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A Flood Plain Palm Forest in the Luquillo Mountains of Puerto Rico Five Years After Hurricane Hugo[1]

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ABSTRACT

Long-term studies are needed to understand the dynamics of tropical forests, particularly those subject to periodic disturbances such as hurricanes. We studied a flood plain *Prestoea montana* palm forest in the Luquillo Mountains of Puerto Rico over a 15-yr period (1980–1995), which included the passage of Hurricane Hugo in September 1989. The passage of the hurricane caused the dominant species to become more dominant and created low instantaneous tree mortality (1% of stems) and reductions in tree biomass (−16 Mg/ha/yr) and density, although not in basal area. Five years after the hurricane, the palm flood plain forest had exceeded its prehurricane aboveground tree biomass, tree density, and basal area. Aboveground tree biomass accumulated at a rate of 9.2 Mg/ha/yr, 76 percent of which was due to palms. Before the hurricane this rate was on the order of 3 Mg/ha/yr. Forest floor litter decreased to prehurricane levels (6.7 Mg/ha), within 5 yr, mostly due to the disappearance of woody litter. Thirteen tree species not represented in the canopy entered the forest by regeneration, and 2 species suffered almost 20 percent/yr mortality over a 5-yr period after the storm (floodplain average of 2%/yr). Delayed tree mortality was twice as high as instantaneous tree mortality after the storm and affected dicotyledonous trees more than it did palms. Regeneration of dicotyledonous trees, palms, and tree ferns was influenced by a combination of factors including hydroperiod, light, and space. Redundancy Data Analysis showed that the area near the river channel was the most favorable for plant regeneration. Palm regeneration was higher in locations with longer hydroperiods, while regeneration of dicotyledonous trees was higher in areas with low risk of flooding. This study shows how a periodic disturbance provides long-term opportunities for species invasions and long-term ecosystem response at the patch scale of <1 ha.

Key words: ecological disturbance; flood plain forest; forested wetlands; Hurricane Hugo; Luquillo Experimental Forest; palms; Prestoea montana; *secondary forests; tropical tree succession; tropical wetlands.*

A DISTURBANCE SUCH AS A HURRICANE acts as a selective force that favors or hinders the survival of tree populations by means of two mechanisms: (1) through mechanical damage and differential mortality; and (2) by opening the canopy and creating a patchwork of environmental conditions along gradients of topography and hydrology on which tree populations can regenerate and grow. To understand how particular tree populations respond to hurricanes, it is necessary to study the same sites over long time periods both before and after the passage of the hurricane. Walker *et al.* (1991) describe such an opportunity with the passage of Hurricane Hugo over the Luquillo Mountains of Puerto Rico.

Long-term studies in progress at the Luquillo Experimental Forest, Puerto Rico, since the early 1940s (Wadsworth 1995) have facilitated the study of the tabonuco (*Dacryodes excelsa*) forest (*cf.* Walker *et al.* 1991), colorado (*Cyrilla racemiflora*) forest (Weaver 1995), dwarf or elfin cloud forest (Weaver 1995), and palm (*Prestoea montana*) slope forests (Lugo *et al.* 1995). These four forest types represent the dominant vegetation in the Luquillo Mountains which also occur throughout the wet mountains of the Caribbean. However, there are less common forest types for which long-term plots do not extend as far back as the early 1940s but whose structure, species composition, and physiography give them an ecological importance exceeding their geographic coverage. An example is the flood plain palm forest at high elevation on sandy soils (Frangi & Lugo 1985).

The flood plain palm forest was found to be more productive and to exhibit faster tree growth than adjacent forest stands (Frangi & Lugo 1985, Weaver & Murphy 1990). Flood plain palm forests contrast in structure with the more common palm

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slope forest but are dominated by the same species, *Prestoea montana.* The dominance of one species in contrasting environments provides an opportunity to study how palm forests respond to hurricanes when growing under dramatically different ecological conditions (*i.e.*, a flood plain with periodic inundation versus steep slopes with prolonged periods of soil saturation). Studies on the effects of Hurricane Hugo on palm forests situated on steep slopes are in progress.

In this paper we report the results of a 15-yr study (1980–1995) of a flood plain palm forest in the Luquillo Mountains. Our goals were to determine: (1) the recovery of vegetation 5 yr after Hurricane Hugo; and (2) how tree species responded to the interaction between the availability of canopy space following the passage of the hurricane and factors associated with the microtopography of the flood plain. This information is required to improve our understanding of the resilience function of tropical forests.

