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An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico

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Summary

1 The controls over above-ground primary productivity following hurricane damage were investigated in a lowland subtropical wet forest (350–500 m altitude) and a lower montane elfin forest (1050 m) in Puerto Rico. Responses of understorey and canopy vegetation to addition of a complete nutrient fertilizer (both altitudes) or hurricane debris removal (lowland only) were monitored for 47–50 months. Treatments were initiated 1–6 months after Hurricane Hugo severely damaged both forests (18 September 1989).

2 Fertilization stimulated leaf litter production in both forests, but the recovery to prehurricane levels occurred earlier in the lowland forest (20 months after initiation of treatment) than in the elfin forest (38 months). Debris removal also increased leaf litter production in the lowland forest.

3 Tree diameter growth was 10-fold greater at low than at high altitude but the only treatment effect was a time by treatment interaction in the lowland forest, indicating that diameters of trees in the debris removal treatment did not increase as rapidly as in the control or fertilizer treatments.

4 Fertilization altered understorey biomass in the elfin forest (graminoids increased 10-fold, bryophytes decreased three-fold) but not in the lowland forest. Debris removal had no effect on understorey biomass in the lowland forest although woody seedling densities were highest in the debris removal plots. In control plots, understorey biomass was 12-fold greater at high than at low altitude. Saplings of a pioneer tree, *Cecropia schreberiana* were three- to five-fold denser in fertilized plots than in control or debris removal plots in the lowland forest.

5 The study showed that establishment of woody species by seeds was more important to posthurricane regeneration in the lowland than in the elfin forest and that the recovery of forest productivity was less responsive to increased nutrient availability in the elfin forest. Opportunistic, rapid responses to nutrient addition by *Cecropia* (low altitude) or graminoids (both high and low altitude) contrasted with the relatively slow responses of mature forest trees. These results suggest that factors regulating primary productivity following disturbance are influenced not only by the physical characteristics of the site but also by the range of potential species-specific responses represented in the flora.

Keywords: Cecropia, disturbance, elfin forest, litter, tropical forests

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Introduction

High-altitude forests in the tropics (also called cloud, dwarf or elfin forests) are generally of smaller stature and have lower productivity than tropical lowland forests (Grubb 1977; Tanner *et al.* 1992). Many reasons have been suggested for this phenomenon, including factors directly affecting tree stature or survival (e.g. mechanical abrasion by wind, poor root

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support from shallow soils, and reduction of photosynthesis by clouds or cold temperatures), genetic constraints, and limited availability of nutrients (Lawton 1982; Chapin *et al.* 1986; Weaver *et al.* 1986; Weaver 1990, 1995; Vitousek *et al.* 1995). Nutrients may be limiting due to poor soil development, saturated soils, slow decomposition, or low nutrient uptake as a result of reduced transpiration (Tanner 1980, 1985; Medina *et al.* 1981). Little experimental work has been done to ascertain the causes of reduced primary productivity and dwarfism in high altitude tropical forests (but see Tanner *et al.* 1992; Vitousek *et al.* 1993).

Tropical forests have generally been considered to be more benign than temperate forests, such that biotic interactions (e.g. pollination, fruit dispersal, herbivory and competition) may be more central in determining their structure and function (Giller 1984; Waide & Lugo 1992). However, tropical vegetation is now considered to be as susceptible to both natural and anthropogenic disturbance as other biomes (Pickett & White 1985; Lugo & Lowe 1995). The cumulative impact of such disturbances as fires (Sanford *et al.* 1985), landslides (Garwood *et al.* 1979), hurricanes (Brokaw & Walker 1991), tree-fall gaps (Denslow 1987), and human exploitation for timber, fuel, and pasture land (Lanly 1995) on species distributions and plant community dynamics may be the ultimate control over primary productivity in tropical forests (Waide & Lugo 1992). Although the lowland tropical forests have been most impacted to date (cf. Lanly 1995), high altitude tropical forests are being increasingly disturbed (Hamilton *et al.* 1993).

