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Hurricane Damage to a Flood Plain Forest in the Luquillo Mountains of Puerto Rico[1]

Jorge L. Frangi

Universidad Nacional de La Plata, 1900 La Plata, Argentina

and

Ariel E. Lugo

Institute of Tropical Forestry, U.S.D.A. Forest Service, Southern Forest Experiment Station, Call Box 25000, Río Piedras, Puerto Rico 00928-2500, U.S.A.

ABSTRACT

Hurricane Hugo caused low to moderate damage to a flood plain forest that was partially protected by its topographic position. Treefalls and the location of damage suggested N to NW wind direction during the storm. Thirty percent of the trees, or 693 trees/ha, had some damage and 84 percent of the damage was to the canopy. Most of the damage to trees was caused by direct wind impact (83%) as opposed to secondary effects (16%). Over 80 percent of the snapped, leaning, and uprooted trees were dicotyledonous. Tree mortality was only 1 percent, and most of the damage to the sierra palm *Prestoea montana* (R. Grah.) Nichols was loss of leaves. Rapid refoliation, epicormic branching, adventitious root production, resprouting, and regeneration from seed in open areas were observed nine months after the event. Ten percent of the aboveground biomass and 12–16 percent of the nutrient stocks (N, P, K, Ca, Mg) were transferred to the forest floor, mostly in the form of woody biomass and nutrient-rich leaves. Palm leaves were the dominant leaf component of necromass. Instantaneous *in situ* fine and coarse necromass production was 10 and 9.2 Mg/ha, respectively. Net changes in aboveground mass, N, P, K, Ca, and Mg (in percent of prehurricane value) were 8, 3, 0, 3, 12, and 1, respectively, in spite of a high rate of loss by export. The source of additional mass and nutrients were boles from upland forests that fell into and remained inside the flood plain.

RESUMEN

El Huracán Hugo causó poco o moderado daño a un bosque inundable protegido parcialmente del viento por su posición topográfica. La caída de árboles y la ubicación del daño sugieren que la dirección del viento durante la tormenta era del N al NO. Treinta porciento de los árboles (693/ha), tenían algún daño y el 84 por ciento del daño fue en el dosel. La mayor porción del daño (83%) a los árboles se debió a impacto directo del viento y el resto (16%) se debió a causas secundarias. Sobre 80 por ciento de los árboles partidos, inclinados, o volteados eran dicotiledoneos. La mortalidad arborea fue solamente de 1 por ciento y el daño mayor a las palmas de sierra (*Prestoea montana* (R. Grah.) Nichols) fue la pérdida de hojas. Nueve meses después del huracán se observó refoliación rápida, ramas epicórmicas, producción de raíces adventicias, re-brotes y regeneración de semillas en claros. Diez porciento de la biomasa y 12–16 por ciento de los nutrientes (nitrógeno, fósforo, potasio, calcio y magnesio) se transfirieron al piso del bosque, mayormente en forma de madera y hojas. Ramas de palma era el componente dominante de la necromasa. Producción instantánea de necromasa fina y gruesa fue de 10 y 9.2 Mg/ha, respectivamente. Cambios netos en masa aérea, nitrógeno, fósforo, potasio, calcio y magnesio, expresados en porciento del valor previo al huracán, fueron 8, 3, 0, 12 y 1, respectivamente, a pesar de pérdidas considerables debido al transporte hidráulico. Fuentes adicionales de masa y nutrientes fueron los troncos caídos en las laderas y transportados al valle inundable.

On 18 September 1989 Hurricane Hugo struck the Luquillo Experimental Forest (LEF) with winds of up to 227 km/hr (Scatena & Larsen 1991). This was the first passage of a hurricane of this size over the LEF in 57 yr. Our study was conducted at an elevation of 750 m in a *Prestoea montana* (R. Grah.) Nichols (sierra palm) flood plain forest. We had prehurricane information for the flood plain forest dating back to the spring of 1980, when we established a permanent 5 × 5 m grid on 2525 m² of the stand (Frangi & Lugo 1985). This gave us the opportunity to study hurricane effects on the structure of the flood plain forest including species-specific responses, estimates of aboveground nutrient and biomass accumulation and their transfer to the forest floor after the hurricane, coarse and fine debris retention by the flood plain 9 mo after the hurricane, and any forest recovery since the hurricane until June 1990.

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TABLE 1. *Criteria used to evaluate damage and tree response to damage.*

A. Type of damage
1. Uprooting and/or treefall: treefalls or steep inclination with partial or total uprooting.
2. Snapping of boles: fracturing of boles above or below the lower limit of the main canopy.
3. Defoliation or debranching: partial or total loss of canopy. The percentage loss of foliage and/or branching relative to a "normal" canopy for the species and its location was estimated.
4. No visible damage: tree was apparently undamaged.

B. Tree responses
1. Regrowth of new branches and/or new leaves: in branches of surviving boles showing evidence of damage or total loss of canopy (as in palms). Branches tend to restore the original canopy.
2. Vegetative regeneration on stems: presence of regrowth along stems, often as an opportunistic response to new conditions of space and light.

