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Hurricane Georges Accelerated Litterfall Fluxes of a 26 yr-old Novel Secondary Forest in Puerto Rico

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1. Introduction

Defoliation and fallen debris are common visible effects of hurricanes and are accompanied by invisible effects such as altered element fluxes, changes in element concentration of plant parts, and variability of processes (Lugo 2008). While ecologists are increasingly documenting visible effects of hurricanes and other disturbances (Everham and Brokaw 1996, Lugo 2008, Turton 2008) less work has been conducted on the invisible effects of hurricanes, which center on the functional attributes of forests. One such functional attribute with both visible and invisible components is litterfall and associated mass and element fluxes. Examples of studies of tropical forests where litterfall mass and element fluxes were monitored before and after a hurricane include work in Puerto Rico (Lodge et al. 1991, Frangi and Lugo 1991, Scatena et al. 1996, Beard et al. 2005, Van Bloem et al. 2005), Hawaii (Herbert et al. 1999), and Mexico (Whigham et al. 1991). These studies cover a range of climates (dry, moist, and wet) and focused on mature native vegetation. To avoid repetitive citations to these papers, we will refer to them by country when the information cited is supported by all of them.

The expansion of human populations and changes in land cover due to deforestation, use, and land abandonment, cause increases in the cover of tropical secondary forests (Brown and Lugo 1990) and there is a need to learn about their functioning and resilience (Lugo and Helmer 2004, Chazdon 2008, Lugo 2009). We had an opportunity to contribute to this research need when Hurricane Georges passed over a study area (Fig. 1) where we were monitoring litterfall and element fluxes of a secondary forest with a novel composition of introduced and native tree species (below). The hurricane moved at 24 km/h over Puerto Rico between 21 and 22 September 1998 as a Category 3 hurricane in the Saffir Simpson scale with maximum sustained winds of 184 km/h and occasional gusts of 240 km/h.

We addressed two questions: How resilient to hurricane winds are the fluxes of litterfall mass and chemical elements in a young secondary forest and how do resilience and fluxes in this forest type compare with those of mature forest vegetation in dry, moist, and wet climates? The comparison with mature forests sheds light on the effects of age in forest response to hurricane winds. Moreover, since our study forest had a mixed composition of introduced and native species and the mature ones were dominated by native species, the comparison adds value to the question of the effects of introduced species on ecosystem functioning.

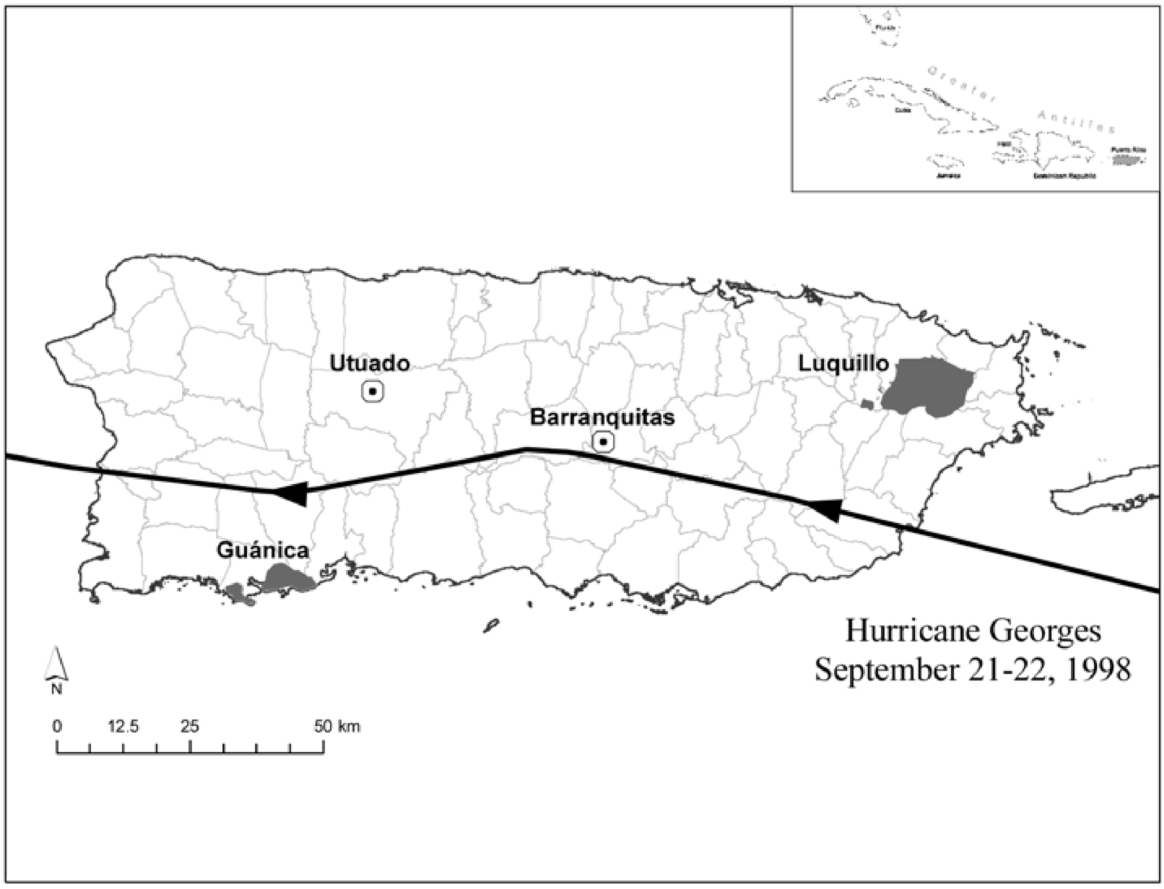


Fig. 1. Location of the study site in relation to the path of Hurricane Georges.

2. Methods

Study area - The study area is located at 416 m elevation in the Jácanas sector, Caguana ward, Utuado, Puerto Rico (lat 18°17’07.995” N, long 66°43’57.446”W NAD 83 (CONUS) CORS96). The site is in the subtropical warm wet moist forest life zone (*sensu* Holdridge 1967) with an annual rainfall of 2331 mm (NOAA 1998). The soil was classified as an Inceptisol and is now classified as a vertic Eutopeps, specifically Múcara clay (Lugo López 1977). The Múcara soil group is a fine, montmorillonitric soil. The Múcara clay sub order is moderately deep, well drained, and occurs on side slopes of humid volcanic uplands. The parent material at the site is non-carbonate sedimentary rock, adjacent to intrusive rocks.

The site was used for coffee production between 1910 and January 1972. Thus, the forest was 26 yr-old when the hurricane passed, although some of the canopy trees were older as they provided shade for coffee trees during the period of active production. Before the hurricane, the stand had tall coffee shade canopy trees (mean of the tallest three trees was 26 m) dominated by native (*Miconia prasina, Schefflera morototoni*) and naturalized (*Syzygium jambos*) tree species. Average tree height was 9.4 ± 0.4 m, n = 168 (Popper *et al.* 1999). *Syzygium jambos, Miconia prasina*, and *Coffea arabica* (also a naturalized species) dominated the understory. There were 15 to 20 (three years before and four years after the hurricane, respectively) canopy tree species, 18 to 23 understory tree species, and 26 seedling and sapling species in 0.1 ha (21 m^2 for the seedling and sapling species count). Tree basal area ranged from 20 to 25 m^2/ha (Lugo et al. 2005). Because of the high Importance Value of introduced and naturalized species (23 percent for canopy trees, 67 percent for understory trees, and 34 percent for seedlings and saplings), the forest is an example of new or novel forests on abandoned agricultural lands (*sensu* Lugo and Helmer 2004, Hobbs et al. 2006). These forests are highly fragmented over the landscape, with most fragments being < 1 ha (Lugo 2002).