In this study, we address the interaction of disturbance responses and productivity gradients. Is the response of a plant community to a disturbance (e.g. its recovery trajectory) mediated by and predictable from its primary productivity (cf. Grime 1979; Grubb 1985; Tilman 1988; Grace & Tilman 1990; Grace 1993)? For example, are low productivity (stressed) systems populated by species with certain life forms and life history characteristics that respond differently to disturbance when compared with species from high productivity systems? We used experimental manipulations to examine controls over primary productivity in two tropical forests in Puerto Rico (lowland and montane) following a major natural disturbance (Hurricane Hugo 1989). Hurricanes are a common disturbance in the Caribbean, striking the island of Puerto Rico every 21 year (Salivia 1972). We hypothesized that nutrients limited primary productivity at both altitudes, but that the elfin forest would be less responsive to nutrient additions because of the additional effects of other factors. In addition, we investigated the importance of disturbance in controlling primary productivity by comparing our results with measurements made before the hurricane.

Methods

STUDY AREA

We compared controls over above-ground primary production at a low altitude site (El Verde or EV) and a high altitude site (Pico del Este or PE). Both sites are located in the Luquillo Experimental Forest (LEF) in eastern Puerto Rico (Fig. 1). El Verde (18°19'N, 65°49'W) is the site of a 70-ha research forest that is 350–500 m a.s.l. and receives a mean annual precipitation of 3460 mm; mean monthly temperatures range between 21 and 25°C (Brown *et al.* 1983). The vegetation is classified as subtropical wet forest (Ewel & Whitmore 1973) and lies in the tabonuco zone which is dominated by *Dacryodes excelsa* Vahl. (tabonuco) and *Prestoea montana* (R. Grah.) Nichols (sierra palm). Nomenclature follows Liogier & Martorell (1982). Before Hurricane Hugo (see below), the forest had a closed canopy at 20–25 m, many understorey trees and shrubs, and generally sparse vegetation on the forest floor. Although Wadsworth (1951) reported 168 tree species in the tabonuco zone, 99% of the total tree density was due to just 40 of these species (Smith 1970). The soils at El Verde are a complex of upland Ultisols and Oxisols (Zarzal–Cristal complex; Soil Survey Staff 1995) and are mostly well-drained clays and silty clay loams.

Pico del Este (18°16'N, 65°45'W) is a summit area (1051 m a.s.l.) that receives a mean annual pre-

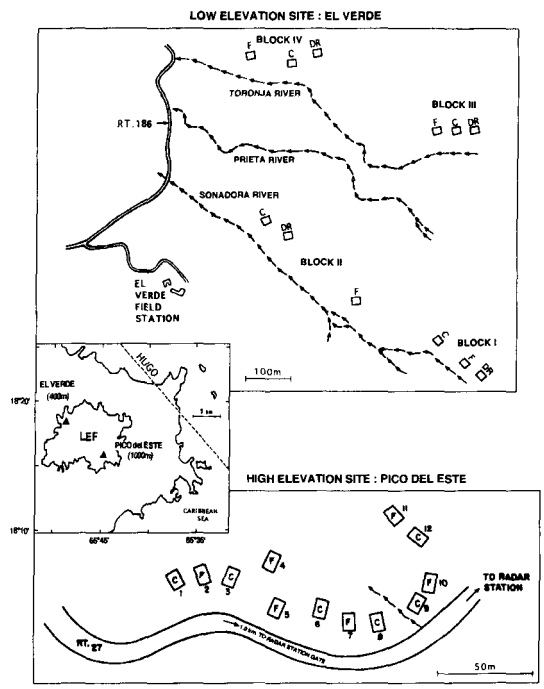

Fig. 1 Location of the low altitude study site El Verde (EV) and the high altitude site Pico del Este (PE) in the Luquillo Experimental Forest (LEF) in north-eastern Puerto Rico. Also shown are the trajectory of Hurricane Hugo (September 1989) and the locations of each plot with letters to indicate treatments (C = control, F = fertilization, DR = debris removal).

cipitation of 4200 mm (7% of which is intercepted mist). Mean monthly temperatures range between 17 and 20°C (Brown *et al.* 1983). The vegetation is considered lower montane rain forest (Ewel & Whitmore 1973), and forms a canopy at 2–6 m. Seven tree species are found in the elfin forest of which three species (Tahebuia *rigida* Urban, *Ocotea spathulata* Mez, and *Calyptranthes krugii* Kiaersk.) account for 80% of total tree density (Howard 1968). Epiphytes are common and the understorey is dominated by bryophytes. Soils at PE are silty loams in the Ultisol order and the Guayabota series, are usually saturated, and have slow permeability (Brown *et al.* 1983).

