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Changes in Necromass and Nutrients on the Forest Floor of a Palm Floodplain Forest in the Luquillo Mountains of Puerto Rico

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ABSTRACT.—We studied changes that occurred between 1980 and 2000 in forest floor biomass (necromass + biomass of herbaceous plants), nutrient stocks, and plant composition of a *Prestoea montana* floodplain forest. The forest was located in the Luquillo Mountains of Puerto Rico. Several storms and hurricanes passed near the study site during that period, the most severe being hurricane Hugo in 1989, and Georges in 1998. Hugo opened the canopy and increased the nutrient and biomass stocks of the forest floor. Six years after the passage of Hugo and two years after Georges, the forest floor necromass was at prehurricane (1980) levels. By October 2000, fine litter mass and nutrient stocks were below 1980 and 1990 levels (respectively). However, the distribution of biomass and nutrients on the forest floor in 2000 was different from pre-Hugo conditions due to the growth of herbaceous vegetation that included grasses and ferns that were not present in 1980. These plants concentrated nutrients in disproportion to their biomass and had leaves with low C/N. Attention to change in species composition on the forest floor as well as to necromass and nutrient distribution in fine litter, improves understanding of the recovery of the forest floor from disturbance.

INTRODUCTION

The litter of mature forests in the Luquillo Mountains of northeastern Puerto Rico should be at steady state with respect to nutrients and necromass for two main reasons. First, annual litterfall is relatively constant in these forests (Lugo and Scatena 1995) and secondly, litter stocks are relatively small, which allows the compartment to quickly reach steady state after a perturbation (Scatena 1995). Notwithstanding this fact, the litter compartment oscillates on a monthly basis due to variation in litterfall (Frangi and Lugo 1985, Lugo 1992). These oscillations do not affect the annual steady state behavior of the litter compartment because stocks remain at a mean level of necromass. However, high wind events interrupt the steady state. These events increase the input of litter and temporarily overwhelm litter decomposition processes (Ostertag et al. 2003). The relation between wind speed (x in km/h) and monthly litterfall (y in g/m^2) for the tabonuco forest at the Luquillo Experimental Forest (LEF) is $y = 1.347x - 63.483$ ($r^2 = 0.92$). Wind events that last hours, add 1.2 to 1.9 times the annual input of organic matter and nutrients to the forest floor (Lodge et al. 1991).

Another effect of wind events on the forest floor is the change in microclimate (e.g., increased light, temperature), which can facilitate the invasion of herbaceous plants. Soon after hurricane Hugo for example, the forest floor in the Bisley Experimental Watersheds at LEF experienced a rapid increase in the biomass of herbaceous vegetation in response to increased availability of light and nutrients (Scatena et al. 1996). Five years after the hurricane, the biomass of the herbaceous layer on the forest floor was still three times higher than prehurricane conditions, particularly because the invasion of herbaceous species not previously recorded for these sites (Chinea 1999).

After hurricane Georges, Ostertag et al. (2003) monitored nutrient stocks and necromass in litter of several forest types in the Luquillo Mountains and found that within two to ten months these parameters had reached pre-hurricane values. A *P. montana* palm brake forest had the slowest rate of decomposition among the sites studied (k = 0.74/yr ± 0.12).

We report data for the year 2000 on the necromass and nutrient content of fine litter and ground vegetation in a *P. montana* palm floodplain forest in the Luquillo Mountains. We compare our data with published information for the same forest (Frangi and Lugo 1985, 1991, 1998). Because the methodology used since 1980 was the same as ours in 2000, we were interested in establishing the time required for the forest floor to recover from hurricane disturbances. Prior to hurricane Hugo, this forest had a low necromass and no herbaceous understory (Frangi and Lugo 1985), and a hurricane had not passed over the site since 1932. The study site is within the protected LEF and the forest type is a mature community (Lugo et al. 1995).

