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Short-Term Disappearance of Foliar Litter in Three Species Before and After a Hurricane[1]

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ABSTRACT

Litter disappearance was examined before (1989) and after (1990) Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico using mesh litterbags containing abscised *Cyrilla racemiflora* or *Dacryodes excelsa* leaves or fresh *Prestoea montana* leaves. Biomass and nitrogen dynamics were compared among: (i) species; (ii) mid- and high elevation forest types; (iii) riparian and upland sites; and (iv) pre- and post-hurricane disturbed environments. Biomass disappearance was compared using multiple regression and negative exponential models in which the slopes were estimates of the decomposition rates subsequent to apparent leaching losses and the y-intercepts were indices of initial mass losses (leaching). *Cyrilla racemiflora* leaves with low nitrogen (0.39%) and high lignin (22.1%) content decayed at a low rate and immobilized available nitrogen. *Dacryodes excelsa* leaves had moderate nitrogen (0.67%) and lignin (16.6%) content, decayed at moderate rates, and maintained the initial nitrogen mass. *Prestoea montana* foliage had high nitrogen (1.76%) and moderate lignin (16.7%) content and rapidly lost both mass and nitrogen. There were no significant differences in litter disappearance and nitrogen dynamics among forest types and slope positions. Initial mass loss of *C. racemiflora* leaves was lower in 1990 but the subsequent decomposition rate did not change. Initial mass losses and the overall decomposition rates were lower in 1990 than in 1989 for *Dacryodes excelsa*. *Dacryodes excelsa* and *C. racemiflora* litter immobilized nitrogen in 1990 but released 10–15 percent of their initial nitrogen in 1989, whereas *P. montana* released nitrogen in both years (25–40%). Observed differences in litter disappearance rates between years may have been due to differences in the timing of precipitation. Foliar litter inputs during post-hurricane recovery of vegetation in Puerto Rico may serve to immobilize and conserve site nitrogen.

Key words: Cyrilla racemiflora; Dacryodes excelsa; *decomposition; hurricane; nitrogen;* Prestoea montana; *Puerto Rico; tropical forest.*

HURRICANES ARE AN INTEGRAL PART OF THE ECOSYSTEMS in Puerto Rico and other Caribbean islands. On average, 4.6 hurricanes pass through the Caribbean annually. The recurrence interval for hurricanes in Puerto Rico is about 20 years (Scatena & Larsen 1991), and they clearly have the potential to alter the structure of Puerto Rican forests (Crow 1980; Weaver, 1986a, b, 1987; Basnet *et al.* 1992a; Zimmerman *et al.* 1996). Special issues of *Biotropica* have addressed the immediate impacts and short-term ecosystem responses to hurricane Hugo (Walker *et al.* 1991) as well as long-term responses (Zimmerman *et al.* 1996). Hurricane disturbance may influence decomposition dynamics by affecting the biotic and abiotic agents of litter decay. Immediate impacts on the forest may include altered forest floor quality (*e.g.*, increased forest floor litter and nutrient availability, altered carbon quality, and carbon:nitrogen ratios) and altered microclimate conditions (*e.g.*, increased air flow, increased substrate temperature, increased insolation, and altered moisture availability). These factors have been shown to affect decomposition rates (Bonner & Fergus 1960, Witkamp & Van der Drift 1961, Swift *et al.* 1979, Covington 1981, Dwyer & Merriam 1981, Day 1983, Waring & Schlesinger 1985, Moore 1986, Cornejo *et al.* 1994).

The range of elevations in Puerto Rico results in several vegetation types. This study was conducted within the Luquillo Experimental Forest (LEF) and included the two most common forest types: the tabonuco forest association and the colorado forest association. The tabonuco forest type has been examined extensively (Odum & Pigeon

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1970, Brown *et al.* 1983), but the colorado forest type has received much less attention. Long-term studies of foliar decomposition in tabonuco forests have included: (i) the effects of radiation on forest floor litter disappearance (Weigert 1970); (ii) the effects of successional stage and leaf structure on decomposition and nutrient dynamics (La Caro & Rudd 1985); and (iii) examinations of fine root and foliar decay (Bloomfield *et al.* 1993, Zou *et al.* 1995).

This study, as one component of a study on riparian nitrogen cycling in two forest types (Bowden *et al.* 1992; McDowell *et al.* 1992, 1996), was originally designed to examine short-term disappearance of foliage from three important montane tree species: *Prestoea montana* (R. Grah.) Nichols, *Dacryodes excelsa* (Vahl), and *Cyrilla racemiflora* L. Several studies have examined the long-term decomposition of *D. excelsa* and *P. montana* (*e.g.*, Frangi & Lugo 1985, La Caro & Rudd 1985, Bloomfield *et al.* 1993, Zou *et al.* 1995, Vogt *et al.* 1996). We are not aware of any previous studies on the decomposition of *C. racemiflora* foliage.

