BIOTROPICA 28(4a): 424–440 1996

The First Five Years in the Reorganization of Aboveground Biomass and Nutrient Use Following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico[1]

F. N. Scatena, S. Moya, C. Estrada, and J. D. Chinea[2]

International Institute of Tropical Forestry, USDA Forest Service, P.O. Box 25000, Río Piedras, Puerto Rico 00928-2500, U.S.A.

ABSTRACT

Five years after Hurricane Hugo reduced the aboveground biomass by 50 percent in two forested watersheds in the Luquillo Experimental Forest of Puerto Rico, regeneration and growth of survivors had increased the aboveground biomass to 86 percent of the pre-hurricane value. Over the 5 yr, the net aboveground productivity averaged 21.6 $Mg \cdot ha^{-1} \cdot yr^{-1}$ and was faster than most plantations and secondary forests in the area. Woodfall and associated nutrient fluxes never attained pre-storm values but by the fifth yr, mean daily total litterfall, and N, P, K, Ca, and Mg fluxes in litterfall were 83, 74, 62, 98, 75, and 81 percent of their pre-disturbance values, respectively. Aboveground nutrient pools of these nutrients ranged from 102 to 161 percent of their pre-disturbance values and were larger after 5 yr because of higher nutrient concentrations in the regeneration compared to the older wood that it replaced. The following sequence of ecosystem reorganization during this first 5 yr period is suggested. An initial period of foliage production and crown development occurred as hurricane survivors re-leafed and herbaceous vegetation and woody regeneration became established. During this period, 75 to 92 percent of the nutrient uptake was retained in the aboveground vegetation and there was a relatively low rate of aboveground carbon accumulation per mole of nutrient cycled. This initial period of canopy development was followed by a peak in aboveground productivity that occurred as early successional species entered the sapling and pole stages. This period was followed by the establishment of the litterfall nutrient cycle and an increase in the net productivity per mole of nutrient cycled. During this 5 yr period, the Bisley forest had some of the lowest within-stand nutrient-use-efficiencies and some of the highest levels of aboveground productivity ever observed in the LEF. The study demonstrates that high levels of productivity and rapid rates of aboveground reorganization can be achieved with rapid within-system cycling and inefficient within-stand nutrient use.

RESUMEN

Cinco años después que el Huracán Hugo redujera la biomasa en un 50 por ciento en dos cuencas arboladas en el Bosque Experimental de Luquillo de Puerto Rico, la regeneración y el crecimiento de los sobrevivientes han aumentado la biomasa a un 86 por ciento del valor previo al huracán. Durante estos cinco años, la productividad neta del suelo promedió un 21.6 $Mg \cdot ha^{-1} \cdot año^{-1}$, por lo que fue más rápido que en la mayoría de las plantaciones y bosques secundarios del área. Caída de madera y los flujos de nutrientes asociados no recuperaron valores anteriores a la tormenta pero al quinto año, el promedio diario de caída de hojarasca y flujos de N, P, K, Ca, y Mg en la caída de hojas fue de 83, 74, 62, 98, 75 y 81 por ciento de sus valores previo al a la perturbación, respectivamente. Los nutrientes en la biomasa se distribuyeron entre 102 y 161 porciento de sus valores previo a la perturbación y fueron mayores después de cinco años debido a la alta concentración de nutrientes en la regeneración comparado a la madera vieja que reemplazaba. Durante el periodo de estos primeros cinco años se sugiere la siguiente secuencia de reorganización del ecosistema. Un periodo inicial de producción del follaje y desarrollo de las copas mientras los sobrevivientes del huracán reverdecían (releafed) o echaban hojas y se establecía la vegetación herbacea y regeneraba la madera. Durante este periodo, el 75 al 92 por ciento de la toma de nutrientes se retuvo en la vegetación del suelo y hubo una proporción relativamente baja de acumulación de carbono en el suelo por mol de ciclo de nutrientes. Ese periodo inicial en el desarrollo de la copa fue seguido por un aumento en la productividad, lo cual ocurrió tan temprano como las especies de sucesión entraron en etapas de arbolitos. A este periodo le siguió el establecimiento de ciclos de nutrientes de hojarascas y un aumento de la productividad neta por mol de nutrientes reciclados. Durante este periodo de cinco años, el Bosque de Bisley tuvo uno de las menores "within-stand" eficiencias de uso de nutriente y unos de los niveles más altos de productividad que se hayan observado jamás en el LEF. Este estudio demostró que altos niveles de productividad y rápidas proporciones de reorganización del ecosistema se puede obtener con rápidos "within-system" ciclos e ineficiente "within-stand" uso de nutrientes.

Key words: *biomass; hurricanes; nutrient use; Puerto Rico; recovery.*

---

[1] Received 15 September 1995, revision accepted 10 April 1995.

[2] Present address: Department of Forestry, University of Illinois, Urbana, Illinois 61801, U.S.A.

THE IMPORTANCE OF NATURAL AND ANTHROPOGENIC disturbances in transferring biomass and nutrients within and between ecosystems is well documented (Pickett & White 1985, Scatena & Lugo 1995). The role of hurricanes in structuring Caribbean forests is also well documented (Crow 1980, Weaver 1986, Lugo & Scatena 1995). While the importance of disturbances in structuring these ecosystems is widely acknowledged, the rates of forest reorganization following catastrophic disturbances are less well understood. This paper documents the 5 yr reorganization of aboveground biomass, nutrient pools, litterfall, throughfall, and nutrient use efficiencies (NUE) in two forested watersheds in the Luquillo Experimental Forest of Puerto Rico that were severely affected by Hurricane Hugo on 18 September 1989.

The premise that efficient nutrient use occurs when a relatively large amount of organic matter is produced per unit of nutrient uptake, and the notion that efficient within-stand nutrient use may indicate nutrient limitations (Grubb 1977, Vitousek 1984), or adaptations to nutrient limitations (Chapin 1980), have been dominant themes in the ecology of humid tropical forest for decades. While it needs to be recognized that maximum within-system efficiencies are not necessarily the efficiencies that produce the maximum benefit to a ecosystem (Odum 1983), and that plant nutrient use can be more complex than simple indices may indicate (Chapin 1980, Grubb 1995), comparisons of NUE between tropical forests have produced considerable insights (*e.g.,* Vitousek 1984, Lugo 1992, Silver 1994). However, because most studies have focused on mature ecosystems and only a few studies have discussed how nutrient cycling responds to hurricanes (Waterloo 1994), or how NUE vary over successional time (Brown & Lugo 1990), less is known about how forest nutrient use responds to catastrophic disturbances. The studies and model simulations that have been conducted have indicated that the effects of hurricanes on intra-system nutrient cycling are large and may last for years or decades (Sanford *et al.* 1991, Waterloo 1994). In this study, variations in the amount of carbon fixed per unit of nutrient cycled and other indices of NUE are compared after Hurricane Hugo created a pulse of high-quality nutrients into an already nutrient-rich system. The emphasis of this paper is on the initial description and graphical display of ecosystem level changes that occurred over the 5 yr period. Subsequent papers will use the unique data set described here to address mechanisms of reorganization and species-specific responses to the disturbance.

The study area, the Bisley watersheds 1 and 2 of the Luquillo Experimental Forest (LEF), drain 13 ha of subtropical wet life zone forest (Ewel & Whitmore 1973). These watersheds have an elevation of 260 to 450 masl, receive between 3000 to 4000 mm of precipitation each yr (Fig. 1), and are steep, highly dissected, and covered with mature secondary Tabonuco-(*Dacryodes excelsa*) type forest (Scatena 1989a, Scatena & Lugo 1995). This forest type is part of the Dacryodes-Sloanea association of the Lesser Antilles (Beard 1949, Crow & Grigal 1979). On 18 September 1989, Hurricane Hugo passed over the region and caused extensive damage to vegetation of the LEF (Scatena & Larsen 1991). The Bisley watersheds were located in one of the most severely affected areas in the LEF (Boose *et al.* 1994) and experienced considerable crown damage, snapping, and uprooting of vegetation (Basnet *et al.* 1992, Scatena & Lugo 1995). The net result of this catastrophic event was to reduce the live aboveground biomass in the watersheds from 226 Mg/ha to 113 Mg/ha (Scatena *et al.* 1993). The corresponding reductions in the size of the aboveground nutrient pools of N, P, K, Ca, and Mg ranged between 45 and 48 percent. The hurricane-induced pulse of fine litter and associated nutrients to the forest floor was 419 to 451 times the mean daily value (Lodge *et al.* 1991).