METHODS

The site is a floodplain forest located at 750 m in the Luquillo Mountains of Puerto Rico. In March 1980, we established a 5 × 5 m grid on the 0.2525-ha forest (Frangi and Lugo 1985). Trees in this grid were inventoried in 1980, 1990, 1995, and 2000. Fine litter accumulation was measured in 1980, 1990, 1996, and 2000 with 20-1.0 × 0.5 m subplots selected at random. Samples were sorted into palm leaves, dicotyledonous leaves, ferns, wood <2 cm diameter, wood ≥2 cm diameter, flowers and fruits, miscellaneous <0.85 mm, and miscellaneous ≥0.85 mm. We excluded logs and large branches (coarse woody debris ≥4 cm diameter) from the sampling and followed the methods of Frangi and Lugo (1985, 1991, 1998). In 1980 and 2000, sampling included herbaceous vegetation of the forest floor. We clipped all aboveground live herbaceous biomass on 20 randomly selected 1.0 × 0.5 m subplots. Plots were selected randomly each sampling date. We sorted vegetation into three plant groups: dicotyledonous, grasses, and ferns.

All samples were oven dried to constant weight, ground individually by sorted category with a Wiley mill (1 mm^2 mesh), and sent to the International Institute of Tropical Forestry laboratory for chemical analysis. We digested sample aliquots with concentrated HNO_3 and 30 percent H_2O_2 (Luh Huang and Schulte 1985). The concentration of P, K, Ca, Mg, Mn, Fe, and Al was determined with a plasma emission spectrometer (Beckman Spectra Span V). Total carbon and nitrogen concentration in samples were determined according to the dry combustion method recommended by Tabatabai and Bremmer (1991) using a LECO CNS-2000. Before 1991, we only measured biomass in the fine litter samples. Ash content was obtained by incineration of aliquots in a microwave oven. The precision of chemical analyses was obtained by running samples of known chemical composition every forty determinations. Control plant material consisted of pine, peach, and citric leaves from the National Bureau of Standards (USA).

We estimated necromass by dividing the dry weight of a sorted category by the area sampled. We estimated the standing stock of elements for each sample by multiplying element concentration by the necromass, or biomass in the case of herbaceous vegetation, of the respective category. We then averaged values by category. We compared the mean concentration and stocks of elements among categories of the forest floor herbaceous vegetation and fine litter with ANOVA and the Tukey test for multiple comparisons (Sokal and Rohlf 1979). We used the Barlett test for homogeneity of variance. When variances were homogeneous we used a $p = 0.05$ for significance. When the variance was not homogeneous, we used a significance of $p = 0.01$ to reduce the probability of erroneously rejecting the null hypothesis.

RESULTS

In October 2000, the forest floor had five times more necromass as fine litter than live herbaceous vegetation (Table 1). Wood, miscellaneous, and dicotyledonous and palm leaves, were the most important categories in terms of necromass on the forest floor. Ferns and reproductive parts were minor components of fine litter necromass.

TABLE 1. Mean dry weight (DW), carbon, and mineral content in herbaceous vegetation and fine litter on the forest floor of a floodplain forest in the Luquillo Mountains of Puerto Rico. Standard errors are shown below the mean (n = 20). Different letters within herbaceous vegetation or fine litter compartment significant differences for an element content among compartments. Difference between total herbaceous and total fine litter storages are in bold. Data 2000. Empty cells = no data.

