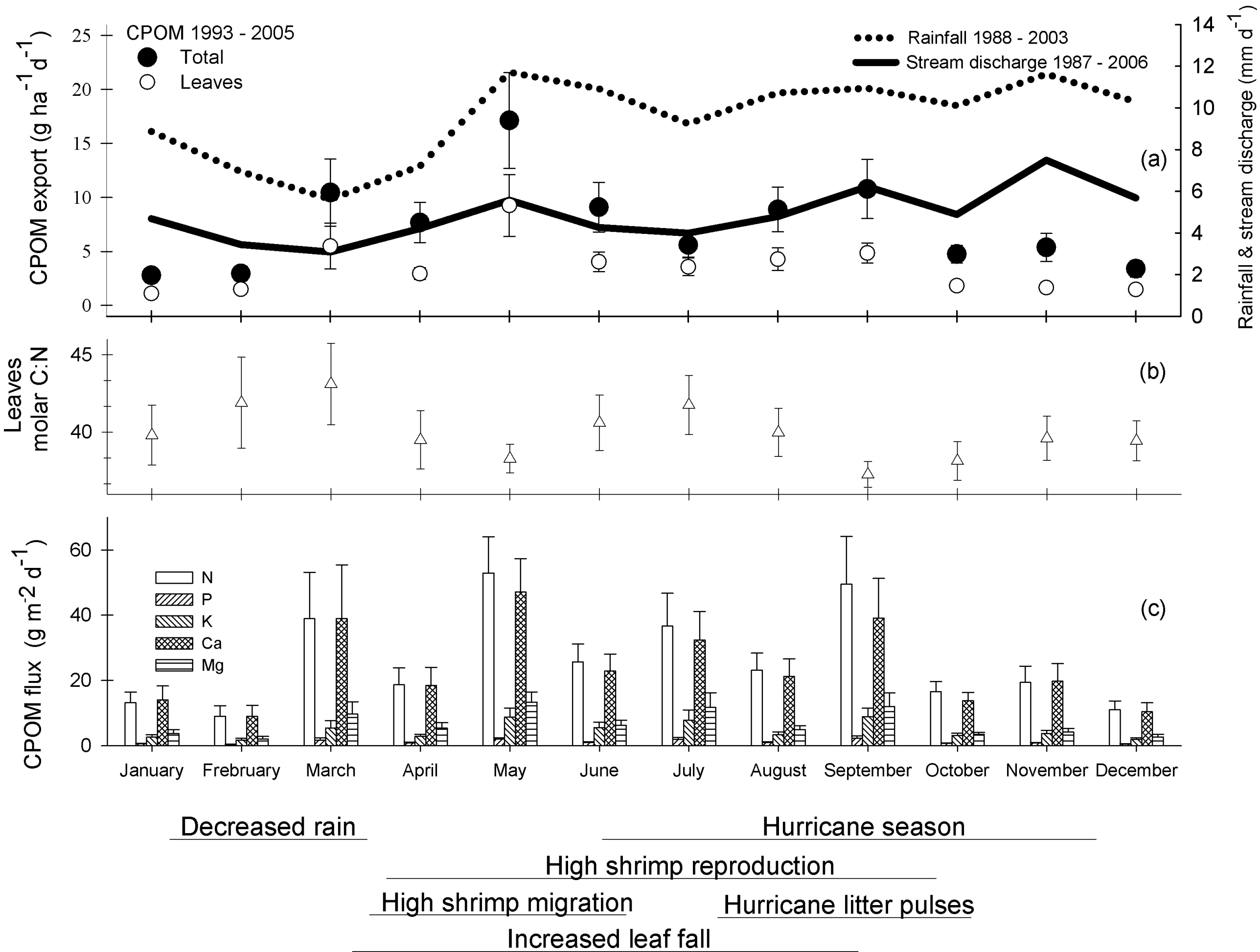

Figure 5. Mean monthly values and 1 SE for export of CPOM (≥12.7 mm) in the Bisley Experimental Watersheds, Luquillo, Puerto Rico. Total and leaf CPOM export on left y-axis, rainfall and stream discharge on right y-axis (a), molar C:N ratios for leaves from CPOM export (b), total CPOM element flux (c) and timing of selected ecological events in the study ecosystems (d). Data on the timing of ecological events are from Scatena (2001) and Heartsill Scalley *et al.* (2001).

