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Species-specific Seedling Responses to Hurricane Disturbance in a Puerto Rican Rain Forest[1]

Lawrence R. Walker

Department of Biological Sciences, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, Nevada 89154-4004, U.S.A.

D. Jean Lodge

USDA Forest Service, Center for Mycology Research, Forest Products Laboratory, P.O. Box 1377, Luquillo, Puerto Rico 00773-1377, U.S.A.

Sandra M. Guzmán-Grajales

River Parishes Community College, P.O. Box 310 John LeBlanc Blvd., Sorrento, Louisiana 70778, U.S.A.

and

Ned Fetcher

Department of Biology, University of Scranton, Scranton, Pennsylvania 18510-4625, U.S.A.

ABSTRACT

Seedling dynamics were followed in a Puerto Rican forest for 20 months following a severe hurricane to study the interactive effects of hurricane debris, nutrients, and light on seedling diversity, density, growth, and mortality. Three treatments (debris removal, an unaltered control with hurricane debris, and chemical fertilization added to hurricane debris) altered levels of forest debris and soil nutrients. Canopy openness was measured twice using hemispherical photographs of the canopy. We examined the demographic responses of six common species to treatments over time. Seedling densities increased for all six species but the only significant treatment effects were increased densities of the pioneer tree *Cecropia* and the shrub *Palicourea* in the debris removal treatment. Seedling growth declined with declining light levels for four species but not for the pioneer tree *Alchornea* or the non-pioneer tree *Dacryodes*. Only *Cecropia* and the non-pioneer tree *Chionanthus* had treatment effects on growth. Mortality also differed among species and tended to be highest in the fertilized plots for all but *Cecropia* and *Dacryodes*. We found only some of the expected differences between pioneer and non-pioneer plants, as each species had a unique response to the patchy distributions of organic debris, nutrients, and light following the hurricane. High local species diversity was maintained through the individualistic responses of seedlings after a disturbance.

RESUMEN

Seguimos la dinámica de plántulas en un bosque en Puerto Rico durante 20 meses después del huracán Hugo para estudiar el efecto de la interacción de hojarasca de huracán, nutrientes, y luz sobre la diversidad de especies, la densidad, el crecimiento, y la mortalidad. Establecimos tres tratamientos (remoción de hojarasca, control con la hojarasca de huracán inalterada, y fertilizante químico añadido a la hojarasca del huracán) para alterar los niveles de hojarasca en el bosque y los nutrientes en el suelo. Medimos luz directa e indirecta dos veces usando fotografías hemisféricas del dosel. La diversidad y la uniformidad en la distribución de especies pero no la riqueza de especies fueron reducidas en presencia de fertilización. Durante el estudio examinamos respuestas demográficas de seis especies communes a los tratamientos. La densidad de plántulas aumentó para todas las seis especies pero el único efecto de tratamiento fue el aumento en la densidad del árbol pionero *Cecropia* y el arbusto *Palicourea* en el tratamiento de remoción de hojarasca. El crecimiento de plántulas disminuyó según los niveles de luz disminuyeron para cuatro de las especies pero no para el árbol pionero *Alchornea* o el árbol no-pionero *Dacryodes*. Sólo el crecimiento de *Cecropia* y del árbol no-pionero *Chionanthus* fue affectado por los tratamientos. La mortalidad fue diferente entre las especies y tuvo una tendencia a ser mayor en las parcelas fertilizadas. Sólo encontramos algunas de las diferencias esperadas entre plantas pioneras y no-pioneras. Cada especie respondió de forma única a la distribución en parches de hojarasca, nutrientes, y luz luego del huracán. La alta diversidad local de especies se mantuvo a través de las respuestas individualizadas de las plántulas después de la perturbación.

Key words: *canopy openness; hurricane; light; nutrients; organic debris; regeneration; secondary succession; tropical forest.*

HIGH SPECIES DIVERSITY IN TROPICAL FORESTS AT THE LOCAL SCALE (plots and stands) has variously been attributed to differential responses of species to microhabitat and resource heterogeneity (Denslow 1987, Cornelissen 1994, Van der Meer *et al.* 1998), random lottery effects resulting from limited seed availability (Barik *et al.* 1992, Dalling *et*

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al. 1998), and high mortality near conspecifics due to herbivory (Janzen 1970, Connell 1978, Clark & Clark 1984) or disease (Augspurger 1983, Gilbert *et al.* 1994, Lodge *et al.* 1996). The patchy availability of seeds of most species (Hubbell *et al.* 1999) acting together with differences in seedling responses to microhabitat variation (Brokaw 1985, Swaine & Whitmore 1988, Denslow *et al.* 1990) may determine which species are available for recruitment into the canopy and thereby contribute to species diversity at a local scale. Disturbances such as treefalls or hurricanes can alter relative species abundance, but do not necessarily alter species richness (Vandermeer *et al.* 1996, Walker 2000). In this paper, we examine species-specific seedling responses to variation in light, nutrients, and organic debris for 20 months following a hurricane in a subtropical wet forest to determine the extent to which microhabitat variation potentially contributes to local species diversity following disturbance.

Nutrient availability can differentially influence seedling growth, survival, and diversity (Coomes & Grubb 2000, Lewis & Tanner 2000). Background litterfall (Vitousek 1984) and pulses of disturbance-induced debris deposition (Lodge *et al.* 1994, Zimmerman *et al.* 1995) are among the factors that affect nutrient availability in tropical forests. Litter affects not only soil structure, nutrient status, and microclimate but can also affect community structure by limiting seedling emergence (Facelli & Pickett 1991, Guzmán-Grajales & Walker 1991, Molofsky & Augspurger 1992). Fertilization (Tanner *et al.* 1992, Vitousek *et al.* 1995) and debris removal (Zimmerman *et al.* 1995, Walker *et al.* 1996) experiments provide tests of nutrient limitation hypotheses.