METHODS

VEGETATION SAMPLING.—Vegetation was measured in 83 permanent circular plots (5 m diameter) that were established at the nodes of a 40 × 40 m grid that covered the two watersheds. (*cf.* Scatena & Lugo 1995). In 1988, and again 3 mo (December 89) and 5 yr (September 94) after Hurricane Hugo, the plots were censused for stems with diameters at 1.3 m (DBH) of 2.5 cm or greater. In addition, in September 1990, 25 of the permanent circular plots were randomly selected for detailed measurements of regeneration. At each of these 25 circular plots, five permanent 1 × 1 m subplots were established and censused at 12, 18, 24, 30, 36, 48 and 60 mo after the hurricane. During each census, the percent cover of herbs, ferns, and seedling species was determined. Seedling regeneration was tallied into three height classes: 0.2 to 0. 5 m (subsequently referred to as class 1); 0.5 to 1.3 m (class 2); and greater than 1.3 m (class 3). For individuals in regeneration class 3, a diameter was also mea-

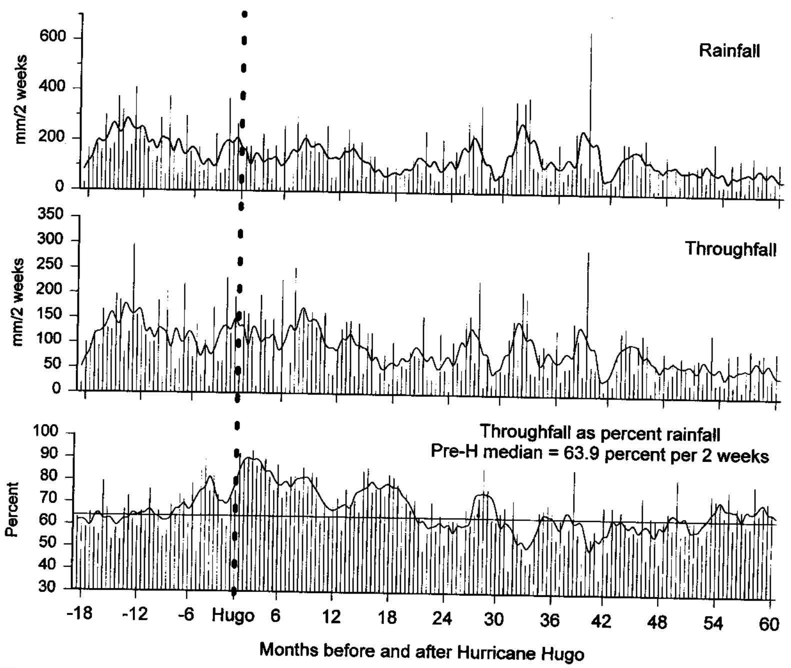

FIGURE 1. Rainfall, throughfall, and throughfall as percent rainfall for two week sampling periods in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Horizontal line is the median of pre-hurricane value, the curved line is the two month running average.

sured. Species names follow Liogier & Martorell (1982) and Chinea *et al.* (1994).

LITTER AND THROUGHFALL COLLECTION.—Total weekly rainfall was collected on a canopy level walk-up tower located in the center of the two watersheds. Total weekly throughfall was measured in 30 collectors that were systematically located along a elevational and topographic transect that traverses the watersheds (*cf.* Scatena 1989b for additional details on the rainfall and throughfall measurements). Litterfall was collected every other week for 1.5 yr prior to, and 5 yr following the hurricane. The litter was collected in 60 baskets (0.25 m^2)

TABLE 1. *Watershed mean and standard error of mean for aboveground biomass and nitrogen in the Bisley Experimental Watersheds prior to, immediately after, and by month following Hurricane Hugo (18 September 1989). NA = not applicable. See text for details.*

			Months after Hurricane Hugo						
	Pre	Post	12	18	24	30	36	48	60
Biomass, Mg·ha^{-1}									
Herbs, vines, ferns	0.4	0.3	1.0	0.8	0.9	1.2	1.0	0.7	0.7
Post-hurricane regeneration	NA	NA	6.0	12.7	28.9	35.8	42.6	62.0	67.7
Hurricane survivors	NA	113.0	115.9	117.3	118.6	119.9	121.2	123.8	126.5
Total biomass	226.3	113.3	122.9	130.7	148.4	156.9	164.8	186.6	195.0
Standard error	26.0	24.9	19.2	20.1	23.1	24.5	25.7	29.1	30.4
Nitrogen, kg·ha^{-1}									
Herbs, vines, ferns	6.8	4.0	14.3	10.6	11.9	17.9	14.0	10.6	10.6
Post-hurricane regeneration	NA	NA	68.6	118.8	176.2	186.4	195.9	317.4	296.7
Hurricane survivors	NA	299.5	318.6	326.1	333.6	341.1	348.7	363.7	378.8
Total N	669.7	303.5	401.5	455.5	521.7	545.4	558.6	691.7	686.1
Standard error	76.4	66.3	53.8	61.0	81.2	73.1	74.9	92.7	91.9

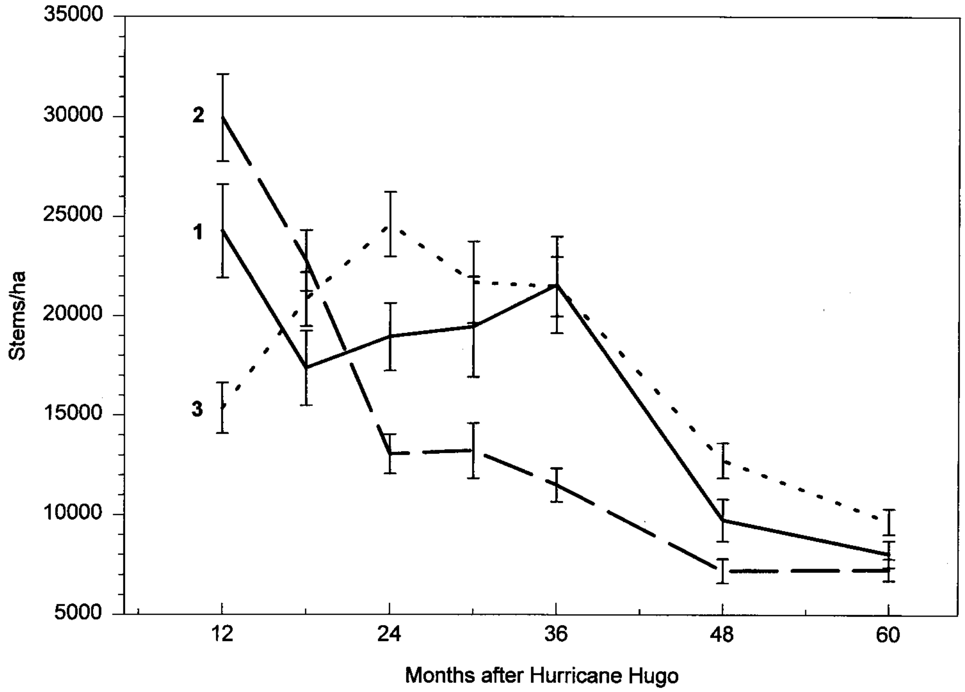

FIGURE 2. Seedling density by height class in the Bisley Experimental Watersheds during the months following Hurricane Hugo (18 September 1989). 1 = 0.2 to 0.5 m height class, 2 = 0.5 to 1.3 m, and 3 = individuals greater than or equal to 1.3 m in height.

that were systematically placed along the same transect as the throughfall collectors and are the same collectors that were used to estimate the litterfall induced by Hurricane Hugo (Lodge *et al.* 1991). The litter was oven-dried at 65°C to a constant weight and sorted into leaf, wood, fruits and flowers, and miscellaneous fractions. For nearly every 2 wk sample period, the nutrient content of the separated fractions was determined using the laboratory methods described below. For the few sample periods where there was insufficient material in a fraction to analyze, the average nutrient concentra-

TABLE 2. *Watershed mean and standard error of mean for aboveground phosphorus and potassium in the Bisley Experimental Watersheds prior to, immediately after, and by month following Hurricane Hugo (18 September 1989). NA = not applicable. See text for details.*

	Months after Hurricane Hugo								
	Pre	Post	12	18	24	30	36	48	60
Phosphorus, kg·ha^{-1}									
Herbs, vines, ferns	0.4	0.2	1.0	0.7	0.9	1.2	1.0	0.7	0.7
Post-hurricane regeneration	NA	NA	4.0	6.9	10.3	10.7	11.0	15.2	15.7
Hurricane survivors	NA	16.7	17.9	18.5	19.0	19.5	20.0	21.0	22.1
Total P	36.8	16.9	23.0	26.1	30.2	31.4	32.0	37.0	38.5
Standard error	4.1	3.7	3.4	3.9	5.0	4.7	4.8	5.5	5.8
Potassium, kg·ha^{-1}									
Herbs, vines, ferns	5.0	2.8	18.6	14.1	16.9	23.1	18.4	13.7	13.3
Post-hurricane regeneration	NA	NA	100.7	173.9	244.7	250.1	254.8	322.3	359.7
Hurricane survivors	NA	268.6	280.5	285.0	289.5	294.1	298.6	307.6	316.7
Total K	561.9	271.4	399.8	473.0	551.2	567.3	571.7	643.6	689.8
Standard error	61.3	59.4	52.8	62.4	91.2	74.9	75.5	85.0	91.1

