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Forest Floor Decomposition Following Hurricane Litter Inputs in Several Puerto Rican Forests

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Abstract

Hurricanes affect ecosystem processes by altering resource availability and heterogeneity, but the spatial and temporal signatures of these events on biomass and nutrient cycling processes are not well understood. We examined mass and nutrient inputs of hurricane-derived litter in six tropical forests spanning three life zones in northeastern Puerto Rico after the passage of Hurricane Georges. We then followed the decomposition of forest floor mass and nutrient dynamics over 1 year in the three forests that experienced the greatest litter inputs (moist, tabonuco, and palm forests) to assess the length of time for which litter inputs influence regeneration and nutrient cycling processes. The 36-h disturbance event had litterfall rates that ranged from 0.55 to 0.93 times annual rates among the six forests; forest floor ranged between 1.2 and 2.5 times prehurricane standing stocks. The upper-elevation forest sites had the lowest nonhurricane litterfall rates and experienced the lowest hurricane litterfall and the smallest relative increase in forest floor standing stocks. In the three intensively studied forests, the forest floor returned to prehurricane values very quickly, within 2–10 months. The palm forest had the slowest rate of decay ($k = 0.74 \pm 0.16\ y^{-1}$), whereas the tabonuco forest and the moist forest had similar decay rates (1.04 ± 0.12 and 1.09 ± 0.14, respectively). In the moist forest, there were short-term increases in the concentrations of nitrogen (N), phosphorus (P), calcium (Ca), and magnesium (Mg) in litter, but in the other two forests nutrient concentrations generally decreased. The rapid disappearance of the hurricane inputs suggests that such pulses are quickly incorporated into nutrient cycles and may be one reason for the extraordinary resilience of these forests to wind disturbances.

Key words: forest floor; nutrient pulses; resilience; resistance; resource heterogeneity; tropical forests; Puerto Rico.

Introduction

Landscape-scale disturbances such as hurricanes are important events in both temperate and tropical forests that can rapidly redistribute mass and nutrients in ecosystems and have the potential to alter community composition, structure, and function (Pickett and White 1985; Bellingham 1991; Whigham and others 1999). Hurricanes result in the loss of leaves, damage to branches and stems, and elevated mortality above background levels (Foster and Boose 1992; Lugo and Waide 1993; Lugo and Scatena 1996). Defoliation is the most prevalent type of damage, occurring even when there is no large-scale structural damage to stems. These litter inputs can be substantial in terms of mass and spatial heterogeneity. For example, in Hawaii, the litterfall associated with Hurricane Iniki

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was 1.4 times greater than the previous year's annual input (Herbert and others 1999). Similarly, in two wet forests and a cloud forest in Puerto Rico, hurricane litterfall was 1.2 to 1.9 times greater than annual litterfall (Lodge and others 1991); and in a dry forest in Mexico, hurricane litter was about 1.3 to 2.0 times greater than the average litterfall over the previous 4 years (Whigham and others 1991).

Previous studies have shown that large, disturbance-related inputs of litter to the forest floor can affect forest recovery in many ways (Lodge and others 1994). Although tree damage patterns have been quantified at the landscape scale (Bellingham 1991; Basnet and others 1992; Foster and Boose 1992; Boose and others 1994; Foster and others 1999), few studies have examined hurricane-related litter production and decomposition across plant communities. It is known that forest communities differ in their ability to resist defoliation and branch or stem damage (Brokaw and Walker 1991). Therefore, hurricane-related litter inputs are likely to be linked to the inherent characteristics of a forest, such as species composition, stature and structure, net primary productivity (NPP), and topographic and edaphic conditions. It has also been suggested that the amount of hurricane inputs can significantly alter ecosystem structure and functioning (Lodge and others 1991). Hurricane litter does not undergo retranslocation before it falls; therefore, it is not only more abundant but also can have higher nutrient concentrations than nonhurricane litter (Lodge and others 1991; Herbert and others 1999). This abundant forest floor material may decrease solar radiation hitting the ground and modify soil temperature and moisture (Facelli and Pickett 1991). The combination of relatively nutrient-rich disturbance-generated litter and fine-root and plant mortality (Parrotta and Lodge 1991; Silver and Vogt 1993) can affect rates of litter decomposition and mineralization, leading to temporary alterations in ecosystem-scale carbon (C) and nutrient cycling rates (Sanford and others 1991) and increasing nutrient export in stream water (Schaefer and others 2000). These modifications of the physical and chemical environment of the forest floor can also affect processes such as seed germination, seedling establishment, and the relative ranking of species, often in complex and species-specific ways (Facelli and Carson 1991; Guzmán-Grajales and Walker 1991; Molofsky and Augspurger 1992; Everham and others 1996; Harrington and others 1997). Although these observational, experimental, and modeling studies have demonstrated that hurricane litter can affect many ecosystem processes, the length of time that this hurricane-generated forest floor mass remains elevated above predisturbance levels, and thus has a direct physical and biogeochemical effect on ecosystem processes, is poorly documented. The rate at which hurricane litter pulses are incorporated into the ecosystem is directly related to the establishment of other recovery mechanisms (for example, plant and microbial uptake, seed bank germination, and so on) and can be considered a measure of the resilience of the ecosystem to these perturbations.

In this study, we examined the production and disappearance of hurricane-generated litter inputs to six forest types in three life zones in northeastern Puerto Rico. Because all the sites are part of the National Science Foundation–sponsored Long Term Ecological Research (LTER) Program in Puerto Rico, data were available on prehurricane litterfall rates, forest floor standing stocks, and climate, allowing us to document the direct impacts of the disturbance on pools and rate processes. We chose these sites because they differ in climate, elevation, and species composition—factors that might affect both the resistance of forests to damage (for example, litter inputs) and the recovery of forest floor pools to predisturbance levels (for example, decomposition).