Increased light availability in treefall gaps also influences local tropical tree species diversity. The availability of gaps (Brokaw 1985, Denslow 1995), differences in gap size (Denslow 1980, Barton 1984, Thompson *et al.* 1992), and within-gap heterogeneity (Vitousek & Denslow 1986, Brandani *et al.* 1988) may be predictors of species diversity at a stand level. Gap specialists or pioneers germinate and grow best in gap environments (Swaine & Whitmore 1988). Gap opportunists or non-pioneers grow best in high light environments but tolerate shaded conditions (Lebrón 1979, Boot 1996) aided by brief periods of sunlight (Chazdon & Pearcy 1991). Rather than a dichotomy, seedling responses to light gaps are actually a continuum of growth responses to light (Augspurger 1984, Swaine & Whitmore 1988, Kobe 1999), and species responses to light are complex in terms of their photosynthesis, growth, nutrient uptake, and carbon allocation (Fetcher *et al.* 1987, Popma & Bongers 1988). Recruitment limitation (rather than light limitation) may make species composition of gaps unpredictable (Hubbell *et al.* 1999).

Most experimental approaches for determining species-specific responses to key enviromental variables in tropical forests (Cornelissen 1994, Burslem 1996, Dalling *et al.* 1999) exploit the changes in light and nutrient availability associated with natural disturbances; however, with such approaches, light and nutrient availability are often confounded. In this study, we manipulated debris deposition resulting from a hurricane, together with fertilization, to isolate the effects of nutrients on seedlings. We used decreasing light levels following the hurricane as a covariate for our manipulations. We hypothesized that if seedling growth of a given species were limited by nutrients, growth rates would be highest in plots where fertilizer was added to hurricane debris and lowest in plots where hurricane debris was removed. In addition, we hypothesized that small-seeded species (putative pioneer species) would grow fastest under conditions of high light and nutrients while large-seeded species would be relatively unresponsive to these variables. Further, we hypothesized that recruitment and growth of pioneers in plots with high nutrient and light availability would depress seedling species diversity.

METHODS

STUDY SITES AND EXPERIMENTAL TREATMENTS.—The strong winds associated with Hurricane Hugo on 18 September 1989 opened much of the forest canopy in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico and deposited a large amount of debris in one day (*ca* 420–450 times the mean daily input in fine litterfall; Lodge *et al.* 1991). Nutrient concentrations in the fine hurricane litter were higher than in normal litterfall and similar to those of living plants (Lodge *et al.* 1991). Although the hurricane debris initially increased nutrient availability to plants, decomposition of woody debris stimulated nutrient immobilization by microorganisms, thereby decreasing nutrient availability to plants beginning about one year after Hurricane Hugo (Zimmerman *et al.* 1995). Uprooting of trees and snapping of boles and branches by the hurricane resulted in an increase in light levels at the forest floor. These light levels were

TABLE 1. *Total Kjeldahl nitrogen, resin-extractable phosphorus, and light availability for three treatments: debris removal (DR), control (C), and fertilized (F) ($\bar{x} \pm SE$; N = 4 plots). There were no significant differences (P < 0.05) among treatments for soil nutrients. Light availability at 1 m above ground is reported as direct (DSF) and indirect (ISF) site factors for two dates: March 1990 and February 1991. Light varied by time and there was a significant time × treatment interaction; see text for details..*

	Soil nutrients (ppm)		Light			
			DSF		ISF	
	Nitrogen	Phosphorus	March 1990	February 1991	March 1990	February 1991
DR	38.0 ± 1.0	0.1 ± 0.0	0.177 ± 0.037	0.103 ± 0.014	0.170 ± 0.039	0.100 ± 0.016
C	39.2 ± 1.6	0.4 ± 0.2	0.217 ± 0.014	0.158 ± 0.044	0.161 ± 0.047	0.138 ± 0.012
F	35.3 ± 1.1	0.7 ± 0.2	0.269 ± 0.035	0.103 ± 0.003	0.226 ± 0.038	0.085 ± 0.009

similar to values previously observed in large gaps (>400 m^2; Fernández & Fetcher 1991).

Four study sites (blocks) were located on ridges with slopes less than 30° near El Verde Field Station in the LEF of eastern Puerto Rico (18°20′N, 65°49′W) at elevations between 300 and 450 m, at least 300 m from each other, and all within a 0.6 x 1 km study area. The study sites were within the tabonuco forest association dominated by *Dacryodes excelsa* Vahl and classified as subtropical wet forest according to the Holdridge life zone system (Ewel & Whitmore 1973). At each block, we established three 20 x 20 m plots at least 30 m apart and randomly assigned each to one of three treatments: debris removal, no debris removal, and fertilization. Details of the study design and a map of the plots are found in Walker *et al.* (1996). The sampling area within each plot consisted of ten nonoverlapping 1 m^2 subplots (total area 40 m^2 for each treatment) that were randomly located within a 10 x 10 m area centrally located within the plot. In the debris removal treatment, we removed all organic debris (snapped trees, branches, and pre- and post-hurricane leaf litter) from the entire 20 x 20 m plot in October 1989 and repeated the debris removal from the 1 x 1 m subplots every 2 months during the 20-month study period. We applied fertilizer to the entire 20 x 20 m plot for the fertilization treatment in November 1989 and repeated the application every 3 months for 20 months, at an annual rate of 300 kg/ha N (as urea and ammonium nitrate), 100 kg/ha P (as triple–super phosphate), 100 kg/ha K (as muriate of potash), 8 kg/ha B, 15.4 kg/ha Cu, 2.2 kg/ha Fe, 25 kg/ha Mn, 26 kg/ha Zn, and 19 kg/ha Mg. These rates approximated 3, 30, and 2 times the mean annual fine litterfall inputs of N, P, and K, respectively (Lodge *et al.* 1991).