METHODS

During March 1980, we established a permanent 5 × 5 m grid that encompassed the whole of a 0.2525 ha flood plain palm forest at 750 m elev. in the Luquillo Mountains of Puerto Rico (Frangi & Lugo 1985). We determined the structure of this forest by a complete inventory in 1980, and in 1990 and 1995 after the passage of Hurricane Hugo on 18 September 1989. In addition, Frangi and Lugo (1991) reconstructed the structure of vegetation just prior to the passage of Hurricane Hugo in 1989.

During June 1995, we relocated the grid in the study area (*cf.* Frangi & Lugo 1985, 1991). We remeasured: (1) all plants tagged in 1990 [DBH (diameter at breast height of 1.3 m) ≥4 cm]; (2) identified to species and measured the height and stem diameter (at DBH if >1.3 m or at the midpoint of the stem if ≤1.3 m tall) of all dicotyledonous trees with DBH <4 cm and over 1.0 m tall; (3) counted and measured the DBH of all tree ferns (*Cyathea portorricensis*) >1.3 m tall; (4) palms ≥2.5 m tall, and (5) measured the stem diameter of ferns and palms >0.7 m tall. For tree ferns and palms with heights <1.3 m, we measured their stem diameter at the midpoint of the stem. We used the plant nomenclature of Little and Woodbury (1976) and Liogier and Martorell (1982).

Tree density and basal area of all trees with DBH ≥4 cm, palms taller than 0.7 m, and tree ferns >2.5 m tall were calculated from field measurements. The importance value of each species was calculated as the sum of their relative basal area and relative stem density, the sum expressed in percent.

Because trees were tagged in 1990, we were able to note tree mortality in the ≥4 cm DBH category for dicotyledonous species and for ferns and palms >0.7 m tall. Tree mortality rates, expressed as stems/ha/yr, were calculated as the number of trees dying per hectare divided by the time interval since the last measurement. Mortality rate was also expressed as the percent of the living trees at the beginning of the interval (*i.e.*, total number that died divided by the number alive in 1990, divided by the time interval in years). Some trees found dead in 1995 had been alive but damaged in 1990, according to one of the following four damage classes: uprooting and/or treefall, snapping of boles, defoliation or debranching, and no visible damage (Frangi & Lugo 1991). Other trees found dead in 1995 were alive and undamaged in 1990. For this reason, we calculated rates of mortality from 1990–1995 for trees that survived the hurricane with some damage in 1990 (termed delayed mortality; *sensu* Walker 1995) and those that escaped damage during the hurricane ("other mortality"). The sum of "delayed" and "other" mortality was the total tree mortality in the flood plain.

Aboveground biomass of trees in the entire flood plain forest was estimated from a regression equation for tropical wet forests in Brown *et al.* (1989; Eq. 7) for dicotyledonous trees and tree ferns, and in Frangi and Lugo (1985) for palms. The Brown *et al.* equation was: kg/tree = $\exp\{-3.302 + 0.9439 \ln (d^2h)\}$, where d is the DBH in cm and h is total height in m ($R^2 = 0.90$). The Frangi and Lugo equation was: kg/palm = 8.4 (height in m)—10.6 ($R^2 = 0.94$). The equation of Brown *et al.* is based on tree allometry without hurricane effects and may overestimate branch biomass in hurricane-damaged trees. We don't compare the 1980 biomass data for dicotyledonous trees with that of the 1990's because contrary to the procedure with the palm, we used a different biomass regression and a different minimum tree diameter (≥1 cm DBH) in 1980 (Frangi & Lugo 1985). We report aboveground biomass data for dicotyledonous trees using the same equations and diameter limits (≥4 cm DBH) for 1989 (prehurricane), and 1990 and 1995 (posthurricane).

To further assess flood plain recovery after the hurricane, we measured fine litter accumulation on the forest floor from 20–1.0 × 0.5 m subplots selected at random. We generally followed the same methodology reported earlier in Frangi and Lugo (1985, 1991); however, the August 1990 and June 1995 measurements were based on a one time sampling, while the 1980 data were based on 11 monthly measurements with 20 replicates each. Samples were oven-dried at 60°C to constant weight and sorted prior to weighing into palm leaves, dicotyledonous leaves, two size classes of wood (<2 cm and ≥2 cm diameter), fruits and flowers, tree fern litter, and miscellaneous.