We first hypothesized that hurricane litter inputs could be best predicted from prehurricane rates of litterfall such that sites that experience high litterfall NPP would also have the highest hurricane litter inputs. Our justification for this hypothesis is that litterfall NPP integrates many climatic, edaphic, topographic, and compositional factors that are likely to influence resistance to disturbance in plant communities. Furthermore, forests with higher litterfall production often have greater standing biomass and thus more potential for litter production when disturbances occur. We also hypothesized that hurricane litter would decompose relatively rapidly; therefore, its direct physical influence on regeneration and ecosystem nutrient processes would be limited to the first few months after a hurricane. Finally, we predicted that upper-elevational sites with lower NPP would experience less damage to trees and therefore have smaller litter inputs but slower decomposition rates than lower-elevation sites. We determined initial hurricane litter inputs in the six forest types and then followed the turnover of the forest floor material for 1 year in the three forests that had the greatest hurricane-generated inputs. These forests spanned the range in life zones of the larger sample, thus affording us the opportunity to examine patterns in decay across life zones and plant community type.

Table 1. Description of the Study Sites Where Litterfall and Forest Floor Litter was Collected Directly After Hurricane Georges

Site	Elevation (m a.s.l.)	Mean Annual Rainfall (mm)	Holdridge Life Zone	Soil Temperature
Moist	300–500	2500	Moist	Not available
Tabonuco	265–395	3500	Wet	Not available
Palm	700–900	4442	Lower montane rain	20.2 ± 0.03
Colorado	600–750	4735	Lower montane rain	20.9 ± 0.03
Short Cloud	750–1050	4097	Lower montane rain	19.7 ± 0.03
Tall Cloud	750–1000	4596	Lower montane rain	20.0 ± 0.03

All forests fit in the subtropical category for life zone description; classifications based on Ewel and Whitmore (1973).
Data from Scatena and others (1993) and W. L. Silver and others (unpublished).

Methods

Site Descriptions

This study was conducted within the Luquillo Experimental Forest (LEF) in six forests where we had previously been collecting data on litterfall production and nutrient dynamics. These forest types are distinguished by differences in rainfall, elevation, and species composition (Table 1)—factors that relate to litterfall rates and that we hypothesized would lead to variation in resistance to storm damage and different rates of decay of forest floor mass and nutrients. Detailed descriptions of the palm, colorado, and tabonuco forest types and life zone classification can be found in Ewel and Whitmore (1973), Brown and others (1983), and Scatena (1989). The palm forest is dominated by the sierra palm, *Prestoea montana* (Graham) Nichols, although dicot trees are also present. The moist forest is a drier site, located in the Cubuy annex of the LEF. It was formerly pasture, but it was reforested in the mid to late 1930s with single and mixed species plantings and natural regeneration (Marrero 1947) and is now a diverse closed-canopy forest containing 75 tree species.

Description of Hurricane Georges

On 21 September 1998, Hurricane Georges made landfall on the southeastern coast of Puerto Rico. The eye of the storm traversed the island from east to west in approximately 6 h (Figure 1). The hurricane had sustained winds of 51 m/s, gusts of 67 m/s, and was a Category 3 storm on the Saffir-Simpson scale. Both the intensity and damage of the storm were less than those associated with Hurricane Hugo in 1989 (Scatena and Larsen 1991). Nevertheless, there was loss of foliage and damage at all the study sites. Storm rainfall at the different study sites ranged between 125 and 250 mm, and mean hourly wind speeds were elevated for about 36 h.

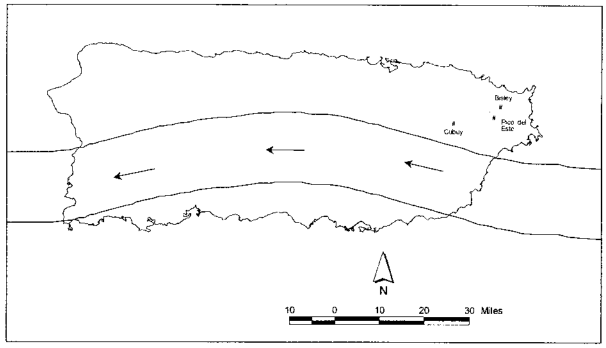

Figure 1. Map of Puerto Rico, showing the location of the study sites with the Luquillo Experimental Forest in relation to the path of Hurricane Georges. Cubuy represents the site name of the moist forest; Bisley, the tabonuco forest. The short and tall cloud forest, colorado, and palm forest are all on the mountain known as Pico del Este.

Storm Inputs to the Forest Floor

At all sites, we had preexisting plots, as well as recent prehurricane litterfall and forest floor data. Our sampling design was based on making posthurricane data as comparable as possible to prehurricane data, and therefore varied between forests in the number of replicates and the size of sampling area (see footnotes in Table 2).

Prehurricane sampling was done 2–3 months before the storm in all forests except the tabonuco forest. At this site, we estimated prehurricane values based on the brown litter on the forest floor immediately after the hurricane, similar to what was done by Lodge and others (1991) and Vogt and others (1996). Our value of 660 (50 SE, n = 20) g/m^2 is comparable to a nearby plot in this forest

Table 2. Litterfall and Forest Floor Values (Not Ash-Corrected) of the Study Sites Sampled Directly After Hurricane Georges

Site	Nonhurricane Litterfall (g/m²/d)	Hurricane Georges Litterfall Input (g/m²/d)	Annual Litterfall (%)	Prehurricane Forest Floor Litter (g/m²) (x ± SE (*n*))	Total Posthurricane Forest Floor Litter (g/m²) (x ± SE (*n*))	Significance
Moist	3.22	868	74	752 ± 51[a] (*n* = 73)	1946 ± 161[d] (*n* = 20)	< 0.0001
Tabonuco	2.38	477	55	660 ± 50[b] (*n* = 20)	1137 ± 111[e] (*n* = 20)	0.0001
Palm	1.41	290	56	617 ± 110[c] (*n* = 15)	958 ± 132[f] (*n* = 21)	0.1 NS
Colorado	2.36	710	82	1591 ± 164[c]	1990 ± 205[f]	NS
Short Cloud	0.82	280	93	545 ± 108[c] (n=15)	616 ± 68[f] (n=21)	ns
Tall Cloud	1.41	314	61	562 ± 66[c] (n=15)	681 ± 94[f] (n=21)	ns

[a]*sampled July 1998, 15 × 15 cm² template*
[b]*estimated based on brown litter, 50 × 50 cm² template*
[c]*sampled June 1998, 15 × 15 cm² template*
[d]*sampled 3 d after hurricane, 15 × 15 cm² template*
[e]*sampled 15 d after hurricane, 50 × 50 cm² template*
[f]*sampled 15 d after hurricane, 15 × 15 cm² template*

sampled previously at 682 (89 SE, n = 13) g/m² (Silver and others 1996).

