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Fine Litterfall and Related Nutrient Inputs Resulting from Hurricane Hugo in Subtropical Wet and Lower Montane Rain Forests of Puerto Rico[1]

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ABSTRACT

On 18 September 1989 Hurricane Hugo defoliated large forested areas of northeastern Puerto Rico. In two severely damaged subtropical wet forest sites, a mean of 1006–1083 g/m^2, or 419–451 times the mean daily input of fine litter (leaves, small wood, and miscellaneous debris) was deposited on the forest floor. An additional 928 g/m^2 of litter was suspended above the ground. A lower montane rain forest site received 682 times the mean daily fine litterfall. The concentrations of N and P in the hurricane leaf litter ranged from 1.1 to 1.5 and 1.7 to 3.3 times the concentrations of N and P in normal leaffall, respectively. In subtropical wet forest, fine litterfall from the hurricane contained 1.3 and 1.5–2.4 times the mean annual litterfall inputs of N and P, respectively. These sudden high nutrient inputs apparently altered nutrient cycling.

RESUMEN

El 18 de septiembre de 1989 el Huracán Hugo defolió grandes extensiones de bosque al noreste de Puerto Rico. En dos localidades en un bosque muy húmedo subtropical donde el daño fue severo, cayó un promedio de 1006–1083 g/m^2, o 419–451 veces el promedio diario de hojarasca (hojas, pequeñas ramas y misceláneas deyección). Una cantidad adicional de hojarasca, 928 g/m^2, quedó suspendida sobre el suelo. En otra localidad en un bosque pluvial montano bajo se recibió 682 veces el promedio diario de hojarasca. Las concentraciones de N y P en la hojarasca del huracán fueron entre 1.1 a 1.5 y 1.7 a 3.3 veces, respectivamente, las concentraciones de N y P que se encuentran en la hojarasca que cae normalmente. En el bosque muy húmedo subtropical, la hojarasca del huracán contenía entre 1.3 y 1.5–2.4 veces el promedio anual de N y P respectivamente. Este aumento repentino en la entrada de nutrimentos aparentemente alteró el ciclo de nutrimentos.

PHYSICAL DISTURBANCES TO FORESTS such as fire, wind, and ice storms may induce pulses of litterfall (Bruederle & Stearns 1985). Such massive inputs of litter can affect nutrient cycling (Sanford *et al.* 1991), seedling survival (Guzmán-Grajales & Walker 1991), and terrestrial animals (Woolbright 1991). Depending on the type, season, and magnitude of the event, the litter generated by these disturbances may have properties different from normal litterfall (Polunin 1984). In particular, green leaves have higher nutrient concentrations than normal leaffall for those nutrients that are translocated during senescence.

On 18 September 1989 Hurricane Hugo defoliated extensive areas of the Luquillo Experimental Forest (LEF; see map in Scatena & Larsen 1991) causing a large pulse of litter deposition. North-facing slopes and ridges were more damaged than southern slopes and protected valleys (D. Foster,

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pers. comm.; Walker 1991; D. J. Lodge, pers. obs.). This paper integrates available data on fine organic matter and related nutrient inputs in three severely damaged sites located on ridges and north-facing slopes within the LEF. Two of these sites, Bisley (260–455 m elevation) and El Verde (350–430 m elevation), were in tabonuco forest in the subtropical wet forest life zone (Ewel & Whitmore 1973). This forest type is dominated by *Dacryodes excelsa* (tabonuco) and *Sloanea berteriana*. One site (East Peak; 1000 m elevation) was in dwarf forest within the lower montane rain forest life zone (Ewel & Whitmore 1973). These forest types and study sites are described in detail elsewhere (Howard 1968, Lyford 1969, Odum & Pigeon 1970, Brown *et al.* 1983, Scatena 1989).

METHODS

In this study, litterfall is defined as all leaf, wood <1 cm in diameter, and miscellaneous plant material deposited on the forest floor. Boles and large branches are excluded. Litter on broken branches and crowns that did not reach the ground immediately after the storm was classified separately as "suspended litter."

In the Bisley watersheds (13 ha), hurricane litterfall was collected from 0.25 m^2 baskets from which litter had been collected every 2 weeks for 2 years preceding the hurricane. Litter was collected 9 days after the storm on the regularly scheduled collection date. Sample statistics were calculated on 41 of the 60 original baskets that survived the storm. The baskets were located close to the ground where they were generally protected from high velocity winds, so litterfall should have remained in the baskets. This is supported by measurements of posthurricane litter standing stocks, which were approximately equal to the sum of prehurricane standing stocks (F. N. Scatena & W. Silver, pers. comm.) and hurricane litterfall as measured by the baskets.