Frangi and Lugo (1991) identified the number of trees that were damaged after the hurricane in each of the 25 m^2 subplots of the entire grid. Damage to trees with DBH ≥4 cm was given in 7 categories from least damaged, 0–6, the most damaged. The number of the category represents the number of damaged trees per subplot, (*e.g.*, damage class 3 means that 3 trees in the subplot were damaged). We identified 45–25 m^2 subplots representative of each of 7 forest damage categories; we refer to this as a hurricane damage gradient. The number of subplots inventoried for each damage category, starting with category 0 and ending with category 6 was: 15, 8, 5, 6, 7, 1, and 3, respectively. Most plots escaped the hurricane without measurable damage (class 0); from these plots we randomly selected 15 for this analysis. The variation in the number of subplots for the other damage categories reflects the actual effect of the hurricane over the flood plain as we inventoried 100 percent of the 0.25 ha plot. In each of the selected subplots we identified to species, tagged, and measured the stem diameter of all dicotyledonous trees, tree ferns, and palms that had regenerated 5.75 yr after the passage of Hurricane Hugo. The following size limits were used to define regenerating stems: <1.0 m tall with stem diameters≤4 cm for dicotyledonous trees, between 1.0 and 2.5 m tall for tree ferns, and <2.5 m tall with pinnate leaves for palms.

To explore the pattern of regeneration for palms, tree ferns, and dicotyledonous trees in relation to two spatial and two hurricane-effect variables, we used Redundancy Data Analysis (RDA; ter Braak 1987, ter Braak & Prentice 1988; Palmer 1993) in the CANOCO Program (ter Braak 1988). The variables were: (1) distance between the center of each of the 45–25 m^2 subplots and the edge of the stream channel; (2) the elevation at the center of each subplot relative to the elevation of the bottom of the stream channel; (3) the percent of trees with DBH ≥4 cm damaged by Hurricane Hugo in each subplot; and (4) the percent of dead trees in each subplot in 1995.

We used the elevation of the flood plain relative to river base flow in 50 cm contour intervals (Frangi & Lugo 1985) to assess the propensity to flooding of each of the 45–25 m^2 subplots. These data showed that water movement (flow and volume turnover) increased towards the river. Therefore, the first spatial variable [(1) above] was an indicator of the rate of water volume turn over and water flux during flood stage. The second spatial variable was an indicator of the length of the hydroperiod; the hydroperiod was longer in the lower elevations of the flood plain and shorter in the higher elevations. The percent of damaged trees in 1990 [variable (3)] and dead trees in 1995 [variable (4)] were used as indicators of the availability of space and light intensity at each subplot. The greater the damage or mortality was, the greater the availability was of space and light for plant growth.

In summary, the ordination used distance to the river, relative elevation inside the flood plain, hurricane damage to trees, and dead trees as independent variables, and the density of regenerating palms, ferns, and dicotyledonous trees as the dependent variables. The ordination results were verified against our earlier observations of hurricane effects at the site (Frangi & Lugo 1991).

RESULTS

Flood plain structure.—During 1990–1995, tree density for trees with DBH ≥4 cm increased by 35 percent and basal area increased by 2 percent (Fig. 1). Basal area increased by about 11 percent since 1980 without any apparent interruption, but tree density decreased as a result of Hurricane Hugo and then increased again as the stand reorganized following the disturbance.

The number of tree species in the ≥4 cm DBH size class changed from 23 in 1980 to 21 in 1990 and 1995 (Table 1). However, this apparently small change in the number of tree species masks the actual number of tree species that appeared at different times in the size class. At the time of each inventory, different species entered and exited the size classes. About 32 tree species (≥4 cm DBH) were observed between 1980 and 1995. Eight tree species present in 1980 were absent in 1995. Between 1990 and 1995, four species entered the size class and four present in 1990 were not found in 1995. Three species observed in 1990 were not present in 1980 or 1995.

The palm gained greater dominance in 1995 than it had in 1990 by increasing both its basal area and tree density (Table 1). For all other species, with the exception of *Magnolia splendens* and