SOIL NUTRIENTS.—Soil samples were taken from four randomly chosen points within the ten subplots in each plot during September 1990 (total = 40 samples) using 10 cm diameter PVC cores and sampling to a depth of 10 cm after removal of any surface debris. All samples were oven-dried at 40°C to a constant dry mass, then analyzed for total Kjeldahl nitrogen following acid digestion (Page 1982) and available phosphorus from resin bag extractions (Siebbesen 1977). Available (KCl-extractable) nitrogen was measured in the same plots by Zimmerman *et al.* (1995).

SITE FACTOR ESTIMATION.—Hemispherical photographs of the forest canopy were taken in March 1990 and February 1991 to estimate the potential light levels reaching the forest floor. The camera was placed 1 m above the ground surface at each of the four corners of each inner 10 x 10 m plot (total = 48 photos/date) and results from the four photographs were averaged per plot. Digitization and analysis of the photographs were performed using the program CANOPY (Rich 1989) and relative values were determined ranging from 0, which represents a complete obstruction of the sky, to a value of 1 where there is no obstruction. This program estimates the proportion of total annual direct radiation (direct site factor, DSF) and indirect or diffuse radiation (indirect site factor, ISF) that can penetrate the canopy and is corrected for latitude, longitude, and the trajectory of the sun at that time of year. Our measurements were not adjusted for local cloud conditions.

SEEDLING RESPONSES.—We identified, marked, and counted all woody seedlings (trees, shrubs, and lianas) that were 10–200 cm tall every 2 months for 12 months beginning in October 1989 for each treatment. Seedlings less than 10 cm tall were considered in Guzmán-Grajales and Walker (1991) and Guzmán-Grajales (1992). Some seedlings greater than 10 cm tall of each targeted species except *Cecropia* were present in the understory when the hurricane damaged the canopy (*Alchornea*: 0–0.2 seedlings/m^2; *Palicourea*: 0–0.3; *Rourea*: 0.8–1.3; *Chionanthus*: 0.7–1.7; *Dacryodes*: 1.4–1.6; Guzmán-Grajales 1992). Regular sampling ended in October 1990. We conducted one additional census in May 1991, 20 months after Hurricane Hugo. We calculated species richness, the Shannon diversity index (H′), evenness (E), and density for all species. We also examined seedling density and height growth of six species that had sufficient sample sizes. These species represented a range of seed size, abundance, life-form and successional status. The species *Cecropia schreberiana* Miq. (seed length 1.6 mm) and *Alchornea latifolia* Sw. (6.4 mm) are pioneer trees (*sensu* Swaine & Whitmore 1988) that commonly grow in gaps. All but a few seedlings of these two pioneer species germinated following the hurricane, and in the case of *Cecropia* soon became part of the canopy (Walker 2000). Two species of intermediate successional status provided different life-forms for contrast with the trees. The shrub *Palicourea riparia* Benth. (seed length 5.0 mm) and the woody vine *Rourea surinamensis* Miq. (seed length 10.0 mm) grow in both gaps and understory (Lebrón 1979, Fetcher *et al.* 1996). In addition, *Rourea* was the most abundant species in this study. *Chionanthus domingensis* Lam. (seed length 19.0 mm) and *Dacryodes excelsa* Vahl (25.4 mm) are non-pioneer forest trees, the latter having the highest basal area in the forest (Briscoe & Wadsworth 1970).

To analyze growth in response to light, we calculated mean monthly height growth of all individuals less than 1 m tall during two time intervals, each bracketing the timing of measurements for canopy openness (March 1990 and February 1991). The first interval (8 mo) included growth increments from October 1989 to June 1990, while the second interval (7 mo) included growth increments from October 1990 to May 1991. Survival curves for the six most abundant species were generated using the univariate survival platform of the JMP statistical package (SAS 1996) and analyzed with the proportional hazards model of Cox and Oakes (1984). Species nomenclature follows Liogier and Martorell (1982) and Taylor (1994).

RESULTS

Soil nutrients.—No significant differences were found 12 months after Hurricane Hugo when the treatments were compared for total N or for resin-extractable P (Kruskal–Wallis nonparametric ANOVA; $P > 0.05$; Table 1).

Site factors.—Both the direct (DSF) and indirect (ISF) site factors declined significantly between March 1990 and February 1991 (Table 1; two-way ANOVA using treatment, time, and their interaction; DSF: $P = 0.04$; ISF: $P < 0.001$). There was a significant time x treatment interaction (DSF: $P < 0.001$; ISF: $P = 0.005$) because the canopy closed faster in the fertilization and debris removal treatments than in the control. There were also significant time x block interactions ($P < 0.001$) for both DSF and ISF, suggesting that canopy closure (at 1 m above the ground) occurred at different rates throughout the forest.

Seedling responses.—A total of 73 species of woody seedlings (including 3 spp. of perennial herbs with woody stems and 8 spp. of vines) were found one year after the hurricane during the October 1990 census (Appendix A; Guzmán-Grajales 1992). Both the number of species (54, 55, and 54) and species densities (x ± SE: 3.60 ± 0.34 species/m^2, 3.37 ± 0.37, 3.35 ± 0.35; $F = 0.15$, df = 2, $P > 0.05$) were similar among treatments (debris removal, control, and fertilization, respectively). Both diversity (H′: 2.71 ± 0.12, 2.84 ± 0.13, 1.84 ± 0.14; $F = 16.97$, df = 2) and evenness (E: 0.76 ± 0.03, 0.81 ± 0.02, 0.53 ± 0.04; $F = 28.66$, df = 2; for the debris removal, control, and fertilization treatments, respectively) were lowest (one-way ANOVA; $P < 0.0001$) in the fertilization treatment due to high dominance by several species including *Eugenia stahlii.* All treatments had increases in the total number of species during the 20-month study period but the fertilization treatment had the fewest colonists (debris removal: 80%; control: 78%; fertilization: 61%; Fig. 1a; Appendix A).