To obtain an estimate of hurricane litter input at El Verde, where litter baskets were not in use, all litterfall and suspended litter (up to 3 m above the forest floor) were collected 3 to 10 days after the hurricane in 36 plots. These 0.25 m^2 plots were located at regular intervals along 4 transects with random compass orientations (245 m total length) that traversed defoliated ridges and upper slopes. We avoided streams and areas in which surface flow had moved litter. An additional 7 samples were collected from defoliated areas at East Peak 13 days after the storm.

Litter resulting from the hurricane was easily distinguished from prehurricane litter by its green color, shredded appearance, and attachment to twigs. Litterfall and suspended litter were not separated in 24 of the 36 samples collected at El Verde. Therefore, we subtracted the mean weight of suspended litter (394, 364, and 170 g/m^2 of leaves, fine wood, and miscellaneous debris, respectively) from the total weight of litter in these samples (double sampling with a difference estimator; Cunia 1985) to obtain unbiased estimates of litterfall at that site. The mean suspended litter mass of each component was calculated from the 12 separated samples.

All litter was oven-dried to a constant weight and sorted into leaf, fine wood, and miscellaneous components. After separation, dried samples were weighed to the nearest 0.1 g and ground with a Wiley mill through a 0.85 mm (20 mesh) stainless steel sieve. Ground samples from all of the baskets at Bisley were then combined, mixed, and subsampled for digestion. For each hurricane litter component at El Verde, seven samples were selected randomly for nutrient analysis. These samples were ground and digested separately, so that standard errors are representative of spatial variation.

Hurricane samples from both sites were digested with H_2O_2 and concentrated HNO_3 (Luh Huang & Schulte 1985) and analyzed for P, K, Ca, and Mg with a Beckman plasma emission spectrometer (Spectra Span V) at the Institute of Tropical Forestry (ITF). Bisley N concentrations were determined using the semimicro Kjeldahl method (concentrated H_2SO_4 digestion; Chapman & Pratt 1979). El Verde samples were analyzed for N at the Center for Energy & Environment Research (CEER) by direct combustion in a C-H-N analyzer (Carlo-Erba model 1106). Twenty-one of the El Verde samples were reanalyzed for N by the ITF laboratory; N values did not differ significantly between laboratories.

The nutrient concentrations of prehurricane litterfall from Bisley are average concentrations of sorted samples taken from the same baskets and analyzed by the same techniques as the hurricane samples. These averages represent 84 samples from 2 years of biweekly sampling. Bisley litter was pooled among baskets on each collection date for nutrient analysis, so standard errors are representative of temporal variation. Normal leaf litterfall P concentrations at El Verde are from Lugo (in press). The nutrient concentrations of prehurricane leaf litter (except P) at El Verde are means of 31 samples of leaves collected within 24 hours of abscission from a 1 ha plot during March, May, and October 1980, and 5 samples from another 1 ha plot in May 1980 (C. Zucca, pers. comm.). Standard errors for pre-

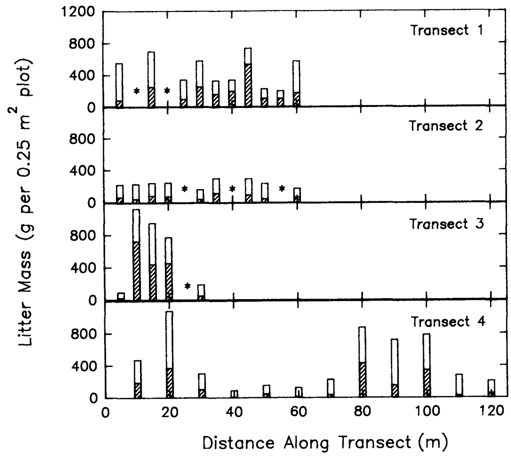

FIGURE 1. Spatial distribution of total fine litter (fallen plus suspended) resulting from Hurricane Hugo along four transects at El Verde. Hatched portion of bar indicates wood litter (<1 cm dia.), and clear portion of bar indicates leaf and miscellaneous litter. Asterisks indicate samples lost in processing.

hurricane nutrient concentrations at El Verde are therefore representative of temporal and spatial variation. A subset of these samples ($N = 16$) was sent to the ITF laboratory to confirm the analyses. Hurricane litter samples from East Peak (seven plots) were analyzed by the ITF laboratory as described above. Nutrient concentrations in aboveground biomass were from samples of live trees collected at Bisley in June 1989 and analyzed by the ITF laboratory as described above. Nutrient concentrations were determined by species, and these values were weighted by the biomass of each species to give the mean forest biomass nutrient concentrations.