METHODS

We reestablished the 5 × 5 m grid by relocating and replacing, where necessary, each of the 161 grid points. Then we identified to species and measured the height and dbh of all dicotyledonous trees ≥4 cm dbh, and all palms ≥0.7 m tall. The rate of change of tree density and basal area was calculated as the difference between 1980 and 1990 measurements divided by the time interval in years. The importance value of each species was calculated by adding their relative basal area and relative stem density and expressing the sum in percent. All new measurements for this study were conducted 9 mo after the hurricane, during June 1990, except the fine litter accumulation which was measured in August 1990.

To assess hurricane damage, we mapped to scale all fallen trees and all standing trees with evidence of damage to the canopy or stems. For each tree we assessed the type of damage (using four damage classes, Table 1), the cause of damage (direct wind damage or indirect damage *i.e.,* caused by the fall of other trees), the height at which damage occurred, and any visible recovery or response to the damage (two categories, Table 1). For leaning or fallen trees we recorded the lean angle and the compass orientation of the downed stem.

To estimate aboveground plant biomass before (1989) and after (1990) the hurricane, we entered the diameter and height of each tree into allometric regressions. All live trees in 1989 (even if downed in 1990) were used for the 1989 estimate. Only live trees in 1990 were used for the 1990 estimate. Total aboveground biomass of sierra palms was estimated with the regressions in Frangi and Lugo (1985), which require only the diameter of the palm. Total aboveground biomass of dicotyledonous trees was obtained from regression equation number 7 in Brown *et al.* (1989) which requires diameter and height data. Aboveground biomass was partitioned among leaf, branch, and bole compartments using their relative proportions before the hurricane (Frangi & Lugo 1985).

Mass transfer to the forest floor due to the hurricane was the sum of the mass of all fallen trees (distributed into leaves, branches, and boles), plus an estimate of leaves and branches that fell from trees that survived the hurricane as standing trees. This estimate was based on the mass of leaves and branches in the canopy prior to the hurricane, corrected by the fraction of the canopy that was observed to be missing after the hurricane. Data for each tree were used in the regressions and summed by species.

The mass of trees from adjacent colorado (*Cyrilla racemiflora* L.) forest stands that fell on the flood plain and of trees from the flood plain that fell outside the forest plot was estimated by regression using measurements of height and dbh of each downed tree. We corrected for the fraction of the tree that remained at either side of the perimeter of the flood plain. Missing from our estimate of inputs and outputs to and from the forest floor are decomposition rates and debris exchanges caused by hydrological flows. Estimates of minimum exports were calculated by differences between inputs and change in storage according to the conservation of mass law.

Aboveground accumulation of N, K, Ca, and Mg and their input to the forest floor were estimated by chemically analyzing stored samples from the study of Frangi and Lugo (1985). That study reported P concentration data only, which we used here to estimate its content and distribution before and after the hurricane. In addition, we collected and analyzed fresh samples of colorado wood that fell in the flood plain and samples of tree species that were new to the plot since the 1980 study.

The methodology for the handling and preparation of samples and for measuring P concentrations are given in Frangi and Lugo (1985). The methodology for chemical analyses of N, K, Ca, and Mg is described in Lugo *et al.* (1990). The appropriate biomass estimates for leaf, branch, and