Seedling densities for each of the six studied species changed differently in response to time and treatment (Table 2; Fig. 1b–g). *Dacryodes* seedling densities decreased with increasing canopy openness, but the seedling densities of the other species were unaffected (ANCOVA with respect to DSF and ISF with treatment and time effects; *Dacryodes*, $P < 0.01$; all other species $P > 0.10$). Each species was analyzed separately using square-root transformed data, the slopes of ISF and DSF were fitted individually, and linear contrasts were used to compare treatments and time intervals (SAS 1996). *Dacryodes* seedling densities decreased with time following the hurricane; however, the seedling den-

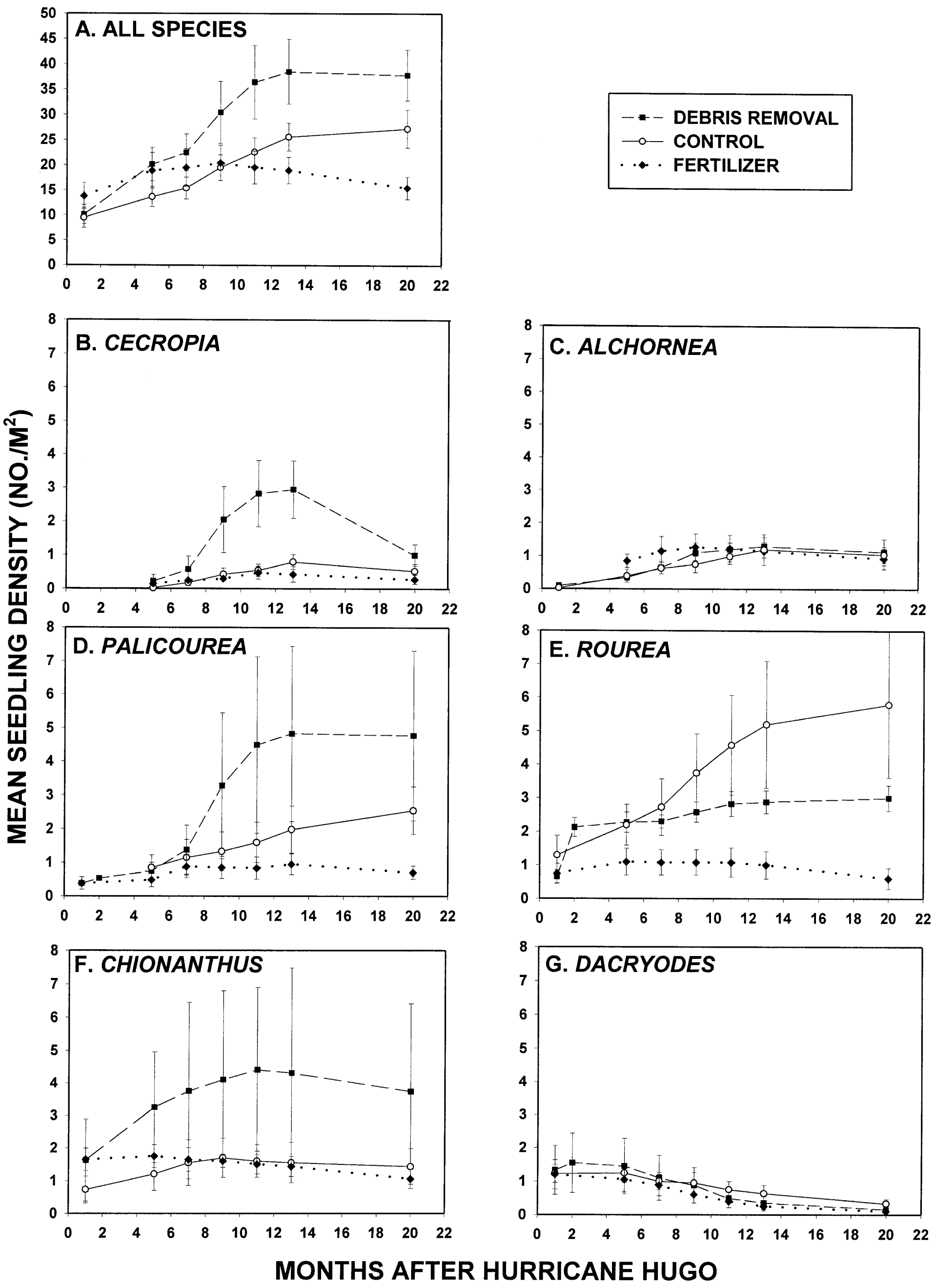

FIGURE 1. Mean density of seedlings for (A) all species in the plots, (B) *Cecropia*, (C) *Alchomea*, (D) *Palicourea*, (E) *Rourea*, (F) *Chionanthus*, and (G) *Dacryodes* ($\bar{x} \pm$ SE, $N = 4$ blocks). Treatments are debris removal, control, and fertilizer. Zero values were omitted.

sities of the other five species increased although that of the shade-intolerant pioneer *Cecropia* declined after 13 months. Seedling densities of three species were influenced by the experimental treatments. *Dacryodes* seedling densities declined least in the control treatment and densities of *Cecropia* and *Palicourea* increased most in the debris removal treatment.

TABLE 2. *Results from an ANCOVA with repeated measures analysis of seedling densities for six species. Treatments were debris removal, control, and fertilization. The covariate was DSF, a measure of direct solar radiation. Similar results were obtained with ISF, or indirect radiation. Significance levels are indicated as * (<0.05), ** (<0.01), and *** (<0.001).*

			F-ratios					
Factor	Num. df	Denom. df	*Cecropia*	*Alchornea*	*Palicourea*	*Rourea*	*Chionanthus*	*Dacryodes*
Treatment	2	6	13.22**	5.12	6.45*	3.07	0.84	0.13
Time	5	34	10.66**	9.84***	8.01***	6.07***	3.97**	9.16***
Treatment × Time	10	34	3.14**	1.5	2.27*	0.37	1.59	4.81***

Height growth rates declined significantly between the first and second time intervals in this study for four of the studied species but not for *Alchornea* or *Dacryodes* (two-way repeated measures ANOVA on log transformed growth increments; Table 3 and Fig. 2). *Cecropia* and *Chionanthus* were the only species with significant differences in growth rates among treatments; however, in an ANCOVA to predict height growth of each species, treatment was also significant for *Palicourea* ($P < 0.05$). *Chionanthus* was the only species with a significant time x treatment interaction because of the stable, low growth in the debris removal treatment.