PLOT DESIGN AND TREATMENTS Al EL VERDE

At EV (Fig. l), four study sites (blocks) were located on ridge tops (<30° slope). At each block, five 20-m × 20-m plots were marked within 30 m of each other and all trees in each plot that had a diameter $\geqslant 5$ cm at 1.3 m (d.b.h.) were identified, measured (height and d.b.h.) and permanently tagged in April-June 1989. In September 1989 Hurricane Hugo severely defoliated > 50% of the trees in the forest (Walker 1991). Using data for annual litterfall collected from 1980 to 1981 (Zou *et al.* 1995) in two plots located in the midst of our study sites, Lodge *et al.* (1991) estimated that the hurricane deposited 1.2 times the mean annual fine litterfall (leaves and twigs) on the forest floor. An equal amount of fine litterfall was suspended above the forest floor on broken crowns, branches, and uprooted trees. Lodge *et al.* (1991) further estimated that the fine litterfall deposited by the hurricane contributed 1.3 and 1.5-2.4 times the mean annual inputs of N and P, respectively. Approximately 85% of hurricane-generated debris was coarse woody debris > 5 cm in diameter (Zimmerman *et al.* 1994).

To adjust for the large input of debris by Hurricane Hugo to our plots, we altered our plans for a factorial fertilization experiment. In October 1989, three plots per block were randomly assigned to one of three treatments: debris removal (D R), fertilizer (F), or control (no manipulation; C) (total of four plots per treatment). The treatments were applied to the whole 20-m × 20-m plot but all measurements except estimates of hurricane-induced mortality (Walker 1991; Walker 1995) were made in the central 10-m × 10-m portion of each plot. Within three weeks after the hurricane, all organic debris (snapped trees, branches, and pre and posthurricane leaf litter) was removed from the DR plots. Seedling dynamics in these DR plots was followed by removing fine and coarse woody debris every 2 months for 19 months (then every 6 months for 29 months) from 10 1 m^2 plots randomly located within the 10-m × 10-m plot (Guzmán-Grajales & Walker 1991). No woody debris was removed from the F or C plots. Fertilization was applied to the ground surface of the F plots in October 1989 (EV) and subsequently every 3 months until December 1993. Nutrients were added at an annual rate of 300 kg ha^{-1} N, 100 kg ha^{-1} P, 100 kg ha^{-1} K, 8 kg ha^{-1} B, 15.4 kg ha^{-1} Cu, 2.2 kg ha^{-1} Fe, 25 kg ha^{-1} Mn, 26 kg ha^{-1} Zn and 19 kg ha^{-1} Mg. These rates are ≈ 3, 30 and 2 times mean annual inputs of N, P and K, respectively, from fine litterfall (Lodge *et al.* 1991). The C plots were not altered after the hurricane.

To determine if hurricane damage at EV differed among plots, we recorded trunks that were uprooted or snapped, and removal of tree limbs by the hurricane (in four categories: none, few, some, many). Tree trunks that were uprooted or snapped were common in our plots (17.5–22%) but differences among treatments were not significant ($G = 1.21$, $P < 0.45$; log-likelihood ratio). There were small but significant differences among treatments in the frequency of trees with broken branches ($G = 38.22$, $P < 0.001$). Treatments received increasing branch damage in the order DR < C <F.