We sampled initial hurricane inputs to the forest floor within 2 weeks of the storm. Hurricane inputs were measured in preestablished plots using preexisting litter baskets to capture litterfall and by sampling the quantity of litter on the forest floor in the vicinity of the litter baskets. We could not gain immediate access to litterfall baskets in the moist forest due to hurricane damage, so in the 1st month we sampled in forest areas near our preestablished plots. Forest floor sampling consisted of randomly locating a template on the forest floor (see Table 2), and then carefully collecting all dead material within the inner area of the template. Another site was randomly selected if more than one-third of the area was rock or exposed root. Leaves still attached to plants, live moss, roots, and rocks were not collected.

After forest floor samples were collected, they were sorted into leaves, wood, and miscellaneous material. Leaves included all leaf parts, including the blade, petiole, petiolule, and rachis (for palms), and leaves of all life forms were considered (palms, ferns, dicotyledons). The wood category included stems, branches, and woody vines. Miscellaneous material included fruits, flowers, pendunctes, small leaf and wood fragments, and any unidentified material. Each component was dried at 65°C for at least 48 h, weighed, and then bulked by plot and collection date, ground in a Wiley mill (18 mesh), and analyzed for nutrients. Because forest floor samples often harbor soil particles, we express all mass and nutrient concentrations on an ash-free basis. Ash-free dry mass was calculated as (100-% ash)·(mass)/100; ash-free nutrient concentrations were calculated as (100· mg/g nutrient)/(100-% ash). The nutrient concentrations for phosphorus (P) and cations were determined at the USDA Forest Service International Institute of Tropical Forestry in Puerto Rico. The samples were digested with H_2O_2 and concentrated HNO_3 (Luh Huang and Schulte 1985), and concentrations of P, potassium (K), calcium (Ca), and magnesium (Mg) were determined with a Beckman Spectra Span V (Fullerton, CA) plasma emission spectrometer. Carbon and nitrogen (N) were determined at the University of California at Berkeley on samples run in duplicate on a CE Elantec (Lakeworth, NJ) CN 2100 analyzer, with a standard run every 10 samples.

Changes in Forest Floor Mass, Nutrients, and Soil C and N over Time

To determine changes in the hurricane litter over time at the three intensively studied sites (moist, tabonuco, and palm), forest floor and litterfall samples were collected from plots at approximately 2, 3, 4, 6, 8, 10, 12, 16, 20, 24, 28, 32, 36, 40, 44, 48, and 52 weeks after the hurricane. At each sampling, forest floor was collected from templates that were randomly placed around existing litter baskets within each plot. Within each site, the plots were considered replicates, and the samples taken within each plot were considered subreplicates and averaged. To be consistent with the prehurricane sampling at each of the sites, the number of plots and samples within a plot varied slightly. In both the moist forest and palm forest sites, seven forest floor samples were collected per plot; the sites had three and four plots, respectively. The tabonuco forest site had five plots with four samples per plot. Sampling in both the tabonuco and palm sites was done using a 50 × 50 cm template; a 15 × 15 cm template was used at the moist site to be consistent with the prehurricane data that was collected there the month prior to the hurricane. Over the course of the study, 476, 357, and 340 forest floor samples were collected and sorted from the moist, palm, and tabonuco forest, respectively. Litterfall was collected in existing baskets at the same time as the forest floor samples were taken. At intervals of at least every 3 months, we also sampled soils (0–10 cm) using a 2-cm–diameter corer to evaluate changes in total soil C and N. Soil samples were taken directly underneath each forest floor sample, so the number of replicates per plot and site are the same as described above. Each soil sample was ground and analyzed separately (not composited), then run in duplicate on a CE Elantec CN 2100 analyzer, with a standard run every 10 samples. Stand-level tree damage was quantified in a 10-m radius in every plot and composited for a site. Damage was assessed on all stems at least 5 cm diameter at breast height (dbh), and we noted whether individuals were broadleaf trees, ferns, or palms. Branch damage of broadleaf trees was classified as none, light (less than 25% of crown), moderate (25–50% of crown), or heavy (more than 50% of crown); stem damage was characterized as none, snapped, uprooted, or defoliated.

Statistical Analyses

All statistical analysis was performed using JMP V.3.1 (SAS Institute, Cary, NC, USA); data were tested for normality and equal variance assumptions and transformed where appropriate. Student *t*-tests were used to compare posthurricane forest floor mass to prehurricane values (Table 2); tests were not paired due to differences in sample size. Regression analyses were used to determine relationships between hurricane-generated litter inputs and forest floor standing stocks with prehurricane litterfall, prehurricane forest floor, average elevation, and mean annual rainfall.

Our objective was to follow the initial cohort of hurricane-generated litter over time, similar to a litterbag decomposition study; therefore, we used a standard decay model. To do this, we subtracted the corresponding posthurricane litterfall inputs measured in the nearest basket from the forest floor standing stocks collected at each sampling date. Thus, every sample was adjusted with a value specific to that sampling area. However, because litter inputs were generally low following the hurricane, these subtractions did not significantly change the decay rates or conclusions of the study. In general, litterfall and ash-free dry mass correction factors, decreased mass values by 8%–19%, mainly due to the ash correction.

Decay rates were determined by calculating k values, a decomposition rate constant in y^{-1}, for each plot based on the following exponential decay model:

$$\ln(x_t/x_0) = -kt$$

where x_t = forest floor mass remaining at time t, x_0 = original forest floor mass, k = decomposition rate constant, and t = time (Olson 1963).

Linear and double exponential decay models were also tested, but these had much lower R^2 values. The calculation of the k value does not require steady state conditions and has been done in numerous decomposition studies in forests at various successional stages and also after hurricanes (Herbert and others 1999; Sullivan and others 1999). For comparison, we also calculated annual litter turnover (k_L), which is based on steady-state conditions, as litterfall divided by prehurricane standing stocks using values from Table 2, and t_{50}, the time it would take for 50% of the forest floor mass to disappear. One-way analysis of variance (ANOVA) was used to compare k, k_L, and t_{50} values among forest types.