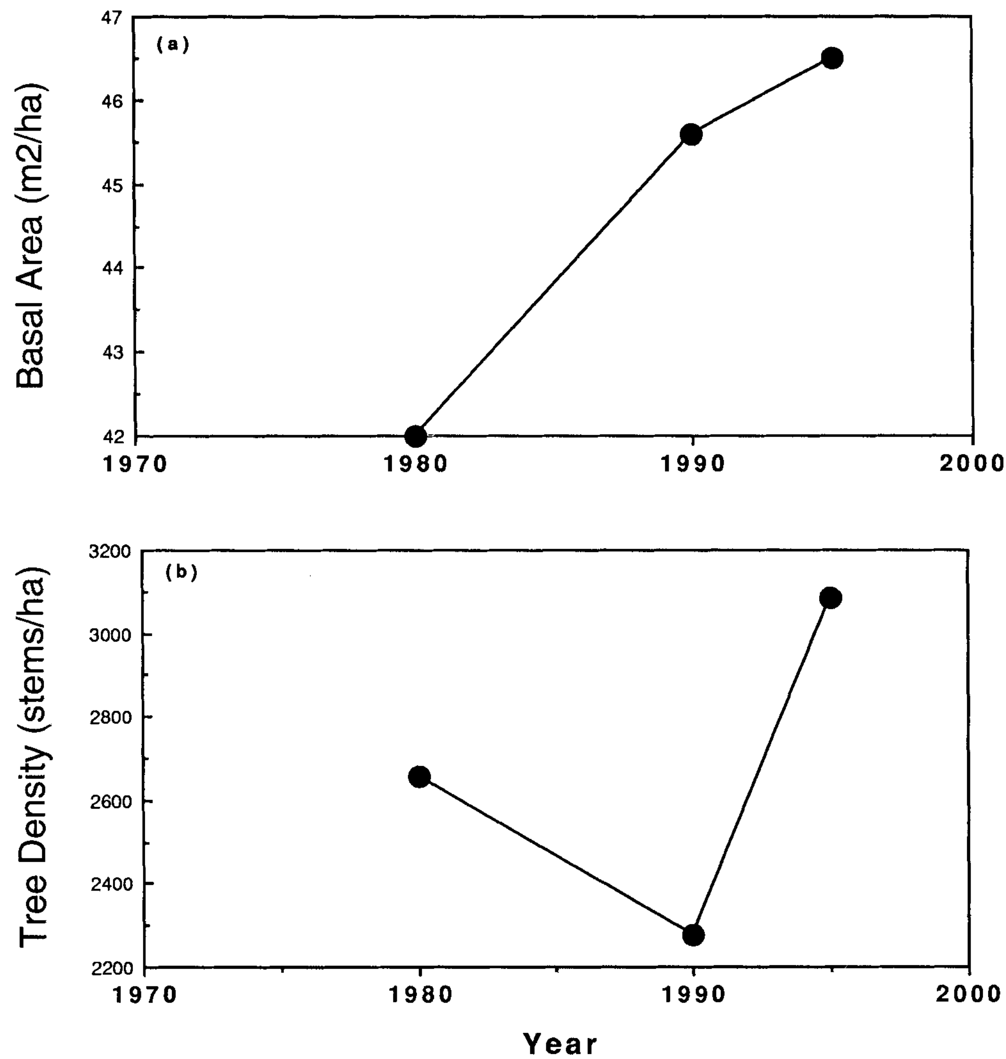

FIGURE 1. Temporal pattern in (a) the basal area and (b) tree density (for trees with DBH ≥4 cm and palms taller than 0.7 m) in a flood plain palm forest in the Luquillo Mountains of Puerto Rico. Hurricane Hugo passed over the stand in 1989.

Myrcia sp., their importance value decreased during the 5-yr posthurricane period. The importance value of 9 of the 21 species found in 1995 increased relative to 1980 and 2 remained at the same value. Among the more common species, *Calicogonium squamulosum* had the highest reduction in importance value and dropped its ranking from fifth in 1980 to sixth in 1995. In spite of the large number of seedlings observed in 1990, we found very few *Cecropia peltata* trees in the flood plain. The species ranked among the least important in 1995 and was never present in 1980 and 1990.

ABOVEGROUND TREE BIOMASS.—Between 1990 and 1995, aboveground tree biomass increased by 28 percent from 162 Mg/ha to 208 Mg/ha (Table 2). The error associated with the use of the same regression for damaged and undamaged trees should be small due to the low fraction of damaged trees (Frangi & Lugo 1991). Thus, the net aboveground tree biomass accumulation for the 1990–1995 period was at least 9.2 Mg/ha/yr. The palm retained biomass dominance in the plot, but *Micropholis chrysophylloides* had 26 percent of the flood plain's total aboveground biomass. However, the palm ex-

TABLE 1. *Species importance values based on relative basal area and relative stem density for dicotyledonous trees with DBH ≥4 cm and palms and ferns with height of ≥ 0.7 m. Species are listed in order of importance value in 1995; some were combined by genera and empty fields mean that the species was not recorded that year. Hurricane Hugo passed over the stand in 1989.*

Species	Importance value (%)		
	1980	1990	1995
Prestoea montana	46.4	43.8	53.5
Micropholis chrysophylloides	19.5	20.8	18.9
Croton poecilanthus	12.7	11.8	7.6
Micropholis garciniaefolia	5.7	7.2	6.9
Magnolia splendens	2.9	2.4	3.0
Calicogonium squamulosum	3.2	4.4	2.5
Eugenia eggersii	2.7	2.2	1.8
Sloanea berteriana	1.6	2.1	1.4
Cyrilla racemiflora	1.1	1.5	1.3
Ditta myricoides	0.9	0.9	0.6
Byrsonima wadsworthii	0.1	0.4	0.6
Tabebuia rigida	0.2	0.5	0.4
Cyathea sp.	0.1	0.5	0.4
Myrcia sp.	0.5	0.2	0.3
Guarea sp.	0.1	0.2	0.2
Eugenia borinquensis	0.2	0.2	0.2
Ocotea spatulatha	0.7	0.1	0.1
Psychotria berteriana	0.1		0.1
Didimopanax morototoni			0.1
Cecropia peltata			0.1
Unknown			0.1
Xylosma schwaneckeanum		0.5	
Clusia clusiodes		0.2	
Casearia guianensis		0.2	
Ilex sideroxyloides	0.1	0.1	
Ocotea leucoxylon	0.3		
Miconia tetrandra	0.4		
Torralbasia cuneifolia	0.2		
Ilex nitida	0.1		