PLOT DESIGN AND TREATMENTS AT PICO DEL ESTE

Hurricane Hugo also severely defoliated the elfin forest at PE (Brokaw & Grear 1991), adding 1.9 times the mean annual litterfall, and 1.5, 1.7 and 3.1 times the annual fine litterfall inputs of N, P and K, respectively, (Lodge *et al.* 1991). However, apart from the defoliation and some twig damage at PE, there were no large structural changes at PE resulting from the hurricane. The experimental design at PE (Fig. 1) resembled the design at EV without the debris removal treatment. Twelve 9-m × 14-m plots were located at least 5 m apart, and with the long axis orientated along a slope near a ridge top, Plots were located on mineral soils, as were the nearby plots used in previous studies by Weaver *et al.* (1986) which yielded the prehurricane litterfall. Other previous studies in this area, however, used plots with deep accumulations of organic matter (Howard 1968). The plots were not placed in one depression where the height of the tree canopy exceeded 7 m. Adjacent pairs of plots (blocks) were assigned at random to either of two treatments: fertilization (F) or control (C) (total of 6 plots per treatment). A complete fertilization was initially applied in April 1990 (6 months after the hurricane) and subsequently every 3 months until December 1993, The 6-month delay in treatment initiation at PE compared to EV was due to the difficulties of plot establishment (and precautions taken to avoid trampling) at PE. Nutrients were added at the same annual rates as at EV (see above) but at this site they represented a greater additional input, being 15, 166 and 30 times mean annual leaf litterfall inputs for N, P and K, respectively, (Lodge *et al.* 1991). Treatments were applied to the entire 9-m × 14-m plot but all measurements were made in a

5-m × 9-m plot located in the centre of the larger plot. Only general observations (no statistical comparisons) were made about contrasts between the lowland and the elfin forest because the plots at both altitudes represented a limited geographical area within each forest type.

MEASUREMENTS

Litter production was monitored in litter baskets (40 cm × 40 cm; 0.16 m^2) that were placed 1 m off the ground surface. The baskets were placed in 10 random locations in each 10-m × 10-m plot at EV and in six random locations in each 5-m × 9-m plot at PE (1.6 and 1.0 m^2 total surface area, respectively), Litter was collected every two weeks, dried at 60' C to a constant mass, sorted into leaves, wood, and miscellaneous, and weighed. Collections began in March 1990 at both EV and PE.

Standing litter was harvested once (October 1993) from the biomass plots at each site (see below) and sorted into leaves, wood, and miscellaneous before drying and weighing.

Tree diameter increments were measured with stainless steel dendrometers imprinted with a Vernier scale to detect small changes (0.01 inch; 0.25 mm) in circumference (Walker 1988). All values were later converted to diameter in mm. The bands were initially placed on all trees > 5 cm d.b.h. at EV in February 1990 and at PE in April 1990. Bands were read at least four times per year for 4 years and replaced as necessary.

Live understorey biomass was harvested in October 1993 for all plants < 2 m tall (except seedlings and sprouts; see below) from four subplots (EV, 1 m^2; PE, 0.25 m^2), located at or near each inside corner of each inner measurement plot (EV, 48 m^2; PE, 12 m^2, total sampled area) but avoiding trees and trampled areas. Samples were combined within each plot by major life forms (graminoids, bryophytes, ferns, herb, vines, woody seedlings, and epiphytes), and dried at 60°C. to a constant mass. Woody seedlings (which included stem and root sprouts at PE only) were harvested only if they were < 25 cm tall in order to avoid long-term impacts on woody vegetation.

Understorey vegetation was measured at EV every 6 months for 4 years (beginning in October 1989) in 10 1-m^2 subplots randomly located within each 10-m × 10-m plot (total = 120 plots). Understorey vegetation was also measured at PE every 6 months for 4 years (beginning in April 1990) in 100.25-m^2 subplots randomly located within each 5-m × 9-m plot (total = 120 plots). Density of all woody seedlings (< 200 cm tall; including stem and root sprouts at PE) was measured every 6 months for 4 years. Percent mortality and recruitment were calculated by dividing the number of seedlings dying or new seedlings appearing during the 4-year period by the number of seedlings initially present at the first census. Mortality and recruitment were calculated for all species of woody seedlings and sprouts at PE but only for seedlings of the 12 most common species at EV (highest overall density; the palm, *Prestoea montana* was excluded because its morphology made consistent measurements difficult). The cover of dominant life forms in the understorey (graminoids, bryophytes, ferns, herbs, vines, and woody seedlings) within 2 m of the ground surface was estimated every 6 months in five cover classes: 0%, 1–25%, 26--50%, 51–75% and > 75%.