We conducted a decomposition study using litterbags from June to August of 1989. Hurricane Hugo struck Puerto Rico about five weeks after the last sample collection. The hurricane provided a unique opportunity to study the effects of this type of natural disturbance on decomposition. With some modifications to the design, we repeated the study in 1990. The research design allowed for comparisons of short-term foliar litter biomass and nitrogen dynamics: (i) among the three tree species, *P. montana*, *D. excelsa*, and *C. racemiflora*; (ii) between the colorado and Tabonuco forest types; (iii) between riparian and upland sites; and (iv) between pre- and post-hurricane environments.

MATERIALS AND METHODS

Forest types.—Beginning at elevations of *ca* 200 m, the Luquillo forest is classified as a subtropical wet forest (Holdridge 1970, Ewel & Whitmore 1973). Temperatures average *ca* 25°C, rainfall averages *ca* 3500 mm/yr with little seasonality, and soil drainage is relatively rapid (Briscoe 1966, Scatena 1989). The forest at these elevations (tabonuco forest), typically has a canopy height of 30 m with two subcanopy layers and is dominated by *D. excelsa* and *Manilkara bidentata* (Crow 1980); however, the relative importance of *D. excelsa* in the Luquillo forest fluctuates and these shifts have been linked to natural and anthropogenic disturbance (Crow 1980, Garcia-Monteith & Scatena 1994). The tabonuco forest extends to the elevation of average cloud condensation (*ca* 600 m). The increase in moisture above 600 m results in a gradient in vegetation to the subtropical lower montane wet forest association (colorado forest type). The nearest weather station to our study site in the colorado forest (La Mina, 716 m) records about 4700 mm of rainfall annually with temperatures generally about 2°C lower than the tabonuco sites.

The increase in precipitation at higher elevations could increase litter mass loss through leaching. Conversely, the decrease in temperature could decrease mass loss by lowering biological activity. Soil moisture drainage in the colorado forest is often impeded by a gley horizon resulting in water filled depressions on the forest floor at some sites. Canopy gaps and herbaceous ground cover are common. The dominant species, *C. racemiflora*, is found as a small tree or shrub along the southeastern coast of the United States from Virginia to southeastern Texas but can grow to a height of 15 m and a diameter of 2 m at higher elevations in the Greater Antilles (Weaver 1986a, Little & Wadsworth 1989).

About half (*ca* 5900 ha) of the LEF is the colorado forest type and roughly half (5300 ha) is the tabonuco type (adapted from Brown *et al.* 1983). A third forest type, the montane palm floodplain forest, consists of nearly pure stands of *P. montana*, a small- to medium-sized palm (<15 m height). *P. montana* is usually found along streams above 600 m (Frangi & Lugo 1985) but is also interspersed throughout the colorado and tabonuco forests (Little & Wadsworth 1989).

Study sites.—A study site was established in the colorado forest between 620 and 630 m elevation within the Rio Icacos watershed (18°16′15″N, 65°46′58″W). The Icacos area has not been studied extensively, although Brown *et al.* (1983) and Weaver (1987) have described the colorado forest type. The second study site was established at an elevation of 240 m (18°18′43″N, 65°45′0″W) within the Luquillo Long-Term Ecological Research Site, a tabonuco forest in the Bisley watershed. The Bisley area has been described by Brown *et al.* (1983), Scatena (1989), Basnet *et al.* (1992a, b), and Garcia-Monteith and Scatena (1994). In general, the Bisley study plots are in an area with relatively steep slopes (*ca* 32%) and poorly defined riparian zones. The Icacos area also has steep slopes (*ca* 25%) but has a well-defined riparian zone.

Hurricane Hugo passed over the northeast corner of Puerto Rico on 18 September 1989. The

recurrence intervals for wind velocity (148 km/hr at San Juan), stream discharge, and precipitation were 50, 10–31, and 5 yrs, respectively (Scatena & Larsen 1991). Of six hurricanes that passed over Puerto Rico between 1899 and 1989, Hugo was moderate in intensity but was ranked second in terms of damage to the Luquillo Experimental Forest (Scatena & Larsen 1991).

The post-disturbance study began nine months after the hurricane. Although it arguably may have been better to begin the study immediately after the hurricane, a short-term study would have missed a potentially important stage of post-hurricane response. Recovery of vegetation after the hurricane was delayed, perhaps because of a drought lasting approximately three months caused by unusual regional weather patterns and microclimate changes induced by the hurricane (Scatena & Larsen 1991). In late October 1989, shoots had just begun to develop from adventitious buds of fallen or standing stems and early successional woody or herbaceous species had not become established near the study sites. The state of the forest, however, changed rapidly. When the post-hurricane study was implemented, vines, grasses, and pioneer trees had become established. This early successional stage lasted longer than the non-vegetated/defoliated stage. Most trees were defoliated by the hurricane, and thus could not produce litterfall until well after they had refoliated. Therefore, placement of foliar litter from less disturbed sites to hurricane disturbed study plots would be contradictory to a natural sequence of events. Refoliation prior to the 1990 study was evidenced by our ability to collect foliage near the Icacos plots. Disturbance to the area around the Icacos site due to Hurricane Hugo was variable; fallen trees created canopy gaps, trees in some areas were defoliated or had branches broken, and some areas were minimally disturbed. The forest surrounding the Bisley site was altered more uniformly and severely than the forest surrounding the Icacos site. Most trees were toppled and only the main stem remained of those that were not fallen (Basnet 1992a). It was both necessary and desirable to establish some additional study plots for the post-hurricane study to replace pre-hurricane plots that were inaccessible due to fallen trees and also to include severely disturbed sites when pre-hurricane plots were minimally disturbed.