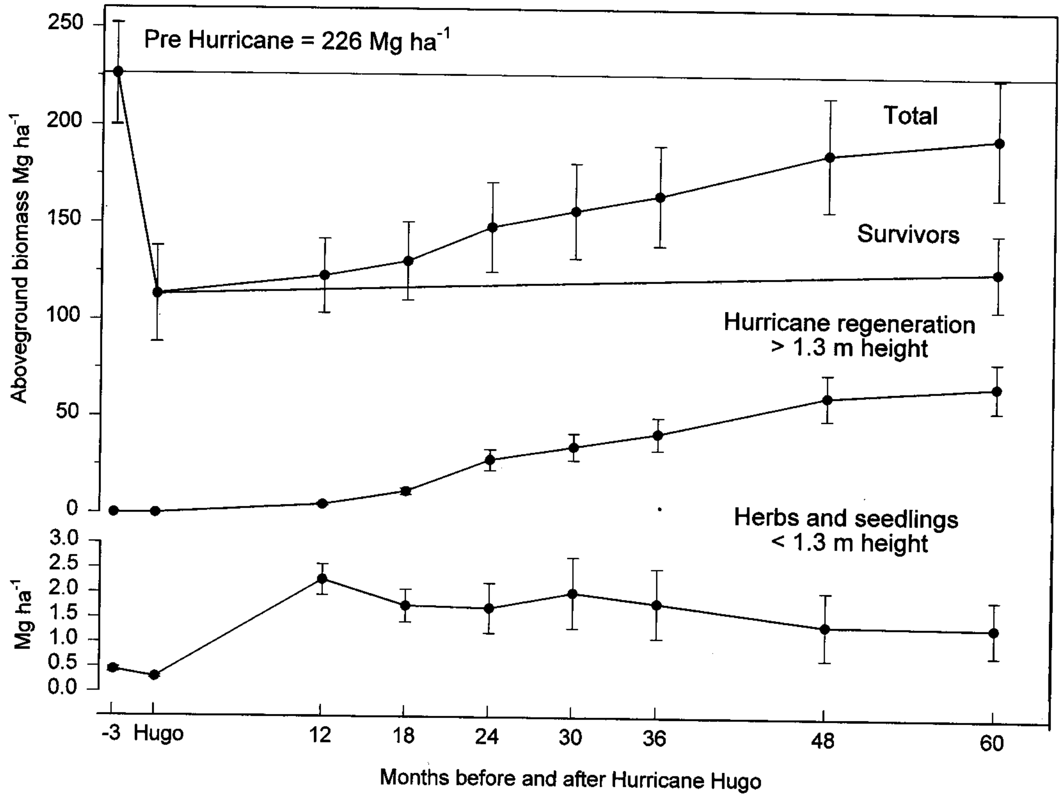

FIGURE 3. Aboveground biomass in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Error bars are standard errors of the mean of all sample plots. Survivors indicate the biomass of individuals that survived the hurricane.

TABLE 3. *Watershed mean and standard error of mean for aboveground calcium and magnesium in the Bisley Experimental Watersheds prior to, immediately after, and by month following Hurricane Hugo (18 September 1989). NA = not applicable. See text for details.*

	Months after Hurricane Hugo								
	Pre	Post	12	18	24	30	36	48	60
Calcium, kg·ha^{-1}									
Herbs, vines, ferns	3.0	1.7	6.0	4.2	5.2	7.1	5.5	4.4	4.1
Post-hurricane regeneration	NA	NA	30.0	53.2	97.6	102.4	107.0	161.0	168.7
Hurricane survivors	NA	228.2	259.6	274.4	289.3	304.1	319.0	348.7	378.3
Total Ca	480.1	229.9	295.5	331.8	392.0	413.7	431.5	514.0	551.2
Standard error	52.3	50.4	84.2	94.6	111.7	101.0	107.9	123.0	146.5
Magnesium, kg·ha^{-1}									
Herbs, vines, ferns	1.9	1.6	2.9	2.2	2.2	4.1	3.0	2.5	2.5
Post-hurricane regeneration	NA	NA	18.4	44.9	82.0	89.4	96.6	133.7	140.5
Hurricane survivors	NA	65.8	70.5	72.0	73.5	75.1	76.6	79.6	82.7
Total Mg	139.3	67.4	91.7	119.1	157.7	168.6	176.2	215.8	225.7
Standard error	15.2	14.7	15.6	20.2	26.8	30.1	31.2	36.7	38.4

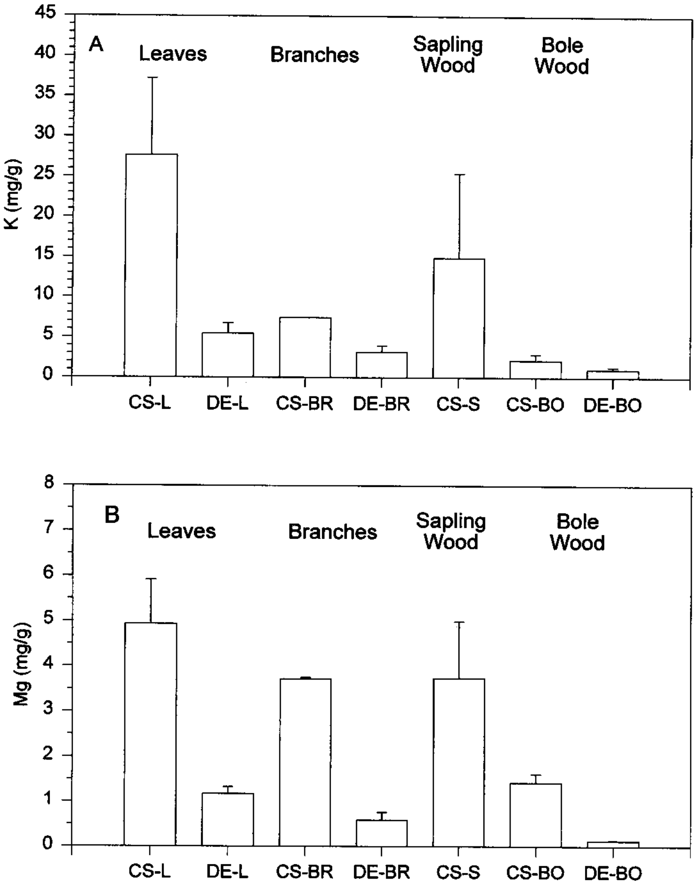

FIGURE 4. Average nutrient concentrations of potassium (A) and magnesium (B) by plant part for *Cecropia schreberiana* and *Dacryodes excelsa* in the Bisley Experimental Watersheds, Puerto Rico. CS = *C. schreberiana*, DE = *Dacryodes excelsa*, L = leaves, BR=branch wood, S = sapling wood, BO = bole wood.