Category	DW	C	N	P	K	Ca	Mg	S	Mn	Fe	Al	Ash
	(Mg/ha)		(kg/ha)									
					Herbaceous layer[1]							
Dicotyledonous	0.28 a	0.13 a	2.93 a	0.14 a	2.06 a	2.20 a	1.04 a	0.70 a	0.11 a	0.40 a	2.26 a	265.12 a
	0.12	0.05	1.01	0.05	0.74	0.90	0.44	0.23	0.04	0.19	1.15	10.40
Grasses	0.09 a	0.04 a	2.01 a	0.08 a	1.47 a	0.16 a	0.25 a	0.47 a	0.05 a	0.18 a	0.35 a	13.67 a
	0.03	0.01	0.77	0.03	0.50	0.05	0.09	0.15	0.01	0.05	0.09	4.04
Ferns	0.16 a	0.07 a	2.02 a	0.09 a	1.23 a	0.66 a	0.54 a	0.82 a	0.05 a	0.32 a	0.62 a	22.20 a
	0.32	0.03	0.85	0.04	0.51	0.34	0.28	0.47	0.03	0.12	0.23	10.33
Total herbaceous[2]	0.53 **a**	0.25 **a**	6.96 **a**	0.32 **a**	4.75 **a**	3.02 **a**	1.83 **a**	1.98 **a**	0.20 **a**	0.90 **a**	3.24 **a**	61.99 **a**
	0.13	0.07	1.67	0.07	1.12	0.98	0.52	0.55	0.06	0.22	1.17	15.15
					Fine litter[3]							
Palm leaves	0.53 ab	0.25 ab	4.16 ab	0.15 ab	0.60 ab	1.92 ab	0.89 ab	0.93 b	0.15 ab	1.13 a	2.08 a	53.79 a
	0.14	0.07	1.29	0.05	0.22	0.67	0.40	0.32	0.04	0.32	0.62	15.61
Dicotyledonous leaves	0.47 ab	0.24 ab	5.08 a	0.13 ab	0.81 bc	3.05 bc	0.84 ab	0.90 ab	0.23 ab	1.29 a	2.60 a	55.30 a
	0.08	0.04	0.93	0.03	0.17	0.56	0.15	0.16	0.05	0.25	0.49	9.08
Ferns	0.02 a	0.01 a	0.22 bc	0.01 a	0.04 ac	0.10 ac	0.05 a	0.04 ab	0.01 a	0.07 a	0.15 a	3.68 a
	0.01	0.00	0.09	0.00	0.01	0.03	0.01	0.02	0.00	0.02	0.05	1.44
Wood <2 cm	0.77 b	0.39 b	4.92 ac	0.12 ab	0.81 bc	4.63 b	0.72 ab	0.86 ab	0.24 ab	0.78 a	1.44 a	36.95 a
	0.18	0.09	1.14	0.03	0.18	1.07	0.19	0.20	0.09	0.18	0.36	8.59
Wood ≥2 cm	0.42 ab	0.26 ab	2.98 ab	0.07 ab	0.34 ab	1.60 ab	0.30 ab	0.47 ab	0.09 ab	1.17 a	2.10 a	49.25 a
	0.18	0.10	1.15	0.03	0.12	0.59	0.11	0.18	0.04	0.59	1.06	24.00
Flowers and fruits	0.01 a	0.00 a	0.06 b	0.00 a	0.01 a	0.03 a	0.01 a	0.01 a	0.00 a	0.02 a	0.03 a	—
	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01	—
Miscellaneous	0.61 ab	0.18 ab	5.26 a	0.21 b	0.89 b	2.19 ab	1.09 b	0.84 ab	0.29 b	5.99 b	7.97 b	249.60 b
	0.13	0.04	1.22	0.05	0.22	0.53	0.27	0.19	0.08	1.72	2.02	60.65
Total litter[2]	2.83 **b**	1.34 **b**	22.69 **b**	0.70 **b**	3.50 **b**	13.5 **b**	3.90 **b**	4.05 **b**	1.01 **b**	10.45 **b**	16.35 **b**	448.60 **b**
	0.40	0.20	3.20	0.11	0.52	2.11	0.64	0.58	0.21	1.95	2.69	68.99
Total Forest floor	3.37	1.58	29.65	1.02	8.26	16.5	5.88	5.88	1.21	11.35	19.59	510.50
	0.38	0.20	3.27	0.11	1.09	2.02	0.78	0.65	0.21	1.96	2.97	72.41

1. For N and K, p = 0.05; for others, p = 0.01
2. For P, Mg, and S, p = 0.05; for others, p = 0.01.
3. p = 0.01.

The weighted concentration of N, P, K, Mg, and S of herbaceous vegetation in 2000 was higher than that of fine litter (Table 2). However, fine litter had higher concentration of Fe and higher C/N. The concentration of C, Ca, Mn, Al, and ash was similar in both categories.