A grid of 10 m x 10 m plots was overlaid over a 50 m x 20 m forest area and on February 25, 1998, we randomly placed two 50 cm x 50 cm wire baskets with plastic lining in each plot to collect litterfall. Our measurements do not estimate coarse wood fall (macro litter), which requires larger plots (Newbould 1967). The 20 baskets were set above the soil and emptied every two weeks over a period of two years (February 25, 1998 when baskets were placed in the forest to February 15, 2000, the last time baskets were emptied). The sampling consisted of 47 biweekly collections, 20 baskets per collection. For each collection we averaged the weights of each of the 20 baskets. However, for the statistical analysis we used all baskets or 940 observations.

The collection interval was affected by the hurricane, as we could not gain access to the site for 61 days, *i.e.*, between the last pre-hurricane collection of September 10, 1998 and the hurricane collection of November 10, 1998. Fortunately, all baskets were intact and collected at that time. We estimated the instantaneous hurricane-peak fluxes of mass and elements by subtracting from the hurricane collection the litter that fell previous to September 21 and after September 22, and assumed the site was exposed for 24 hr to hurricane winds. We based this assumption on the direct observations of Van Bloem *et al.* (2005) at Guánica Forest just south of our site. For the material that fell before September 21, we extrapolated the rate of the last pre-hurricane collection by 11 days. Similarly, we estimated the post-hurricane fall by extrapolating the first post-hurricane rate between November 10 and December 1, 1998 by 49 days (the time between September 23 and November 10, 1998).

Samples were sorted in the laboratory into leaves, wood ≤ 2 cm diameter, wood > 2 cm diameter, flowers and fruits, and miscellaneous. Sorted litter was oven-dried to constant weight at 65 ^{o}C and ground through an 18-mesh (1 mm) sieve with a Wiley Mill. All ground litter samples were analyzed for P, K, Ca, Mg, Al, Mn, and Fe with a Beckman plasma emission spectrometer (Spectra Span V). Samples were digested with concentrated HNO_3 and 30 percent H_2O_2 using the digestion method recommended by Luh Huang and Schulte (1985). Ash was determined by igniting 1 g samples in a muffle furnace at 490 ^{o}C for at least 10 hr (Wilde *et al.* 1979). Total N, total C, and total S were analyzed using the dry combustion method in LECO Corp. (1995) by means of a LECO CNS-2000 analyzer. In this method, a sample of known weight is combusted by heating it to a high temperature (1300 ^{o}C) inside a resistance furnace and in a stream of purified oxygen. Precision for all analyses was assured by running samples of known chemical composition every forty determinations. These control samples (citrus leaves [NBS-1572], peach leaves [NIST-1547] and pine needles [NIST-1575]) were obtained from the National Institute of Standards and Technology, USA. The calibration standards (tobacco leaves, orchard leaves, and alfalfa) used in the total C, N, and S analysis were obtained from LECO Corporation in St. Joseph, MI.

Our chemical analysis of 91 litterfall samples were distributed as follows: 22 leaf fall, 20 wood fall with diameter ≤ 2 cm, 11 wood fall with diameter > 2 cm, 21 flowers and fruits fall, and 17 miscellaneous fall. The number of samples depended on the availability of sufficient material for all chemical determinations. For the purpose of estimating element return, we combined samples with low amounts for analysis such that we analyzed litterfall samples representing all the months between the first collection in March 10, 1998 and September 21, 1999. This pooling of samples corresponded to 38 of the 47 biweekly collection of litterfall. We did not have chemical analyses for litterfall samples collected after September 21, 1999. For the estimate of element return in these remaining 9 biweekly collections of litterfall (those collected after September 21, 1999), we used the mean element concentration of all analyses for the particular element and litterfall component.

We converted element concentration data into units of element mass per ground area by multiplying element concentration by the corresponding mass of litterfall. The annual weighted element concentration was estimated by dividing the annual element mass return in a litterfall compartment by the annual mass fall of that compartment. Within-stand nutrient use-efficiency is the inverse of the weighted nutrient concentration of litterfall (Vitousek 1982). To estimate the C/N and N/P element molar ratios, we divided the concentrations of C, N, and P by 12, 14, and 30.97, respectively, to express them in molar units.

Litterfall mass and element mass fluxes, and element concentration data were tested for normality and homogeneity of variance prior to further statistical analysis. We used the Shapiro-Wilk W test for goodness of fit of the normal distribution and four tests (O'Brien [.5], Brown-Forsythe, Levene, and Bartlett) for equal variances. When the assumptions of normality and equal variances were met, we used Oneway ANOVA to determine significant difference at $p < .05$.

A repeated measures analysis of variance (ANOVA) with a generalized linear model (GLM) procedure was used for the analysis of mean differences of litterfall rates (total, wood, leaf) among collection periods (using all 940 individual basket observations coded for date of collection). When significance differences were found, the post hoc Ryan-Einot-Gabriel-Welsch multiple range (REGWQ) test was used to compare means among collection periods. These statistics were done with SAS Version 9.1, SAS Institute 2003 at alpha <.05. We also used version 7.0 of the SAS Institute Inc. (2007) JMP program for Macintosh for calculating descriptive statistics.

3. Results

Litterfall Mass—Total litterfall rates spanned four orders of magnitude, and two large pulses dominated the pattern of biweekly litterfall (Fig. 2a). Peak rates of litterfall occurred in the hurricane collection and on the December 15, 1998 collection (post-hurricane fall). These two rates were the only significantly different rates among the 47 bi-weekly collections. Two weeks after the hurricane collection and one month after the second pulse, total litterfall rate reached a low value. After the second low value, litterfall rates increased until the end of the study. Leaf fall was 57 percent of total litterfall until September 10, 1998 when the proportion changed and wood fall became the highest fraction of litterfall (77 percent). Leaf fall followed a similar temporal pattern to that of total litterfall with the exception that leaf fall did not exhibit a post-hurricane pulse (Fig. 2a). After the hurricane collection, leaf fall rate decreased to low values and then increased steadily for a year. Both the hurricane pulse and the low value after the pulse were statistically different from other leaf fall rates in the record. The proportion of leaf fall increased rapidly after the hurricane from a low of 16 percent reaching 86 percent of total litterfall at the end of the study.