Two plots (each 8 × 16 m) were established at each of the Icacos and Bisley study sites in 1989, thus allowing us to make comparisons of decomposition among riparian and upland plots within watersheds and between watersheds. Similar plots were established in 1990 (riparian and upland, Bisley & Icacos). Since the Icacos upland plot was only minimally disturbed (defoliated), a fifth plot (hereafter referred to as 1990 Icacos upland blowdown plot) was established in an adjacent area that was severely disturbed. To summarize:

1989: (2 watersheds × 2 slope positions)
= 4 plots

1990: (2 watersheds × 2 slope positions)
+ 1 blowdown plot = 5 plots

LITTERBAG PREPARATION AND COLLECTION.—The use of mesh litterbags to study decomposition has been criticized (*e.g.*, Wieder & Lang 1982) because the litter is placed in an unnatural environment and the resulting data may not describe true rates of decay (Swift *et al.* 1979, Anderson *et al.* 1983, Stewart & Davies 1989). The fine-mesh litterbag method as used in this study may underestimate decomposition rates but does allow comparison of species, site, and other treatment effects.

Recently abscised *D. excelsa* leaflets for each year were collected immediately prior to each study period from the forest floor near the El Verde field station (350 m elev.). Recently abscised *C. racemiflora* leaves were collected at or near the Icacos site for each year and also *ca* 1.5 km south of the El Verde field station in 1990 (575 m elev.). Fresh (green) palm foliage was used due to the inconsistent and gradual way the species replaces fronds. Fronds were collected near the Icacos site; leaflets were stripped from the fronds and cut into 15- to 20-cm segments. The rhacises of the fronds were discarded.

Foliage for the 1989 study was stored as collected for two days before being weighed. To improve our estimates of initial dry mass, the foliage collected for the 1990 study was air-dried for three days before being weighed. An unknown amount of moisture was lost from litter during storage in 1990. Foliage from a single species was weighed and placed in 20 × 30 cm litterbags (*ca* 1 mm fiberglass mesh). A sample of approximately one per six litterbags (randomly stratified across the processing interval) was retained and dried to later estimate the initial moisture, nitrogen, lignin, cellulose, and ash content of treatment samples. Between 8 and 14 g (oven-dried equivalent; Table 1) of foliage were placed in each litterbag, although the dry mass per litterbag varied by < 1 g for a given species and study year.

TABLE 1. *Initial quantities and qualities of foliage.* P-*values are for* t-*tests for nitrogen and ash content between years.*

		Cyrilla racemiflora				*Dacryodes excelsa*				*Prestoea montana*			
Number of litterbags		184				211				208			
Dry mass/litterbag (g)		8–12				10–13				9–14			
Leaves/litterbag (approx.)		60				18				12[a]			
Initial subsample	Year	N	$\bar{x}$	SE	$P > \|t\|$	N	$\bar{x}$	SE	$P > \|t\|$	N	$\bar{x}$	SE	$P > \|t\|$
Nitrogen (%)	89	11	0.43	(0.009)	0.0000	8	0.67	(0.007)	1.0000	9	1.77	(0.045)	0.2641
	90	18	0.35	(0.005)		17	0.67	(0.007)		16	1.74	(0.020)	
Ash (%)	89	5	0.25	(0.06)	0.0000	11	11.36	(0.06)	0.7051	10	8.14	(0.28)	0.0090
	90	18	1.81	(0.02)		18	11.47	(0.18)		17	7.33	(0.14)	
Lignin (%)		18	22.1	(0.90)		18	16.6	(0.30)		17	16.7	(0.71)	
Cellulose (%)		18	25.8	(0.58)		18	43.5	(1.04)		17	42.9	(0.63)	

[a] Leaf segments.

Each 8 × 16 m plot was divided into a grid of 2 × 2 m subplots. With three species and five replicates per species to distribute, 15 subplots were randomly selected from the 32 total subplots. Assignment of species per subplot also was selected randomly. Litterbags were placed on the forest floor within the subplots and tethered to an anchor. The 1989 samples were distributed on 2 June and the 1990 samples were distributed on 7 July (Bisley) and 10 July (Icacos). A single litterbag was collected from each subplot after: (i) 14, 35, 52 (Bisley), 55 (Icacos), and 78 days in 1989; (ii) 12, 23, 45, 73, and 102 days at Icacos plots in 1990; and (iii) 11, 22, 42, 69, and 99 days at Bisley plots in 1990. Samples were collected more frequently at the beginning of each study period to account for the rapid changes that occurred in litter during this period. To summarize:

1989: (3 spp.) × (4 plots) × (5 replicates) × (4 collections) = 240 litterbags

1990: (3 spp.) × (5 plots) × (5 replicates) × (5 collections) = 375 litterbags

MASS AND QUALITY ANALYSES.—Foliage samples were oven-dried on the day of collection (*ca* 50°C), shipped to Durham, New Hampshire, redried (65°C), removed from the litterbag, separated from loose soil, weighed, and milled to pass through a 1-mm sieve. The ash content of each sample was estimated by combusting a *ca* 1-g subsample (500°C for 6 h). Estimates of ash content were used to adjust the biomass and nitrogen values for soil contamination; therefore, disappearance rates were calculated on an ash-free basis. Total nitrogen was estimated using a micro-Kjeldahl digestion method and Technicon Autoanalyzer (Bremner & Mulvaney 1973, Technicon 1983). Initial lignin and cellulose content was estimated using a near-infrared reflectance (NIR) spectrometer (Pacific Scientific, CITY, Oregon, Wessman *et al.* 1985, McLellan *et al.* 1991).