Nutrients in the forest floor components over time were compared using the same methodology as for the initial inputs of forest floor, pooling all samples within a plot. One-way ANOVA was used to compare values of C:P and C:N across sites, after natural log (ln) transformation. Nutrient contents were calculated by multiplying concentration by mass to express nutrients on a kg/ha basis. Soil C and N were analyzed with one-way ANOVA.

Results

Initial Inputs of Forest Floor Mass and Nutrients

Hurricane Georges litterfall ranged from 0.55 to 0.93 times annual litterfall, and forest floor mass increased 1.1 to 2.5 times above prehurricane values (Table 2). Forest floor mass increased significantly above prehurricane values in the moist, tabonuco, and palm forests, whereas in the colorado,

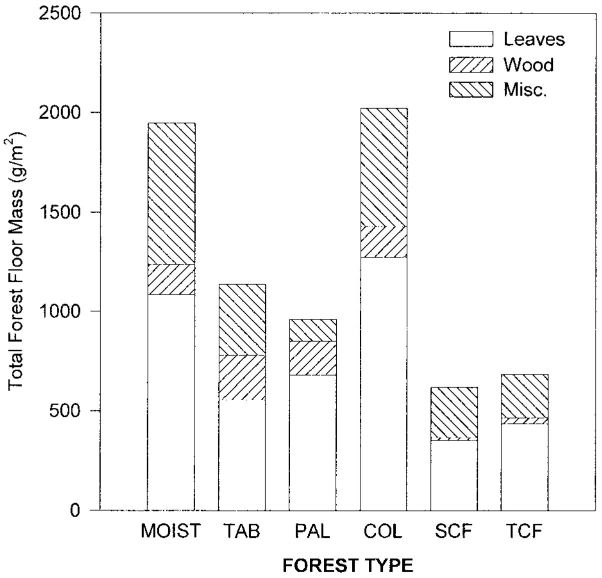

Figure 2. Ash-free dry mass of various components of the forest floor litter collected immediately after the passage of Hurricane Georges. Within the Luquillo Experimental Forest, Puerto Rico, we took samples in moist forest (MOIST), tabonuco forest (TAB), palm forest (PAL), colorado forest (COL), short cloud forest (SCF), and tall cloud forest (TCF) (see Table 1).

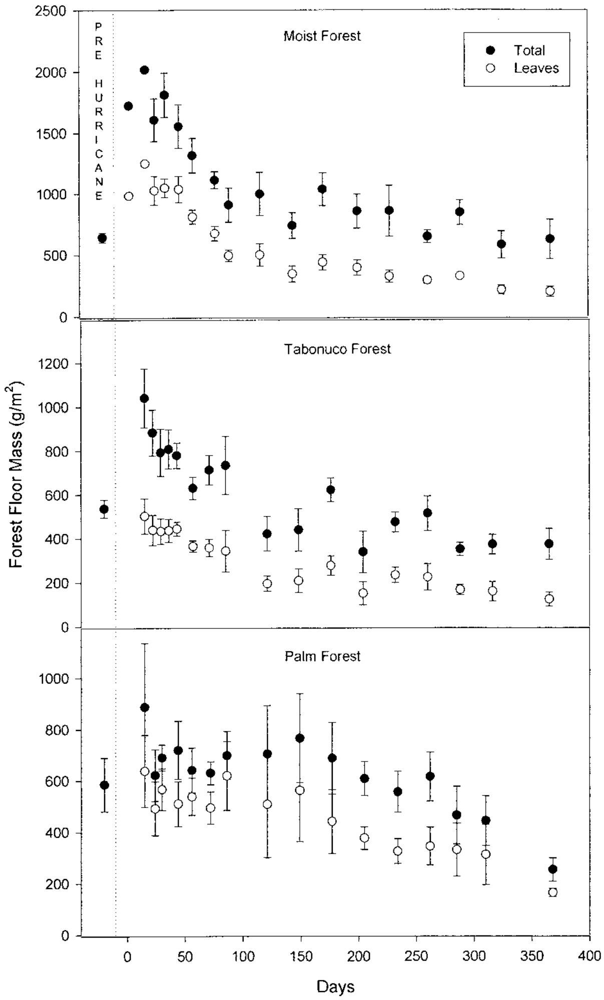

Figure 3. Changes in total forest floor mass and leaf mass over time in the three forest types followed for 1 year. Values represent plot-level means and SEs. Each value is expressed on an ash-free dry mass basis and was corrected for incoming litterfall. Points to the left of the dotted lines are from samples taken prehurricane using the same methodology.

short cloud, and tall cloud forests forest floor inputs were not significant compared to prehurricane levels. Of the three sites with significant litter inputs, the moist forest had the largest storm litterfall inputs and the greatest increase in forest floor mass. The sites also varied in the types of litter inputs to the forest floor (Figure 2). In five sites, approximately 50%–60% of the forest floor mass consisted of leaves, and 30%–40% consisted of wood. The palm forest was an exception, with proportionally more leaf mass (71%) and proportionally lower wood mass (11%) as well as high values for miscellaneous component (18%) due to the input of fruit and infructescences (Figure 2).

Prehurricane litterfall rates explained 86% of the variability in hurricane-generated litter inputs ($P < 0.01$). Only 57% of the variability in hurricane-generated forest floor mass was explained by prehurricane standing stocks ($P = 0.08$), due primarily to the large prehurricane forest floor standing stock in the colorado forest type. There were no patterns in hurricane-generated litterfall or forest floor mass in relation to elevation or mean annual rainfall.

The initial hurricane inputs of nutrients to the forest floor were substantial (Table 3), rivaling levels of fertilization used in agricultural practices and similar to other hurricane studies (Harrington and others 1997). Nitrogen ranged from approximately 67 to 309 kg/ha, P ranged from 1.5 to 8.4 kg/ha, and K ranged from 7.6 to 79.9 kg/ha. The moist forest inputs consistently had the higher nutrient content due to larger mass inputs (Table 2). We calculated ratios of C:N and C:P as common indices of litter quality (Table 3). C:N varied across sites in leaves ($P < 0.003$) but not in wood, with the upper elevational sites tending to have higher ratios (Table 3). C:P varied among leaves ($P = 0.003$) and wood ($P < 0.012$), with higher values again at the upper-elevational sites. Among the three forests studied intensively over time, there were no differences in either ratio (Table 3).