hibited the fastest rate of biomass accumulation after the hurricane (Table 2). The rate of biomass accumulation in palms accelerated after the hurricane from 2 to 7 Mg/ha/yr after a reduction of 16 Mg/ha/yr in the year following passage of the hurricane (Fig. 2).

FOREST FLOOR LITTER.—The mean mass of forest floor litter in June 1995 was within the prehurricane range of 1.6–8.0 mg/ha (Table 3). However, both the 1980 and 1995 mean values were lower than measured in August 1990 (Table 3). The proportion of the wood fraction decreased considerably between 1990 and 1995, as did the miscellaneous fractions. Tree fern litter appeared as a new and significant component of the forest floor litter in 1995, and the other litter fractions remained unchanged.

TREE MORTALITY.—The rate of total tree mortality continued to be low in this flood plain (2.0%/yr; Table 4). However, more palms died in the 5-yr interval after the hurricane than did immediately after the event: 9/ha (Frangi & Lugo 1991) versus 84/ha in Table 4. In fact, 57 percent of those palms found dead in 1995 had no visual hurricane damage when recorded live in 1990. This is "other mortality" in Table 4. For the flood plain forest as a whole, "other mortality" was 29 percent. Delayed mortality (*i.e.*, mortality during the 1990–1995 interval of trees damaged by Hurricane Hugo), was higher in the dicotyledonous trees than it was in the palms. Delayed mortality was also higher than "other mortality" for the flood plain as a whole. Because of its abundance or low rate of mortality, the fraction of the total population that died was low for palms (1.8%/yr) and *M. garciniaefolia* (1.6%/yr). However, for *Ilex sideroxiloides* and *Casearia guianensis*, delayed tree mortality was high relative to the population size before the hurricane (19.0%/yr).

POSTHURRICANE PLANT REGENERATION.—In 1995, more tree species were represented in the regenerating cohort than in the canopy of the forest (*i.e.*, 30 vs. 21 species). Seven canopy tree species were not represented in the posthurricane regeneration and 13 tree species in the posthurricane regeneration were not present in the canopy. Stem density of posthurricane regeneration was higher than that of trees with DBH ≥4 cm (*i.e.*, 3756 vs. 3084 stems/ha). Among posthurricane regeneration, the palm was also dominant in terms of density, but contributed little to basal area as did all the other 29 species (a total basal area of 0.27 m^2/ha for all regeneration). Tree fern density increased to 33 stems/ha during the 5-yr posthurricane period.

PATTERNS OF POSTHURRICANE PLANT REGENERATION.—Redundancy Data Analysis revealed that the horizontal axis along which regeneration subplots were aligned corresponded very closely with distance to the river (*i.e.*, distance increasing as values were more positive in the horizontal axis; Fig. 3). Elevation above the river (arl) increased as values became more positive on the vertical axis. Damage by Hurricane Hugo increased as values became more negative on the vertical axis. This means that the damage of Hurricane Hugo was greatest in the lower elevations near the river.

TABLE 2. *Aboveground biomass by species for June 1989, 1990, and 1995, and biomass production from 1990 to 1995 for dicotyledonous trees with DBH ≥4 cm and ferns and palms ≥0.7 mm tall in a flood plain palm forest in the Luquillo Mountains of Puerto Rico. Hurricane Hugo passed over the stand in November 1989. Data for 1989 and 1990 are from Frangi and Lugo (1991).*