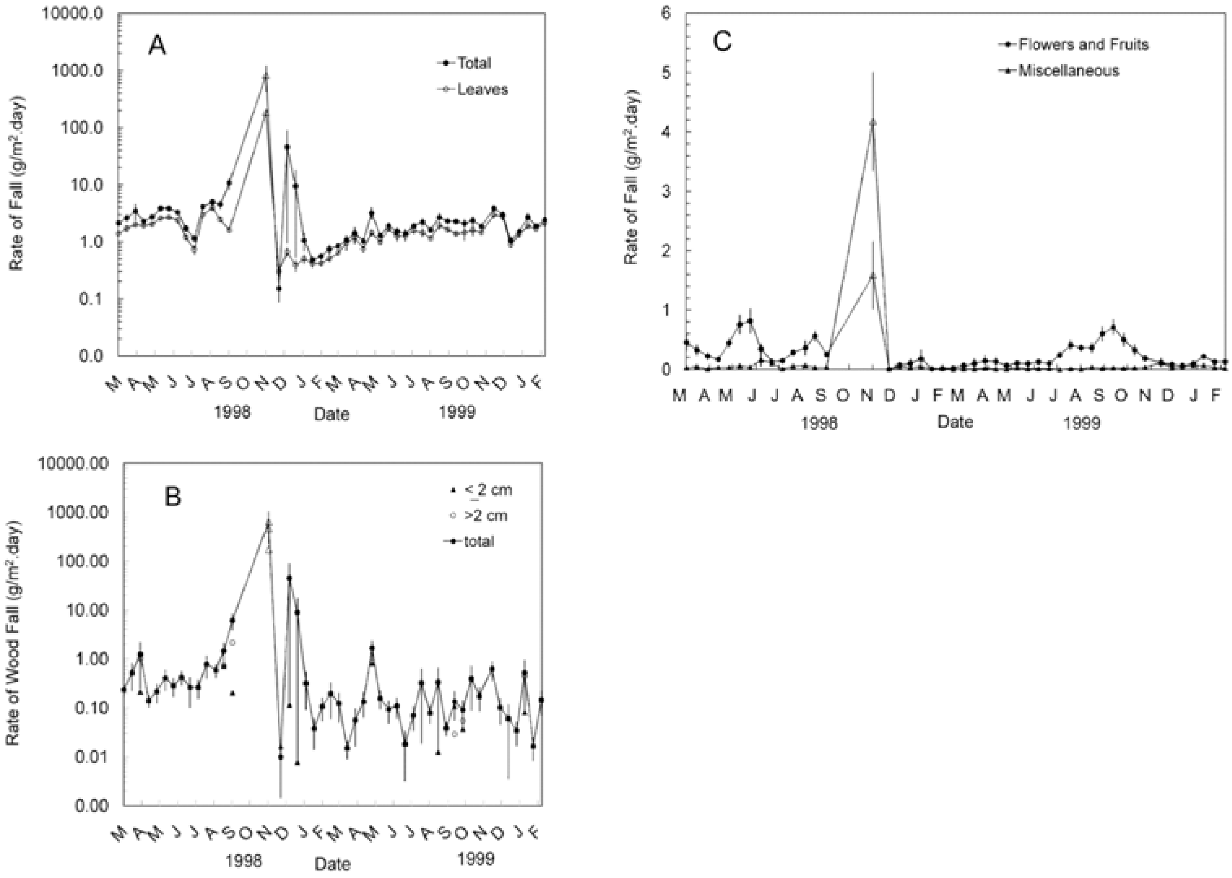


Fig. 2. Leaf and total litterfall (A), wood fall (B) and flowers and fruit fall and miscellaneous fall (C) in a secondary forest at Utuado, Puerto Rico. Vertical lines are 1 standard error of the mean, n = 20. Note the logarithmic scale for A and B. The datum reflecting peak hurricane fall is shown with a large open triangle. The line in 2B connects total wood fall.

Wood fall ranged five orders of magnitude with significantly high pulses in the hurricane collection and the December 15, 1998 collection (Fig. 2b). One month after the post-hurricane pulse, wood fall rates were not different from pre-hurricane rates. Most of the peak wood fall fluxes were due to wood > 2 cm. Flowers and fruits fall had four significant pulses: two pre-hurricane, the hurricane flux, and a post-hurricane pulse a year later (Fig. 2c). Flowers and fruits fall rates decreased after the hurricane and were different from a peak flowers and fruits fall eleven months after the hurricane. Miscellaneous fall was low throughout the study period but had a significant pulse in the hurricane collection and quickly returned to pre-hurricane levels (Fig. 2c).

The annual quantity of total, leaf, and wood fall combined was four times higher in the first year of measurement (February 25, 1998 to February 23, 1999), which included the hurricane, than in the second year (February 23, 1999 to February 15, 2000) (Table 1). The first year, 69 percent of the litterfall was wood fall, while leaf fall was 76 percent of the total litterfall in the second year. For the second year of study, flowers and fruits comprised 11 percent of the total annual litterfall.

		Mass	N	P	K	Ca	Mg	Mn	Al	S	Fe	Ash
Leaves												
	98-99	8.7	181	4	33	55	19	6	24	27	2	444
	99-00	5.5	105	3	29	38	13	4	11	15	1	287
Wood												
	98-99	22.0	259	8	62	229	35	12	152	33	2	1045
	99-00	0.8	11	0.2	2	5	1	1	2	1	0.1	25
Flowers and fruits												
	98-99	0.9	20	0.8	5	3	1	0.3	2	2	0.2	28
	99-00	0.8	17	0.8	4	3	1	0.4	1	2	0.2	26
Miscellaneous												
	98-99	0.2	0.2	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	1
	99-00	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.5
Total												
	98-99	31.9	459	13	100	287	55	18	178	62	3	1518
	99-00	7.2	133	4	35	46	15	5	13	18	1	338

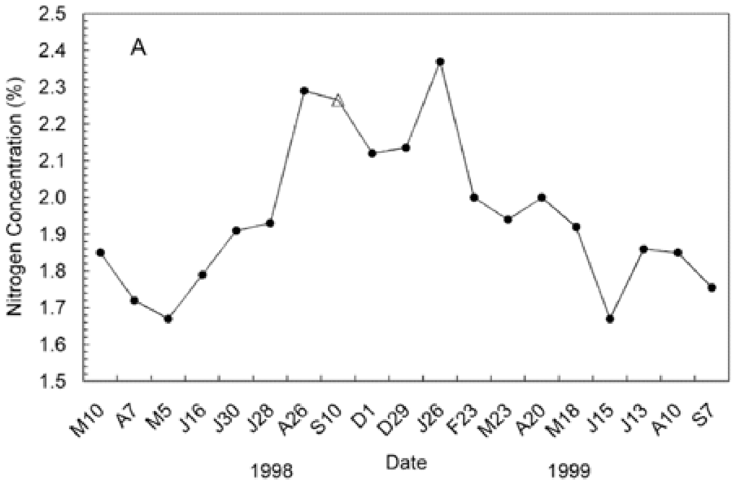
Table 1. Annual litterfall (mass in Mg/ha) and element return (kg/ha) in litterfall for a secondary forest in Utuado, Puerto Rico. The time interval is from March to February for both years (1998 to 1999 and 1999 to 2000). Hurricane Georges struck in the 1998 to 1999 interval. Element return columns might not add to the total because of rounding to the nearest kg or 0.1 kg.

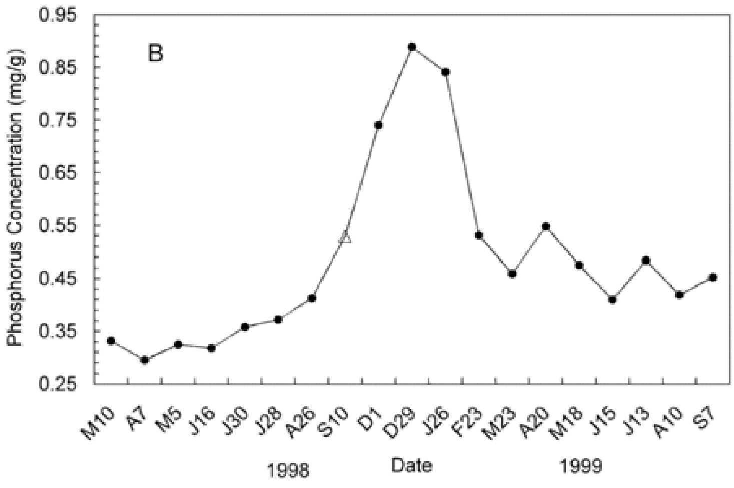
Element Concentrations and Molar Ratios—Leaf fall had the highest concentrations of Ca, Mg, S, and ash among litterfall components (Table 2). Flowers and fruits fall had the highest concentrations of N, P, K, Fe, and C among litterfall components. Wood fall had the highest C/N, and with leaf fall, shared the highest N/P and Al and Mn concentrations. Wood fall had the lowest concentrations of N, P, K, Mg, S, and ash among litterfall components (Table 2).