In the proportional hazards analysis of seedling survivorship, treatment, species, and their interaction were highly significant ($P < .0001$). As shown in Figure 3, survival of *Cecropia* and *Dacryodes* was less than the other species, whereas that of *Rourea* and *Palicourea* was greater. For all six species combined, survival was highest in the control treatment and lowest in the fertilization treatment. The interaction arose largely because survival of *Cecropia* was much greater in the fertilized plots than in the other treatments (data not shown).

DISCUSSION

Nutrients and canopy openness both affected the dynamics of the seedling community at the Luquillo Experimental Forest (LEF) in Puerto Rico following a hurricane in 1989 and some of their effects were mediated by hurricane debris. Responses of pioneer and non-pioneer species to nutrients, canopy openness, and debris did not conform strictly with our expectations. Instead, each species had a unique response. To the extent that our results are representative, they have implications for the maintenance of species diversity in disturbed tropical forests.

Disturbances frequently alter resource availability (Canham & Marks 1985) but the availability of nutrients to plants will depend on whether the nutrients are immobilized or mineralized (La Caro & Rudd 1985). In the LEF, a large pulse of nutrients (especially P) became available from the litterfall during the hurricane (Lodge *et al.* 1991, 1994), but subsequent immobilization of nutrients occurred in sites where debris was not removed (control and fertilization treatments; Zimmerman *et al.* 1995). Nutrient immobilization, increased decomposition, or dilution of N and P by rapid seedling growth may each contribute to the lack of treatment differences in our measurements of total soil N or available P despite some significant seedling responses to our treatments. Experimental removal of debris combined with fertilization in an extension of this study (Guzmán-Grajales 1992) showed that fertilization had the strongest positive effect on seedling densities when debris was not present. We show here that debris removal increased densities of seedlings greater than 10 cm tall most in the absence of fertilizer. Similar re-

TABLE 3. F*-ratios from a two-way ANOVA with repeated measures analysis of rates of seedling height growth for the six species and three treatments in Table 1. Significance levels of the* F*-ratios are indicated as <0.05*, <0.01**, and <0.001***.*

			F-ratios					
Factor	Num. df	Denom. df	*Cecropia*	*Alchornea*	*Palicourea*	*Rourea*	*Chionanthus*	*Dacryodes*
Treatment	2	6	16.56**	2.89	1.50	2.15	6.26*	0.39
Time	1	7	50.59***	0.08	30.68**	98.61***	29.98***	2.80
Treatment × Time	2	7	0.28	0.05	0.54	0.34	11.74**	0.26