Table 3. Nutrient Characteristics of the Floor at the First Sampling Period for the Six Forests

Site	C:N Leaves (x ± SE)	C:N Wood (x ± SE)	C:P Leaves (x ± SE)	C:P Wood (x ± SE)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)
Moist	27.2	46.3	96.6	197	308.8	8.4	79.9	168.0	42.2
Tabonuco	26.7 ± 2.1^{a}	47.5 ± 6.6^{a}	$95.7 \pm 12.1^{a,c}$	162.8 ± 22.9^{a}	193.7	5.7	40.0	104.9	21.5
Palm	$28.0 \pm 1.1^{a,b}$	52.6 ± 6.5^{a}	70.6 ± 2.4^{a}	155.0 ± 31.7^{a}	142.9	6.1	21.8	49.6	19.5
Colorado	43.0 ± 2.4^{b}	59.4 ± 6.7^{a}	$163.3 \pm 27.7^{b,c}$	$294.5 \pm 32.8^{a,b}$	214.2	5.8	43.3	123.5	28.5
Short Cloud	37.8 ± 1.8^{b}	68.4 ± 8.2^{a}	164.3 ± 16.4^{b}	490.3 ± 123.0^{b}	66.6	1.5	7.6	18.2	7.1
Tall Cloud	42.3 ± 1.5^{b}	83.3 ± 36.8^{a}	$151.3 \pm 7.0^{a,b}$	$236.7 \pm 78.8^{a,b}$	79.7	1.7	10.4	28.2	8.2

Sampling occurred within 2 weeks of Hurricane Georges.
To obtain values on a kg/ha basis, nutrient concentration values were multiplied by the posthurricane forest floor mass values shown in Table 2 and Figure 2.
Nutrient ratios were compared across sites, but the moist site could not be included because only one plot was accessable during the initial sampling.
C, carbon; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium
Letters denote significant differences among means within a column.

Table 4. Damage to Trees at Least 5.0 cm dbh Within a 10-m Radius of the Forest Floor Sampling Sites

Tree Damage						Branch Damage			
Site	Tree Type	Defoliation	Snap	Uproot	None	Light	Moderate	Heavy	None
Moist	Broadleaf	194	26	14	1	77	80	59	11
	Palm	1	1	0	0				
	Fern	0	0	0	0				
	All	195 (82.3)	27 (11.4)	14 (5.9)	1 (0.4)	77 (33.9)	80 (35.2)	59 (26.0)	11 (4.8)
Tabonuco	Broadleaf	159	12	1	20	71	36	27	58
	Palm	31	0	0	19				
	Fern	0	0	0	3				
	All	190 (77.3)	12 (4.1)	1 (0.4)	42 (18.2)	71 (37.0)	36 (18.8)	27 (14.1)	58 (30.2)
Palm	Broadleaf	47	8	5	4	32	11	8	11
	Palm	100	0	3	2				
	Fern	34	1	3	3				
	All	181 (86.2)	9 (4.3)	11 (5.2)	9 (4.3)	32 (51.6)	11 (17.7)	8 (12.9)	11 (17.7)

Total numbers are listed by life form and for all trees (percentage in parentheses) for each forest type.
Trees were classified based on damage to canopy (defoliation) or trunk (snap, uproot). Canopy damage of broadleaf trees was further classifed based on damage to the branch structure.
Light damage constituted less than 25% of canopy damage, moderate was 25–50% damage, and heavy damage was more than 50% canopy damage.

Tree Damage and Changes in Forest Floor Mass and Nutrients over Time

We quantified tree damage at the three intensively studied sites. Defoliation was the most common form of damage, accounting for 77% to 86% of all tree damage (Table 4). Snaps were relatively common (11.4%) in the moist forest, but they were less common in the other two sites. Uprooted trees were common in both the moist (5.9%) and palm forests (5.2%). Part of these differences relate to life form, because broadleaf trees tended to snap more than other life forms. Broadleaf trees were also the only life form in which branch damage could be quantified; this damage was greatest at the moist forest site. Overall, the three forests had very similar tree densities, but it is clear that the moist forest had the most structural damage because of its higher proportion of snapped and uprooted trees, and broadleaf trees with heavy branch damage (Table 4).

Litterfall remained low in the year following the hurricane. Leaffall and total litterfall were 0.93 ± 0.23 SE and 1.22 ± 0.30 g/m^2/d in the moist forest, 1.21 ± 0.19 and 1.39 ± 0.19 g/m^2/d in the tabonuco forest, and 0.58 ± 0.08 and 0.66 ± 0.12 g/m^2/d in the palm forest, respectively. These values were 38% to 58% of prehurricane litterfall values (Table 2).

Decay of the hurricane-generated litter tended to follow an exponential pattern for both the dead leaf component and total mass at all three sites (Figure 3). For the leaf component, R^2 values for k calculated for each plot were 0.83 ± 0.03 SE for the moist forest, 0.69 ± 0.10 for the tabonuco forest, and 0.64 ± 0.08 for the palm forest. For the total

Table 5. Decomposition Fate Constants (k) (in y^{-1}) and Half-Life for Litter (t_{50}) for the Three Sites

Site	kleaf	t50leaf	ktotal	t50total	kL
Moist	1.76 ± 0.14	0.40 ± 0.04	1.09 ± 0.14	0.67 ± 0.10	1.56
Tabonuco	1.45 ± 0.20	0.52 ± 0.08	1.04 ± 0.12	0.70 ± 0.08	1.32
Palm	1.03 ± 0.11	0.69 ± 0.06	0.74 ± 0.16	1.25 ± 0.53	0.84
	$F_{2,9} = 3.75$	$F_{2,9} = 3.73$	$F_{2,9} = 1.51$	$F_{2,9} = 1.69$	
	$P = 0.065$	$P = 0.066$	$P = 0.272$	$P = 0.239$	