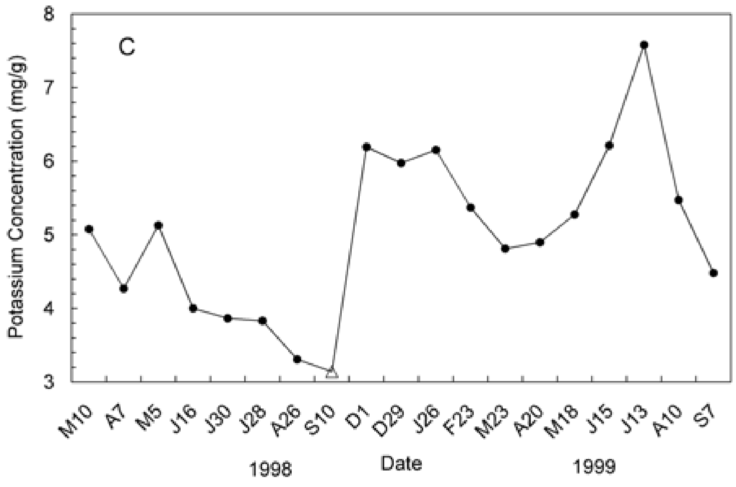
Element or Combination	Leaf	Wood < 2cm	Flowers and Fruits
Nitrogen	19.5 (0.5)	13.2 (0.6)	22.4 (0.8)
Phosphorus	0.48 (0.04)	0.32 (0.02)	1.04 (0.06)
Potassium	5.0 (0.3)	2.6 (0.1)	6.1 (0.4)
Calcium	6.5 (0.2)	5.6 (0.5)	4.2 (0.4)
Magnesium	2.3 (0.1)	1.6 (0.1)	1.9 (0.1)
Sulphur	2.9 (0.1)	1.7 (0.1)	2.4 (0.1)
Aluminum	2.5 (0.4)	2.2 (0.5)	1.4 (0.3)
Manganese	0.70 (0.04)	0.70 (0.01)	0.46 (0.05)
Iron	0.13 (0.01)	0.09 (0.01)	0.33 (0.05)
Carbon	530 (2)	527 (3)	542 (4)
Ash	52 (1)	31 (2)	38 (3)
C/N	32 (1)	49 (2)	29 (1)
N/P	96 (5)	101 (8)	49 (2)

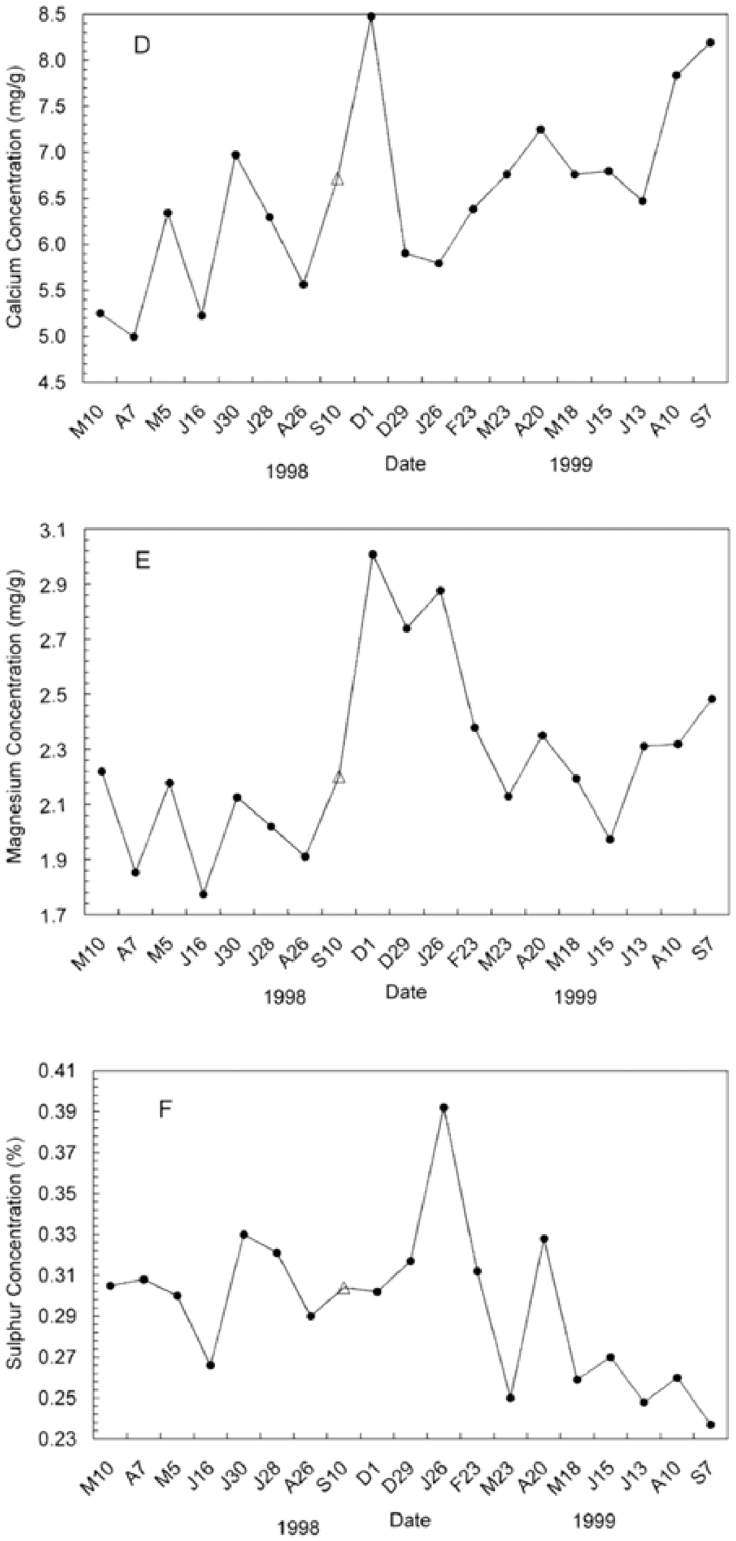
Table 2. Mean element and ash concentrations (mg/g), and mean molar ratios of litterfall components of a novel secondary forest in Utuado, Puerto Rico. Standard error is in parenthesis and the n values were 19, 19, and 21 for leaf, wood, and flowers and fruits, respectively. Results are rounded.