TABLE 4. *Leaf, wood and total litter (leaf + wood + miscellaneous fractions) mass, in g·m^{-2}·d^{-1}, in the Bisley Experimental Watersheds, prior to and following Hurricane Hugo (18 September 1989). Means, medians, and standard errors of mean are for 60, 0.5 m × 0.5 m traps that were collected every 2 wk. See text and figures for details.*

		Months after Hurricane Hugo							
		Pre-Hugo	0–12	12–18	18–24	24–30	30–36	36–48	48–60
Littermass, g·m^{-2}·d^{-1}									
Total	mean	2.38	0.63	1.10	1.53	1.11	1.68	1.95	1.98
	median	2.40	0.65	0.97	1.69	1.19	1.59	1.96	2.01
	SE	0.18	0.08	0.13	0.15	0.11	0.13	0.09	0.10
Leaf	mean	1.54	0.39	0.71	1.20	0.85	1.38	1.43	1.41
	median	1.35	0.30	0.66	1.32	0.83	1.38	1.35	1.51
	SE	0.09	0.05	0.07	0.12	0.09	0.10	0.08	0.07
Wood	mean	0.45	0.10	0.12	0.08	0.05	0.10	0.16	0.14
	median	0.38	0.09	0.08	0.07	0.05	0.08	0.13	0.12
	SE	0.07	0.01	0.02	0.02	0.01	0.01	0.02	0.13

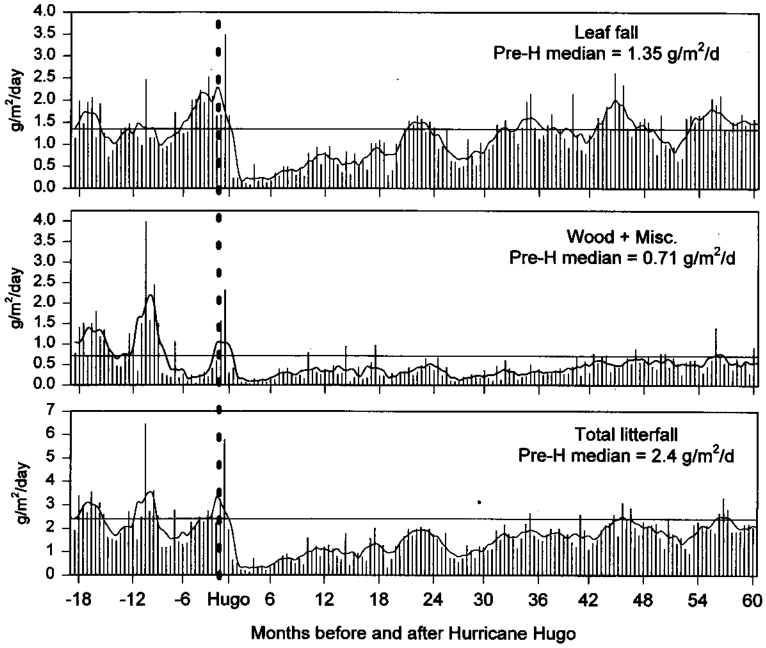

FIGURE 5. Leaf fall, wood and miscellaneous fall, and total litterfall in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Horizontal line is the median of pre-hurricane values, the curved line is the two month running average.

TABLE 5. *Total litter nutrient flux in the Bisley Experimental Watersheds prior to and following Hurricane Hugo. (18 September 1989). Means, and standard errors of mean are for 60, 0.5 m × 0.5 m traps that were collected every 2 wk. See text and figures for details.*

		Months after Hurricane Hugo						
	Pre-Hugo	0–12	12–18	18–24	24–30	30–36	36–48	48–60
Litter N, g·m^{-2}·d^{-1}								
Mean	288.2	93.5	166.8	200.6	138.4	185.9	214.5	212.0
SE	19.4	11.8	24.5	18.9	13.8	14.6	43.8	10.4
Litter P, g·m^{-2}·d^{-1}								
Mean	11.7	4.3	6.9	8.6	5.5	7.3	8.1	7.3
SE	0.9	0.6	1.1	1.1	0.7	0.7	0.5	0.4
Litter K, g·m^{-2}·d^{-1}								
Mean	85.8	30.3	49.3	67.2	48.4	54.3	73.0	84.2
SE	6.3	4.5	5.9	5.8	5.6	3.2	4.2	5.7
Litter Ca, g·m^{-2}·d^{-1}								
Mean	178.3	49.1	95.5	122.7	99.0	125.0	115.1	133.4
SE	12.0	6.5	13.4	11.9	10.3	11.9	9.3	7.4
Litter Mg, g·m^{-2}·d^{-1}								
Mean	50.5	15.3	30.0	37.5	29.9	42.1	41.7	40.7
SE	3.4	2.2	3.9	3.8	3.2	3.6	2.5	2.3

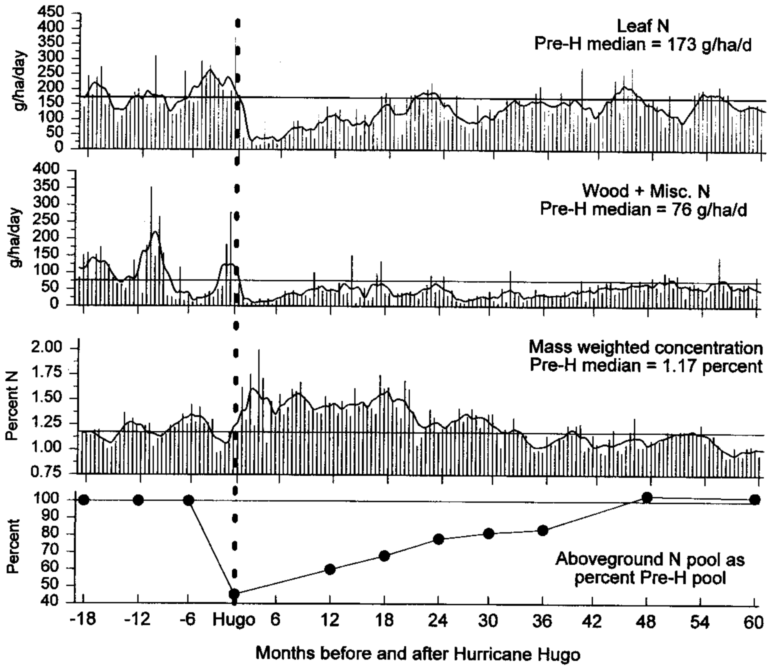

FIGURE 6. Nitrogen flux in leaf litter, wood and miscellaneous litter, the mass weighted concentration of total litter, and the aboveground N pool as a percent of the pre-hurricane pool, in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Horizontal line is the median of pre-hurricane values, the curved line is the two month running average.

tion of the two adjacent sample periods was used to estimate nutrient fluxes.

All the rainfall, throughfall, and litterfall values reported here are from the same 6.5 yr period of overlapping measurements and are graphed using the same 2 wk litter sampling periods. All graphs were developed using Sigma Plots for Windows, Version 2.0, Jandel Scientific. All other statistics were calculated using SAS for Windows, Version 6.01.

LABORATORY NUTRIENT ANALYSIS.—The nutrient concentration of dried vegetation and litter was determined at the International Institute of Tropical Forestry laboratory using identical procedures to those used to measure the tissue concentrations prior to the hurricane (Scatena *et al.* 1993) and the nutrient concentrations of hurricane litterfall (Lodge *et al.* 1991). After separation into different plant parts, 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. The ground samples were then digested with H_2O_2 and concentrated HNO_3 (Luh Huang & Schulte 1985) and analyzed for P, K, Ca, and Mg, with a Beckman Spectra Span V plasma emission spectrometer. Nitrogen concentrations were determined using the semi-micro Kjeldahl method and a H_2SO_4 digestion (Chapman & Pratt 1979). Pine and peach leaf standards from the U.S. National Bureau of Standards were run every 40 samples. The detection limits for N, P, K, Ca, and Mg were 0.1, 0.09, 0.02, 0.009, and 0.08 mg/g respectively.

ABOVE-GROUND BIOMASS AND NUTRIENT POOLS.—Aboveground biomass and nutrient pools were determined for herbaceous species, regeneration in the three height classes, and survivors of the hurricane. For each sample period, the biomass of herbs and class 1 and 2 seedlings was determined by destructively sampling 25-1 × 1 m plots that were censused in the same manner as the 125 regeneration quadrats. The herbaceous biomass in each of these destructively sampled plots was sorted by species, dried, weighted, and analyzed for nutrient content. Watershed level estimates of herbaceous biomass for each sample period were then estimated by multiplying the average percent cover in the 125 regeneration plots by the average weight of a species per unit percent cover that were measured in the destructively sampled plots at that sample period. The biomass and nutrient content of class 1 and 2 seedlings were also estimated from the average weight and nutrient concentrations of each species in each size class measured in the destructive plots multiplied by the average density of seedlings measured in the regeneration plots. The biomass and nutrient pools of aboveground vegetation with diameters greater than 2.5 cm DBH (Class 3 regeneration and survivors) were calculated using allometric equations that were developed specifically for the trees and species in the watersheds (*cf.* Scatena *et al.* 1993 for details of allometry and the estimates of pre and post hurricane biomass). The tissue nutrient concentrations used to derive nutrient pool sizes were both species, component, and size-class specific.

After calculating the biomass and nutrient pools of the herbaceous vegetation, post hurricane regeneration, and hurricane survivors by species within the individual sample plots, watershed mean values were estimated as the mean of the sum from the sample plots. Specifically:

$$\text{Mean watershed biomass} = (\Sigma_p(\Sigma_s(\Sigma_c(B_{p,s,c})))/n) \tag{1}$$

$$\text{Mean watershed nutrient pool} = (\Sigma_p(\Sigma_s(\Sigma_c(N_{p,s,c}B_{p,s,c})))/n) \tag{2}$$

Where:

s = species
c = plant part; *i.e.*, bole, branches, or leaves
B = biomass
N = nutrient concentration
p = individual plot
n = number of sample plots

Stand-level standard errors of the means of the plots were calculated separately for each vegetative compartment and the sum of the compartments. These estimators are identical to those used previously in the watersheds (Scatena *et al.* 1993) and are measures of the variation in biomass between the plots and are not estimators of total measurement or estimation error.