Saplings >2 cm d.b.h. that recruited into the EV plots were permanently marked and measured (d.b.h. and height) approximately every 6 months (beginning 11 months posthurricane (August 1990) for 4 years. No saplings recruited into the PE plots.

Results

LITTER FALL

Leaf litter production (pooled per plot per 3-month period for analysis by repeated measures ANOVA; SAS 1987) differed among treatments at both EV (Fig. 2; fertilization [F] > debris removal [DR] > control [C]; $P = 0.01$) and PE (Fig. 3; fertilization > control; $P = 0.045$). Leaf litter production increased significantly with time at both EV ($P < 0.001$) and PE ($P < 0.001$) but there was no time-treatment inter-

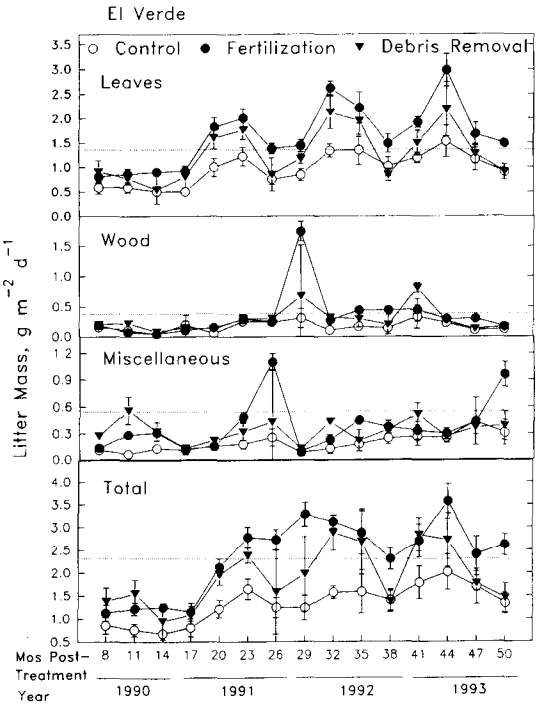

Fig. 2 Comparison of leaf, woody, miscellaneous, and total components of litter trapped in control, fertilized, and debris removal plots following Hurricane Hugo (September 1989) at the El Verde site (EV) in Luquillo Experimental Forest. Dotted line indicates prehurricane annual mean litter mass (collected by Zou *et al.* 1995 in two plots in the midst of our study sites) (mean ± SE, n = 4 plots per 3-month period).

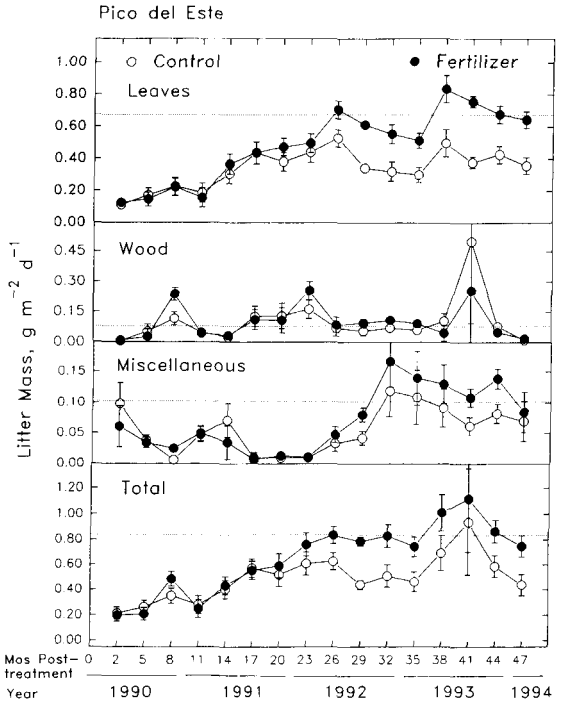

Fig. 3 Comparison of leaf, woody, miscellaneous, and total components of litter trapped in control and fertilized plots following Hurricane Hugo (September 1989) at the Pico del Este site (PE) in Luquillo Experimental Forest. Dotted line indicates prehurricane annual mean litter mass (collected from 1977 to 1978 in one plot adjacent to our plot 10; Weaver *et al.* 1986)(mean ± SE, n = 6 plots per 3-month period).