Intra-annual patterns have distinct peaks that originate mainly from rainfall patterns, and to a lesser extent from seasonal phenology. Interannual patterns were related to hurricanes, storms and droughts, and the successional status of the forest. Overall CPOM export follows the seasonal pattern of rainfall and streamflow. However, we also found that the variation in the quantity and quality of CPOM exported depends on traits of particular input events and the successional status of forest. More than 10 events in our study period that were not hurricane-related had exports of more than 75 g ha^{-1} d^{-1}. Most of these non-hurricane events were associated with intense but localized rainfall of more than 60 mm d^{-1}. At smaller time scales, a positive relationship of organic matter export with rainfall and stream discharge had been reported for this site (Larsen *et al.* 1999, Ortiz Zayas 1998).

There were distinct seasonal patterns in both quantity and quality of exports. The seasonal pattern of CPOM exported followed a combination of the monthly rainfall patterns and seasonal litterfall patterns, with distinct peaks in May and September (Figure 5). The greatest exports of leaves typically occurred during April, May and September, which have intense rain showers (Heartsill Scalley *et al.* 2007) and the greatest numbers of species (at least 16) synchronously having leaf-fall events (Zalamea & González 2008, Zou *et al.* 1995). Variation in the quality of exports, as expressed by C:N ratios, were typically highest during March, when litterfall increases. Dry-season element absorption before leaf abscission may lead to higher C:N values than those observed in the rainy season when leaf fall was driven by intense rainfall and winds. During March, the leaf CPOM exports also increased in part because of species-specific leaf-fall events, such as those of the thick-leaved lianas *Schelegelia brachyantha* and *Marcgravia sintenissii* (Zalamea & González 2008). Relative to trees in this forest type, lianas contribute high amounts of leaf litter to riparian areas (Heartsill Scalley 2005).

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Table 3. Mean ± 1 SE of element concentration (mg g^{-1}), per cent carbon and carbon to nitrogen ratios of coarse particulate organic matter (CPOM ≥12.7 mm), leaves, wood and miscellaneous (flowers, fruits and other particulates) exported 1993–2005, Bisley Experimental Watersheds, Luquillo, Puerto Rico.

	Leaves	Wood	Miscellaneous
Bisley 1			
N	10.3 ± 0.19	4.84 ± 0.13	10.7 ± 0.32
P	0.37 ± 0.01	0.16 ± 0.01	0.66 ± 0.03
K	1.57 ± 0.07	0.76 ± 0.03	5.84 ± 1.20
Ca	7.72 ± 0.17	4.42 ± 0.21	7.65 ± 0.29
Mg	1.94 ± 0.06	0.90 ± 0.03	2.73 ± 0.06
Al	6.27 ± 0.36	1.75 ± 0.13	11.0 ± 0.60
Fe	7.74 ± 0.54	2.35 ± 0.23	18.2 ± 1.25
Mn	1.55 ± 0.25	0.32 ± 0.04	2.84 ± 0.57
Bisley 2			
N	11.4 ± 0.20	5.71 ± 0.13	8.61 ± 0.28
P	0.48 ± 0.01	0.20 ± 0.01	0.59 ± 0.01
K	1.87 ± 0.06	1.01 ± 0.05	2.51 ± 0.13
Ca	10.6 ± 0.18	6.23 ± 0.16	8.43 ± 0.26
Mg	2.62 ± 0.06	1.17 ± 0.02	3.85 ± 0.09
Al	7.63 ± 0.41	1.88 ± 0.11	13.3 ± 0.55
Fe	10.0 ± 0.61	2.55 ± 0.19	21.6 ± 1.10
Mn	1.04 ± 0.23	0.30 ± 0.05	3.08 ± 0.75
Carbon (%)	37.9 ± 0.30	45.8 ± 0.11	27.4 ± 0.58
Molar C:N	29.2 ± 0.30	89.9 ± 2.00	24.2 ± 0.48
n	324	470	272