Values are mean ± SE.
The first two columns show values for the leaf component; the third and fourth columns show values for total forest floor mass, calculated for each plot and then averaged.
F and P values are from one-way ANOVA comparing forest types.
The last column shows the total annual litter turnover rate (kL), calculated as annual litterfall dividing by the litter standing stock.

mass, R^2 values generally were not as high (moist forest, 0.66 ± 0.06; tabonuco forest, 0.47 ± 0.19; palm forest, 0.54 ± 0.10). The main reason for the lower R^2 values on the total mass data is the wood component, which has substantial mass but decays much more slowly than recently dead leaves. After the initial increase, forest floor mass returned to prehurricane values rapidly: within 5–10 months for the moist forest, 4–5 months for the tabonuco forest, and 1–2 months for the palm forest (Figure 3). The palm forest site had little wood; therefore, the total and leaf curves sometimes coincided. The palm forest tended to have lower k and the highest t_{50} values, but these were not significantly different from the other two sites; k_L values were lower than k values at all three sites (Table 5).

Patterns in nutrient concentrations of the forest floor litter declined on a similar time scale as forest floor mass, although patterns of nutrient accumulation and release were dependent on the site and on the nutrient (Figure 4). Potassium quickly decreased from leaves at all three sites, most likely due to leaching losses. Nitrogen, P, Ca, and Mg concentrations increased above the initial storm input levels in leaves in the moist forest, suggesting some nutrient accumulation at this site. Similar patterns were also seen for wood at this site. In the tabonuco and palm forests, there was no pattern of nutrient accumulation in either leaves or wood. Some Mg loss occurred early on in the palm forest, as evidenced by sharp decreases in leaf Mg concentrations after the first three sampling periods. As litter decomposed, there were no detectable changes in soil C or N concentrations over time within a site (Figure 5).

Discussion

The long-term impact of a disturbance on ecosystem structure and process results from the interaction of the initial damage and the recovery and repair mechanisms that operate during the subsequent phase of reorganization. In this study, we compared initial damage (for example, hurricane litter inputs) and recovery (for example, decomposition) of different forest floor ecosystems following the passage of Hurricane Georges. Hurricane litter inputs were strongly related to prehurricane litterfall, a measure of productivity. This result coincides with work by Harrington and others (1997), who noted that leaf area index (LAI) loss was correlated with prehurricane LAI and canopy height. Recovery of forest floor mass was rapid at the three sites that were studied intensively over time, despite considerable variation in the level of initial structural damage (Table 4), the magnitude of litter inputs (Table 2, and plant community composition and physiognomy (Tables 1 and 4). Generally, within 6 months, the sites approached prestorm forest floor mass levels (Figure 3). This return time was related both to the degree of initial damage and to the rate of decomposition. Because initial litter masses at all three sites were not dramatically dissimilar in their C:N and C:P, differences in decomposition rates are likely to be related to climatic factors and secondary chemistry (Bloomfield and others 1993).

Other studies suggest that hurricanes and their associated canopy openings do not increase decomposition in these forests. In a previous short-term study (approximately 100 days) in the tabonuco forest, mass loss of leaves from litterbags was generally slower after Hurricane Hugo than before the hurricane in several species, site, and topographic combinations (Sullivan and others 1999). In a tropical wet forest in Costa Rica, the decomposition rates of freshly fallen leaf material were not accelerated in canopy openings as compared to intact forest (Denslow and others 1998). Finally, a similar result was seen in a litterbag study of *Metrosideros polymorpha* leaves in Hawaii, where green leaves decomposed faster than brown leaves only for the