In 2000, dicotyledonous herbs had the highest concentration of Ca and Mg. Grasses had the highest concentration of K, S, and ash, the lowest concentration of C, and the lowest C/N. Grasses and dicotyledonous herbs had the highest concentrations of N and P. Ferns had the lowest Mn concentrations, and with dicotyledonous herbs, the highest C/N. There was no difference in the concentration of Fe and Al of herbaceous vegetation.

In 2000, there was no difference in the concentrations of C, N, Ca, S, Mn, Fe, Al, ash, and C/N in leaf litter (palms, dicotyledonous leaves, and fern leaves; Table 2). Fern litter had high concentration of P and Mg, while fern and dicotyledonous litter had high concentration of K. The high Ca concentration in fern leaves was not significantly different from that of other litter. Palm leaf litter was low in K. Woody litter had the highest C/N of all litter material while the miscellaneous fraction had the lowest C/N. Miscellaneous litter, particularly the finest fraction, had the highest ash, Fe, and Al concentrations and the lowest C concentration.

The highest element stocks in fine litter relative to total forest floor stocks were Fe and ash at 92 and 88 percent, respectively (Table 1). The lowest were N, S, P, and Mg at 77, 69, 69, 66, and 42 percent respectively. Manganese, Al, and Ca occurred in the same proportion as dry matter (82 to 84 percent). All three herbaceous vegetation categories had the same mineral element stocks. In the case of K, the stock in vegetation was higher than the stock in fine litter.

Discussion

The forest floor of this palm floodplain forest has undergone changes in biomass (Fig. 1), nutrient stocks (Fig. 2), and species composition since it was first studied for 12 months in 1980 (Frangi and Lugo 1985). In 1980, forest floor vegetation was composed mostly of palm and dicotyledonous seedlings with a combined biomass of 0.03 Mg/ha and traces of P. There was no evidence of ferns or grasses in this system, although bryophytes were abundant (Frangi and Lugo 1992). Fine litter averaged 5.5 Mg/ha and 1.4 kgP/ha (Frangi and Lugo 1985).

Hurricane Hugo increased the amount of coarse and fine woody debris into the forest floor and opened several canopy gaps (Frangi and Lugo 1991). In 1998, hurricane Georges further added to the organic load of the forest floor but not as significant as did hurricane Hugo (Ostertag et al. 2003). Ferns appeared in 1995 and grasses in 2000. In 2000, biomass of herbaceous plants was 17.7 times higher than it was in 1980.

Woody material comprised most of the increase in fine litter stocks after hurricane Hugo and we found no increase in litter stocks attributed to hurricane Georges (Fig. 1). By 1995, wood and total litter standing stocks were at pre-hurricane levels. The standing stock of dicotyledonous and palm leaves in fine litter remained constant between 1980 and 1996, and declined after 1996. However, this component is subject to high variation due to exports by floods (Frangi and Lugo 1985). We believe we missed the hurricane pulses of leaf addition to the forest floor because we sampled the material several months after the passage of hurricane Hugo and two years after hurricane Georges, and it is likely that leaf litter was decayed or flushed from the floodplain by the time we sampled. The same is true of flowers and fruits, and other litter components. Moreover, the floodplain forest exhibits mast fruit production that can significantly influence their standing stock on the forest floor (Lugo and Frangi 1993).