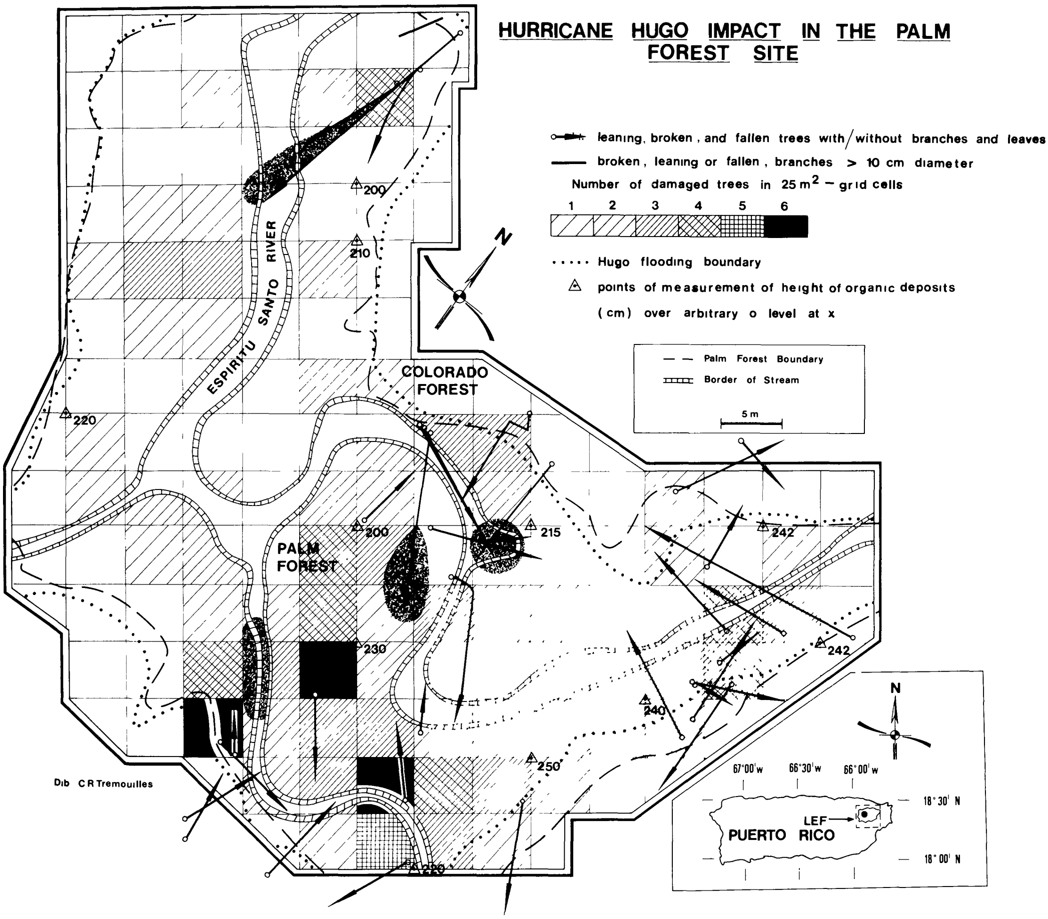

FIGURE 1. Location of the study area in the Luquillo Experimental Forest and geographic depiction of the impact of Hurricane Hugo to flood plain vegetation. The fallen tree with a zigzag shape near the center of the map had probably fallen, resprouted, and grew in a different direction during previous disturbances to the site.

bole compartments of individual trees were multiplied by the corresponding nutrient concentration in the compartment to estimate its nutrient content in 1989 and 1990.

The height of piles of debris that accumulated on tree trunks and other obstructions to debris flow in the flood plain was also noted. We mapped the area and height of the hurricane flood by projection of height measurements of debris piles.

Twenty rectangular plots (1 m × 0.5 m) were established at random on the forest floor for the collection of fine litter as in Frangi and Lugo (1985). All fine litter was removed from each plot, dried to constant weight at 60°C, sorted into plant parts (palm leaves, dicotyledonous leaves, wood, fruits and flowers, and miscellaneous), and weighed. Samples were then ground through a 0.85 mm (20 mesh) stainless steel sieve and used for chemical analysis (N, P, K, Ca, and Mg). Nutrient content was estimated by multiplying nutrient concentration in tissue by its mass per unit area.

RESULTS

CHANGES IN FOREST STRUCTURE: 1980–1990.—We found 21 tree species in June 1990, including four that were not recorded in 1980. Stand basal area (45.6 m^2/ha) increased by 7.6 percent while stand density (2278 trees/ha) decreased by 26 percent. The top three species maintained their ranking in terms of importance value but there was considerable change in ranking among the rest of the species. The basal area (m^2/ha), stem density (trees/ha), and importance value (%) of the top five species were (respectively): *Prestoea montana* (18.9, 1049, 43.8), *Micropholis chrysophylloides* Pierre (12.0, 349, 20.8), *Croton poecilanthus* Urban (4.0, 335, 11.8), *Micropholis garciniaefolia* Pierre (4.3, 115, 7.2), and *Calycogonium squamulosum* Cogn. (1.5, 124, 7.2).

EFFECTS ON VEGETATION.—Damage to vegetation was unevenly distributed within the flood plain (Fig. 1). Greater damage was observed in those sectors of the flood plain that were unprotected from N–NW winds or along moderate slopes that allowed wind tunneling. The direction of trees felled by wind (as opposed to secondary causes) reflected the N–NW direction of wind at this site, in spite of the modification of treefall by slope and the presence of obstacles such as understory trees.

Thirty percent of the trees (693 damaged trees/ha) had some damage caused by the hurricane. Sierra palms (48%) and dicotyledonous trees (52%) suffered equal proportion of this damage. The rank order of damage to vegetation, with percentage of total damage in parenthesis, was: loss of crown (84), uprooting and tree falls (8), tree snapping (7), twisting and leaning of stems (6), and fall of standing dead trees (2). Several of the fallen trees originated outside the flood plain, in the adjacent steeper lands of the colorado forest (Fig. 1).

The main damage to sierra palms was the loss of their crown due to wind. Very few palms were snapped (3/ha), uprooted (8/ha), or leaning (8/ha). In contrast, the greatest fraction of stem snapping (92%), uprooting and upturning (86%), and leaning (82%), occurred in dicotyledonous trees.

Direct wind damage caused 83 percent of the recorded tree damage and all height classes experienced direct wind damage (Fig. 2a). Most of the remaining damage was due to secondary effects (16%). Only the shorter trees experienced indirect damage (Fig. 2b).