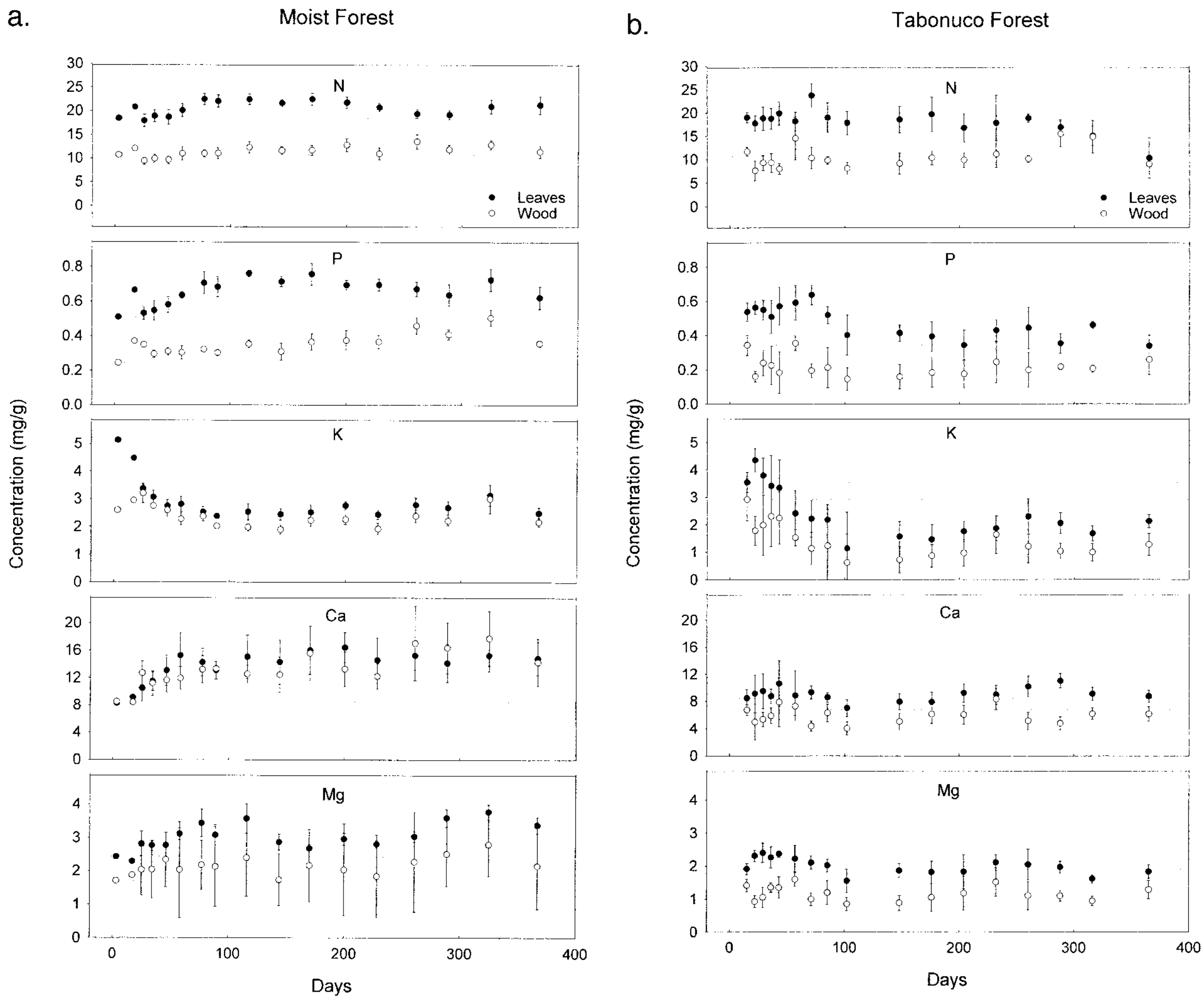

Figure 4. Changes in nutrient concentration for various nutrients at the three sites: (**a**) moist forest, (**b**) tabonuco forest, and (**c**) palm forest. Leaf and wood components are considered separately. Dotted lines represent initial nutrient concentration values. Points above the line represent net accumulation; points below the line represent net release.

1st month of a 24-month study (Herbert and others 1999). We therefore suspect that decomposition rates were probably not accelerated after the hurricane, and that these forests, with their relatively high decomposition rates typical of tropical forests (Anderson and Swift 1983), are simply capable of processing hurricane litter on time scales of less than 1 year. Such brisk recovery of forest floor processes suggests that the length of time for which fine litter inputs may affect processes such as nutrient cycling and seedling regeneration is on the order of months in these tropical forests. This rapid litter decomposition and its incorporation into nutrient cycles appears to be one reason why these forests can reorganize quickly following wind storms and are thus highly resilient to these disturbances.

The moist forest had the greatest proportional increase of litter on the forest floor, but because decomposition rates in this forest were similar to the wetter tabonuco type forest, both sites returned to prehurricane values at similar times (Figure 3 and Table 5). The upper-elevation palm forest had smaller litter inputs but generally slower decomposition rates (Table 5), leading to relatively fast recovery of the forest floor. These site differences may be due in part to the ability of different life forms to resist storm damage. For example, palms and ferns snap and uproot infrequently compared to the other forest types (Frangi and Lugo 1991; Zimmerman and others 1996). They also have proportionally more leaves and fruit, which decay more rapidly than wood (Figure 2).

Inputs of hurricane litter nutrients, although

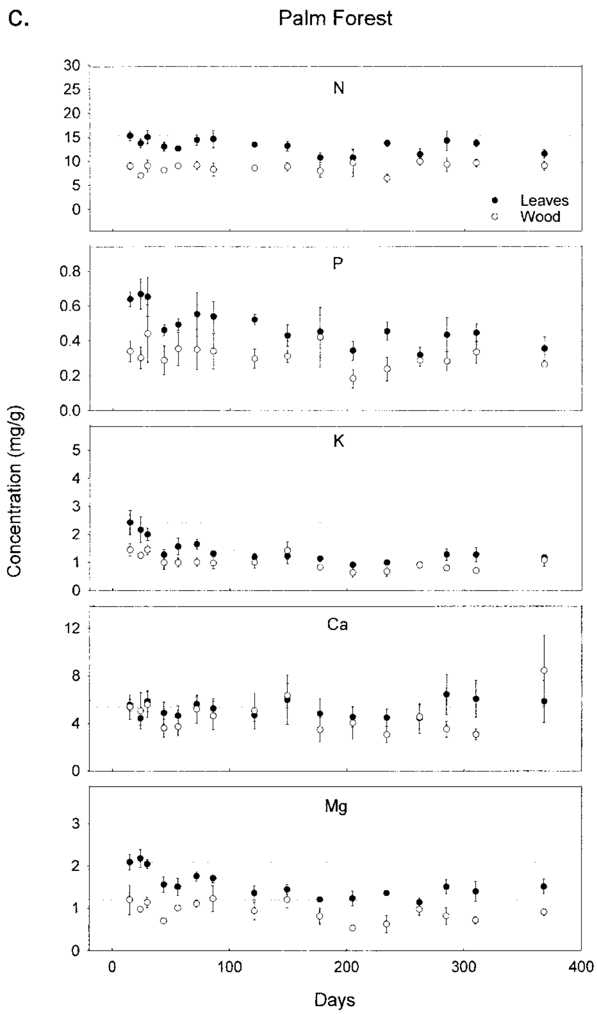

Figure 4. (Continued)