DATA ANALYSES.— The fraction of the initial biomass remaining (FBMR) and the fraction of initial nitrogen remaining (FNR) were examined using several approaches. Foliar litter generally displays a negative exponential pattern of disappearance during early stages of decomposition (Jenny 1949, Swift *et al.* 1979, Wieder & Lang 1982). This decomposition rate often is described by the model: $y = e^{-kt}$, where y = FBMR, t is the elapsed time in years, and k is a litter-specific constant. We used a simple least squares regression [ln(FBMR) = $-kt$] to fit a model to our data for comparing the results of this study to other studies (CRC–STATA 1990); however, application of this general model across all litter types and species often has been found to underestimate initial mass loss (Wieder & Lang 1982, McClaugherty & Berg 1987, Gallardo & Merino 1993). Models that factor the variable mobility of litter constituents and the multi-stage nature of decomposition better describe mass loss (Ezcurra & Becerra 1987). Forcing the y-intercept to zero as in the $y = e^{-kt}$ model can assert an undesirable leverage when modeling and other statistical procedures are applied. This artificial affect is particularly influential when applied to a study focusing on short-term decomposition dynamics. For example, immigration and incorporation of decomposer organisms can increase litter mass or biomass loss through leaching, but may not occur immediately upon placement on the forest floor.

The single exponent model described above was modified to test for differences among species,

site, and year categories. The rate component of the modified model was renamed k' and the model included a y-intercept term:

$$\ln(\text{FBMR}) = -k't + y_{int}$$

The y-intercept in this model may be viewed as an index of the initial leaching losses or delay in mass loss that can occur. The slope (k') may be viewed as the second stage in the multistage process of decomposition. We used regression techniques to fit this model with category indicator variables to simultaneously and efficiently test for differences in biomass loss among categories (Hamilton 1990, Bloomfield *et al.* 1993). Binary indicator variables (1 or 0) were factored for each category (*e.g.*, year, watershed, slope position) along with elapsed time such that the influence of the category was reflected by a deviation in the rate and a deviation in the y-intercept (an example interpretation is included in the results section).

The pattern of the fraction of nitrogen remaining over time was curvilinear and the degree and shape of curvilinearity varied among sample groups. No single transformation technique would linearize the data for analyses using regression. Consequently, nonparametric Kruskal-Wallis rank sum tests were used to compare nitrogen response (FNR) over time and among sites for each study year. Statistical comparisons between study years were complicated by unequal sampling intervals. To address this, the data were divided into groups with year, species, and treatment interval in common (Kruskall-Wallis comparisons of FNR among sites showed that sites did not differ significantly in nitrogen dynamics). The fraction of nitrogen remaining at a given sampling time in 1989 was compared to the closest two sampling times (before and after) in 1990. For example, the 35-day samples from 1989 were compared to both 23- and 44-day samples from 1990.

RESULTS

Initial foliage quality.—Abscised *C. racemiflora* foliage contained relatively low concentrations of nitrogen and cellulose (*ca* 0.38 and 26%, respectively) and a relatively high lignin concentration (22%; Table 1). The *D. excelsa* and *P. montana* initial state samples had similar lignin (*ca* 17%) and cellulose (*ca* 43%) concentrations. The abscised *D. excelsa* foliage, however, had about one third the N concentration of fresh *P. montana* (0.67 vs. 1.77%). Thus, foliar litter of these three species span a wide range of nitrogen and carbon quality. The nitrogen concentration of the foliage collected for the study did not differ significantly between years for *D. excelsa* and *P. montana* (Table 1). Although there was a statistically significant difference in nitrogen content between years for *C. racemiflora*, the difference was less than 0.1 per cent N.

Biomass disappearance.— The rates of disappearance among the three species varied significantly ($P<0.0005$); therefore, the species were modeled separately for further comparisons. The relationships among watersheds, slope positions, and study years can be described by simultaneously factoring all indicator variables (Table 2). The rate of biomass disappearance was lower in 1990 than in 1989 for most combinations of species, site, and slope position (Fig. 1). Using *D. excelsa* as an example, Table 2 can be interpreted as follows: (1) the slope of the base model for this species ($k' = -1.174$, $P<0.001$) and intercept (-0.073, $P<0.05$) are significant; (2) there was a significant difference between pre- and post-hurricane litter disappearances (deviation due to year $= -0.619$ in 1989 for the slope and -0.063 for the intercept); and (3) there were no significant differences among watersheds and slope positions.