The daily average export (7.39 g ha^{-1} d^{-1}) and the CPOM export relative to the amount of litter falling into the stream channel (2.3%), or the entire watershed (0.024%) is comparable with other available studies. During 1 y, CPOM (>2 mm) exports from southern Amazonian streams were 0.03% of watershed leaf-litter inputs (Selva *et al*. 2007). In Appalachian streams, CPOM (>4 mm) exports ranged between 1.8–3.8% of riparian litterfall inputs over a 9-y period (Wallace *et al.* 1995). For headwater streams in Hawaii, Larned (2000) reported a very large range of CPOM (>4 mm) exports. During drought periods, exports were 8% of riparian litter, but in non-drought periods exports were as high as 40% of inputs (Larned 2000). All of these studies indicate a high level of instream processing and breakdown of litter.

Measurements of litter falling directly into streams, riparian and upland areas indicate that Bisley streams receive slightly less litterfall and have more temporal variation in litter inputs than adjacent riparian and upland areas (Beard *et al.* 2005, Crowl *et al.* 2006). Overall the watersheds have a high internal processing efficiency and only a small percentage (0.02–0.03%) of mean litter falling across the entire watersheds is exported as CPOM. Likewise, over 97% of the litter inputs to the active channel are either decomposed in place or broken into fine fragments that were transported as fine particulates.

Previous studies indicate that during 1 y CPOM (including both coarse and fine) accounted for 14% of carbon exports from the watersheds (Ortiz Zayas 1998, Ortiz Zayas *et al.* 2005). From these exports, Ortiz Zayas (1998) estimated that most of the carbon was respired (45%) with the rest (41%) exported as dissolved organic carbon. During dry years, particulate exports (coarse and fine) can decrease to 12% while in wet years it can increase to 32% (Ortiz Zayas 1998). In nearby and similar-sized streams in the same forest type, dissolved organic carbon (DOC) exports was 204 g ha^{-1} d^{-1} and fine particulate organic carbon (POC) was 20.6 g ha^{-1} d^{-1} representing 90% and 9.0% of exports (McDowell & Asbury 1994). The contribution of coarse particulate organic carbon (CPOC) from Bisley CPOM (≥12.7 mm) is 3.0 g ha^{-1} d^{-1} and represents 1.3% of stream exports (Table 2).

The carbon turnover length, which measures the rate at which organic material is lost from streams relative to the rate at which it is used (Webster *et al.* 1995), is estimated at a relatively small 0.4 km for these streams, and further indicates these streams have high carbon retention relative to downstream export (Ortiz Zayas 1998). The measured CPOM exports reported here support these previous studies and indicate that both local site conditions and the time between export events promotes the breakdown and in-stream processing of large amounts of CPOM. Rapid leaf processing occurs in these streams and most leaves can lose between 63% and 79% of their mass in 6 mo and over 90% within 1 y (Beard *et al.* 2005, Crowl *et al.* 2006). In-stream leaf-litter decomposition rates also vary by species, are related to the amount and timing of precipitation, and to processing by detritivore fauna (Beard *et al.* 2005, Crowl *et al.* 2006, Sullivan *et al.* 1999). In stream reaches near our collection nets, leaf consumption by the dominant macro-invertebrate consumers (*Xiphocaris elongata* and *Atya lanipes*) is estimated at 350 g m^{-2} y^{-1}, or 40% of direct litterfall inputs (Cross *et al.* 2008, Crowl *et al.* 2006).