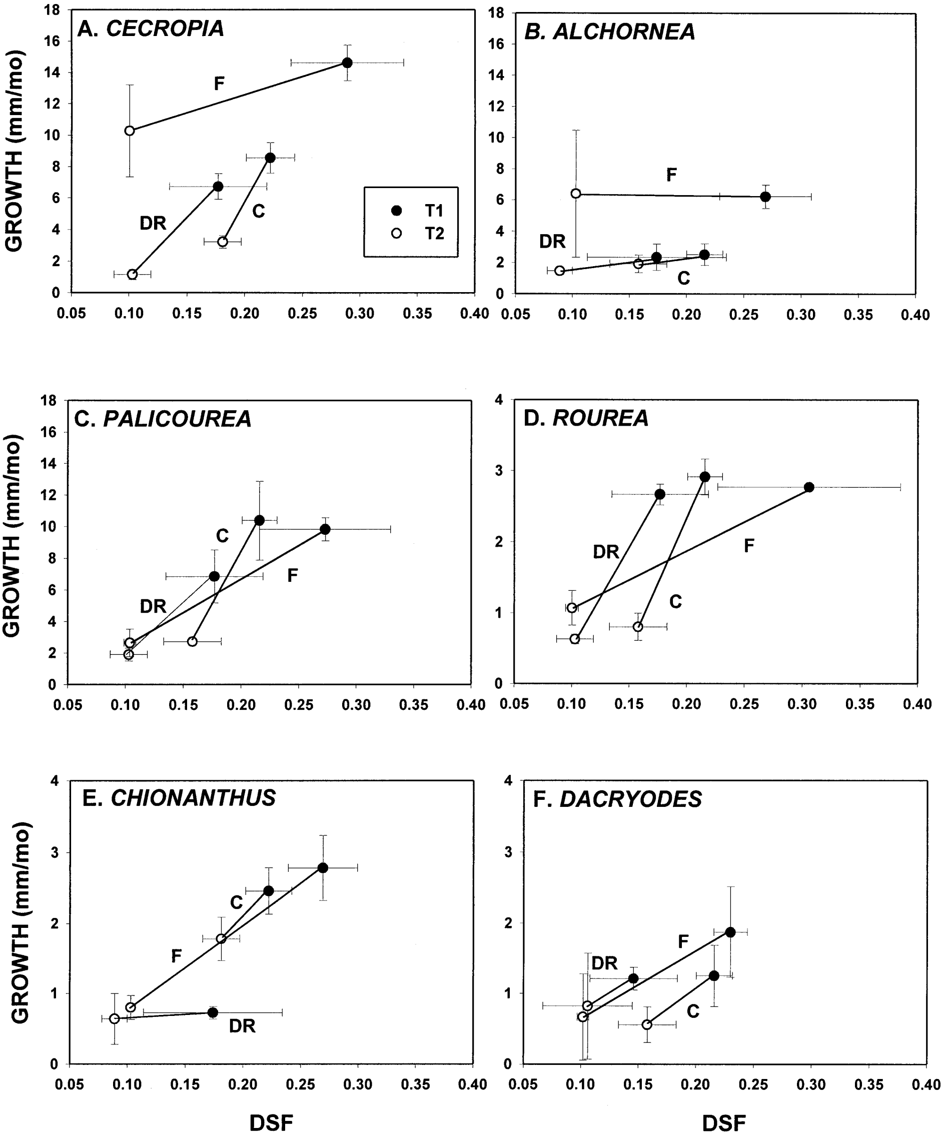

FIGURE 2. Seeding height growth as a function of DSF (direct site factor) during two time periods (T1 and T2; 1–9 mo and 13–20 mo after the hurricane) for three treatments (DR = debris removal, C = control, and F = fertilization) for (A) *Cecropia*, (B) *Alchornea*, (C) *Palicourea*, (D) *Rourea*, (E) *Chionanthus*, and (E) *Dacryodes* ($\bar{x}$ ± SE for both growth and DSF; $N = 2$, 3, or 4 blocks because each species was not present in each treatment/time combination). Patterns of ISF (indirect site factor) values were similar to DSF values and were not plotted. Note variable *y*-axes and that light levels decrease from T1 to T2.

sponses occurred for those seedlings less than 10 cm tall (Guzmán-Grajales & Walker 1991), in which high levels of recruitment in the debris removal (but not fertilization) treatment 5–11 months following the hurricane led to increased densities of seedlings greater than 10 cm tall 9–20 mo after the hurricane (Fig. 1; Guzmán-Grajales & Walker 1991). These findings contradict our initial assumption that fertilizer and debris would have additive effects. In the low-nutrient, newly exposed mineral soils from uprooted trees following Hurricane Hugo, seedling densities (but not species richness and diversity) were lower than in forest plots (Walker 2000), again suggesting that nutrient levels impact seedling densities.

The differential growth responses of each spe-

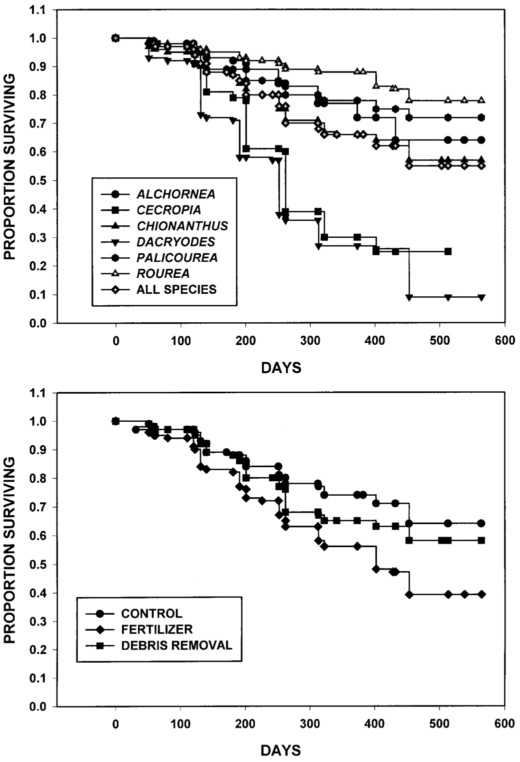

FIGURE 3. Survival of all seedlings that appeared during the study period by (A) species and (B) treatment.

cies to our treatments probably further altered nutrient pools, increasing the patchiness of resources. For example, the rapid growth of the pioneer species *Cecropia* (particularly in the fertilization treatment) after the hurricane probably sequestered nutrients that otherwise might have been lost from the system (Scatena *et al.* 1996, Silver *et al.* 1996). These nutrients are gradually released through wood decomposition (Vogt *et al.* 1996); however, the other pioneer species *Alchornea* did not have highest growth in the fertilization treatment, contrary to our expectations.

Palicourea shrubs and *Rourea* vines did not respond to fertilization, as may be typical of some mid-successional species (Parrish & Bazzaz 1982). *Palicourea* did respond with relatively rapid growth in all three treatments, but was most common in the debris removal treatment. *Rourea* seedlings, the most common of the six species in the control treatment, were, in contrast to *Palicourea*, slow-growing and unresponsive to fertilizer. *Rourea* seedlings may eventually be outcompeted by faster-growing vines or the grass *Ichnanthus pallens* (Sw.) Munro (Walker 1994, Schnitzer *et al.* 2000).

The late successional trees (*Chionanthus* and *Dacryodes*) also did not respond to fertilization, although *Chionanthus* growth was reduced by the debris removal treatment. The rapid decline in *Dacryodes* seedling density in the fertilized plots may have been because of damage to the mycorrhizae on which this "litter-rooted" species depends (Edmisten 1970).

Canopy cover increased from very open conditions immediately following the hurricane to *ca* 50 percent canopy cover ten months later (Fernández & Fetcher 1991). Growth of seedlings and saplings as well as resprouting of trees (Walker 1991) contributed to the rapid closure of the canopy. Our February 1991 light measurements confirmed the conclusion of Zimmerman *et al.* (1995) that canopy closure was faster in the fertilization and debris removal than in the control treatment. The pioneer tree species *Cecropia*, as we expected, responded strongly to canopy openness only when nutrients were abundant. In light gaps with low nutrient availability (from uprooted trees), however, *Cecropia* can grow fast enough to reach the canopy, presumably by tapping nutrient sources in the adjacent forest floor (Walker 2000). In contrast, *Alchornea* growth did not respond to light availability.

Palicourea growth increased significantly with relatively small changes in light availability, suggesting that this common understory plant responds rapidly when the canopy opens, particularly when hurricane litter is present. At higher light levels, however, its growth was inhibited. Lebrón (1979) called *Palicourea* a gap opportunist in Puerto Rico and noted its broad ecological amplitude. Its rapid growth at low light levels may allow it to colonize smaller gaps than the more light-demanding *Cecropia* (Popma & Bongers 1988). The variety of responses to decreasing light levels following the hurricane suggests a partitioning of the light gradient (Kobe 1999) that may promote species diversity. Growth of all species except *Alchornea* responded to light reduction, contradicting our assumption that only pioneer species would respond. Nutrient addition (fertilization treatment; *Cecropia*) and removal (debris removal treatment; *Chionanthus*) occasionally altered the light response.