The y-intercept for the *C. racemiflora* model differed between years (deviation $= -0.112$, $P<0.001$), but the decomposition rate did not ($k'_{1990} = -0.724$ and $k'_{1989} = -0.724 - 0.119$ or 0.843). The only significant differences among watersheds and slope positions occurred for *C. racemiflora* in which initial disappearance (y-intercept) was significantly greater on the upland plots than on riparian plots. This difference is particularly notable for pre-hurricane Bisley samples (Fig. 1). The decomposition rate and y-intercept for *P. montana* did not differ significantly among years, watersheds, or slope positions.

The y-intercepts from the k' models were significantly less than 0 ($P< 0.0005$), indicating that the traditional single exponent model (k) underestimated the initial rate of biomass loss. Nonetheless, the two decay coefficients, k and k', suggest the same relationships among species and study years. The rate of litter biomass disappearance using k follows the same pattern: *P. montana* > *D. excelsa* > *C. racemiflora* and 1989 > 1990 for each species. Apparent differences in k between upland and riparian sites in 1989 were due to the leverage of the y-intercept = 0 term; k' models indicate these sites did not differ after initial leaching losses. The fit of regression models based on the tradi-

TABLE 2. *Multivariate regression models by species for predicting biomass remaining over time. Category indicator variables (1 or 0) were factored to simultaneously test for differences among sites and between study years. Parameters for study year, watershed, and slope position indicate the change in the base parameters when the category variable is 1. The standard error is in parentheses with the significance level indicated as ** = P < |t| = 0.001, * = P < |t| = 0.05, and NS = not significant.*

	Base model		Change in base parameter due to:					
			Study year 1989 = 1, 1990 = 0		Watershed Bisley = 1, Icacos = 0		Slope position Upland = 1, Riparian = 0	
	Slope (k')	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept
Cyrilla racemiflora	−0.724	0.044	−0.119	−0.112	−0.025	−0.029	0.138	−0.04
N = 184, R^2 = 0.70	(0.094)	(0.014)	(0.117)	(0.016)	(0.098)	(0.015)	(0.098)	(0.015)
	**	*	NS	**	NS	NS	NS	*
Dacryodes excelsa	−1.174	−0.073	−0.619	−0.063	−0.102	0.004	0.002	−0.009
N = 211, R^2 = 0.68	(0.148)	(0.023)	(0.171)	(0.025)	(0.153)	(0.024)	(0.154)	(0.024)
	**	*	**	*	NS	NS	NS	NS
Prestoea montana	−2.707	−0.042	−0.303	−0.042	0.179	0.020	0.365	−0.023
N = 208, R^2 = 0.75	(0.197)	(0.030)	(0.231)	(0.034)	(0.205)	(0.031)	(0.206)	(0.031)
	**	NS	NS	NS	NS	NS	NS	NS

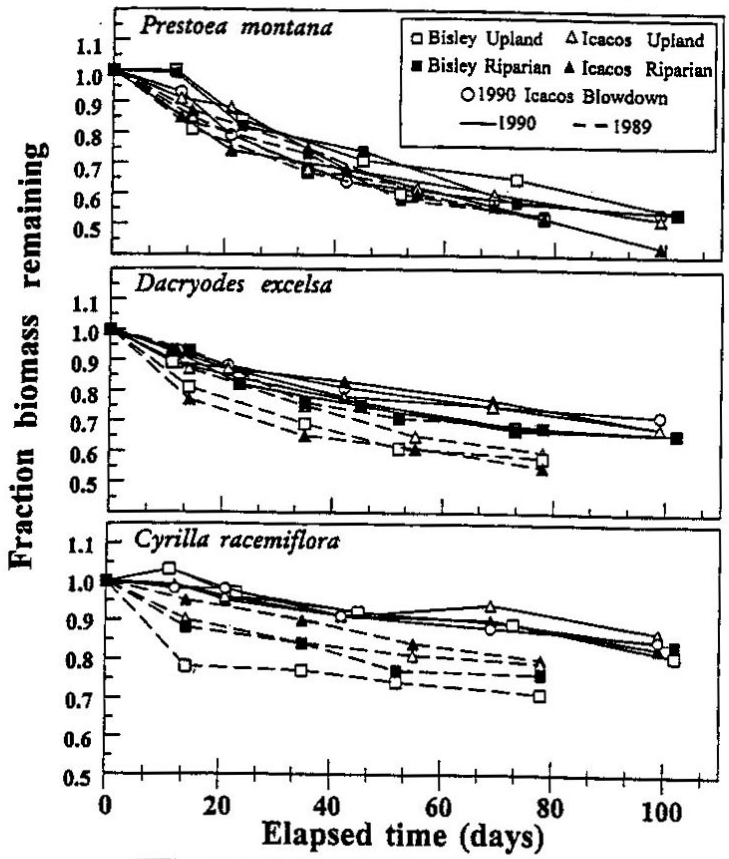

FIGURE 1. Short-term biomass loss over time by species, site, and two study periods.