Long-term average litterfall for this forest type ranges from 2.38 to 3.45 g m^{-2} d^{-1} (Beard *et al.* 2005, Lodge *et al.*

Table 4. Mean ± 1 standard error of element export from coarse particulate organic matter (CPOM >12.7 mm) 1993–2005, Bisley Experimental Watersheds, Luquillo, Puerto Rico.

	N	P	K	Ca	Mg	Al	Fe	Mn
Mass-weighted (mg g^{-1})	4.39 ± 0.14	0.18 ± 0.01	0.84 ± 0.08	3.96 ± 0.17	0.95 ± 0.04	2.60 ± 0.11	3.38 ± 0.17	0.56 ± 0.08
Element flux (mg ha^{-1} d^{-1})	26.3 ± 2.40	1.13 ± 0.11	4.72 ± 0.52	23.7 ± 2.20	6.63 ± 0.73	20.3 ± 2.58	28.9 ± 4.13	3.73 ± 0.82
Flux from leaves (%)	68.8 ± 1.45	67.7 ± 1.46	64.8 ± 1.59	67.2 ± 1.46	67.2 ± 1.43	72.6 ± 1.37	70.2 ± 1.42	69.7 ± 1.40
n	284	286	286	286	286	286	286	286

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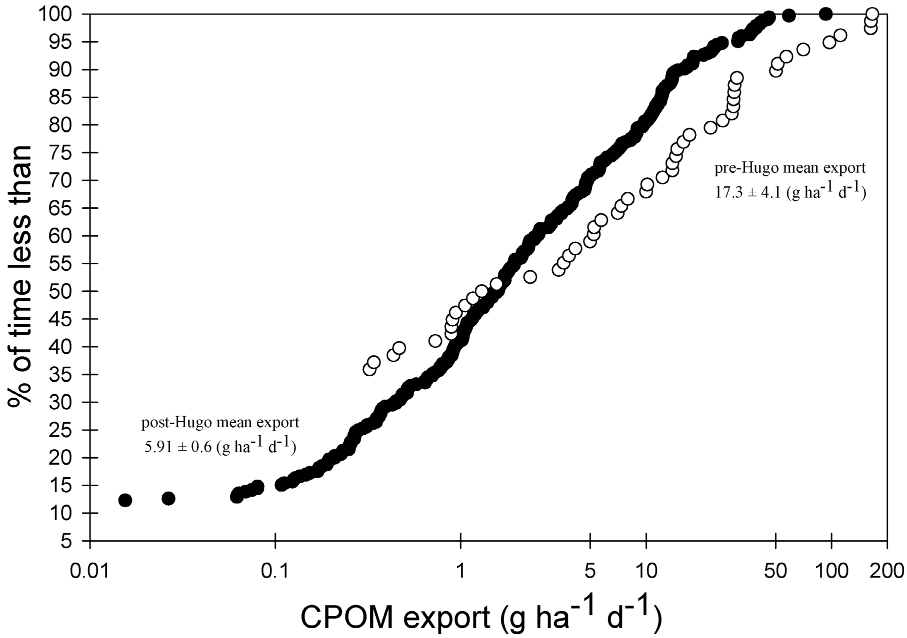

Figure 6. Export duration curves, expressed as per cent of time export is less than a given value, for the combined Bisley Experimental Watersheds, Luquillo, Puerto Rico. Total CPOM (≥12.7 mm) exports pre-hurricane Hugo in empty circles and post-hurricane Hugo in filled circles.