Woody seedlings also had a wide range of responses to debris removal. Diversity was lowest when fertilizer was added to hurricane debris (Appendix A; Fig. 3), supporting our hypothesis. This result was primarily due to a decrease in evenness rather than species richness and could have resulted from competition by a few, rapidly growing individuals (Fetcher *et al.* 1996) or from direct negative effects of fertilizer (Walker *et al.* 1996). Debris removal resulted in high densities of *Cecropia* and *Palicourea* and modest increases in *Chionanthus* and *Dacryodes* (the pattern indicated in Fig. 3), but *Alchornea* and *Rourea* densities were highest in the fertilization and control treatments, respectively. Higher seedling densities in the debris removal treatment were not matched with higher growth. The relatively small-seeded *Cecropia* and *Palicourea* apparently benefited from the removal of debris, a phenomenon that occurs naturally on steep slopes in this forest (Lodge & Asbury 1988); however, the larger-seeded *Chionanthus* and *Dacryodes* also apparently benefited from debris removal. The debris removal treatment provided the advantages of reducing the number of competing plants, the removal of the potentially negative effects of litter (Denslow *et al.* 1991; Guzmán-Grajales 1992), and higher initial nutrient availability (Zimmerman *et al.* 1995). The disadvantages of the debris removal included potentially higher susceptibility to drought (Everham *et al.* 1996; the 3 mo following Hurricane Hugo were unusually dry, Scatena & Larsen 1991) as well as an eventual decrease in nutrient availability (Zimmerman *et al.* 1995). Natural variation in the distribution and depth of organic debris on the forest floor results in maximal seedling diversity because of the variable responses of seedlings (Molofsky & Augspurger 1992, Everham *et al.* 1996, Benitez-Malvido & Kossmann-Ferraz 1999).

Our results indicate the importance of simultaneously examining the influence of nutrients, light, and organic debris to determine their interactive effects on seedling dynamics. There were some obvious effects of nutrients, light, or debris on individual species, but the biggest influence on density and growth of seedlings was time. Seedling densities increased overall, but some had reached a plateau and others were declining by the end of this study. As light levels declined, seedling growth rates also declined. Canopy opening and the interaction of treatment and time, however, were so confounded as to preclude detection of a response to canopy openness as long as treatment and time were included in the models. We inferred that the treatments influenced light availability through their effects on canopy closure and seedling density.

The pioneer trees and *Palicourea* had greater absolute height growth in all treatments; thus they should be better competitors than the non-pioneer trees and *Rourea*, even at low nutrient levels, until light becomes limiting. Species in this study showed a continuum of responses to both available light and nutrients, suggesting that a partitioning of those resources is possible. Traditional groupings into pioneer and non-pioneer species are problematic, however, as we found very different responses to the treatments, even between the two putative pioneer trees as well as between the two non-pioneer trees. For example, mortality was greatest for the pioneer *Cecropia* and the late successional *Dacryodes* but lower for the pioneer *Alchornea* and late successional *Chionanthus*. These results suggest such categories should be used with caution.

Differential species responses to the variety of microsites helped maintain species diversity after a major disturbance. Some species were most responsive to increases in light, others to increases in nutrients, or to increases in light if accompanied by a pulse of nutrients. Other species may have a delayed response to changing conditions if they still depend on seed resources. Patchy distributions of nutrients and light as well as competition between individuals are important determinants of the pattern of regeneration following disturbance and the replacement of pioneer species by non-pioneers. The variety of responses in density, growth, and mortality of woody seedlings, while ensuring the maintenance of high species diversity in tropical forests, makes prediction of such replacement patterns difficult.

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APPENDIX A. *Number of woody seedlings 10–200 cm tall of each species per treatment followed by frequency (number of plots) per treatment (October 1990 census only). Treatments are DR = debris removal, C = control with no debris removal, and F = fertilization but no debris removal. Total seedling numbers in all treatments and total frequencies are in the final column (TL). Species (N = 73) are presented first in descending order of seedling number by the October 1990 census for the C treatment and then in descending order by total abundance. Symbols denote increase (+), decrease (−), or no change (=) in number from the first census (October 1989). "a" denotes species absent from a treatment; "a−" was used for species present in October 1989 but not in October 1990; superscripts denote vines (v), herbs (h), shrubs (s), and trees (t).*