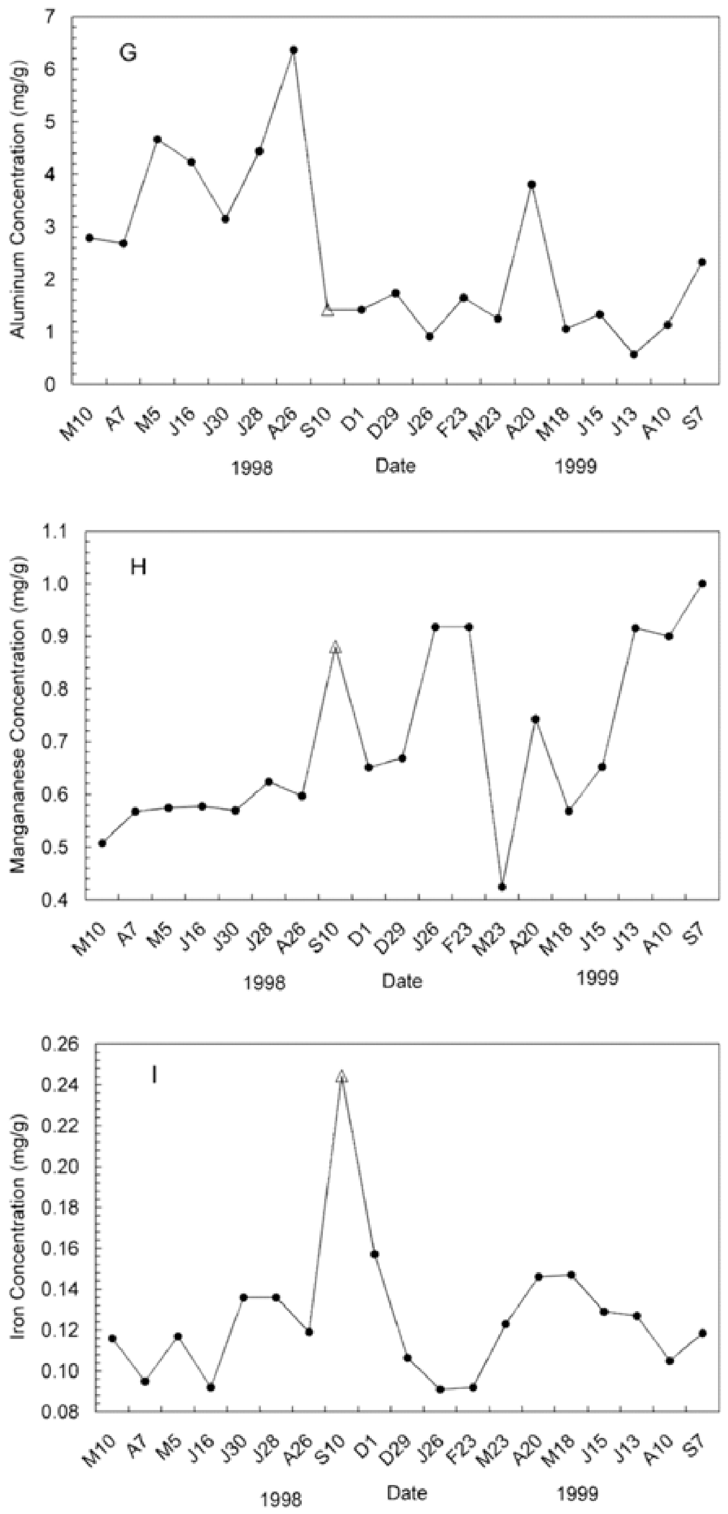
Except for two instances, wood fall and flowers and fruits fall did not exhibit differences in the temporal pattern of element concentration, but for leaf fall, there were several significant patterns of temporal change in element concentration (Fig. 3). The two exceptions were the pattern for changes in P concentration in flowers and fruits fall, which was similar to the one in leaf fall (Fig. 3b) and the pattern of N/P in wood fall, which was similar to that of leaf fall (Fig. 3l).








D
Calcium Concentration (mg/g)
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
E
Magnesium Concentration (mg/g)
3.1
2.9
2.7
2.5
2.3
2.1
1.9
1.7
F
Sulphur Concentration (%)
0.41
0.39
0.37
0.35
0.33
0.31
0.29
0.27
0.25
0.23
M10
A7
M5
J16
J30
J28
A26
S10
D1
D29
J26
F23
M23
A20
M18
J15
J13
A10
S7
1998
Date
1999


G
Aluminum Concentration (mg/g)
0
1
2
3
4
5
6
7
M10
A7
M5
J16
J30
J28
A26
S10
D1
D29
J26
F23
M23
A20
M18
J15
J13
A10
S7
1998
Date
1999
H
Manganese Concentration (mg/g)
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
M10
A7
M5
J16
J30
J28
A26
S10
D1
D29
J26
F23
M23
A20
M18
J15
J13
A10
S7
1998
Date
1999
I
Iron Concentration (mg/g)
0.08
0.10
0.12
0.14
0.16
0.18
0.20
0.22
0.24
0.26
M10
A7
M5
J16
J30
J28
A26
S10
D1
D29
J26
F23
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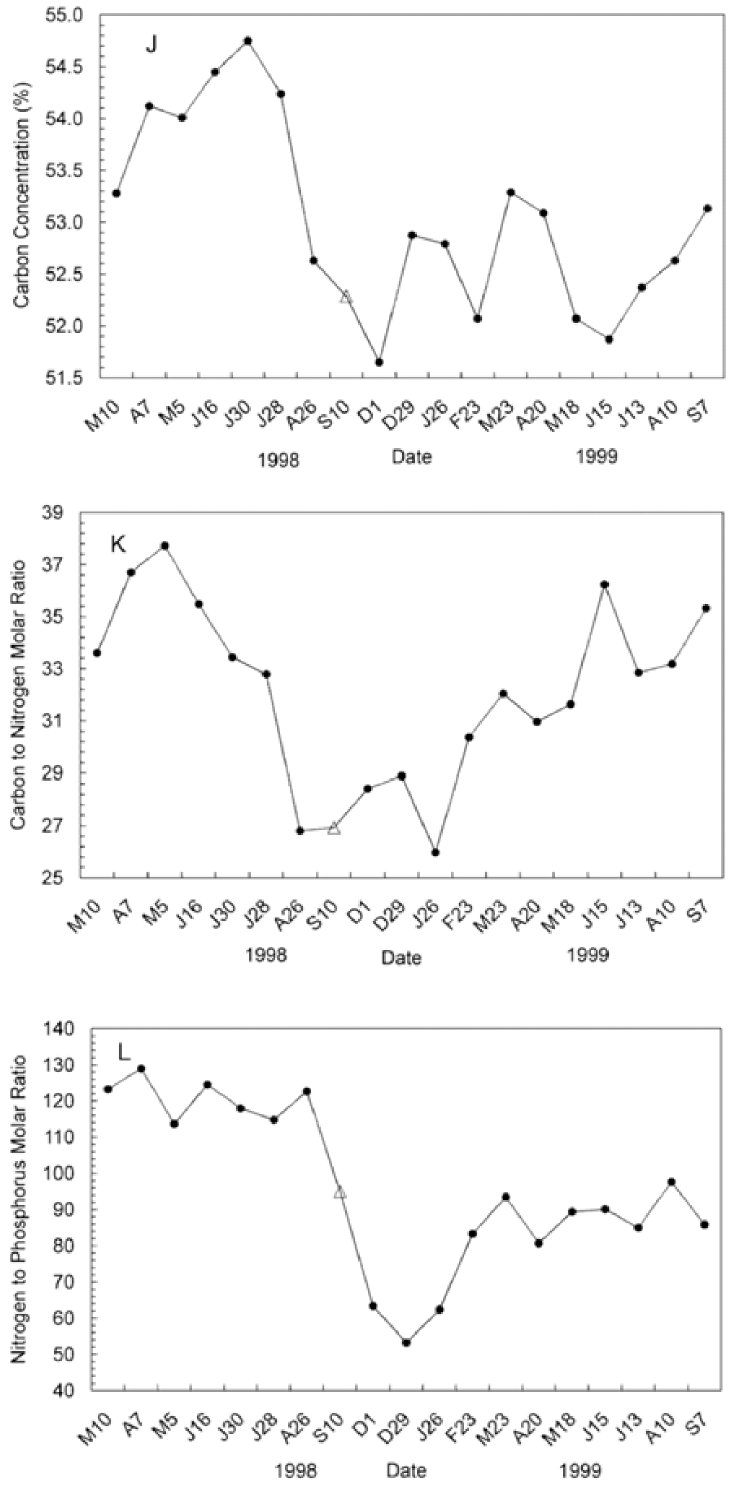

Fig. 3. Element concentrations and C/N and N/P molar ratios in leaf fall of a secondary forest at Utuado, Puerto Rico. The elements are: nitrogen (A), phosphorus (B), potassium (C), calcium (D), magnesium (E), sulphur (F), aluminum (G), manganese (H), iron (I), and carbon (J). Molar ratios are: carbon to nitrogen (K) and nitrogen to phosphorus (L). Data for the first collection after the passage of Hurricane Georges are shown with an open triangle in each graph. The date shows the abbreviation for the month followed by the day of collection.