1991, Ostertag *et al.* 2003, Scatena *et al.* 1996). However, defoliation associated with the passage of hurricanes (e.g. Hugo, Georges) has produced average daily litter falls of 477 to 1083 g m^{-2} d^{-1} (Lodge *et al.* 1991, Ostertag *et al.* 2003). Following hurricane Hugo, it took approximately 5 y for litterfall rates in the watersheds to return to pre-Hugo levels (Scatena *et al.* 1996). Various other storms and hurricanes affected the study area for an additional 4 y; therefore, a total of eight of the 18 study years (44% of the record) were directly influenced by storms and hurricanes. Extended periods of below-average rainfall (i.e. meteorological droughts) occupied an additional 10% of the study period (Heartsill Scalley *et al.* 2007). During these droughts, which mostly occurred in January and February, there were consistently low to no exports of CPOM. The sequence of storms and the successional status of the forest also influenced CPOM exports. For example, one of the largest events occurred on 27 July 2004 and was associated with a local tree fall that produced an equivalent of 192 g ha^{-1} d^{-1} of CPOM exports. The following week had a relatively high weekly rainfall of 80 mm d^{-1} (Figure 2) but the organic matter exported was only a fourth of the previous week. Events that transported more than 10 g ha^{-1} d^{-1} of material occurred 17% of the time or on average once every 2.8 mo post-Hugo and on average once a month pre-Hugo (Figure 6).

Most of our hypotheses were confirmed, as indeed (1) CPOM export follows the seasonal pattern of rainfall and streamflow, (2) exported CPOM is a very small percentage relative to litterfall entering these streams, (3) there is seasonal variation in CPOM quality. However, hypothesis (4) CPOM export recovers at the same time scale as does litterfall following hurricane defoliation was not confirmed. We initially expected that the recovery of CPOM export would follow the same general pattern as watershed litterfall rates, which took only 5 y to return to pre-hurricane amounts (Scatena *et al.* 1996). After 10 y of succession in the study watersheds, riparian vegetation was just beginning to return to pre-hurricane stem density, while species composition had not (Heartsill Scalley *et al.* 2010).

The actual exports that occurred during hurricane Hugo are unknown because storm flows broke the collection nets and limited access to the collection sites. Culverts and bridge crossings across the region were clogged with plant debris and large trees fell in and around the Bisley Experimental Watersheds riparian zones. In Bisley 2, several large introduced mahogany trees fell across the channel where they remained suspended in the air for nearly a decade before they decomposed and fell into the adjacent riparian area. However, across the Luquillo Mountains most of the large, hurricane-induced debris dams were naturally removed within 5 y of the hurricane event (Scatena & Gupta 2012). It was calculated that 1083 g m^{-2} of litter fell across the watershed during the storm (Lodge *et al.* 1991). Considering the average exports relative to litterfall that occurred with other large storms in the series, Hugo should have transported over 1000 g ha^{-1}d^{-1} or over 100 times the average daily exports.

In general, 16 y after hurricane Hugo median daily exports and exports during low-flow conditions were similar to those observed pre-Hugo. High-flow exports

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and storm-associated exports have not returned to pre-hurricane values after 16 y, although median values did (Figure 6). These observations raise two questions. First, why do subsequent hurricanes fail to produce similar high amounts of POC export as with Hurricane Hugo? Second, what controls the long-term temporal pattern of POC export in these streams?

Part of the explanation to the first question involves the magnitude of the events and the type of forest they interacted with. Post Hugo, hurricanes had lower wind speeds and affected a young, rapidly regenerating forest. Thus, they did not result in the same levels of defoliation or biomass reduction as hurricane Hugo. This indicates that the long-term pattern of CPOM export (and hurricane effects on vegetation) is associated with the level of maturity of watershed vegetation in relation to the intensity of the passing hurricane event. The greater the maturity of the vegetation, i.e. level of biomass, structural development, tree height, forest-floor debris, the greater is the potential for hurricane effects on vegetation and larger the CPOM exports. In contrast, storms that affect younger, less-mature forests will export less CPOM. Although seasonal patterns in exports, median daily exports, and exports during low-flow periods were similar between the mature (i.e. pre-Hugo) and younger (post-Hugo) forests, this study indicates moderate- and high-flow exports are still less after 16 y of succession. Thus, the state of development or maturity of the vegetation places a limit on how much CPOM can be exported during a storm that is independent of the level of hillslope or stream run-off. In conclusion, the synergy between hurricane intensity and frequency, and level of vegetation maturity dictates the long-term temporal pattern of CPOM export in these watersheds.

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