ABOVEGROUND NUTRIENT USE EFFICIENCIES.—Temporal changes in "within stand" (*sensu* Vitousek 1984) efficiencies of aboveground nutrient use were ascertained by comparing changes in the rates of accumulation of carbon and nutrients over the different sampling periods. These comparsions were made using several indices:

$$\frac{\text{Net aboveground productivity}}{\text{nutrient uptake}} = (dB/dt + dL/dt)/(dUn/dt) \tag{3}$$

$$\frac{\text{Aboveground biomass accumulation}}{\text{nutrient uptake}} = (dB/dt)/(dUn/dt) \tag{4}$$

$$\frac{\text{Aboveground biomass accumulation}}{\text{litterfall return}} = (dB/dt)/(dLn/dt) \tag{5}$$

$$\frac{\text{Aboveground nutrient accumulation}}{\text{nutrient uptake}} = (dBn/dt)/(dUn/dt) \tag{6}$$

$$\frac{\text{Aboveground nutrient accumulation}}{\text{litterfall return}} = (dBn/dt)/(dLn/dt) \tag{7}$$

$$\text{Turnover period of aboveground nutrients by litter} = Bn/(dL/dt) \tag{8}$$

$$\text{Mass weighted nutrient concentration of litter} = (dLn/dt)/(dL/dt) \tag{9}$$

Where:

dB/dt = rate of carbon accumulation in aboveground biomass
dBn/dt = rate of accumulation of nutrient n in aboveground biomass
dL/dt = rate of carbon flux in litterfall
dLn/dt = rate nutrient n in litterfall
dUn/dt = $dBn/dt + dLn/dt$ = rate of plant uptake of nutrient n
Bn = aboveground nutrient n in biomass at time t.

In these indices, net aboveground productivity (NPP) over a sample interval is the sum of net aboveground biomass accumulation plus litterfall. The net plant uptake of a nutrient is the sum of the nutrient accumulation in biomass plus the nutrient returned in litterfall and is a conservative estimate since it does not include nutrient uptake lost by leaching. Because indices of different nutrients are being compared directly and are placed on the same graphs, NUE were calculated on a molar basis. Moreover, the mass of nutrients and carbon have been converted to moles and NUE are expressed on a mole of carbon per mole of nutrient

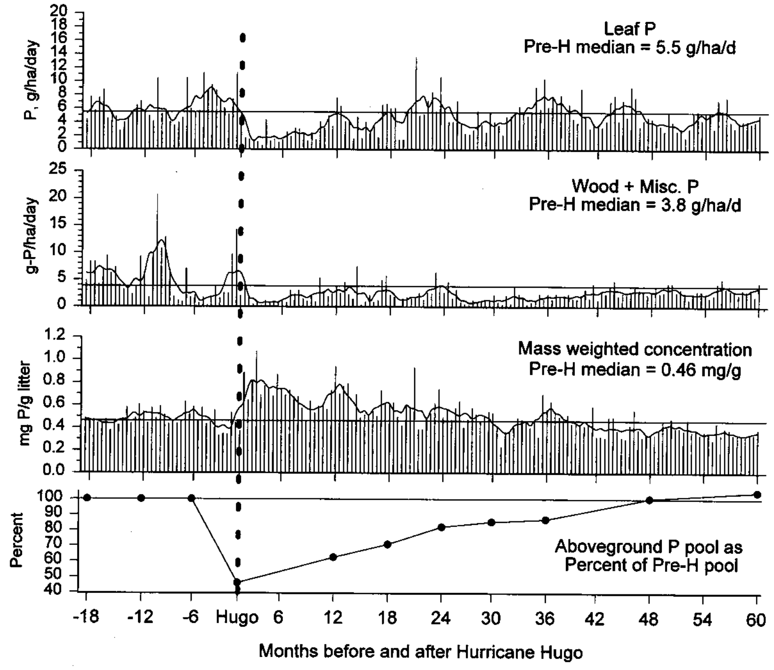

FIGURE 7. Phosphorus flux in leaf litter, wood and miscellaneous litter, the mass weighted concentration of litter, and the aboveground P pool as a percent of the pre-hurricane pool, in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Horizontal line is the median of pre-hurricane values, the curved line is the two month running average.

basis. The concentration of carbon in the aboveground biomass and litterfall was assumed to be 50 percent of the total biomass of these compartments.

Equations 3 and 4 are the ratios of net aboveground carbon production and net aboveground carbon accumulation per unit of nutrient uptake, respectively and are standard measures of resource utilization. Equation five is the ratio of the moles of carbon accumulated in aboveground biomass per mole of nutrient cycled by litter and is considered here as an index of the efficiency of litterfall nutrient return to net aboveground carbon accumulation. Equation six is the fraction of nutrient uptake that remains in aboveground biomass and reflects the relative proportions of a nutrient that is cycled within the system versus that which remains in the aboveground biomass. Equation seven measures the relative amount of a nutrient that accumulates in aboveground biomass compared to that cycled by litterfall. Equation eight is the average turnover time, in yr, of aboveground pools by litterfall (Scatena 1995). Equation 9 is the mass weighted concentration of nutrients in litter and is the inverse of the index of nutrient use efficiency of litter discussed by Vitousek (1984). Although mass weighted concentrations are not indices of resource utility per se, they are commonly used as surrogate indices of NUE and are compared here with more direct measures of resource use.

RESULTS

Forest structure and aboveground biomass and nutrient pools.—The density of post hurricane seedlings peaked at 12 mo and continued to remain high until mo 36 when they declined rapidly (Fig. 2). Like the mature forest is characterized by a few dominant species (Scatena & Lugo 1995), post hurricane regeneration was also characterized by a few species, namely *Cecropia schreberiana* (also known as *C. peltata*), *Psychotria berteriana*, and *Guarea glabra*. The largest individual of post hurricane regeneration observed in the watersheds was a *C. schreberiana* that had a DBH of 27 cm after 5 yr. Many *C. schreberiana* had diameters of 20 cm after 4 yr.

Five yr after the hurricane, the spatial variation in aboveground biomass across the watersheds was

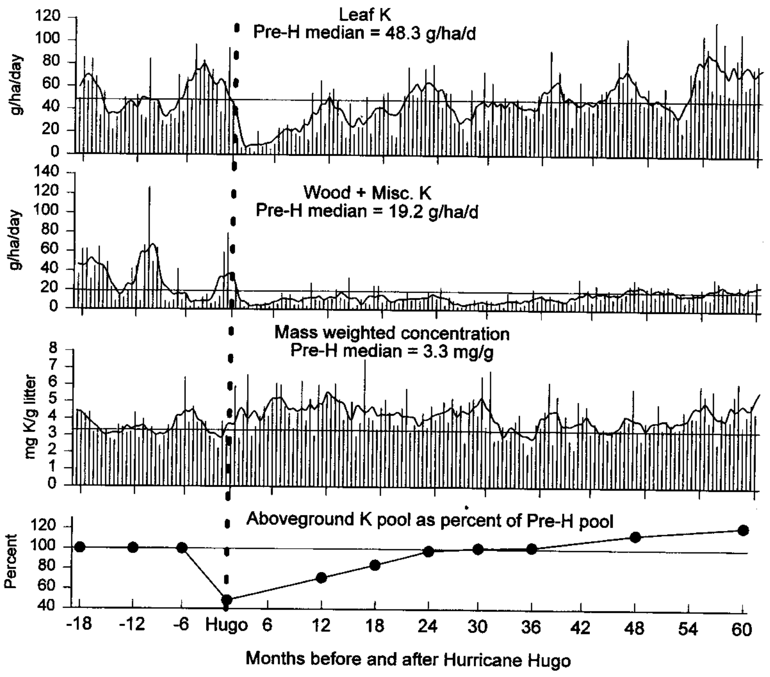

FIGURE 8. Potassium flux in leaf litter, wood and miscellaneous litter, the mass weighted concentration of litter, and the aboveground K pool as a percent of the pre-hurricane pool, in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Horizontal line is the median of pre-hurricane values, the curved line is the two month running average.

greater than that of the pre-hurricane forest (Fig. 3 and Table 1). However, total watershed biomass had attained 86 percent of the pre-hurricane value, 35 percent of which was from the post-disturbance regeneration of trees. The greater spatial variation in post-hurricane biomass resulted because areas dominated by hurricane survivors had attained levels of biomass that were equal to or greater than pre-hurricane levels while other areas were still covered by herbaceous vegetation or young saplings. One yr after the hurricane, the biomass of herbs and class 1 seedlings were over five times the pre-hurricane values. By the end of the fifth yr, the biomass in this compartment was still 3 times larger than pre-hurricane values.