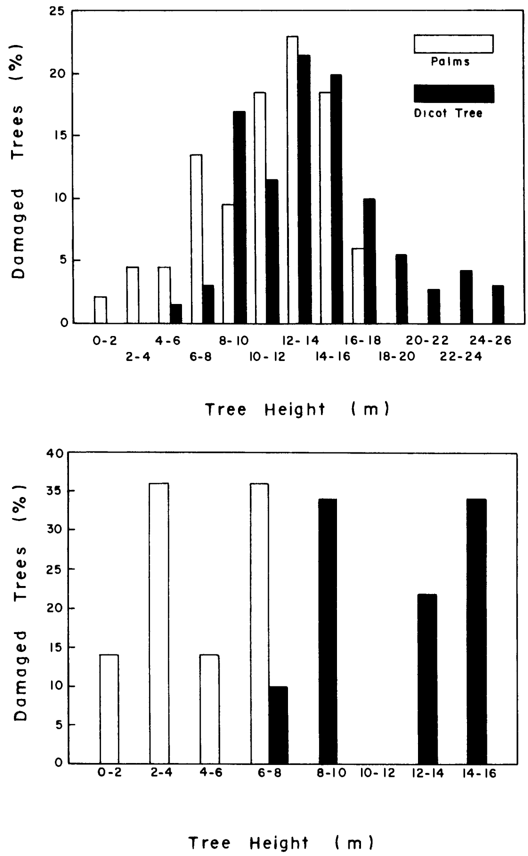

FIGURE 2. Distribution of direct wind damage (a), and indirect damage by falling trees (b) to trees by height class in a flood plain forest in the Luquillo Experimental Forest.

The main plant response 9 mo after the event was refoliation. Of the sierra palms that lost all leaves during the hurricane, 98 percent had restored an average of 4.7 (SE = 1.3, N = 39) leaves on the crown. Among the dicotyledonous species, the ones with the most refoliation were *Croton poecilanthus, Micropholis chrysophylloides,* and to some extent *Magnolia splendens* Urban. On average, these species had new foliage on 21 percent of the damaged trees.

Stem resprouts on damaged trees were also prevalent. The percent of damaged stems that resprouted, with the number of trees counted in parenthesis, was: *C. poecilanthus*—67 (18), *Micropholis garciniaefolia*—50 (2), *M. splendens*—25 (4), and *M. crysophylloides*—8 (38). All stem resprouting developed as stem suckers as described by Halle *et al.* (1978) for the reiteration phenomena. Epitrophy was common in both species of *Micropholis.* Plant mortality was 1 percent (33% of the trees that died were sierra palms). We observed extensive regeneration by *Cecropia peltata* L. (some taxonomists now consider this to be *Cecropia schreberiana*), particularly along the steep banks of streams and in gaps along smaller drainages within the forest.

EFFECTS ON BIOMASS AND NUTRIENT STOCKS.—The hurricane downed 10 percent of the stand's aboveground biomass (Table 2). Leaf and branch biomass suffered a greater proportion of damage (21%) than boles (6%), although when expressed in absolute mass, boles suffered more loss than either leaves or

TABLE 2. *Aboveground biomass estimates (Mg/ha) for tree species in a flood plain forest before and after the passage of Hurricane Hugo over the Luquillo Experimental Forest. Values correspond to trees with diameter at breast height ≥4 cm and palms taller than 0.7 m. Total columns may not add up due to rounding.*

	1989				1990				Loss due to the hurricane			
Species	Leaves	Branches	Boles	Total	Leaves	Branches	Bole	Total	Leaves	Branches	Bole	Total
Prestoea montana	23.0	—	49	71.9	17.7	—	42	60	5.3	—	6.9	12.2
Micropholis chrysophylloides	1.6	8.3	40	49.7	1.1	5.3	38	45	0.5	3.0	1.6	5.0
Croton poecilanthus	1.5	4.0	9.5	14.9	1.5	4.0	9.5	15	0	0	0	0
Micropholis garciniaefolia	0.5	3.3	14.1	18.0	0.5	2.9	13.5	17	0.08	0.4	0.7	1.2
Calycogonium squamulosum	0.5	1.5	4.9	6.9	0.5	1.5	4.9	6.9	0	0	0	0
Magnolia splendens	0.3	1.3	5.0	6.5	0.2	1.0	5.0	6.2	0.06	0.3	0	0.4
Sloanea berteriana	0.2	1.2	4.5	5.9	0.1	0.7	4.5	5.3	0.09	0.5	0	0.6
Eugenia eggersi	0.07	0.1	0.3	0.5	0.07	0.1	0.3	0.5	0	0	0	0
Cyrilla racemiflora	0.1	0.6	2.8	3.5	0.1	0.6	2.8	3.5	0	0	0	0
Ditta myricoides	0.05	0.1	0.3	0.5	0.05	0.1	0.3	0.5	0	0	0	0
Tabebuia rigida	0.04	0.09	0.5	0.6	0.03	0.07	0.5	0.6	0.01	0.02	0	0.03
Cyathea sp.	0.04	—	0.08	0.1	0.04	—	0.08	0.1	0	—	0	0
Xilosma schwaneckeanum	0.01	0.02	0.06	0.1	0.01	0.02	0.06	0.1	0	0	0	0
Byrsonima wadsworthii	0.01	0.04	0.1	0.2	0.01	0.04	0.1	0.2	0	0	0	0
Clusia sp.	0.05	0.1	0.4	0.5	0.05	0.1	0.4	0.5	0	0	0	0
Eugenia borinquensis	†[a]	0.06	0.1	0.2	†	0.06	0.1	0.2	0	0	0	0
Myrcia spp.	0.01	0.05	0.2	0.2	0.01	0.05	0.2	0.2	0	0	0	0
Guarea guidonia	0.02	0.04	0.2	0.2	0.02	0.04	0.2	0.2	0	0	0	0
Casearia guianensis	0.02	0.06	0.1	0.2	0.01	0.03	0.03	0.06	0.01	0.03	0.08	0.12
Ilex sideroxyloides	0.01	0.02	0.05	0.08	0.01	0.02	0.05	0.08	0	0	0	0
Ocotea spathulata	†	†	0.02	0.02	†	†	0.02	0.02	0	0	0	0
Total	28	21	132	181	22	17	123	162	6.0	4.3	9.2	19

[a] † = trace.