RESULTS AND DISCUSSION

MASS.—The mass of fine litter deposited on the forest floor during Hurricane Hugo was *ca* 400 times the average daily input at Bisley and El Verde, and 682 times the daily input at East Peak (Table 1). Under normal conditions in these nonseasonal, evergreen forests, litterfall is distributed relatively evenly throughout the year. Bisley and El Verde did not differ significantly in either the dry mass of total litterfall (1083 *vs.* 1006 g/m^2, respectively) or the mass of fine woodfall (575 *vs.* 319 g/m^2; $P > 0.05$ for Kruskal-Wallis One-way Nonparametric ANOVA; Table 1). The mass of fallen litter varied sevenfold and the mass of fallen plus suspended litter varied twelvefold among plots along the El Verde transects (Fig. 1). The patches of high litter mass were 5–20 m long (Fig. 1) and coincided with fallen tree crowns.

At El Verde, where only heavily damaged sites were sampled, 56 percent of the total fine litter was deposited on the forest floor immediately after the

TABLE 1. *Hurricane litter and mean annual litterfall mass inputs by component in severely damaged subtropical wet forests (El Verde and Bisley) and lower montane rain forest (East Peak) in Puerto Rico. Prehurricane canopy leaf biomass estimates are also shown. Standard errors are given in parentheses after the sample mean.*

	Number of samples	Leaves	Fine wood	Misc.	Total
Hurricane litterfall (g/m^2 day^{-1})					
Bisley	41	377 (22)	575 (75)	131 (12)	1083 (92)
El Verde	36	615 (85)	319 (100)	72 (99)	1006 (203)
East Peak	7	354 (53)	95 (24)	131 (34)	580 (100)
Hurricane suspended litter (g/m^2 day^{-1})					
El Verde	12	394 (143)	364 (133)	170 (129)	928 (263)
East Peak	7	0.57 (0.5)	36 (29)	9 (7.6)	45 (37)
Mean daily nonhurricane litterfall (g/m^2 day^{-1})					
Bisley[a]	3300	1.29	0.55	0.54	2.38
El Verde[b]	2080	1.34	0.40	0.57	2.31
East Peak[c]	—	0.67	0.08	0.10	0.85

[a] F. N. Scatena & A. Lugo, pers. comm.
[b] C. Zucca, pers. comm.
[c] Weaver *et al.* 1986.

TABLE 2. *Mean nutrient concentrations (mg/g) in hurricane litter, normal (prehurricane) litterfall by component, and prehurricane canopy leaves and branches. Standard errors in parentheses represent spatial and/or temporal variation (see Methods).*