TABLE 3. *Nonlinear regression models for estimating decay coefficients (k) in the single exponent model where: fraction biomass remaining = e^{-kt} and t = time in years.*

			Cyrilla racemiflora			*Dacryodes excelsa*			*Prestoea montana*		
			k	*N*	R^2	*k*	*N*	R^2	*k*	*N*	R^2
Bisley	riparian	1989	−1.54	16	0.85	−2.08	22	0.90	−3.31	23	0.96
Bisley	upland	1989	−2.03	13	0.84	−3.08	24	0.91	−3.34	20	0.96
Icacos	riparian	1989	−1.10	20	0.91	−3.22	20	0.92	−3.19	20	0.96
Icacos	upland	1989	−1.30	20	0.88	−2.60	21	0.95	−3.27	20	0.93
Bisley	riparian	1990	−0.61	25	0.93	−1.76	25	0.94	−2.51	25	0.88
Bisley	upland	1990	−0.65	22	0.94	−1.78	25	0.88	−2.28	25	0.93
Icacos	riparian	1990	−0.67	23	0.90	−1.49	25	0.91	−3.24	25	0.94
Icacos	upland	1990	−0.57	45	0.79	−1.48	49	0.95	−2.66	50	0.92
		Overall	−0.85	184	0.71	−1.99	211	0.85	−2.87	208	0.92

tional single negative exponential equation improved as the sample sets became more site specific (R^2 = 0.707–0.964; Table 3), suggesting that samples from the same plot or year were following more closely the same pattern of disappearance over time.

NITROGEN.—Patterns of nitrogen (N) dynamics over time were curvilinear and differed between years. In general, the fraction of nitrogen remaining over time in 1990 exceeded that in 1989. Of 222 paired Kruskal-Wallis tests among plots by year and species, less than ten percent showed a significant difference in FNR with no apparent pattern to the occurrences of these differences (Sullivan 1993). There were significant differences between study years, however, for these three species (Fig. 2; Table 4).

In 1990, *C. racemiflora* samples immobilized nitrogen up to the end of the study (110% of the initial N at 102 days) whereas 1989 samples released about 10 percent of the original nitrogen before the first collection and maintained 90 percent of the initial N mass for the remaining 78 d of the study. Between year relationships for *C. racemiflora* were similar for all sites; *i.e.*, 1990 samples immobilized N and 1989 samples released N before the first collection.

In 1989, *D. excelsa* samples maintained their original N mass for *ca* 20 d and then declined gradually to about 82 percent of the original N mass. The 1990 *D. excelsa* samples maintained the same N mass throughout the study. The patttern of nitrogen dynamics for *D. excelsa* at the Icacos riparian sites in 1990 differed from that of other sites. Nitrogen content was > 100 percent of the initial content throughout the study, although this litter began to release N at 70 d. One or two subplots that contained *D. excelsa* foliage were flooded after litterbag distribution, perhaps leading to these unusual results. In 1989, the first collection of *D. excelsa* litter from the Bisley riparian site had high and variable N mass (89–141% of the initial mass, SD = 21%), although the biomass results (87–101%, SD = 7%) for that replicate set were similar to other plots.

In 1989, *P. montana* samples began to release nitrogen immediately and declined to 60 percent of the initial N mass within 78 d. During the second study year, *P. montana* samples immobilized N briefly (105% at day 12) and declined at a rate similar to 1989 (70% of the initial N). The variability in nitrogen content of *P. montana* differed among sites and years. A brief period of immobilization occurred in 1990 at the Icacos sites, whereas there was a relatively long immobilization period at the Bisley sites. Once the immobilization period had passed, the rate of loss between years was similar.

Nitrogen dynamics between the 1990 defoliated and blowdown plots did not differ for *D. excelsa* and *P. montana*. However, *C. racemiflora* samples from the blowdown plot initially immobilized significantly more nitrogen (*ca* 10% of the initial nitrogen mass) than the defoliated plot ($P < 0.05$).

DISCUSSION

The concentrations of nitrogen and lignin in litter are important controllers of decomposition (Aber & Melillo 1982, Bosatta & Staff 1982, Melillo *et al.* 1982, Gallardo & Merino 1993). Based on these criteria, the species chosen for this study represent a range of litter qualities from low (*C. racemiflora*) to high (*P. montana*). The differences in rates of biomass disappearance for these three species are consistent with expectations based on the initial qualities of the foliage. For example, the very