Expressed on an annual basis, the short term NPP ranged from 11.6 to 41 $Mg{\cdot}ha^{-1}{\cdot}yr^{-1}$ and had a large peak during the 12 to 18 mo period following the hurricane. Simulation modeling of the Tabonuco forest also suggests a peak in forest production two or three yr following a hurricane (Sanford *et al.* 1991). Over the five yr period, NPP averaged 21.6 $Mg{\cdot}ha^{-1}{\cdot}yr^{-1}$ while aboveground biomass accumulated in the watersheds at a rate of 16.3 $Mg{\cdot}ha^{-1}{\cdot}yr^{-1}$, 83 percent of which was from post hurricane regeneration (Table 1). This 5 yr

TABLE 6. *Range and sample size in parentheses of within-stand nutrient use efficiencies of aboveground primary productivity, expressed on a kg per kg basis, for plantations, secondary forests, and the Bisley watersheds of the Luquillo Experimental Forest of Puerto Rico. Data for plantations and secondary forests are from Lugo 1992. Data used to calculate efficiencies for the Bisley watersheds are from Tables 1 and 5 and are average values for the entire 5 yr post-hurricane period. See text for details.*

	N	*P*	K
Pine plantations (2)	131–157	3677–4719	950–839
Mahogany plantations (2)	175–259	5929–6586	553–531
Secondary forests (4)	80–152	1491–3762	278–416
Bisley 0–60 mo	112	2300	148

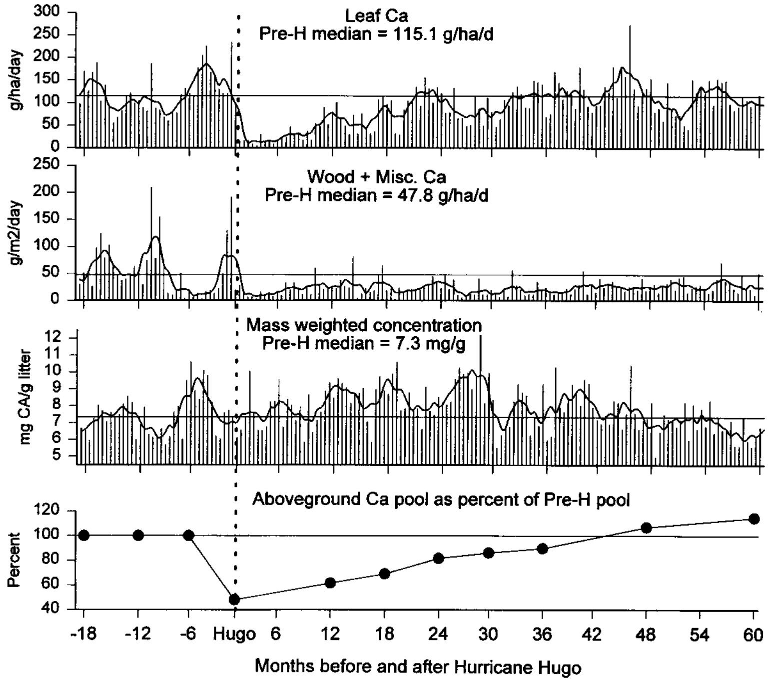

FIGURE 9. Calcium flux in leaf litter, wood and miscellaneous litter, the mass weighted concentration of litter, and the aboveground Ca pool as a percent of the pre-hurricane pool, in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Horizontal line is the median of pre-hurricane values, the curved line is the two month running average.

average NPP was higher than that of nearby plantations (11.4 to 19.1 Mg·ha^{-1}·yr^{-1}) and paired secondary forests (7.9 to 12.3 Mg·ha^{-1}·yr^{-1}, Lugo 1992). Accumulation of aboveground biomass during this first 5 yr was also nearly 7 to 10 times faster than the long-term accumulation rates in mature tabonuco forests (Weaver & Murphy 1990) and 55 yr old landslides in the upper montane forests of the LEF (Zarin 1993, Zarin & Johnson 1995).

Although aboveground biomass only reached 86 percent of the pre-hurricane value, the nutrient content of above-ground vegetation surpassed the pre-hurricane levels after 24 to 48 mo (Tables 1, 2 and 3). The fastest rates of aboveground nutrient accumulation occurred during the first two yr and by the second yr, the aboveground pools of Mg and K were equal to, or greater than their pre-hurricane values. Furthermore, the sizes of these pools continued to increase during the following 3 yr. In contrast, aboveground N and P pools reached pre-hurricane values at 48 mo, 2 yr after Mg and K, and remained constant during the fifth yr. This increase in aboveground nutrients relative to the pre-disturbance forest is a result of the relatively high nutrient concentrations in the young, post-disturbance vegetation compared to that of the pre-disturbance dominants (Fig. 4).

LITTERFALL AND THROUGHFALL.—By the second post-hurricane yr a foliar canopy had developed to the extent that temporal variations in throughfall as a percentage of rainfall (Fig. 1), and the seasonal rhythms in leaf fall (Fig. 5) had attained some resemblance of their pre-storm patterns. Over the fifth yr, the rate of daily average leaffall was 92 percent of pre-storm levels while average and median daily total litterfall rates were both about 83 percent of the pre-hurricane values (Table 4). Total fluxes of N, P, K, Ca, and Mg in litter during the fifth yr ranged between 62 and 98 percent of their pre-hurricane averages (Table 5).

The mass weighted concentrations of N, P, and Ca in total litter were higher than the pre-hurricane median for the first 36 mo, and similar to or lower than pre-hurricane values for the remaining period (Figs. 6–10). In contrast, K and Mg had mass weighted concentrations that were higher than the pre-hurricane values throughout the entire 5 yr. Relatively high nutrient concentrations in post-dis-

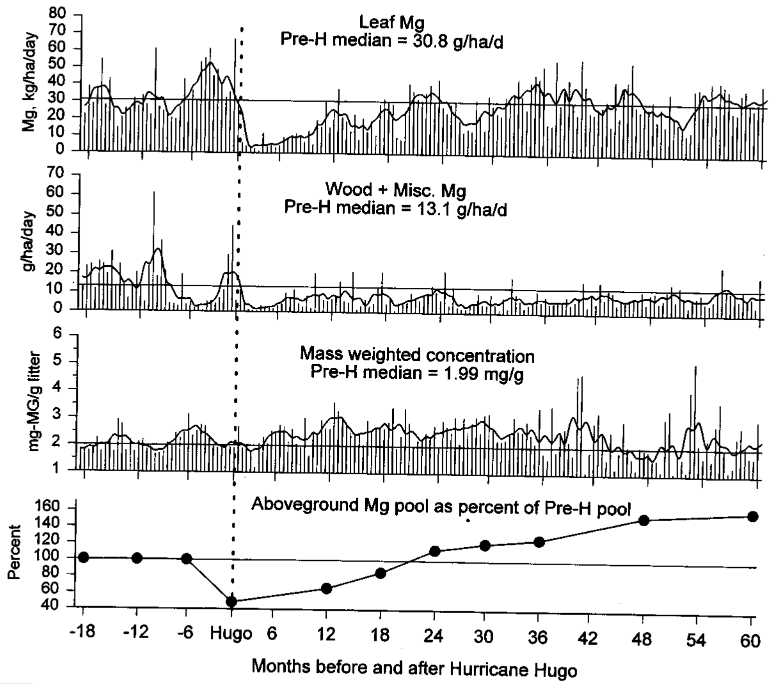

FIGURE 10. Magnesium flux in leaf litter, wood and miscellaneous litter, the mass weighted concentration of litter, and the aboveground Mg pool as a percent of the pre-hurricane pool, in the Bisley Experimental Watersheds, Puerto Rico, before and after Hurricane Hugo (18 September 1989). Horizontal line is the median of pre-hurricane values, the curved line is the two month running average.

turbance needle fall were also observed in pine plantations for several months following the passage of Cyclone Sina over Fiji (Waterloo 1994). The relatively high mass weighted concentrations of nutrients during the first 5 yr in Bisley are attributed to contributions from nutrient rich litter from herbs, young woody regeneration, and from hurricane defoliated litter that remained suspended immediately following the hurricane. This "hanging" hurricane litter had significantly higher nutrient concentrations than normal litter (Lodge *et al.* 1991) and continued to fall during the first post-hurricane yr as pieces of broken canopy gradually disintegrated. The relatively high mass weighted concentrations of K and Mg that were prevalent throughout the 5 yr are attributed to nutrient rich foliage of *C. schreberiana* (Fig. 4).