TABLE 3. *Aboveground nutrient content of tree biomass in a flood plain forest before and after the passage of Hurricane Hugo over the Luquillo Experimental Forest. Values are in kg/ha and correspond to trees with diameter at breast height ≥4 cm and palms taller than 0.7 m.*

	Prestoea montana		*Micropholis chrysophylloides*		*Croton poecilanthus*		*Micropholis garciniaefolia*		*Calycogonium squamulosum*		Other 14 species		Total	
	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
N														
Leaves	275	212	16	12	25	25	5.5	4.7	50	5	9.5	6.3	336	265
Branches	—	—	53	34	31	31	33	28	12	13	17	15	146	121
Bole	266	228	99	95	22	22	90	86	10	10	22	22	509	463
Total	541	440	169	141	78	78	128	119	28	28	47	43	991	849
P														
Leaves	20.8	16	0.7	0.5	1.5	1.5	0.2	0.2	0.3	0.3	0.5	0.5	24	19
Branches	—	21	3.5	3.1	1.4	1.3	1.4	1.1	0.7	0.5	3.0	1.0	10	8
Bole	24.2	21	3.2	3.1	1.3	4.2	1.2	1.1	0.5	0.5	1.6	1.0	32	28
Total	45	37	7.3	5.8	4.2	18	2.8	2.5	1.4	1.4	5.3	4.1	66	55
K														
Leaves	178	137	9.4	6.6	18	18	3.2	2.7	3.7	3.7	7.7	6.0	220	174
Branches	—	—	34	22	22	22	15	13	7.7	7.7	22	18	101	83
Bole	331	284	42	40	6.3	6.3	57.9	55	5.4	5.4	28.4	29	471	420
Total	508	421	85	69	46	46	76	71	17	16.8	60	53	792	677
Ca														
Leaves	74	57	6.8	4.8	9.8	9.8	2.3	2.0	6.2	6.2	4.9	4.2	104	84
Branches	—	—	85	55	50	50	12	11	16	16.2	15	12	178	144
Bole	121	104	34	33	8.0	8	145	138	13	13.1	22	22	343	318
Total	195	161	127	93	68	68	159	150	35	35	41	39	625	546
Mg														
Leaves	48	37	2.2	1.6	6.5	6.5	0.8	0.7	1.1	1.1	1.4	1.1	60	48
Branches	—	—	5.1	3.3	6.1	6.1	3.6	3.2	2.9	29	5.3	4.5	23	20
Bole	67	58	5.0	4.8	5.7	5.6	8.6	8.2	9.6	9.6	8.1	7.8	104	94
Total	115	94	12.3	9.78	18.3	18	13	12	13.6	13.5	14.8	15	187	162

TABLE 4. *Changes in aboveground nutrient content of tree biomass in a flood plain forest after the passage of Hurricane Hugo over the Luquillo Experimental Forest. Values are in kg/ha and correspond to trees with diameter at breast height ≥4 cm and palms taller than 0.7 m.*

	N		P		K		Ca		Mg	
	Before	After	Before	After	Before	After	Before	After	Before	After
Leaves	336	265	24	19	220	174	104	84	60	48
Branches	146	121	10	8	101	83	178	144	23	20
Bole	509	463	32	28	471	420	343	318	104	94
Total	991	849	66	55	792	677	625	546	187	162

branches. Most of the damage to aboveground biomass was inflicted on the dominant tree species, with the notable exception of *C. poecilanthus.* Damage to small individuals of species with low importance values was small or negligible. Some species with low importance values suffered damage to a large single tree (*e.g., Casearia guianensis* (Aubl.) Urban) and this explained high loss of nutrients and mass from aboveground compartments. Palm leaves accounted for most of the damage to leaf biomass.

Prior to the hurricane most of the aboveground nutrient stocks in the forest were stored in sierra palm biomass (Table 3). For N, P, K, Ca, and Mg the proportion of the total stock accumulated in palm biomass was 55, 68, 64, 31, and 61 percent, respectively. For comparison, the proportion of the stand's biomass attributed to sierra palm was 30 percent (Table 2). The species with the highest accumulation of Ca was *M. garciniaefolia* with 25 percent of the stand's total. This species also accumulated a disproportionate amount of K.

After the hurricane the proportion of the stand's aboveground inventory of N, P, K, Ca, and Mg stored in palms did not change substantially (52, 67, 62, 29, and 58%, respectively; Table 3). Twenty-eight percent of the Ca was stored in *M. garciniaefolia.*

Absolute transfer of nutrients from live aboveground compartments to necromass was greater for leaves than for branches or boles (Table 4). The exception was Ca, which was transferred to a greater degree in branches and boles than in the leaf compartment. The amount of nutrients transferred as a percent of the prehurricane nutrient stocks ranged between 12.5 for Ca to 16.3 for P. The relative fraction of nutrient transfer from individual compartments was greater for leaves, followed by branches, and lowest in boles.