Phosphorus (Fig. 3b), K (Fig. 3c), and Mg (Fig. 3e) concentrations in leaf fall had the same pattern of temporal change, which involved a rapid increase in concentration after the hurricane followed by a decreasing trend to pre-hurricane concentrations. We found a rising post-hurricane trend in leaf fall Ca (Fig. 3d) and Mn (Fig. 3h) concentrations. In contrast, S (Fig. 3f) and Al (Fig. 3g) concentrations exhibited a declining post-hurricane trend, while Fe (Fig. 3i) had a high concentration in the hurricane collection and quickly returned to pre-hurricane concentrations. Leaf fall concentrations of C (Fig. 3j) and N (Fig. 3a) contrasted in their temporal patterns. Nitrogen concentrations were rising before the hurricane and declined afterwards, while C concentrations were declining before the hurricane and roused after the event. The C/N molar ratio (Fig. 3k) behaved similar to the C concentration, while the N/P molar ratio (Fig. 3l) declined sharply after the hurricane and then increased somewhat in the following months. All elements with the exception of Al had achieved (N, P, K, Mg, S, Fe, C, C/N, ash) or exceeded (Ca, Mn) pre-hurricane concentrations or molar ratios by November 23, 1999 (Table 2). Only Al and the N/P molar ratio remained below pre-hurricane values.

Element Return Flux—Annual element return flux by miscellaneous fall was insignificant, and we will not address it any further (Table 1). Flowers and fruits fall returned a low but steady amount of elements to the forest floor. Element return was higher in the hurricane year than in the year after. Element return by wood fall was higher than those of leaf fall during the hurricane year, but lower the year after the hurricane (Table 1). The biweekly pattern of total element return to the forest floor is not shown but was similar to the biweekly pattern of total litterfall (Fig. 2).

4. Discussion

Our study documented both the instantaneous and short-term effects (months to years) of Hurricane Georges on litterfall mass and element fluxes of a young novel secondary forest. We first discuss six such effects of this hurricane followed by the reasons why the forest behaved as it did, and the implications of our results to the functioning of tropical forests in the hurricane belt.

Effects on the Pattern of Litterfall—The temporal pattern of litterfall is modified by hurricanes. The modified pattern usually involves a rapid decline in litterfall after the hurricane pulse and a trajectory to pre-hurricane rates in subsequent months (Fig. 2). We also measured a second litterfall pulse (mostly wood fall), which reflects delayed mortality or late return of debris retained in the canopy and caught in branches and the lower canopy where it remains suspended until wind and rain cause it to fall. Lodge et al. (1991) found 9.3 Mg/ha of suspended litter after Hurricane Hugo in the Luquillo Experimental Forest (LEF).

The most obvious effect of a hurricane on litterfall is the instantaneous pulse associated with hurricane winds and crown defoliation (Fig. 2) as measured in Puerto Rico, Hawaii, and Mexico. Pulses of litterfall are also common after heavy rains and wind events associated with low-pressure atmospheric systems (Lugo 1992, Lugo et al. 2007). An example of a rain-induced litterfall event in our data is the peak wood flux in the collection of April 7, 1998, before Hurricane Georges passed over the forest (Fig. 2). That pulse was statistically different from rates before and after the event. However, rainfall events do not reach the high rates that accompany hurricanes because hurricanes have the highest velocity winds and litterfall rates are linearly related to wind speed (Beard et al. 2005).

Effects on the Proportion of Litterfall Components—The hurricane changed the proportion of litterfall components from a predominance of leaves to wood and then back to leaves (Table 1, Fig. 2a, b). This is another common effect of hurricanes (Frangi and Lugo 1991, Whigham et al. 1991, Scatena et al. 1996, Herbert et al. 1999). The norm is the predominance of leaf fall as observed in a similar forest type in nearby Barranquitas (Fig. 1), which had 64 to 82 percent leaf fall in a replicated three-year study (Lugo et al. 1999). The change in the relative fractions of wood and leaves in litterfall has implications to litter chemistry, the quality of material available to soil organisms, and post-hurricane nutrient availability (below). This is reinforced by the predominance of >2 cm wood fall (Fig. 2b). Large wood pieces require longer processing by soil organisms than leaves, flowers and fruits, or miscellaneous materials (Swift et al. 1979). Moreover, one study at the LEF predicted nutrient immobilization, reduced decomposition, and reduced tree growth as a result of the large fraction of wood (including coarse woody debris) returned to the forest floor by Hurricane Hugo (Zimmerman et al. 1995, but see Lugo 2008).

Effects on Litterfall Mass and Element Fluxes—The instantaneous pulse of leaf and total litter fall in the hurricane collection was 176 and 449 times the respective pre-hurricane rates. On an annual basis, total litterfall the year of the Hurricane was 4.4 times higher than that of the year after the hurricane (Table 1). The hurricane transferred a large mass of material to the forest floor, thus temporarily increasing the accumulation of litter. Similar pulses of litter input to the forest floor have been documented in Hawaii, Mexico, and Puerto Rico. In all examples, the instantaneous hurricane pulse exceeds or approaches the normal annual flux of mass.

Pulses of element return accompany the hurricane pulse of litterfall mass. The annual quantities of N, P, K, Ca and Mg returned to the forest floor by total litterfall the year of Hurricane Georges were 3.5, 3.2, 2.9, 6.2 and 3.7 times the quantities returned the year after the hurricane (Table 1). These levels of element return, with the exception of Ca, were close but not proportional to the increase in litterfall mass. The differences are caused by differences in concentration (Fig. 3, Table 2) and the relative proportions of leaf and wood fall in total litterfall mass (Table 1). The higher proportion of Ca return, for example, is attributed to the large wood fall with high Ca concentration.

The ratios of hurricane pulse to pre-hurricane fluxes of mass and element return in litterfall were similar for mass but lower for nutrients in our study (with the exception of Ca) than those measured elsewhere in Puerto Rico after Hurricanes Hugo and Georges (Table 3). The similarity in the mass pulse ratio (except for Guánica and elfin forests) and the differences in the nutrient pulse ratios, suggest ecophysiological differences among sites rather than differences in forest resistance to hurricane winds. The reason is that the mass pulse is the direct effect of winds, while the nutrient content of litterfall reflects in addition the concentration in plant parts, which is unrelated to the wind storm. We will address this issue below.

Effects on the Chemistry of Litterfall and Nutrient Use-Efficiency—The element concentration of the material that falls instantaneously during a hurricane is high because it is mostly composed of live plant parts. Element concentration is higher in live materials than in dead material because of retranslocation of nutrients associated with senescence particularly in leaves (Noodén and Leopold 1988). The higher nutrient concentration in downed hurricane material has already been documented in Puerto Rico, Mexico, and Hawaii. A hurricane or windstorm interrupts senescence and retranslocation processes, which in turn affects element concentrations of falling parts and processing of debris by forest floor organisms (Berg and McClaugherty 2003).