Species	DR	C	F	TL
Rourea surinamensis^{v} Miq.	115/4+	208/4+	40/3+	363/11
Palicourea riparia^{s} Benth.	193/4+	79/4+	38/4+	307/12
Manilkara bidentata^{t} (A. DC.) A. Chev.	34/2+	68/2+	8/3−	110/7
Chionanthus domingensis^{t} Lam.	172/4+	62/4+	57/4−	291/12
Alchornea latifolia^{t} Sw.	52/4+	48/4+	46/4+	146/12
Sapium lauracerasus^{t} Desf.	16/4+	43/4+	13/3+	72/11
Schefflera morototoni^{t} (Aubl.) Decne. & Planch	91/4+	39/4+	54/4+	184/12
Cecropia schreberiana^{t} Miq.	118/4+	32/4+	17/3+	167/11
Inga laurina^{t} (Sw.) Wild.	60/2+	32/2+	41/3+	133/7
Matayba domingensis^{t} (DC.) Radlk.	53/4+	28/3+	19/4=	100/11
Psychotria berteriana^{s} DC.	29/3+	28/4+	14/2+	71/9
Sloanea berteriana^{t} Choisy	12/3+	27/4+	16/3−	55/10
Prestoea montana^{t} (R. Graham) Nichols	38/4+	26/4+	34+	98/12
Byrsonima spicata^{t} (Cav.) HBK	116/3+	26/3+	32/1−	174/7
Dacryodes excelsa^{t} Vahl.	14/4−	25/4−	10/3−	49/11
Guarea guidonia^{t} (L.) Sleumer	19/4+	25/3+	12/2−	56/9
Tetragastris balsaminifera^{t} (Sw.) Kuntze	15/2−	24/2+	14/4+	53/8
Miconia racemosa^{s} (Aubl.) DC	38/2+	18/2+	a	56/4
Ocotea leucoxylon^{t} (Sw.) Mez.	8/1+	16/2−	5/2+	29/5
Ocotea globosa^{t} (Aubl.) Schltdl. & Cham.	10/3+	15/2−	3/2+	28/7
Ormosia krugii^{t} Urban	2/1−	15/1+	3/2=	20/4
Piper glabrescens^{s} (Miq.) C. DC.	22/3+	14/2+	12/2+	48/7
Casearia arborea^{t} (L. C. Rich.) Urban	40/2+	13/4+	5/3+	58/9
Securidaca virgata^{v} Sw.	17/4+	13/3+	26/4+	56/11
Drypetes glauca^{t} Vahl.	49/3+	11/4+	29/3−	89/10
Ixora ferrea^{s} (Jacq.) Benth.	1/1=	11/3+	12/2=	24/6
Tabebuia heterophylla^{t} (DC.) Britton	13/1+	9/2+	13/3=	35/6
Inga vera^{t} Willd.	a	8/1+	a	8/1
Eugenia stahlii^{t} (Kiaersk.) Krug & Urban	28/3+	4/2−	121/3+	163/8
Phytolacca rivinoides^{s} Kunth & Bouche	a	5/1+	2/1+	7/2
Callophyllum callaba^{t} (Jacq.) Camb.	9/1+	4/2+	a	13/3
Casearia sylvestris^{t} Sw.	28/1+	4/3+	6/3+	38/7
Hirtella rugosa^{s} Pers.	6/3+	4/1=	2/1=	12/5
Nectandra turbacensis^{t} (Nees) Mez.	16/3+	4/2+	11/3+	31/8
Trichilia pallida^{t} Sw.	5/3+	4/3+	6/1+	15/7
Roystonea borinquena^{t} O. F. Cook	a	4/2+	a−	4/2
Alchorneopsis portoricensis^{t} Urban	5/2+	3/1+	a	8/3
Guatteria caribaea^{t} Urban	1/1=	3/1+	a	4/2
Psychotria brachiata^{s} Sw.	a	3/1+	2/1−	5/2
Syzygium jambos^{t} (L.) Alst.	9/2+	3/1+	2/1+	14/4
Buchenavia capitata^{t} (Vahl.) Eichl.	a	2/1=	3/1−	5/2
Lasianthus lanceolatus^{s} (Griseb) Gómez Maza	a	2/1+	4/1+	6/2
Micropholis chrysophylloides^{t} Pierre	a	2/1=	a	2/1
Micropholis garciniifolia^{t} Pierre	a	2/2=	a	2/2
Heterotrichum cymosum^{s} (Wendl.) Urban	17/2+	2/1+	a	19/3
Byrsonima coriacea^{t} (Sw.) DC.	a−	1/1−	a	1/1
Cordia borinquensis^{t} Urban	1/1=	1/1=	2/1+	4/3
Guarea glabra^{t} Vahl.	4/1+	1/1+	a	5/2
Myrcia splendens^{s} (Sw.) DC.	3/2=	1/1=	1/1−	5/4
Ocotea floribunda^{t} (Sw.) Mez.	a	1/1+	1/1+	2/2
Paullinia pinnata^{v} L.	a	1/1+	2/1=	3/2
Psychotria patens^{s} Sw.	a	1/1=	a	1/1
Trema micranthum^{t} (L.) Blume	a	1/1+	1/1+	2/2
Zanthoxyllum martinicense^{t} (Lam.) DC.	13/1+	1/1+	1/1+	15/3
Gonzalagunia spicata^{h} (Lam.) Gómez Maza	a	1/1+	a	1/1

APPENDIX A. *Continued.*

Laetia procera^{t} (Poepp. & Endl.)	1/1=	a−	a	1/1
Miconia prasina^{t} (Sw.) DC.	4/2−	a	1/1=	5/3
Myrcia leptoclada^{s} DC.	4/2+	a	4/3+	8/5
Smilax domingensis^{v} Willd.	a	a	6/2+	6/2
Andira inermis^{t} (W. Wright) HBK	2/1+	a	a	2/1
Heteropteris laurifolia^{v} (L.) A. Juss.	4/1+	a	a	4/1
Cordia sulcata^{t} DC.	a	a	1/1+	1/1
Croton poecilantus^{t} Urban	1/1+	a	1/1+	2/2
Daphnopsis philippiana^{t} Krug & Urban	1/1=	a	a	1/1
Hypocratea volubilis^{v} L.	4/2+	a	1/1−	5/3
Forsteronia portoricensis^{v} Woodson	a−	a	1/1−	1/1
Myrcia deflexa^{t} (Poir.) DC.	a−	a	1/1−	1/1
Margaritaria nobilis^{t} L.F.	4/2+	a	a	4/2
Psychotria maleolens^{s} Urban	2/1+	a	a	2/1
Rheedia portorricensis^{t} Urban	3/1=	a	1/1+	4/2
Solanum torvum^{h} Sw.	1/1+	a	1/1+	2/2
Solanum rugosum^{h} Dunal	1/1+	a	1/1+	2/2
Samyda spinulosa^{t} Vent.	a	a	1/1−	1/1
Total no. species 10–200 cm tall	54	55	54	
Total species increases/decreases	43/7	43/6	33/15	
Percent increase in species	80	78	61	
Shannon index of diversity (H′)	2.71	2.84	1.84	
Evenness (E)	0.76	0.81	0.53	