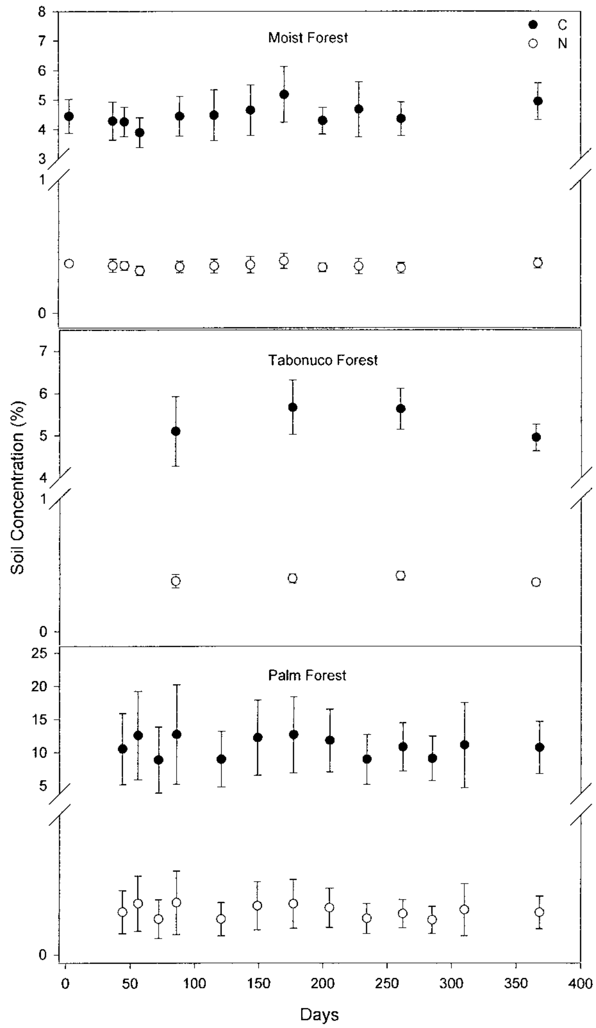

Figure 5. Soil carbon (C) and nitrogen (N) concentrations (0–10-cm depth) with time since hurricane disturbance at the three sites. Values represent plot-level means and SEs expressed on a dry-weight basis.

large, are also not longlasting in these forests due to the rapid decomposition rates. Only in the moist forest site did the nutrient concentrations of forest floor N, P, Ca, and Mg increase over time. The decreases in K nutrient concentrations within the 1st month at all three sites, and in several nutrients at the other two sites, suggest that the release of nutrients during decay might yield short-term soil nutrient pulses. Such pulses may be difficult to pick up in the soil, however, and our sampling may not have been intensive enough to pick up changes to a large pool. We compared our C numbers to previous research in tabonuco forests that found 7.4 t/ha of forest floor C and 21–27 t/ha C in 0–10 cm of soil (McGroddy and Silver 2000). Assuming that the input of 4.77 t/ha hurricane litterfall is 50% C (Table 2), then the total input of hurricane litter is only 6.9%–8.4% of the total amount of C stored in the forest floor and soil.

It has been hypothesized that these litter pulses are an important source of heterogeneity that can affect processes such as regeneration, growth, and competitive interactions among species (Orians 1982; Denslow 1987). However, the nutrient pulses associated with these litter pulses have been difficult to detect in both temperate and tropical forests. For example, after treefall gap formation, no differences were found in soil nutrient pools and N mineralization rates between crown zones and intact forest in 2–24-month-old gaps in Costa Rica (Vitousek and Denslow 1986) or 5-month-old experimental gaps in the Amazon (Uhl and others 1988). Only Denslow and others (1998) were able to detect a difference in soil nutrient pools—an effect that was most pronounced in the first 3 months after gap formation. Similar results have also been noted after larger-scale wind disturbances. For instance, no differences in soil NO_3, NH_4, or PO_4 concentrations were evident 1.5–2 years after Hurricane Opal (Hunter and Forkner 1999). After an experimental blowdown in Harvard Forest, net nitrification was slightly higher at 9–12 months, but at 3 years there was no difference in mean potential net mineralization or nitrification rates (Bowden and others 1993). Only studies that have done measurements within 4 months of hurricane disturbance (Steudler and others 1991; Silver and others 1996) have detected any type of soil nutrient increase. Although modeling exercises on tabonuco type forests in Puerto Rico found large increases in soil organ carbon (SOC) with successive hurricanes (Sanford and others 1991), we were unable to detect a significant increase in total soil organ matter (SOM) after one storm in this and in an earlier study (Silver and others 1996). However, this is not surprising given the large spatial variation in SOM and considering that the total hurricane inputs were only 5%–10% of the C stored in the 0–10-cm horizon of the tabonuco forest (Figure 5).

Based on our results after Hurricane Georges, we believe that litter on the forest floor can be an important source of soil nutrients over short-term time scales, but the nutrients will be difficult to detect unless measurements on a large number of samples are made within days to months after the disturbance. Although we have not followed where these nutrients go after being released from the litter, we hypothesize that a large proportion of the litter nutrients enters the soil and is used for plant uptake rather than being lost via leaching through the root zone or appearing in stream water and groundwater (McDowell and others 1996). We base this hypothesis on the small increases in nutrients seen in streams after hurricanes; for up to 2 years after the more intense Hurricane Hugo, only 1%–3% of the nutrients from hurricane-derived plant litter appeared in stream water (Schaefer and others 2000). Rates of gaseous N loss have been found to increase after hurricanes (Steudler and others 1991), but we noted rapid refoliation (within 3–4 weeks) of the canopy and a vigorous understory of grasses, seedlings, and vines in canopy openings, which are most likely using at least some these litter-derived nutrients.

As large-scale disturbances, hurricanes appear to be affecting nutrient cycling on two different spatial and temporal scales, due to differential consequences between structural damage to trees and defoliation. Structural damage to forests can be quite severe (Brokaw and Walker 1991; Whigham and others 1999) and can lead to long-term (on a decadal time scale) effects on nutrient cycling. However, the degree of structural damage will vary with both wind intensity and time since the last storm. For example, in Puerto Rico, Hurricane Hugo reduced aboveground biomass by 50% and aboveground nutrient content by 45%–48% (Scatena and others 1993), but such a large storm had not hit the Luquillo Mountains for 53 years (Scatena and Larsen 1991). These aboveground decreases were partially due to the production of coarse woody debris, which modeling exercises suggested was induced by net immobilization and decreased NPP (Zimmerman and others 1995). Reestablishment of predisturbance LAI and litterfall rates can take about 1–5 years (Scatena and others 1996; Harrington and others 1997), and aboveground nutrient pools may be enhanced after hurricanes, but the recovery of biomass and decay of coarse woody debris generally occurs on longer time scales (Zimmerman and others 1995; Scatena and others 1996). Hurricane Georges represents a storm of moderate intensity in that it followed Hurricane Hugo after only 9 years and reached Category 3–level winds. A storm with these characteristics may not produce large amounts of coarse woody debris, but even minor windstorm events produce significant amounts of fine litter. These fine-litterpatches are therefore important for their larger spatial extent and as sources of nutrients, which may make them more desirable microsites. Although short-lived, litter pulses after hurricanes provide important physical and biogeochemical properties for the recovering vegetation, and demonstrate remarkable resilience in their C and nutrient cycling processes.

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