	N	P	K	Ca	Mg
Leaves					
Subtropical wet forest					
Bisley					
Hurricane leaffall	16.2 (0.1)	0.734 (0.030)	5.65 (0.67)	6.19 (2.40)	2.09 (0.45)
Prehurricanea leaffall[a]	12.6 (0.2)	0.422 (0.010)	2.57 (0.09)	6.90 (0.15)	2.29 (0.04)
Prehurricane canopy leaves	15.4	0.743	7.41	4.43	2.00
El Verde					
Hurricane leaffall	15.4 (0.1)	0.820 (0.030)	6.37 (0.31)	8.29 (0.58)	2.51 (0.03)
Prehurricane fall[b]	14.4 (0.5)	0.25[c]	7.49 (0.30)	12.14 (0.36)	4.24 (0.12)
Prehurricane canopy leaves[d]	15.2 (0.6)	0.769 (0.027)	9.37 (0.58)	9.02 (0.63)	3.51 (0.21)
Lower montane rain forest					
East Peak					
Hurricane leaffall	11.9 (0.37)	0.427 (0.016)	4.30 (0.18)	4.43 (0.10)	1.77 (0.05)
Prehurricane leaffall[e]	7.7	0.245	1.39	5.31	2.45
Fine wood (< 1 cm diameter)					
Subtropical wet forest					
Bisley					
Hurricane woodfall	8.6 (1.4)	0.339 (0.07)	3.10 (0.66)	7.26 (0.44)	1.62 (0.02)
Prehurricane woodfall[a]	8.6 (0.03)	0.297 (0.010)	1.42 (0.08)	6.87 (0.21)	1.54 (0.09)
El Verde					
Hurricane woodfall	8.5 (0.03)	0.753 (0.026)	6.25 (0.26)	11.86 (0.74)	2.49 (0.08)
Prehurricane woodfall	7.1[c]	0.26[c]	3.0[f]	16.0[f]	2.1[f]
Lower montane rain forest					
East Peak					
Hurricane woodfall	6.7 (0.05)	0.223 (0.047)	2.28 (0.25)	3.77 (0.87)	0.87 (0.14)
Miscellaneous					
Subtropical wet forest					
Bisley					
Hurricane litterfall	17.2 (0.2)	1.034 (0.061)	5.57 (0.09)	6.98 (0.69)	2.47 (0.20)
Prehurricane litterfall[a]	13.4 (0.4)	0.917 (0.022)	5.10 (0.15)	9.09 (0.34)	1.96 (0.03)
El Verde					
Hurricane litterfall	10.5 (1.0)	0.810 (0.067)	8.48 (0.64)	7.49 (0.78)	3.01 (0.29)
Lower montane rain forest					
East Peak					
Hurricane litterfall	9.7 (0.1)	0.351 (0.058)	4.04 (0.52)	3.67 (0.37)	1.86 (0.13)

[a] F. N. Scatena & A. Lugo, pers. comm.
[b] C. Zucca *et al.*, pers. comm.
[c] Lugo (in press) data on nutrient inputs from litterfall at El Verde.
[d] Unweighted mean of tree species (Table 8, Ovington and Olson 1970).
[e] Weaver *et al.* 1986.
[f] Cintron, unpublished data, Institute of Tropical Forestry.

storm. The remainder stayed suspended on broken crowns, branches, and uprooted trees. Deposition of this litter was gradual; a few leaves and much of the fine woody litter remained suspended one year after the hurricane. The suspended masses of leaf (394 g/m^2), fine wood (364 g/m^2) and total fine litter (928 g/m^2) after the storm amounted to 0.8, 1.8, and 1.1 times the normal annual litterfall inputs, respectively (Table 1).

Total fine litterfall resulting from the hurricane was 1.2 times the mean annual litterfall at Bisley and El Verde, and 1.9 times the mean annual litterfall at East Peak. The total mass of suspended and fallen hurricane leaf litter in defoliated areas at

TABLE 3. *Total fine litter nutrient inputs (g/m²) and the ratio of Hurricane Hugo to mean annual litter nutrient inputs at the Bisley watershed and severely damaged sections of El Verde in the Luquillo Experimental Forest of Puerto Rico. Values are calculated from litter masses and nutrient concentrations in Tables 1 and 2.*

	N	P	K	Ca	Mg
Nutrient inputs (g/m²) from total fine litterfall in subtropical wet forest					
Bisley					
Hurricane	13.3	0.61	7.15	7.91	2.04
Mean annual	10.3	0.40	2.39	6.32	1.61
El Verde					
Hurricane					
Fallen	13.0	0.80	6.52	9.42	2.55
Suspended	13.3	0.61	6.23	8.86	2.41
Mean annual	10.5	0.33	5.16	10.17	2.79
Nutrient inputs (g/m²) from leaf litterfall in lower montane rain forest					
Hurricane	4.2	0.15	1.52	1.57	0.63
Mean annual	1.9	0.06	0.34	1.30	0.60
Ratio of hurricane to mean annual total fine litterfall nutrient input					
Bisley	1.29	1.53	2.99[a]	1.25	1.27
El Verde	1.25	2.42[b]	1.26	0.93	0.91

[a] Probably an overestimate because of leaching losses of K from prehurricane litterbasket collections.

[b] This may be high due to differences in classifying fine wood. Hurricane P-inputs were 1.86 times mean annual P-inputs assuming equal P- concentrations in pre- and posthurricane woodfall.

El Verde was within the range of previous leaf biomass estimates for this forest type (259–1024 g/m²; Ovington & Olson 1970). Leaffall in the lower montane site was slightly greater than previous biomass estimates from an adjacent area at East Peak (290 g/m²; Weaver *et al.* 1986). However, our samples were from a stand with mineral soils; whereas, the biomass estimates were from a stand of smaller stature growing on soil with an organic surface (Weaver *et al.* 1986).