Nutrient stocks on the forest floor also reached high values after Hugo (Fig. 2). The only pre-hurricane value that we have is for P in 1980, which was 2.4 times lower. Ten years after hurricane Hugo and two after hurricane Georges, fine litter necromass was lower than in 1980, and nutrient stocks were lower than in 1990. Phosphorus stocks were lower in fine litter but they were much higher in herbaceous vegeta-

TABLE 2. Mean element concentration in herbaceous vegetation and fine litter on the forest floor of a floodplain palm forest in the Luquillo Mountains in Puerto Rico. Standard errors are below the mean. Different letters within herbaceous vegetation or fine litter compartments indicate significant differences for an element concentration among categories. Data are for October 2000. Empty cells = no data.

Category	C (%)	N	P	K	Ca	Mg (mg/g)	S	Mn	Fe	Al	Ash (%)	C/N
						Herbaceous layer[1]						
Dicotyledonous	47.32 a	14.99 ab	0.66 ab	9.11 a	9.30 a	3.96 a	3.60 a	0.47 a	1.52 a	6.77 a	9.49 a	38 a
(n = 17)	0.71	1.58	0.05	0.71	1.12	0.40	0.40	0.07	0.33	1.08	0.79	5
Grasses	41.52 b	21.38 b	0.80 b	15.0 b	2.00 b	2.84 b	5.71 b	0.55 a	2.73 a	5.44 a	17.39 b	22 b
(n = 17)	0.79	1.99	0.05	1.05	0.18	0.17	0.43	0.04	0.40	0.70	1.66	2
Ferns	46.13 a	13.26 a	0.59 a	8.30 a	3.77 b	3.05 b	3.92 a	0.22 b	2.33 a	4.60 a	12.86 a	35 a
(n = 14)	0.92	0.62	0.03	0.77	0.49	0.26	0.35	0.04	0.58	0.84	.134	2
Weighted total herbaceous[2]	44.88 **a**	16.78 **a**	0.70 **a**	11.2 **a**	5.29 **a**	3.42 **a**	4.35 **a**	0.40 **a**	2.23 **a**	5.98 **a**	13.32 **a**	31 **a**
(n = 20)	0.59	1.26	0.05	1.00	0.81	0.26	0.33	0.03	0.34	0.80	0.79	3