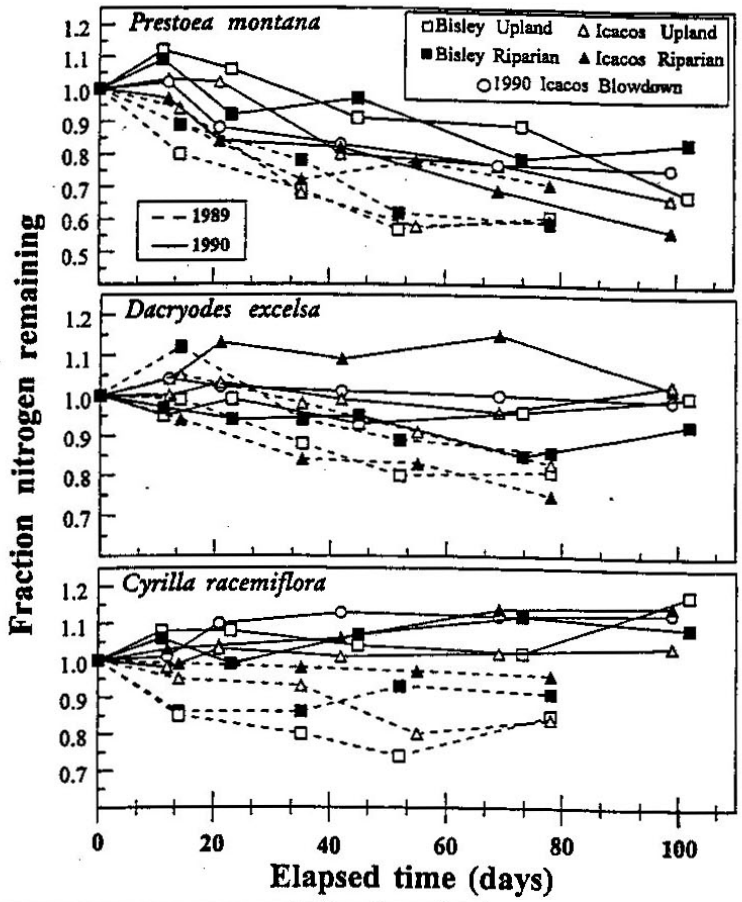

FIGURE 2. Short-term nitrogen dynamics over time by species, site, and two study periods.

low nitrogen and relatively high lignin concentrations of *C. racemiflora* foliage resulted in low decay rates and intermediate N retention despite favorable moisture and temperatures found in this tropical rain forest. *P. montana*, on the other hand, decomposed rapidly but with little N retention. The intermediate N and lignin content of *D. excelsa* led to a moderate disappearance rate.

The overall mean k values for the three species in this study (−0.85, −1.99, and −2.87; Table 3) span ranges reported in other studies of foliar decomposition. Edwards (1982) characterized k values for Neotropical sites as being between −1.1 and −1.7. In a long-term study conducted during nearly the same period as our two study periods, Bloomfield *et al.* (1993) found similar short-term results for *P. montana* and *D. excelsa* (based on their FBMR at 109 d); however, their overall k values (−1.6) were lower than ours for *P. montana*, probably due to the short duration of our study and the effect of initial leaching. Our data also did not reflect the long-term persistence of palm foliage noted by Bloomfield *et al.* (1993) and Frangi and Lugo (1985). Eliminating the opportunity for resorption of nutrients by harvesting fresh fronds, as well as the high nitrogen concentration of the *P. montana* foliage in our study, may have contributed to its relatively high initial disappearance rate.

As in other studies in tropical locations (*e.g.*, Edwards 1977, Ewel 1977, Bloomfield *et al.* 1993), we did not find significant differences in decay rates or nitrogen dynamics among sites for either study year. The direction of orientation of slopes in tropical forests is not as important in terms of energy influx as it is in higher latitudes (*e.g.*, Murdick *et al.* 1994). Environmental differences among subplots were notable. Part of the within-site variability in litter disappearance may have been due to variation in the distribution of decomposer organisms. Mycelium were apparent and abundant in some litterbags, several times within two weeks, while others displayed no visible sign of fungi

TABLE 4. *Results of testing for differences in mean fraction nitrogen remaining (FNR) between study years using nonparametric Kruskal-Wallis rank sum methods. Means from 1989 samples were compared to the two nearest (Mean Elapsed Time [M.E.T.]) means from 1990 samples.*

1989			1990			$P > \|z\|$
M.E.T. (days)	*N*	Mean FNR	M.E.T. (days)	*N*	Mean FNR	between years
Cyrilla racemiflora						
14	18	0.92	12	13	1.03	0.0002
14	18	0.92	23	14	1.04	0.0010
35	19	0.90	23	14	1.04	0.0003
35	19	0.90	44	15	1.05	0.0001
54	14	0.86	44	15	1.05	0.0001
54	14	0.86	71	16	1.08	0.0001
78	17	0.89	71	16	1.08	0.0001
78	17	0.89	102	17	1.12	0.0001
Dacryodes excelsa						
14	22	1.02	12	18	1.00	0.8890
14	22	1.02	23	19	1.02	0.4954
35	21	0.91	23	19	1.02	0.0013
35	21	0.91	44	20	0.99	0.0062
54	21	0.85	44	20	0.99	0.0001
54	21	0.85	71	21	0.98	0.0005
78	23	0.82	71	21	0.98	0.0001
78	23	0.82	102	22	0.99	0.0001
Prestoea montana						
14	21	0.88	12	23	1.05	0.0001
14	21	0.88	23	24	0.94	0.0642
35	21	0.72	23	24	0.94	0.0001
35	21	0.72	44	25	0.87	0.0005
54	20	0.64	44	25	0.87	0.0001
54	20	0.64	71	26	0.78	0.0028
78	21	0.63	71	26	0.78	0.0014
78	21	0.63	102	27	0.70	0.0504