ABOVEGROUND NUTRIENT USE EFFICIENCIES.—The 5 yr average NUE of aboveground productivity for N and P estimated here are similar to, but slightly less than those for young secondary forests in the LEF (Table 6). However, the NUE of abovegound productivity for K was only 43 percent of these secondary forests. The different indices used to estimate NUE in the Bisley forest also varied considerable over the 5 yr period (Figs. 11 and 12). During the first yr of reorganization when the canopy was beginning to close, 75–92 percent of the nutrient uptake was retained in the aboveground vegetation (Fig. 12a). Relatively large nutrient requirements during canopy closure following a hurricane has also been noted in plantations (Waterloo 1994). By the second yr, litterfall began to increase and the rate of aboveground nutrient accumulation per unit of nutrient returned in litter began to stabilize (Fig. 12c). In general, NPP peaked during the second yr while the ratios of carbon fixation and aboveground carbon accumulation per mole of nutrient uptake peaked in the third yr (Fig. 11a, b, c). The peak in NPP during the 18 to 24 mo period is primarily a reflection of the massive recruitment of *C. schreberiana* seedlings into the class 3 size category (Fig. 2). The third yr increases in NPP and the NUE of K with respect to NPP and aboveground accumulation are also due to the increase in the biomass of *C. schreberiana,* which has a relatively high concentration of K in its woody tissue (Fig 4).

In addition to K, the patterns of NUE varied

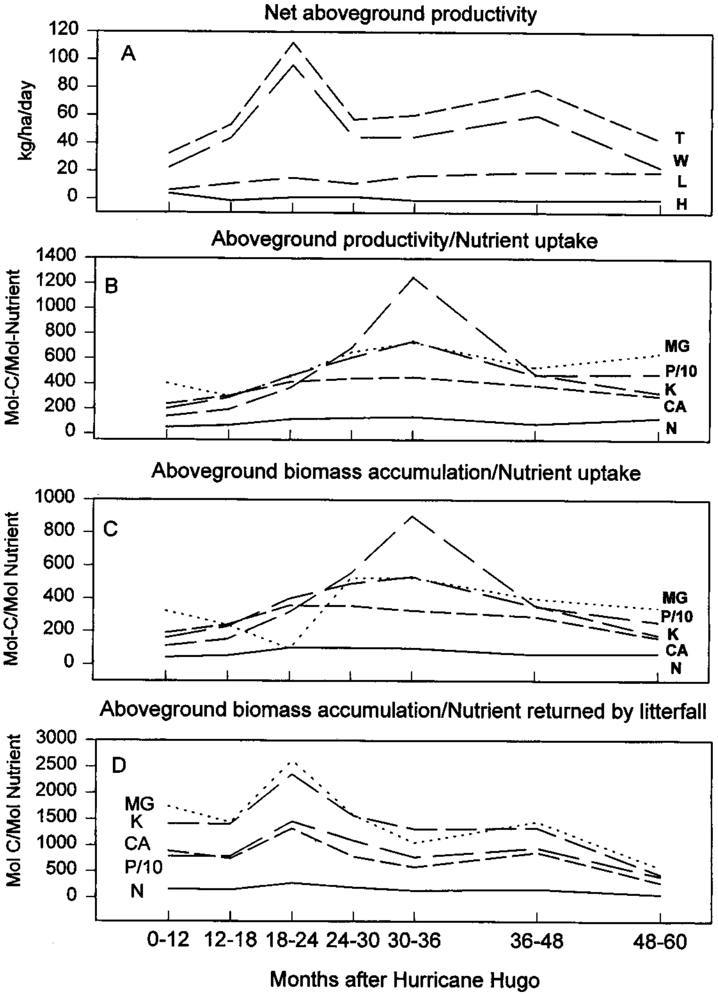

FIGURE 11. Net aboveground productivity (A), net aboveground carbon production per mole of nutrient uptake (B), net aboveground carbon accumulation per mole of nutrient uptake (C), and net aboveground carbon accumulation per mole of nutrient returned in litterfall (D), in the Bisley Experimental watersheds, Puerto Rico by month after Hurricane Hugo (18 September 1989). See text for details.

with other nutrients. In general, the NUE of N was relatively consistent through time in all of the indices (Figs. 11 and 12) and similiar between Bisley and secondary forests in the LEF (Table 6). Furthermore, because of the large quantity of N that cycles through the system, on a molar basis the NUE of N were relatively low compared to other nutrients. In contrast, P is much less abundant and an order of magnitude more carbon is fixed per mole of P cycled than for other nutrients.

Patterns of NUE also varied with the subsystem of the ecosystem being considered. In general, indices related to the NUE of aboveground carbon production or accumulation (Fig. 11b, c) reached their maximum levels during the third yr and had less temporal variability than other indices. In contrast, indices related to the NUE of the litterfall cycle (Fig. 11c, and Fig 12b, c) and the mass weighted concentrations of nutrients in litterfall (Fig. 6–10) had large changes during the first 2 yr of reorganization and were relatively stable during the remaining period.

DISCUSSION

The first 5 yr of reorganization of the Bisley forest following Hurricane Hugo were characterized by the re-leafing of hurricane survivors and the estab-

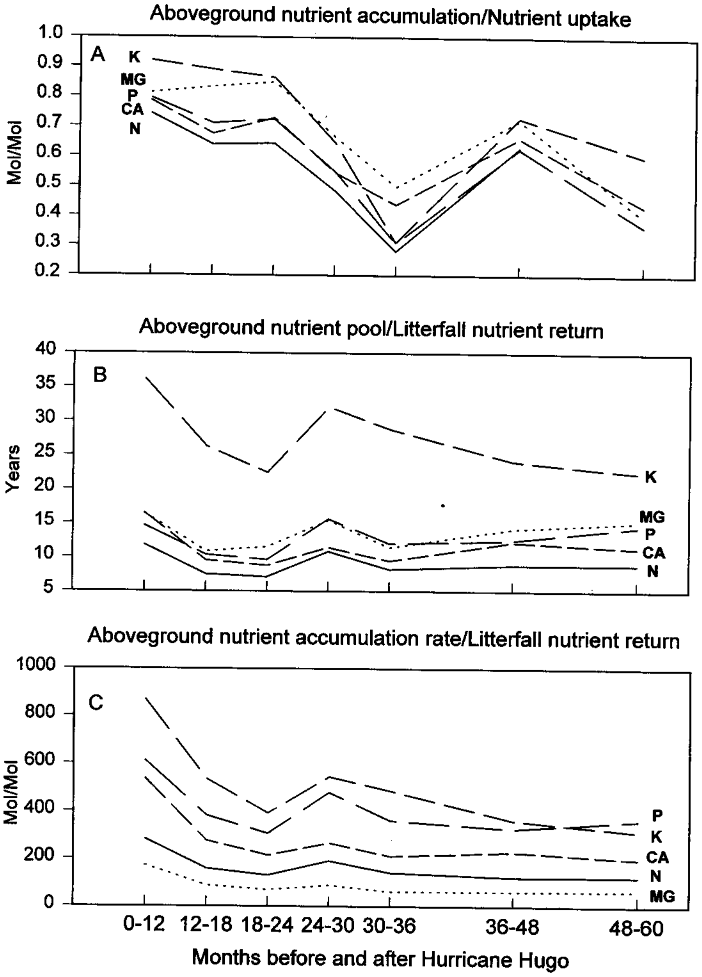

FIGURE 12. Net aboveground nutrient accumulation per mole nutrient uptake (A), the turnover period of the aboveground pool by litterfall nutrient return (B), and the net aboveground nutrient accumulation per mole of nutrient returned in litterfall (C), in the Bisley Experimental Watersheds, Puerto Rico by month after Hurricane Hugo (18 September 1989). See text for details.

lishment of post hurricane regeneration. During the first yr of reorganization, herbaceous vegetation and seedlings were established in a forest that had an open canopy and forest floor levels of solar irradiance that were 5–47 percent of full sunlight (Petty 1993). During this period, canopy throughfall of rainfall was relatively high, litterfall was relatively low, and most of the nutrient uptake remained in the aboveground vegetation. By the end of the second yr a forest canopy had developed and canopy throughfall of rain and leaf-fall approached their pre-storm patterns. During the second yr, the density of class 3 saplings, and aboveground NPP peaked. Furthermore the aboveground pools of K and Mg, a major component of chlorophyll, reached those of the undisturbed forest and their aboveground accumulation and the accumulation of aboveground biomass per mole of nutrient returned in litterfall began to decline.