						Fine litter[3]						
Palm leaves	47.95 a	8.15 a	0.29 ac	1.11 a	3.60 ab	1.32 ad	1.70 ab	0.34 ab	2.87 ac	4.79 a	11.95 a	65 ab
(n = 20)	0.92	0.50	0.02	0.08	0.37	0.14	0.11	0.04	0.48	0.67	1.71	6
Dicotyledonous leaves	50.88 a	10.80 a	0.30 ac	1.83 ab	6.70 ab	1.78 ac	1.92 a	0.50 ab	3.66 ac	6.65 a	12.68 ab	51 ad
(n = 20)	1.06	0.83	0.04	0.22	0.69	0.13	0.08	0.06	0.70	1.11	1.24	3
Fern fronds	46.39 ac	10.81 a	0.50 b	2.46 b	7.51 a	3.31 b	2.03 ac	0.37 ab	4.08 ac	8.29 ab	17.97 a	46 ac
(n = 8)	1.48	0.94	0.05	0.35	1.61	0.55	0.26	0.06	0.74	1.36	1.84	5
Wood <2 cm diam.	53.08 a	7.36 a	0.21 c	1.38 a	6.63 ab	1.04 d	1.26 bc	0.32 b	1.72 a	2.30 a	5.73 a	78 b
(n = 18)	0.35	0.45	0.03	0.23	0.72	0.10	0.06	0.04	0.36	0.29	0.49	6
Wood ≥2 cm diam.	51.81 a	6.53 a	0.15 c	0.88 a	5.43 ab	0.74 d	1.07 bc	0.22 b	1.97 ac	3.56 a	8.78 a	87 b
(n = 7)	1.08	0.95	0.02	0.19	2.20	0.12	0.17	0.08	0.60	0.94	1.92	9
Flowers and fruits	55.22 a	8.59 a	0.44 abc	1.57 ab	4.75 ab	1.57 abcd	1.29 ab	0.25 ab	3.17 ac	4.33 abc	—	64 abc
(n = 2)	0.76	0.24	0.09	0.56	1.79	0.31	0.03	0.10	1.25	1.16	—	3
Miscellaneous <0.85 mm	20.45 b	7.21 a	0.41 ab	1.65 ab	3.09 b	2.14 c	1.11 b	0.51 ab	14.57 b	16.39 c	62.63 c	28 c
(n = 18)	3.59	1.23	0.04	0.12	0.56	0.13	0.20	0.04	1.95	1.65	6.35	1
Miscellaneous ≥0.85 mm	39.99 c	10.75 a	0.40 ab	1.65 ab	4.60 ab	1.70 ac	1.82 ac	0.54 a	7.83 c	12.33 bc	27.17 b	38 c
(n = 20)	1.21	0.42	0.03	0.16	0.51	0.16	0.07	0.07	1.11	1.34	2.45	2
Weighed total fine litter[2]	45.14 **a**	7.97 **b**	0.26 **b**	1.30 **b**	4.59 **a**	1.46 **b**	1.43 **b**	0.37 **a**	4.71 **b**	6.65 **a**	18.76 **a**	59 **b**
(n = 20)	1.47	0.42	0.02	0.09	0.31	0.13	0.07	0.04	0.70	0.81	2.42	3