Species	Biomass (Mg/ha)			Mg/ha/yr
	1989	1990	1995	1990–1995
Presotea montana	71.9	60	94.9	7.0
Micropholis chrysophylloides	49.7	45	53.7	1.7
Micropholis garciniaefolia	18	17	20.6	0.7
Croton peocilanthus	14.9	15	13.3	−0.4
Magnolia splendens	6.5	6.2	9.2	0.6
Sloanea berteriana	5.9	5.3	4.8	−0.1
Calicogonium squamulosum	6.9	6.9	3.5	−0.7
Cyrilla racemiflora	3.5	3.5	3.9	0.1
Eugenia eggersii	0.5	0.5	0.8	0.1
Byrsonima wadsworthii	0.2	0.2	0.8	0.1
Tabebuia rigida	0.6	0.6	0.7	<0.1
Ditta myricoides	0.5	0.5	0.5	<−0.1
Myrcia sp.	0.2	0.2	0.3	<0.1
Cyathea portorricensis	0.08	0.08	0.1	<0.1
Guarea sp.	0.2	0.2	0.2	<0.1
Eugenia borinquensis	0.2	0.2	0.2	<0.1
Didimopanax morototoni	0	0	0.1	<0.1
Unknown	0	0	0.3	0.1
Ocotea spatulatha	0.02	0.02	0.02	0
Cecropia peltata	0	0	0.02	t*
Psychotria berteriana	0	0	0.01	t
Total for flood plain	181	162	208	9.2

* Trace.

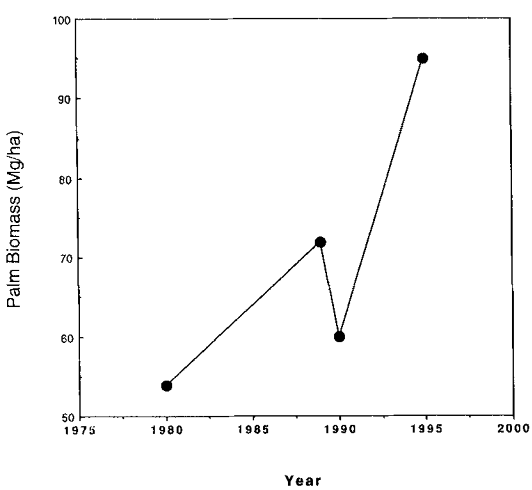

FIGURE 2. Temporal pattern of aboveground biomass for *Prestoea* montana trees in a flood plain palm forest in the Luquillo Mountains of Puerto Rico. Hurricane Hugo passed over the stand in 1989.

Dead trees showed no relationship to any axis. This is because of the low rate of tree mortality, and the fact that most mortality was delayed mortality of palms or small dicotyledonous trees. None of these cause large canopy gaps that would contribute to large increases in light intensity to the forest floor.

Abundant palm regeneration occurred in subplots with the lowest elevation near the river and where the canopy had opened the most as a result of treefall or tree damage after Hurricane Hugo. These sites had the longest hydroperiods with evidence of plant regeneration; we observed no plant regeneration in subplots with stagnant water. However, palm regeneration was not exclusively spatially determined, as there was palm regeneration at high elevation sites. The determinant factors in regulating palm regeneration appear to be edaphic, including soil moisture and short or moderate hydroperiod. These conditions can occur at higher elevation where small tributary channels dissect the flood plain.

Dicotyledonous trees regenerated best in areas with low probability of flooding (higher elevation arl), either close or far from the river. Regeneration of dicotyledonous trees can be high in some sub-

TABLE 3. *Litter accumulation (Mg/ha) on the forest floor of a flood plain palm forest in the Luquillo Mountains of Puerto Rico. Means for August 1990 and June 1995 are based on 20 collections each; SE is in parenthesis below the x. Values for 1980 are based on a weighted annual x derived from 11 monthly samples with 20 replicates for each.*

Year	Palm leaves	Dicot* leaves	Wood ≤2 cm	Wood ≥2 cm	Palm wood	F & F†	Fern litter	Misc‡	Total
1980	1.68	1.80		1.09		0.13	0	0.73	5.45+ (0.5)
1990	1.87 (0.41)	1.72 (0.33)	1.97 (0.51)	3.63 (2.27)	8.80 (8.75)	0.58 (0.25)	0 —	1.03 0.20	19.6 (9.0)
1995	1.96 (0.55)	1.65 (0.36)	0.69 (0.15)	0.98 (0.51)	0 —	0.91 (0.62)	0.16 (0.07)	0.37 (0.08)	6.72 (1.07)

* Dicotyledonous.
† Flowers and fruits.
‡ Miscellaneous.
\+ Range 1.6–8 mg/ha.

plots located at intermediate height and distance from the river. In these instances, the regeneration was associated with hurricane damage (high light intensity due to high mortality and large canopy gaps).

Dicotyledonous trees failed to regenerate far from the river in subplots undamaged by Hugo, regardless of the elevation of the subplot. Low light intensity, waterlogging, and low water turn over can be factors that limit the regeneration of dicotyledonous trees in these locations.

Tree ferns had an intermediate regeneration strategy between that of palms and dicotyledonous trees. We have observed a preference for mineral soil in the regeneration of tree ferns. However, this factor was not included in our ordination and its absence in the analysis could mask the regeneration pattern of this species.