The flood plain gained more mass and nutrients, as a result of the trees that fell across its perimeter than it lost by those from the flood plain that fell outside the perimeter (Table 5). Only one flood plain tree fell completely to the outside of the perimeter (Fig. 1, Table 5). Six trees accounted for a net necromass input of 14 Mg/ha and significant amounts of N, P, K, Ca, and Mg. These inputs were mostly in the form of coarse woody debris.

The flood caused by the hurricane extended throughout all the flood plain and up to its maximum perimeter (Fig. 1). Fine litter accumulation after the event was 10.8 Mg/ha of mass (*vs.* 5.5 Mg/ha in 1980) and significant quantities of nutrients on the forest floor (Table 6). Wood was the most important fraction of fine litter, followed by leaves. Leaf litter of dicotyledonous species had high content of N and Mg. Small diameter woody debris was high in Ca and low in Mg and K. The accumulation of fruits and flowers alone accounted for 0.5 Mg/ha of mass.

DISCUSSION

VEGETATION RESISTANCE AND RESILIENCY.—The flood plain forest was less damaged than other stands exposed to the impact of the storm. For example, at 260–400 m elevation in the tabonuco (*Dacryodes excelsa* Vahl.) forest, tree mortalities of up to 40 percent occurred (Scatena, pers. comm.); the flood plain forest had only 1 percent tree mortality. Two factors account for this large difference. The most important is the location of the flood plain relative to the storm. Because of its low position in a valley, the flood plain forest was protected from direct and prolonged impact of the highest velocity winds. Damage was caused by winds that funnelled up the valley, or those that entered the flood plain in locations where the slopes beyond the flood plain were not as effective in sheltering the stand from direct impacts of the wind. In these sectors of the flood plain we observed treefalls in the direction of prevailing winds.

A second mitigating factor was the resistance or inertia (*sensu* Westman 1978) and resiliency of

TABLE 5. *Input and loss of mass and nutrients (kg/ha) across the perimeter of a flood plain forest after the passage of Hurricane Hugo over the Luquillo Experimental Forest. Total or net inputs may not add up due to rounding.*

	Mass				N				P			
	Leaves	Branches	Boles	Total	Leaves	Branches	Bole	Total	Leaves	Branches	Bole	Total
Input												
Prestoea montana	60	—	480	540	0.7	—	2.6	3.3	0.1	—	0.2	0.3
Cyrilla racemiflora	500	2180	10,120	12,800	3.5	9.6	8.1	21	0.3	1.7	0.2	2.2
Micropholis chrysophylloides	40	200	980	1220	6.1	15	29	50	0.2	0.9	0.8	1.9
Total[a]	600	2380	11,580	14,560	10.3	26	43	79	0.6	2.6	1.3	4.4
Loss												
Micropholis chrysophylloides	†[b]	20	80	100	†	0.1	0.2	0.3	†	†	†	†
Net input	600	2360	11,500	14,460	10.3	25.6	43	79	0.6	2.6	1.3	4.4

TABLE 5. *Continued.*

	K				Ca				Mg			
	Leaves	Branches	Bole	Total	Leaves	Branches	Bole	Total	Leaves	Branches	Bole	Total
Prestoea montana	0.5	—	3.3	3.7	0.2	—	1.2	1.4	0.1	—	0.7	0.8
Cyrilla racemiflora	4.7	17	20	43	0.8	22	2.4	25	0.3	2.2	1.4	3.9
Micropholis chrysophylloides	3.5	9.8	12	25	2.6	24	10	37	0.9	1.5	1.5	3.8
Total[a]	8.7	27	36	72	3.6	46	14	63	1.3	3.7	3.5	8.5
Loss												
Micropholis chrysophylloides	†	0.1	0.1	0.2	†	0.2	0.1	0.3	†	†	†	†
Net input	8.7	27	36	72	3.6	46	14	63	1.3	3.7	3.5	8.5

[a] Includes a small *Byrsonima wadsworthii* tree.
[b] † = trace.

TABLE 6. *Nutrients and mass of fine litter on the forest floor of a flood plain forest 10 mo after the passage of Hurricane Hugo over the Luquillo Experimental Forest. Totals may not add up due to rounding.*

Compartment	Mass	N	P	K	Ca	Mg
	(kg/ha)					
Palm leaves	1870	12.4	0.7	2.2	9.9	3.1
Dicotyledonous leaves	1720	14.8	0.5	2.1	8.7	2.9
Fruits and flowers	500	3.2	0.2	0.7	2.1	1.2
Miscellaneous	1030	10.4	0.5	1.9	2.6	2.0
Wood ≤2 cm dbh	1970	10.5	0.4	1.1	10.5	1.9
Wood ≥2 cm dbh	3630	20.9	1.0	2.6	17.7	2.0
Palm wood	50	0.1	†[a]	0.1	0.2	†
Total	10,770	72.3	3.3	10.8	51.6	13.2

[a] † = trace.

trees. Trees in the flood plain, particularly the sierra palm, quickly recovered from wind damage. Palms did so by the regrowth of canopy leaves after their total loss during the storm. Other trees like *C. poecilanthus* and *M. crysophylloides* had opportunistic resprouting, formation of adventitious roots, epicormic growth, and new branch formation, such that in spite of what appeared to be serious hurricane damage, we found them in a vigorous state of regrowth and recovery. Nearly all fallen trees with the root crown partially buried in the soil survived, resprouted from the stems (see Walker 1991), and were opportunistically reestablishing hereditary crown architecture (*sensu* Halle *et al.* 1978).