1. For C, K, Ca, S, Mn and Al, $p = 0.05$; for others, $p = 0.01$.
2. $p = 0.01$.
3. For P, K, Mg and Mn, $p = 0.05$; for others, $p = 0.01$.

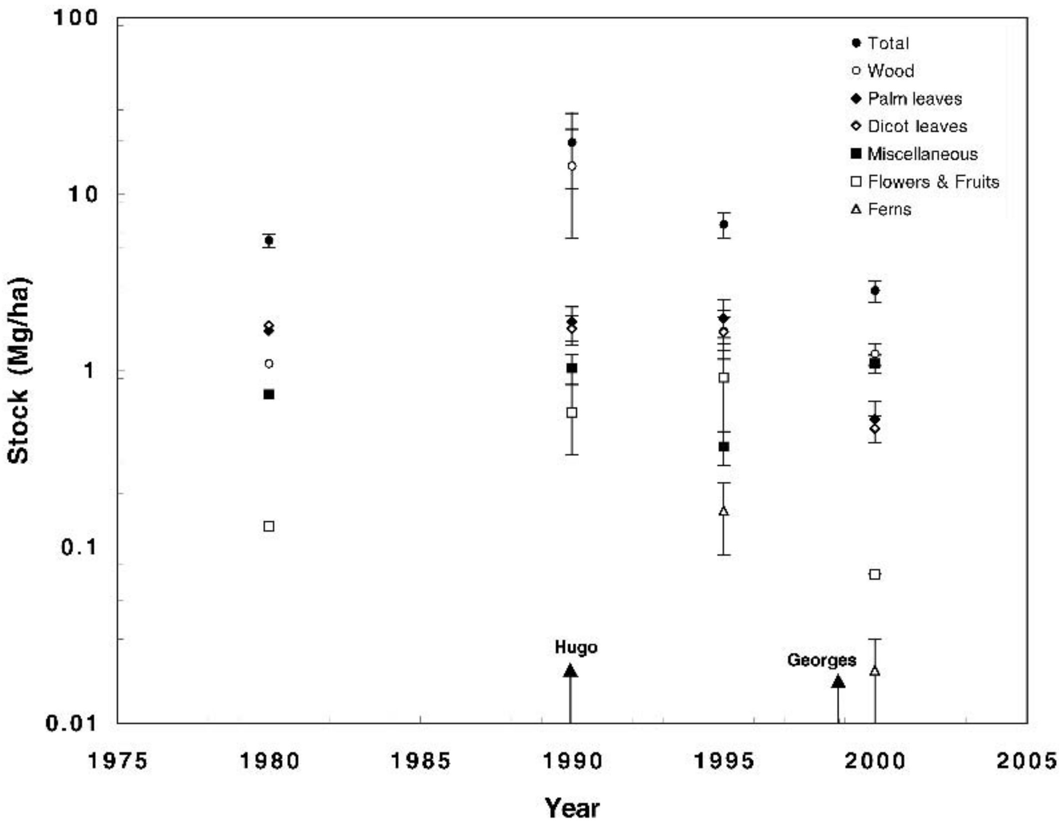

FIG. 1. Temporal pattern in the necromass of fine litter in a *Prestoea montana* floodplain forest, Luquillo Experimental Forest. Standard error bars correspond to n = 20. Data prior to 2000 are from Frangi and Lugo (1998).

tion in 2000 than in 1980. It appears that the litter compartment of the palm floodplain forest was at pre-hurricane levels six years after Hugo. However, the presence of grasses and other herbaceous plants, with their high nutrient concentrations and low C/N, represents a change in the composition and partitioning of nutrients on the forest floor. This aspect of the forest floor had not returned to pre-hurricane conditions ten years after Hugo. Ferns appeared in 1996 fine litter but their contribution decreased in 2000.

The palm floodplain forest has a low forest floor mass and low nutrient content when compared to the forest floors of other forest types in the LEF. This comparison includes secondary forests, mature forests, and plantation forests in the LEF (Lugo 1992, Lugo and Scatena 1995). Biomass stocks in these other forest types are typically higher than 5.5 Mg/ha, which was the mean value measured in the floodplain prior to the hurricane. Nutrient stocks in other LEF forest types are also well above the values measured in the floodplain, in some cases even after the hurricane. For example, the N stocks in fine litter of mature and secondary tabonuco forest and mature mahogany plantations at LEF were (respectively) 87, 50, and 93 kg/ha (Lugo 1992). These values are higher than those in Table 1 and Fig. 2 for the floodplain forest. Periodic flooding prevents litter accumulation in the floodplain and resulting anaerobic conditions limit the growth of understory herbaceous vegetation (Frangi and Lugo 1998). Notably, the accumulation of mass and nutrients in live bryophytes in the floodplain is similar to the stocks measured on the forest floor before the hurricane and in 2000 (compare our Table 1 with Table 1