TABLE 4. *Tree mortality (trees/ha) between 1990 and 1995 in a flood plain palm forest in the Luquillo Mountains of Puerto Rico. Annual mortality (%/yr) is based on the percentage of live trees in 1990 that were dead in 1995 divided by the time interval. Data are for dicotyledonous trees with DBH ≥4 cm and ferns and palms ≥0.7 m tall. The text defines the types of mortality.*

Species	Delayed mortality	Other mortality	Total mortality	Annual mortality
Prestoea montana	36	48	84	1.8
Croton poecilanthus	36	16	52	3.6
Calicogonium squamulosum	16	0	16	3.0
Micropholis garciniaefolia	8	0	8	1.6
Xilosma schwaneckeanum	8	0	8	10.0
Casearia guianensis	4	0	4	19.0
Ditta myricoides	0	4	4	2.8
Ilex sideroxiloides	4	0	4	19.0
Total for flood plain	112	68	180	2.0
Annual rate (trees/ha/yr)	22	13	35	—

DISCUSSION

The disturbance caused by Hurricane Hugo allowed us to study the relative importance of growing space, canopy opening, and flood plain effects (*i.e.*, length of hydroperiod and water turn over) in the reorganization of the palm forest. Because of its location relative to the path of the hurricane, the study site suffered only moderate damage. For example, tree mortality immediately after the event was 1 percent (Frangi & Lugo 1991) and 5 yr later it was 2 percent/yr (Table 4). Both values fall well within the normal range for background tree mortality (*sensu* Lugo & Scatena 1996).

Recovery after the hurricane was fast in terms of basal area (Fig. 1a), tree density (Fig. 1b), immigration and turn over of tree species (Table 1), aboveground tree biomass (Table 2; Fig. 2), and litter accumulation on the forest floor (Table 3). The palm was the clear dominant, particularly in its fast accumulation of aboveground biomass and increase in importance value after Hurricane Hugo (Table 1; Fig. 2). The steep slope of the biomass/productivity curve in Figure 2 is a measure of the high resilience for the palm population in the flood plain, because it directly indicates the recovery of biomass after the disturbance.

In spite of the rapid response and resiliency of the vegetation to the hurricane, several legacies of the hurricane were measurable five years after the event. For example, while the mass of litter on the