During the third yr of reorganization, leaf fall attained pre-hurricane values and the biomass and nutrient pools of the herbaceous vegetation and seedlings began to decline. However, as post-hurricane regeneration rapidly accumulated woody tissue there was a rapid gain in woody biomass relative to gains in the biomass of more nutrient-rich herbaceous and foliar vegetation. Consequently, aboveground NPP per unit nutrient uptake peaked (Fig. 11) and aboveground nutrient accumulation per unit of uptake dropped (Fig. 12). Furthermore, aboveground nutrient accumulation per unit nutrient returned in litterfall and the turnover of aboveground nutrients by litterfall began to decline and stabilize.

By the fourth yr of reorganization, aboveground nutrient pools surpassed pre-hurricane levels and the density of post-disturbance stems had declined. By the fifth yr, total aboveground biomass was still less than pre-hurricane values but herbaceous biomass and aboveground nutrient pools were equal to, or larger than those found in the pre-hurricane forests. These larger post-hurricane nutrient pools were primarily due to the high nutrient concentrations of the tissue in species that dominated the post hurricane regeneration. Moreover, during the reorganization of the forest, the relatively old and low nutrient woody tissue that became necromass during the hurricane was replaced by nutrient rich tissue of early successional species. These species, primarily *C. schreberiana, P. berteriana,* and various ferns and herbs are also known to dominate the regeneration in landslides, tree fall gaps, and irradiated areas in other parts of the LEF (Taylor *et al.* 1995) and may play a similar role in nutrient storage during recovery in those disturbances. The post-disturbance increases in aboveground nutrient pools also reflect the predominance of nutrient uptake by young trees as opposed to a predominance of nutrient re-use by old trees, as occurs in other tropical secondary forests (Brown & Lugo, 1990) and plantations that are recovering from hurricane damage (Waterloo 1994).

During the reorganization of the Bisley forest, the highest aboveground NPP occurred while regeneration was becoming established and hurricane survivors were replacing their defoliated crowns. In contrast, the most efficient use of nutrients in fixing aboveground carbon occurred shortly after, while the early successional species were adding woody biomass and the cycling of leaf litter nutrients started to approach pre-disturbance levels. This lag between the peaks in NPP and the maximum NUE of NPP is a consequence of a reorganization sequence that began by the developement of nutrient-rich foliage. This foliage then provided the energy needed to accumulate woody biomass and recycle nutrients through the system. Moreover, the nutrient cycling strategy observed here consisted of the rapid accumulation of aboveground nutrients during stand closure and the rapid turnover and cycling of nutrients through litterfall as the stand matured. During this 5 yr period, this strategy resulted in the some of the lowest within-stand NUE observed in the LEF and some of the high levels of aboveground productivity and indicates that high levels of NPP can be achieved with rapid within-system cycling and low within-stand NUE.

ACKNOWLEDGMENTS

This research was performed under grant BSR-8811764 from the National Science Foundation to the Terrestrial Ecology Division (University of Puerto Rico) and the International Institute of Tropical Forestry (USDA Forest Service) as part of the Luquillo Long-Term Ecological Research Program. Additional support was provided by the USDA Forest Service.

LITERATURE CITED

Basnet, K., G. E. Likens, F. N. Scatena, and A. E. Lugo. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. J. Trop. Ecol. 8: 47–55.

Beard, J. S. 1949. The natural vegetation of the windward and leeward islands. Oxford For. Mem. 21.

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecol. Monogr. 64: 396–400.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. J. of Trop. Ecol. 6:1–32.

Chapin, F. S. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11: 233–260.

Chapman, H. D., and P. F. Pratt. 1979. Métodos de análisis para suelos, plantas y aguas. Editorial Trillas, Mexico City, Mexico.

Chinea, J. D., R. J. Beymer, C. Rivera, I. Sastre de Jesus, and F. N. Scatena. 1994. An annotated list of flora of the Bisley Area, Luquillo Experimental Forest, Puerto Rico. U.S. For. Serv. Gen. Tech. Rep. SO-94. New Orleans, Lousiana.

Crow, T. R. 1980. A rainforest chronicle: a 30 year record of change in the structure and composition at El Verde, Puerto Rico. Biotropica 12: 42–55.

———, and D. F. Grigal. 1979. A numerical analysis of arborescent communities in the rain forest of the Luquillo Mountains, Puerto Rico. Vegetatio 40: 135–146.

Ewel, J. J., and Whitmore J. L. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. U.S. For. Serv. Res. Pap. ITF-18. Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: With special reference to mineral nutrition. Annu. Rev. Ecol. Syst. 8: 83–107.

———. 1995. Mineral nutrition and soil fertility in tropical rain forests. *In* A. E. Lugo and C. Lowe (Eds.). Tropical forests: management and ecology. pp. 308–330. Ecological Studies 112. Springer-Verlag, New York.

Liogier, H. A., and L. F. Martorell. 1982. Flora of Puerto Rico and adjacent islands: a systematic synopsis. Editorial de la Universidad de Puerto Rico, Río Piedras, Puerto Rico.

Lodge, D. J., F. N. Scatena, C. E. Asbury, and M. J. Sánchez. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rainforests of Puerto Rico. Biotropica 23: 336–342.

Lugo, A. E. 1992. Comparsion of tropical tree plantations with secondary forests of similiar age. Ecol. Monogr. 62: 1–41.

———, and F. N. Scatena. 1995. Ecosystem-level properities of the Luquillo Experimental Forest with emphasis on the tabonuco forest. *In* A. E. Lugo and C. Lowe (Eds.). Tropical forests: management and ecology, pp. 59–108. Ecological Studies 112. Springer-Verlag, New York.

Luh Huang, C. Y., and E. E. Schulte. 1985. Digestion of plant tissue for analysis by ICO emission spectroscopy. Commun. Soil Sci. Plant Anal. 16: 943–958.

Odum, H. T. 1983. Systems ecology: an introduction. John Wiley, New York.

Petty, W. H. 1993. Seedling growth and mortality of four shade-tolerant canopy tree species in the rain forest of Puerto Rico following Hurricane Hugo. Masters Thesis, University of Tennesee, Knoxville.

Pickett, S. T. A., and P. S. White, Editors. 1985. The ecology of natural disturbances and patch dynamics. Academic Press, New York.

Sanford R. L., W. J. Parton, D. S. Ojima, and D. J. Lodge. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modeling. Biotropica 23: 364–372.

Scatena F. N. 1989a. An introduction to the physiography and history of the Bisley Experimental watersheds in the Luquillo Mountains of Puerto Rico. U.S. For. Serv. Gen. Tech. Rep. SO-72. New Orleans, Lousiana.

———. 1989b. Watershed scale rainfall interception on two forested watershed in the Luquillo Mountains of Puerto Rico. J. of Hydrology 113: 89–102.

———. 1995. Relative scales of time and effectiveness of watershed processes in a tropical montane rain forest of Puerto Rico. Natural and anthropogenic influences in fluvial geomorphology. Geophysical Monogr. 89: 103–111, American Geophysical Union, Washington D.C., USA.

———, and M. C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico, Biotropica 23: 317–323.

———, and A. E. Lugo. 1995. Geomorphology, disturbance, and the soils and vegetation of two subtropical wet steepland watersheds of Puerto Rico. Geomorphology 13: 199–213.

———, W. Silver, T. Siccama, A. Johnson, and M. J. Sánchez. 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. Biotropica 25: 5–27.

Silver, W. L. 1994. Is nutrient availability related to plant nutrient use in humid tropical forests? Oecologia 98: 336–343.

Taylor, C. M., R. B. Waide, and W. J. Pfeiffer. 1995. Recovery of a tropical forest after gamma irradiation: A 23 year chronicle. *In* A. E. Lugo and C. Lowe (Eds.). Tropical forests: management and ecology, pp. 258–288. Ecological Studies 112. Springer-Verlag, New York.

Vitousek P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285–298.

Waterloo, M. J. 1994. Water and nutrient dynamics of *Pinus caribaea* plantation forests on former grassland soils in southwest Viti Levu, Fiji. Dissertation. Vrije Universiteit, Amsterdam.

Weaver, P. L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. Caribb. J. Sci. 22: 53–70

———, and P. G. Murphy. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. Biotropica 22: 69–82.

Zarin, D. J. 1993. Nutrient accumulation during succession in subtropical lower montane wet forests, Puerto Rico., Dissertation, University of Pennsylvania, Philadelphia.

———, and A. H. Johnson. 1995. Base saturation, nutrient cation, and organic matter increases during early pedogenesis on landslide scars in the Luquillo Experimental Forest, Puerto Rico. Geoderma 65: 317–330.