throughout the study periods. The increase in light at the forest floor due to toppled trees, fewer branches, and reduced leaf area after the hurricane resulted in dense, herbaceous ground cover. With the exception of the Icacos "defoliated" plot, all other subplots were dominated by herbs. All Icacos upland blowdown subplots, all Bisley upland subplots, most of the Icacos riparian subplots, and half of the Bisley riparian subplots were occupied by herbs. In effect, the canopy was lowered to the forest floor (Brokaw & Walker 1991). Transpiration from herbaceous vegetation along with reduced air circulation at the forest floor may have maintained a high moisture content in foliar litter and decreased the vapor pressure gradient from the litter to the atmosphere, despite apparently increased insolation and temperatures. The herbaceous layer also may have prevented litterbags from being in contact with the litter layer and sources of microbial decomposers. In a similar situation, Maheswaren and Gunatilleke (1988) found that litter disappearance in a cleared tropical lowland forest that was subsequently populated by low-statured vegetation (ferns) was 20 percent less than an adjacent intact rain forest.

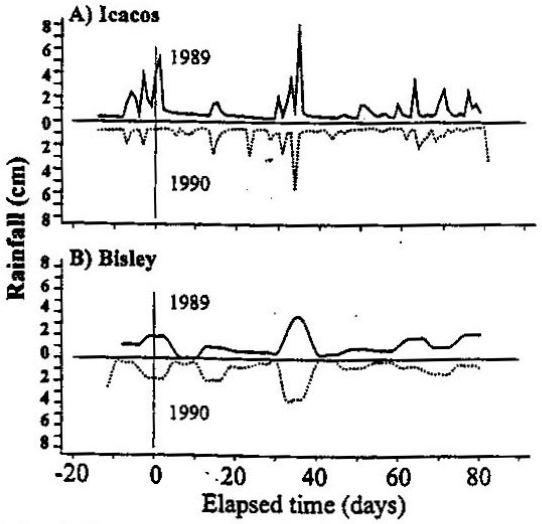

FIGURE 3. Rainfall during the two study periods. The Icacos site rainfall was estimated from daily Rio Icacos stream discharge recorded at gage 50075000 about 100 meters from the study plots (Curtis et al. 1990; 1991). Smoothed-lines were fit to Bisley mean daily rainfall from weekly collections (F. N. Scatena, pers. comm.)

While the comparisons among slope positions and forest types did not suggest statistically different initial decomposition rates, the disappearance rates and nitrogen dynamics of *C. racemiflora* and *D. excelsa* did differ between study years. Leaching by precipitation and the physical impact of rainfall may have interacted to cause differences in biomass loss between years. Leaching can result in significant mass loss. For example, Day (1983) found that *Acer rubrum* leaves lost 30.8 percent of their biomass and 18.7 percent of their nitrogen in a 93-h leaching experiment. In our study, the amount and pattern of precipitation was similar during the two study periods (Fig. 3). Precipitation in 1989, however, was greater than in 1990 during the period in which foliage was being collected for use and for 2 to 3 days after litterbags were deployed. This may have caused the higher initial biomass loss rates for *C. racemiflora* and *D. excelsa*. *P. montana* foliage also displayed this delay in mass loss at the Bisley sites, although not at the Icacos sites. Among year differences in biomass loss and nitrogen dynamics between litterbag distribution and

the first collection corresponds to a period of low rainfall (Bisley) and low stream discharge (Icacos). While rainfall would be expected to alter mass and nitrogen dynamics by removing material through leaching, the physical impacts of precipitation immediately preceding the study may have caused leaves to fall to the forest floor before some soluble compounds could be translocated to woody tissue; thus, apparent initial biomass losses might have been higher than would otherwise be the case. The relative proportions of leachable and non-leachable constituents is not known for this study. The notion that differences in precipitation early in the study periods rather than hurricane disturbance contributed to the differences in initial decomposition rate is supported by the observation that samples from the 1990 defoliated plot and the 1990 blowdown plot did not differ in biomass loss.

The differences between pre- and post-hurricane nitrogen dynamics may have been due to a combination of precipitation and availability of nitrogen in the ecosystem. The brief period of nitrogen immobilization by *P. montana* in 1990 and persistent retention of nitrogen by *D. excelsa* and *C. racemiflora* may have been related to greater availability of inorganic nitrogen due to hurricane litter inputs and, initially, lower precipitation and thus lower losses through leaching (Lodge *et al.* 1991, McDowell *et al.* 1992, Silver & Vogt 1993). When nitrogen is available, some fungal species are capable of increasing nitrogen in mycelium by up to 20 times the minimum nitrogen content (Swift *et al.* 1979). Contact between litterbags and herbs in disturbed sites and leaching from vegetation actively taking in nutrients may have increased nitrogen in litterbags.

The results of this study seemed to be affected by variability in the timing and intensity of weather events. Differences in litter mass disappearance between study years apparently was due to differential initial leaching that may have been related to differences in precipitation. Exploration of the timing, frequency, and intensity of non-catastrophic climatic events, their effect on the amounts of nutrient translocation during leaf senescence and on leaching from fresh litter, and their subsequent effects on hydrologic nutrient export and dynamics could advance our understanding of disturbed ecosystems.

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