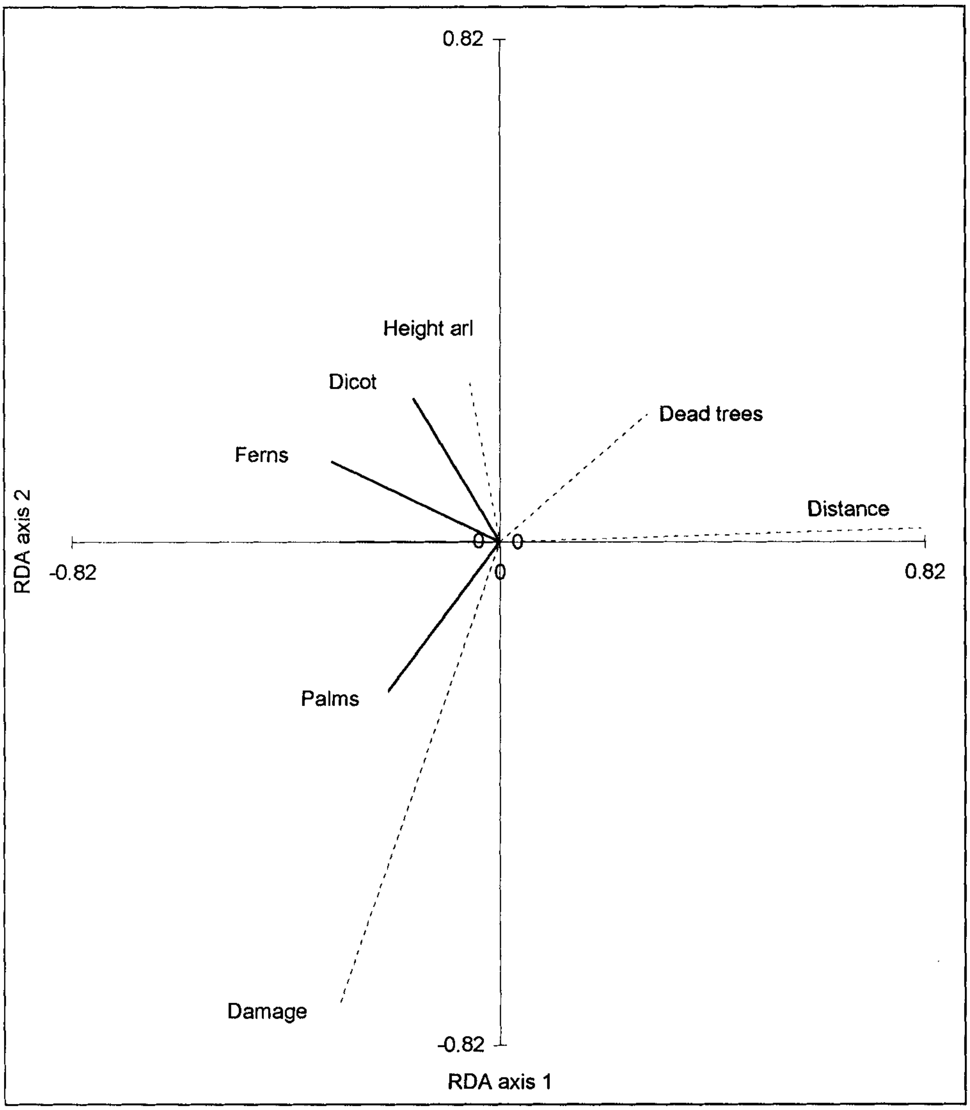

FIGURE 3. Redundancy Data Analysis diagram for tree regeneration in a flood plain palm forest in the Luquillo Mountains of Puerto Rico. Solid lines are independent variables and dashed lines are dependent variables. The angle of the lines with a particular axis is a measure of the degree of correlation. Shallow angles mean higher correlation. The length of the dashed line signifies the significance of the axis in explaining the regeneration.

forest floor returned to prehurricane values, its composition was different from what it was before (appearance of tree fern litter) and immediately after the hurricane (accumulation and then loss of woody litter; Table 3).

Delayed tree mortality had three peculiarities: (1) it was higher than initial hurricane mortality; (2) it was higher than other mortality perhaps unrelated to the hurricane; and (3) its effects were greater on dicotyledonous tree species (Table 4). Species that were poorly represented in the flood plain prior to the hurricane suffered cumulative mortalities of up to 90 percent in the 5 yr after the disturbance (Table 4). These high rates of tree mortality, coupled with the high tree species richness in posthurricane regeneration, help explain the high turn over of species and changes in species' importance values over the 15-yr study.

Posthurricane plant regeneration resulted in 13 new tree species entering the forest floor and in the

TABLE 5. *Matrix of ecological conditions under which trees regenerate in a flood plain palm forest in the Luquillo Mountains of Puerto Rico. The matrix illustrates the interplay between factors associated with microtopography (degree of flooding and water turn over) and light intensity as a result of disturbance (gaps of several sizes), absence of disturbance (no gaps), or the location of the axis for the river channel where light is naturally abundant.*

		Low light		High light	
		No damage to canopy	Small canopy gaps	Along river	Large gaps
Low relief	Stagnant water	No regeneration	No regeneration	Little regeneration	Little regeneration
	Moving water	Low regeneration	Low regeneration palms	Palms regenerate well	Palms regenerate well
High relief	Moving water	Low regeneration dicots*	Low to medium regeneration dicots	All trees regenerate well	All trees regenerate well
	Infrequent flooding	No regeneration	High regeneration of dicots	High regeneration of dicots	High regeneration of dicots

* Dicotyledonous trees.

almost elimination of the initially high density of *Cecropia peltata* observed in 1990 (Frangi & Lugo 1991). Clearly, disturbance events need not be catastrophic to exert selective pressure on the differential survival of trees at the <1-ha patch scale.

The regeneration patterns by species groups (palm, tree fern, dicotyledonous; Fig. 3) suggest the interaction between two types of light environments (high and low light), microtopography, and the hydrodynamics of the flood plain (Table 5). The axis of the river channel provides a "river bank effect" with continuous side light for plants capable of regenerating along the river. This permanent light availability contrasts with the light temporarily made available by the opening of the canopy after the hurricane. Because of the low damage to the canopy by the hurricane, canopy gaps closed quickly by either regrowth of branches in surviving trees or the growth of regenerating plants. Our measurements show that tree regeneration was more prevalent along the river channel axis. Tree regeneration was lower in areas inside the flood plain where the canopy was temporarily opened by Hurricane Hugo.

Trees in the flood plain must cope with the problem of inundation, water stagnation, and anoxia. Results show that very little regeneration occurred in sectors of the flood plain with long periods of stagnant water. Palm regeneration was greatest in high and in low areas of the flood plain, where water flow and turn over was high. Water movement ventilates soils and roots, reducing the period of anoxia. Dicotyledonous trees regenerated in the higher areas of the flood plain where the risk of flooding was lowest. Our results show how two topographic features (the axis of the river channel and microtopography) coupled with moderate hurricane disturbance create ecological conditions of light and hydroperiod on which plant regeneration sorts out according to tolerance to flooding and light (Table 5).

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