Forest Type	Mass	N	P	K	Ca	Mg	Mn	Al	S	Fe
Palm floodplain[1]	36									
Palm floodplain[2]	447		1726							
Tabonuco forest, El Verde[3]	436	448	800	466	336	319				
Tabonuco forest, Bisley[3]	455	475	610	1021	465	510				
Elfin forest[3]	682	430	219	997	417	635				
Guánica dry forest[4]	767	842	1460	520						
This study	449	278	487	316	935	478	442	992	246	522

1. Subtropical wet forest at 750 m elevation after Hurricane Allen (Frangi and Lugo 1985).
2. Same as above after Hurricane Hugo (Frangi and Lugo 1991).
3. Subtropical wet forest after Hurricane Hugo (Lodge *et al.* 1991).
4. Subtropical dry forest after Hurricane Georges (Van Bloem *et al.* 2005).

Table 3. Ratio of instantaneous mass or element return to the forest floor due to a hurricane to pre-hurricane daily average mass or element return to the forest floor. Values used to calculate the ratio are for total litterfall expressed on a daily basis. Empty cells mean there are no data. All sites are from Puerto Rico and all but the study site are mature forests.

Element concentration of leaf fall in our study changed for about a year after the passage of the hurricane probably due to the development and turnover of new leaves in fast-growing trees. For example, both in our study (Fig. 3e) and the LEF (Scatena *et al.* 1996), post-hurricane falling leaves had high Mg concentration. Magnesium is required for chlorophyll production, and it is expected that high quantities of Mg are required for the re-growth of the canopy. The leaves that fell on our litterfall baskets after Hurricane Georges had higher elemental concentrations than did senesced leaves falling before the hurricane. In some instances, leaf fall months after the hurricane had higher nutrient concentrations than live leaves that fell during the hurricane pulse. At the end of the study, leaf litter fall had higher Ca and Mn concentrations than pre-hurricane leaf fall. Ostertag et al. (2003) showed that after Hurricane Georges these high concentrations in leaf fall flux are reflected in the concentration of standing litter where they remain high for several months while soil organisms process the material. They found that N, P, Ca, and Mg increased in concentration in the standing litter of a moist forest but in other forest types this increase was not observed. In our study P concentration increased after the hurricane while N concentration increased just before the hurricane and remained high for three collection intervals before returning to pre-hurricane values. Our concentration data is consistent with Ostertag et al. (2003) observations on ground litter but we have no explanation for the pre-hurricane N concentration increase.

The within-stand nutrient use-efficiency reflects a low nutrient use-efficiency in our study site when compared to other forests and tree plantations in Puerto Rico (Table 4). Brown and Lugo (1990) found that tropical secondary forests in general had lower within-stand nutrient use-efficiency than mature forests and this general pattern applies to the comparison of secondary forests with mature forests in Puerto Rico (Lugo 1992). However, as first demonstrated by Scatena et al. (1996), the within-stand nutrient use-efficiency of forests decreases even more with hurricanes. This means that the weighted nutrient concentrations (the inverse of the within stand nutrient use efficiency in Table 4) in post-hurricane leaf fall in our forest were high, thus reflecting high nutritional quality. Wood fall had lower weighted nutrient concentrations than leaf fall, but it also had a post-hurricane increase in nutritional quality (Table 4). Nevertheless, the predominance of wood in litterfall during and immediately after the hurricane (Fig 2b) dominated nutrient inputs to the forest floor and because of the lower nutritional quality of this material it probably immobilized nutrients relative to the effect of the higher quality material in leaf fall.

Site	N		P		K		Source
	Leaf	Total	Leaf	Total	Leaf	Total	
			Secondary Forests				
Guzmán	132		2652	2747	584		Lugo 1992
Cubuy	117	123	2366	2382	447	477	Lugo 1992
Sabana	66	69	1329	1310	434	490	Lugo 1992
El Verde	91	92	3222	2999	527	565	Lugo 1992
Guánica	97	99	6056	6076	123	134	Lugo and Murphy 1986
Barranquitas	56	57	1553	1544	164	159	Lugo *et al.* 1999
Utuado (H)	48	70	2175	2454	263	319	This study
Utuado (PH)	52	54	1833	1800	190	206	This study
					Plantations		
Pine	198	134	4997	4153	974	992	Lugo 1992
Mahogany	82	92	140	163	537	611	Lugo 1992
Eucalyptus	165		5100				Cuevas and Lugo 1998

Table 4. Nutrient use efficiency in leaf and total litterfall of various secondary forests and plantations in Puerto Rico. Utuado data are for the hurricane (H) year (March 1998 to February 1999), and the post-hurricane (PH) year (March 1999 to February 2000). Empty cells = data not available. Data are in kg organic matter falling as litter/kg element in litter fall.

The lowering of the N/P molar ratio of leaf fall after the hurricane implies an improved availability of P in relation to N to soil organisms (Table 2). The N/P ratio of leaf fall was lowest during the first three months after the hurricane, and remained below pre-hurricane values through the end of the study (Fig. 3l). This, coupled to a decrease in the C/N ratio (Fig. 3k), and lowered within-stand nutrient use-efficiency (Table 4) suggests that conditions for the decomposition of falling leaf litter, and thus subsequent plant uptake, are favorable post-hurricane, particularly when leaves become the dominant component of litterfall. Nutrients such as P, K, Ca, and Mg (Figs. 3b-e) had increased concentrations in post-hurricane leaf fall. Part of the high resilience exhibited by the processing of leaf litter by forest floor organisms in a moist forest was attributed to the high nutrient concentration of incoming leaf fall (Ostertag et al. 2003). Our results support this suggestion.

The Influence of Species Composition on Litterfall Element Fluxes—The young forest that we studied was composed of pioneer and secondary vegetation, including a significant component of introduced species. Although we did not analyze leaf fall chemistry by species, we believe that the species composition influenced the high litterfall element fluxes that we measured. We base our inference on studies of leaf fall chemistry that show the influence of species composition on element concentration and flux data (Cuevas and Lugo 1998, Scatena et al. 1996, Lugo 2004, Lugo et al. 2004, available unpublished data).

It is thus possible that the dominance of pioneer species may be responsible for observed nutrient use-efficiency differences between secondary and mature forests (Brown and Lugo 1990). Fast growing introduced species, which are common in our forest, may accelerate nutrient fluxes even further. Beyond the secondary forest/mature forest comparison; hurricanes influence the nutrient dynamics and use-efficiency of forests in two ways. They favor the fast growth of pioneer species, and they enable the growth of nutrient-enriched leaves. At the LEF, Scatena et al. (1996) measured the highest net primary productivity so far measured at that site and the lowest nutrient use-efficiency after Hurricane Hugo. In our study, the result was that the low nutrient use-efficiency typical of secondary successional vegetation was lowered even more by the hurricane (Table 4). Nutrient use-efficiency was lower than that measured by Scatena et al. (1996), which we attribute to species composition (mostly pioneer and introduced species) and young age (26 yr-old).