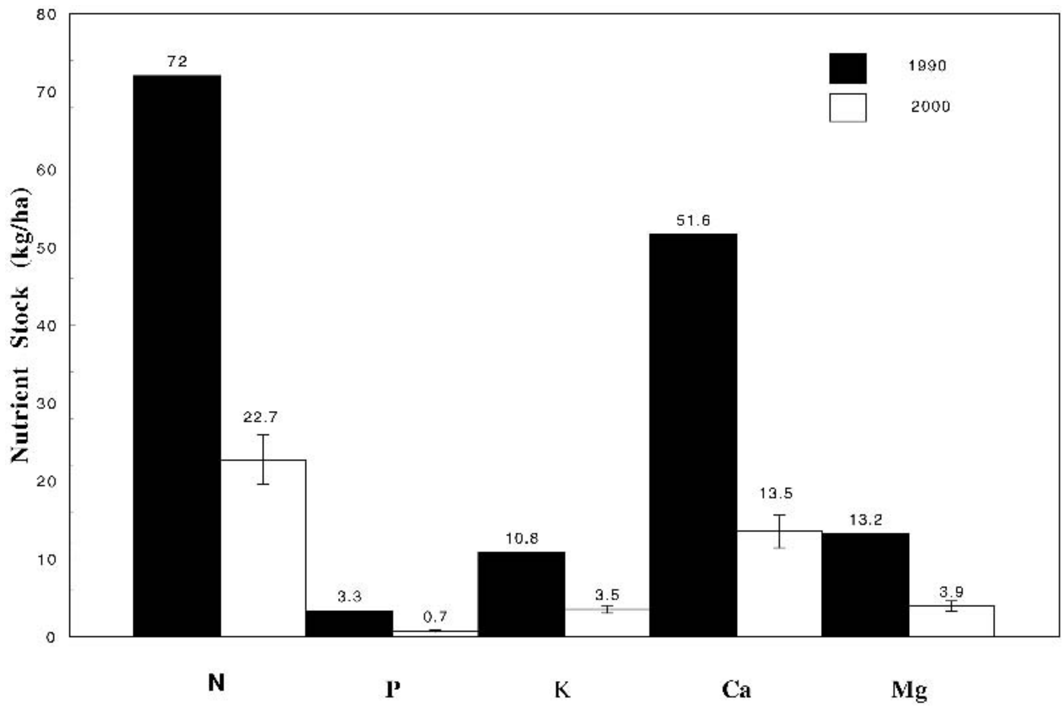

FIG. 2. Change between 1990 and 2000 in the nutrient stocks in fine litter in a *Prestoea montana* floodplain forest, Luquillo Experimental Forest. Standard errors (n = 20) are for 2000 data. The 1990 data are from Frangi and Lugo (1991). In 1980, before hurricane Hugo, the P stock was 1.4 kg/ha.

in Frangi and Lugo 1992). Storage in live plants adapted to flooding doubles the standing stock of biomass and nutrients on the forest floor in this floodplain forest.

We found high rates of palm regeneration and stem turnover in the floodplain forest in 2000 (Lugo and Frangi, unpublished). The wind events created a pulse in stand biomass and nutrient stocks that impacted all levels of forest structure: overstory and forest floor. In 2000, overstory forest vegetation was still in a rapid rate of change and re-adjustment, perhaps still decades from pre-hurricane values. In contrast, the forest floor, with its lower stocks and exposure to periodic flooding, appears to rapidly reach peak values of biomass and nutrient content, followed by a rapid decline (6 yr) to pre-hurricane levels. However, due to the invasion of plant groups such as grasses and ferns, the forest floor in 2000 was still different from what is was in 1980.

The forest floor reaches nutrient and necromass steady state more rapidly than it does in terms of stabilizing the species composition. At the scale of the whole ecosystem, the high dominance of trees overcomes any large-scale effect that changes in herbaceous species composition might have on litter quality or turnover. However, at the scale of the forest floor, the effects of altered understory species composition might be different than they are at larger scales, particularly in light of their disproportional high nutrient concentrations and low C/N. Moreover, the changes in nutrient distribution due to the presence of herbaceous vegetation and the observed temporal pattern of necromass and nutrient stocks (Figs. 1 and 2, Table 1) suggest that the forest is undergoing decadal-level processes of change in its stocks of necromass and nutrients. The length of time required for these processes to return the forest floor to pre-hurricane conditions appear to contradict the one-year turnover rate expected from the ratios of input to accumulation

(Scatena 1995). The reason is that after a disturbance both the input and accumulation of fine litter change in a direction that reduces their ratio. We lack data for the recovery of fine litter input, but the data on accumulation (Fig. 1) show at least a six-year delay in the return of pre-disturbance values.

Two processes acting in concert might explain the results of this study. One is the change in nutrient distribution and tissue quality due to the establishment of an herbaceous plant layer. The other is the apparent delay in woody debris decomposition relative to inputs, which resulted in the accumulation of woody debris on the forest floor in spite of the flushing effect of flooding. The behavior of the woody component accounts for the increase of stocks on the forest floor over the first six years after hurricane Hugo. The invasion of herbaceous plants might remain influential on forest floor processes until the canopy closes.

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