Tree architecture appeared to play an important role in hurricane resistance. We observed that the only palms that fell because of wind impact (as opposed to those that fell due to secondary causes) were old individuals with extensive epiphytic growth and large loads of lianas. The extra material in their crown offered greater resistance to winds and apparently this was the cause of their falling. Crowns of sierra palms stream horizontally during the storm, and having thin stems, offer little resistance to wind. After the storm, most palms had their leaves hanging down and eventually shed them. Tree architecture in turn was greatly affected by the hurricane because trees lost large portions of their crowns and this resulted in a reduced crown-to-basal-area ratio. Deformed tree crowns are a result of hurricane passage.

Biotic resistance to hurricane winds has limits once organisms are exposed to winds that exceed a certain threshold of velocity. In the flood plain forest this was illustrated by differential wind damage to size classes. The distribution of damage across size classes as a result of direct wind action was normally distributed (Fig. 2a). Trees >8 m height were greatly damaged by wind. Smaller individuals were protected by the closed structure of the community and only a few of them suffered direct wind damage. In contrast, indirect wind damage, *i.e.,* by the fall of other trees, showed a bias for smaller height classes (Fig. 2b). Smaller trees were more likely to be damaged by falling trees and less likely to be downed by the direct effects of the wind than larger trees.

Treefalls opened the forest canopy and created numerous gaps that favor the establishment of palms and fast growing tree species. In these areas we observed large numbers of *C. peltata* and seedlings and saplings of the sierra palm.

TRANSFER OF NUTRIENTS AND MASS.—Hurricane Hugo reduced aboveground live-tree biomass by about 10 percent and nutrient stocks by almost 15 percent. The greater impact on nutrient stocks was due to the loss of nutrient-rich but low-biomass leaf canopy and the relatively low impact on biomass-rich but nutrient-poor boles. The sierra palm and *M. garciniaefolia,* which were the two species that accumulated the largest fraction of the nutrient stocks in the flood plain forest, both retained the same proportion of the nutrient inventory that they had prior to the hurricane.

After the hurricane, about 18 percent of both nutrients and mass were found in necromass (Table 7). Calcium was the exception with about 23 percent of its total aboveground stock in the form of necromass. The origin of necromass was from internal sources as well as from trees outside the flood plain. The ratio of *in situ* inputs to outside transfer of mass and nutrients as necromass was 1.3, 1.8, 2.4, 1.6, 1.2, and 2.9 for mass, N, P, K, Ca, and Mg, respectively. However, the input of coarse woody debris from outside the flood plain was a significant source of nutrients and mass to the flood plain forest (Fig. 3).