Effects on Post-Hurricane Litterfall Rates—The post-hurricane production of flowers and fruits is of significance to the survival of wildlife. Several studies in diverse locations show that nectarivorous and frugivorous wildlife populations experience significant reductions after hurricanes as populations migrate to locations where nectar and fruit remain available (Waide 1991a and b, Askins and Ewert 1991, Lynch 1991, Will 1991, Wunderle *et al.* 1992). Months can pass before fruit production returns to some normalcy and allow recovery of wildlife. At the LEF, flowers and fruits fall remained below average for about 2.5 years after Hurricane Hugo (F.N. Scatena, University of Pennsylvania, Personal Communication), while at our site the post-hurricane reduction lasted 10 months (Fig. 2c). Other litterfall fluxes had different levels of resilience (Fig. 4). Leaf fall did so in about eight months while wood fall and total litterfall returned to pre-hurricane rates after the pulses of fall during and within a month of the hurricane. Phosphorus, K, Ca, and Mn in leaf fall reached pre-hurricane fluxes in about 5 months or faster than leaf fall mass and faster than N, Mg, S, and ash fluxes, which required about 8 months to reach pre-hurricane rates.

Leaf expansion after the hurricane is rapid and new leaves have higher element concentrations (Table 2), thus accelerating the recovery of these fluxes. The required time to reach pre-hurricane fluxes in our forest, with one exception, oscillates between 5 and 8 months for leaf fluxes. This level of resilience is shorter than the 20 months in the mature forest studied by Scatena et al. (1996), a forest that had a higher reduction in litterfall fluxes after Hurricane Hugo (Table 3). The exception is Al, the element most affected by the passage of the hurricane at our site, which had a positive slope at the end of our measurements but had not reached pre-hurricane rates after 17 months. Thus, while the hurricane caused a wide oscillation in the pattern of element return, it appears that our forest might reach pre-hurricane litterfall fluxes in one or two years after the event.

Two factors might explain the high litterfall resilience of the study forest to hurricane winds. One is the low level of hurricane effects on the structure of the forest. For example, most of the effects to understory trees were caused by fallen debris, which in most cases bent and injured but did not kill trees (Lugo et al. 2005). As a result, loss of canopy was low in this forest and most trees exhibited rapid increases of growth rate after the hurricane. The other explanation for our results is the nature of the affected species. The tree species that dominated the canopy of our forest were secondary forest species characterized by rapid growth and frequent and profuse flowering (Little and Wadsworth 1964) and the chemical characteristics discussed above. Therefore, in spite of the passage of the hurricane, the forest had the capacity to respond quickly. When fast-growing species are dominant in a forest, they circulate more chemical elements per unit mass (Table 4) and enrich litter and soil (Brown and Lugo 1990, Cuevas and Lugo 1998, Lugo *et al.* 2004). These accelerated fluxes contribute to resilience after hurricanes and other disturbances.

Comparison of Secondary Forests With Mature Forests—The immediate effect of hurricane-force winds on litterfall is the ensuing pulse of mass and element return to the forest floor (Fig. 2). The relative magnitude of this pulse is its ratio to pre-hurricane rates (Table 3). Our results, when compared to mature natural forests elsewhere in Puerto Rico, reflect lower ratios for nutrients and similar ratios for mass flux, except for the Guánica dry forest and the elfin forest. Part of the difference may be due to the timing in the collection of litterfall samples. Both Lodge et al. (1991) and Van Bloem et al. (2005) collected hurricane litterfall quicker after the event than we did. Our hurricane pulse is underestimated due to the decomposition of litter during the 61 days between its fall and collection. However, this underestimate was small in comparison with the hurricane pulse (5 g/m^2 based on the decomposition rate of leaves after Hurricane Hugo in Ostertag *et al.* 2003). This correction does not explain the differences between the forests.

We believe two circumstances explain our results and the differences between forests in Table 3. One is the high ratio of wood fall to leaf fall at our site (3:1) compared to 2:1 for Guánica Forest (Van Bloem et al. 2005) and 1.5:1 for Bisley (Lodge et al. 1991). The larger fraction of wood in our samples lowers the nutrient return of the pulse due to the lower element concentration of wood (Table 2). Calcium concentration in wood is the exception and for that element our forest had the highest pulse ratio of any forest in Table 3. Thus, the relative proportion of leaves and wood in the hurricane pulse, influences the ratio of nutrients in the hurricane pulse to pre-hurricane nutrient fluxes.

The second circumstance is the difference in nutrient concentration in pre-hurricane litter compared to hurricane litter in the various forests. Both Guánica dry forest and the elfin forest produce nutrient-poor litterfall, which is reflected in the within-stand nutrient use-efficiency. For the Guánica dry forest, the N and P nutrient use-efficiency under normal conditions is three and two times, respectively, higher than for our site (Table 4). A lower nutrient return in the absence of hurricanes would accentuate the flux difference between pre- and post-hurricane element return. That is, the nutrient turnover in our study site is normally high and the increase due to the hurricane flux is not as dramatic as in native mature forests with pre-hurricane conservative nutrient fluxes.

Some Implications to Tropical Forests on the Hurricane Belt—A common denominator to our results is the recurrence of pulses of mass fall and element return to the forest floor. These pulses occur at different intensities and times, depending on atmospheric conditions. The highest rates occur after hurricanes. These pulses increase the amount of nutrients entering the litter/soil compartments of the forest and change the quality of decomposing litter through altered C/N and N/P ratios and high leaf fall nutrient concentrations. Sayer et al. (2006) found that increasing litter inputs to the forest floor in a tropical moist forest in Barro Colorado accelerated the decay of wood but not the meso arthropod population abundance in litter. Thus, pulses of litter fall and nutrient return have proven effects on decomposition and recycling processes of tropical forests. They also found greater accumulation of P and N in litter as did Ostertag et al. (2003) after Hurricane Georges in Puerto Rico. However, our study shows that the nutritional quality of the pulse depends on the plant part that dominates the flux. Wood fall pulses have a different nutritional quality than a leaf fall pulse.

The implications to soil processes of rapid changes in litterfall quantity and chemistry, coupled to the disproportional behavior of nutrients and organic mass is poorly known, but is receiving increased attention by ecologists. For example, Lodge et al. (1994) suggest that responses to pulsed inputs to the soil/litter compartment involve complex non-lineal phenomena. Our results are in agreement with previous observations of the nutrient-rich litter environment in tropical secondary forests (Brown and Lugo 1990). However, this high nutrient richness, low C/N ratios, and low N/P ratios apply to leaf fall and not to wood fall, which contains lower quality material and can immobilize nutrients. Falling leaves after a hurricane constitute a favorable environment for supporting high rates of litter decomposition and nutrient cycling (Ostertag et al. 2003). In turn, these ecosystem processes have a practical application for supporting the rehabilitation of soil fertility in degraded lands colonized by new forest ecosystems (Lugo and Helmer 2004, Lugo et al. 2004).

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This book represents recent research on tropical cyclones and their impact, and a wide range of topics are covered. An updated global climatology is presented, including the global occurrence of tropical cyclones and the terrestrial factors that may contribute to the variability and long-term trends in their occurrence. Research also examines long term trends in tropical cyclone occurrences and intensity as related to solar activity, while other research discusses the impact climate change may have on these storms. The dynamics and structure of tropical cyclones are studied, with traditional diagnostics employed to examine these as well as more modern approaches in examining their thermodynamics. The book aptly demonstrates how new research into short-range forecasting of tropical cyclone tracks and intensities using satellite information has led to significant improvements. In looking at societal and ecological risks, and damage assessment, authors investigate the use of technology for anticipating, and later evaluating, the amount of damage that is done to human society, watersheds, and forests by land-falling storms. The economic and ecological vulnerability of coastal regions are also studied and are supported by case studies which examine the potential hazards related to the evacuation of populated areas, including medical facilities. These studies provide decision makers with a potential basis for developing improved evacuation techniques.

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