NUTRIENTS.—The total nutrient input to the forest floor from hurricane-derived litterfall ranged between 1.3 and 3.0 times the annual litterfall transfer at Bisley and El Verde (Table 2). Transfers of nutrients in leaffall at East Peak ranged from 1.0 to 4.5 times the average annual input by leaves (Table 2). Additional nutrients which were temporarily retained in suspended loose litter, broken crowns, and uprooted trees accounted for 48 to 56 percent of the hurricane litter nutrient transfers at El Verde. Because this vegetation did not immediately reach the ground and some remained alive, this suspended litter represents an intermediate-term storage compartment.

Concentrations of some nutrients in Hugo litter were greater than in normal litter and were similar to those in aboveground biomass at Bisley and El Verde (Table 3). The difference in nutrient concentrations between hurricane and normal leaf litterfall reflects leaching and retranslocation that occurs during senescence and early decomposition. Concentrations in hurricane leaf litter at East Peak were 1.5 times higher for N, 1.7 times higher for P and 3.1 times higher for K than previously reported values for normal litterfall (Weaver *et al.* 1986, Medina *et al.* 1981). Potassium is highly mobile and is readily leached from senescent and fallen leaves (Tukey 1970, Golley *et al.* 1975). Although K was twice as concentrated in hurricane litter than in normal leaf litter at Bisley, most of this difference was probably caused by leaching loss from normal litterbasket samples rather than retranslocation. The concentration of K in hurricane leaf litter at El Verde was similar to the concentration in leaves that were collected within 24 hr of normal leaf fall to minimize leaching loss (Table 3).

Hurricane leaf litter had *ca* 2–3 times the P concentration of normal leaf litter at El Verde and Bisley (Table 3). Phosphorus is generally not susceptible to leaching so this difference probably reflects retranslocation. Phosphorus retranslocation is known to be high in tabonuco forest and has been variously estimated as 92 percent (Lugo, in press; as the difference in concentrations between canopy leaves from biomass harvests and leaf litterfall) and 72 percent (calculated using data of Medina *et al.* [1981] on adult green leaves and freshly fallen leaves of five species with the method of Vitousek & Sanford [1986]). We did not calculate retranslocation rates using these differences because the hurricane litter included leaves in various stages of growth and senescence; whereas, retranslocation rates are properly estimated using mature green foliage.

The input of phosphorus contained in total hurricane fine litterfall was 1.5 to 2.4 times normal annual litterfall input in the heavily damaged Bisley and El Verde sites (Table 2). Inputs of P in the hurricane leaffall were 2.5 times the normal annual input of P in leaffall at East Peak (Table 2). Such high magnitude transfers of phosphorus from live vegetation to the forest floor may affect soil fertility and forest productivity (Sanford *et al.* 1991).

The concentration of N was slightly greater in hurricane litter as compared to normal leaf litter at El Verde and Bisley (Table 3). However, the input of carbon and more than a normal year's litterfall-N on a single day (Table 2) together with destruction of vegetation and disturbance of roots and soil contributed to changes in N-cycling (W. McDowell & C. Asbury, pers. comm.; Steudler *et al.* 1991, Sanford *et al.* 1991). After the hurricane, NO_3 concentrations initially declined in stream waters apparently due to microbial immobilization (C. Asbury, pers. obs.). Stream nitrate concentrations subsequently increased dramatically. Because few fine roots were alive after the hurricane (Parrotta & Lodge 1991), it is likely that plant uptake of N was minimal and that the resulting increased soil ammonium stimulated nitrification (Montagnini & Buschbacher 1989) and denitrification (Steudler *et al.* 1991). Nitrification rates (as measured using *in situ* incubations without live roots) were very low in surface soils before the hurricane (C. Asbury & D. J. Lodge, pers. obs.).

Forested areas of northeastern Puerto Rico that were severely affected by Hurricane Hugo received a high-magnitude pulse of fine litterfall. The physical effects of such massive inputs of litter affected seedling and frog recruitment and survival (Guzmán-Grajales & Walker 1991, Woolbright 1991). Furthermore, the flux of nutrients associated with this litter apparently altered nutrient cycles (Steudler *et al.* 1991) and may affect soil nutrient availability and forest productivity (Sanford *et al.* 1991).

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