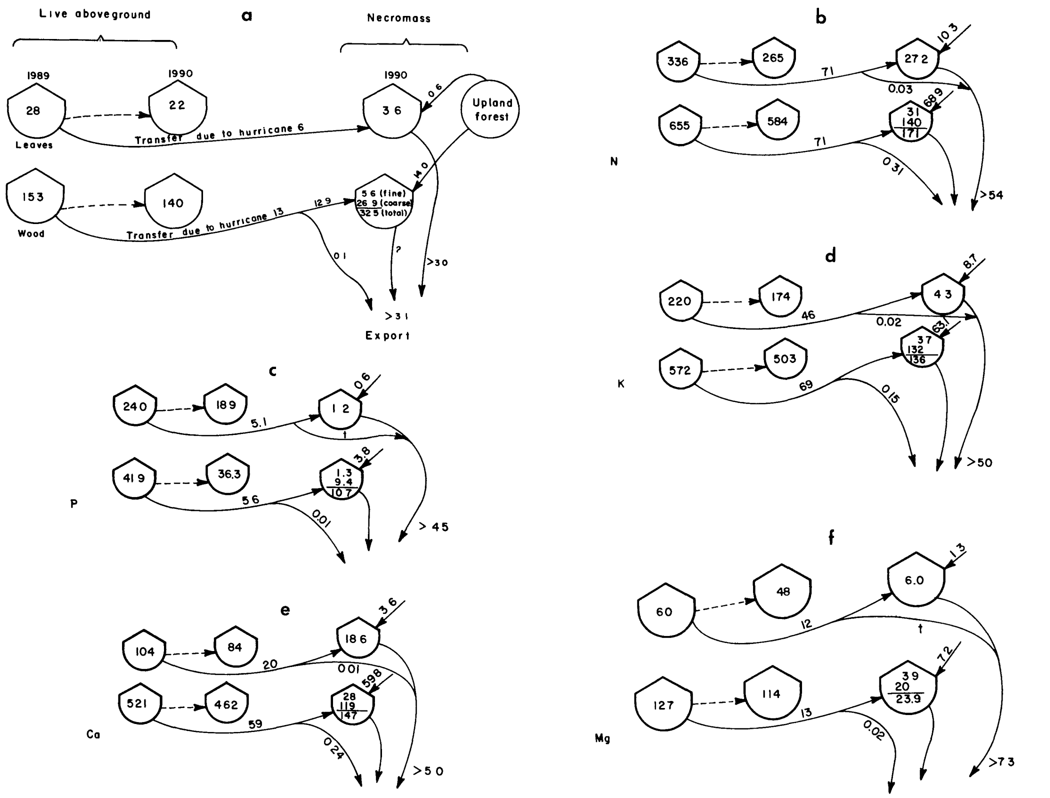

FIGURE 3. Diagrams of mass (a), nitrogen (b), phosphorus (c), potassium (d), calcium (e), and magnesium (f) accumulation and flux after passage of Hurricane Hugo over a flood plain forest in the Luquillo Experimental Forest. Tanks represent accumulation in Mg/ha for mass and kg/ha for nutrients. Aboveground live accumulations before the hurricane (1989) are connected by dotted lines to tanks depicting the corresponding accumulation after the hurricane (1990). Solid lines depict transfer of mass or nutrients to necromass and as import or exports to and from the forest floor. Instantaneous fluxes are reported in Mg/ha for mass and kg/ha for nutrients.

Fine litter fall expressed on a daily basis averaged 2.3 g/m^2 before the hurricane (Frangi & Lugo 1985). In 1980 Hurricane Allen passed 150 km south of the forest and caused a fine litter fall of 83 g/m^2 (Frangi & Lugo 1985). The magnitude of this flux during Hurricane Hugo was 1029 g/m^2. Coarse woody debris added 919 g/m^2 to this one-day input to the forest floor. These calculations exclude inputs from the colorado forest, but underscore the high magnitude of instantaneous fluxes associated with hurricane disturbances to forests.

When expressed on an absolute basis, the transfer of organic matter to the forest floor by Hurricane Hugo was equivalent to twice the normal annual production of fine litterfall by the forest (see Lodge *et al.* 1991). However, in terms of P input, the corresponding value was 4.7 times the annual input reported by Frangi and Lugo (1985). Thus, the effects of the hurricane on the transfer of materials to necromass was proportionally greater for nutrients than for mass.

Much of the leaf material transferred to the forest floor was either exported or decomposed in

TABLE 7. *Fraction of aboveground nutrients and mass in necromass seven months after passage of Hurricane Hugo in a flood plain forest in the Luquillo Experimental Forest.*

Component	Total aboveground (kg/ha)	Necromass (% of total)
Biomass	198,100	18
Nitrogen	1047	19
Phosphorus	67	18
Potassium	817	17
Calcium	711	23
Magnesium	192	16

TABLE 8. *Aboveground biomass (Mg/ha) and nutrients (kg/ha) in a flood plain forest before and after the passage of Hurricane Hugo over the Luquillo Experimental Forest, Puerto Rico.*

Component	Before	After
Mass	183	198
Nitrogen	1007	1047
Phosphorus	67	67
Potassium	794	817
Calcium	636	711
Magnesium	190	192

the time interval between passage of the hurricane and the time of our sampling (Fig. 3). Coarse woody debris has a slower turnover and thus a larger fraction remained on the forest floor. However, because we lack information on the material flow associated with hydrologic fluxes, we cannot estimate the potential export and decomposition of coarse woody debris. Yet, with the information available, we can estimate the minimum export of mass and nutrients from the flood plain forest (Fig. 3). These data suggest that exports of nutrients and mass approach the annual export measured for mass and P at the site (Frangi & Lugo 1985). But, because of the equal magnitude of external input of materials from the colorado forest and its retention in the flood plain as coarse woody debris, it would appear that the flood plain forest gained mass and nutrients after the hurricane. However, the increases in the aboveground compartments (tree biomass and coarse and fine litter) were less than 10 percent except for Ca which was 12 percent (Table 8).

CONCLUSION

Hurricane Hugo had a low to moderate impact on the structure of vegetation in this flood plain forest. Tree mortality was low, damage to the stand was limited to those sectors directly facing the prevailing winds, and the dominant species survived with damage to their leaves and small branches only. Recovery from this damage proceeded rapidly after the hurricane. Sierra palms were able to retain their importance value, conserve their nutrient reservoir, and quickly produce new leaves. The most important dicotyledonous trees performed as did the sierra palm. The forest had experienced a high turnover of species as a result of normal succession during the 10 yr prior to the hurricane. Opening of the canopy will likely induce further changes in species composition in the near future.

The flood plain continued to be a small sink of N, K, Ca, and mass originating from upstream forests retained P and Mg in spite of hurricane damage, and continued to export large amounts of materials, particularly as leaf litter. The hurricane greatly increased the accumulation of coarse woody debris on the forest floor. This material acts as a large reservoir of organic mass and nutrients that remains available to the organisms of the flood plain forest for long periods of time.

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