action at EV (P = 0.249) indicating that the trajectories were statistically parallel. At PE there was a significant time by treatment interaction ($P < 0.001$) because the trajectories diverged after 23 months. Recovery to prehurricane levels of leaf litter production occurred within 20 months in F and DR plots at EV and within 38 months in F plots at PE. Litter in C plots equalled prehurricane levels seasonally at EV within 32 months but did not return to prehurricane levels at PE during the study. Wood and miscellaneous components of the litter increased with time (EV wood, P = 0.01; EV miscellaneous, P = 0.003; PE wood, P = 0.023; PE miscellaneous, $P < 0.001$) but did not differ among treatments at either site. Total litterfall differed among treatments at EV (P = 0.001) but not at PE (P = 0.14) and increased significantly with time at both sites (EV, $P < 0.001$; PE, $P < 0.001$). At neither site was there a significant time–treatment interaction.

Standing litter from October 1993 did not differ among treatments within sites (Table 1), although leaf litter biomass in the F plots at PE tended (P= 0.058; two-way ANOVA) to be lower than in the C plots.

TREE GROWTH

Tree diameters (Table 2) increased with time at both EV ($P < 0.001$) and PE ($P < 0.001$), but treatment effects were not significant at either site. There was a significant time–treatment interaction at EV (P = 0.003; repeated measures ANOVA following adjustment for differences in tree diameter), indicating that diameters of trees in the DR treatment at EV did not increase as rapidly as trees in the C and F treatments. Subsequent ANOVAs on log-transformed data did not alter these results. There was no significant time–treatment interaction at PE. Trees had larger diameters at EV than at PE. Analysis by dominant tree species at each site (e.g. *Dacryodes excelsa* at EV, *Tabebuia rigida* at PE), pooled across plots within treatments, gave similar results (time effect at both sites, time-treatment interaction only at EV).

UNDERSTOREY

Live understorey biomass was lower at EV than at PE in all categories (Table 1). Graminoids at PE had 10-fold greater biomass in F plots (P = 0.045; two-way ANOVA) and bryophytes at PE had three-fold greater biomass in C plots (P = 0.009), but total biomass did not differ between treatments at PE. No other treatment differences were found for biomass at either site. Because significant cover (> 25%) of herbs was limited to one plot, data on herb biomass were not analysed.

Vegetation cover class data, presented as frequency distributions, were analysed by comparing plot means of midpoints of each cover class with repeated measures ANOVA. Means were transformed to arcsine-square roots prior to analysis. Cover of graminoids at EV (Fig. 4a,b) varied with time (P = 0.01) but not among treatments (P = 0.26). A significant time by treatment interaction ($P < 0.001$) occurred in part due to a sudden increase in cover of the grass, *Ichnanthus pallens* (Sw.) Munro in F plots at EV during the first 6 months after the hurricane (Fig. 4b). During the same time period there was no grass cover in C (Fig. 4a) and DR plots (data not shown). Cover of ferns at EV (data not shown) had no significant treatment or time effect but a gradual decline in F plots was indicated by a significant time by treatment interaction (P = 0.004). Maximal fern cover was reached 12–23 months after treatment initiation (5% of the plots with > 75% cover, 40% with < 75% cover). Cover of vines at EV (data not shown) was greatest (P = 0.04) in the C plots. Vine cover dropped in all plots during the first 18 months after the hurricane (to ≈ 30% of plots with 1-25% cover; significant time effect; $P < 0.001$) but the recovery of vines was less rapid in the F plots than in the C or DR plots (final vine cover in C and DR plots: 80% of plots with l–25% cover, 5–10% of plots with 51–75% cover; significant time by treatment interaction; P = 0.002). Cover of herbs and bryophytes was minimal at EV (< 25% in at least 80% of the plots and no cover values > 25%) and was not analysed. Cover of graminoids at PE (Fig 4c,d; primarily *Scleria canescens* Boeck. and *Panicum laxum* Sw.) did not differ between treatments (P = 0.11), because of large variation

Table 1 Components of understorey live biomass and standing litter (mean ± SE, g m $^{-2}$) in plots located in low altitude forest (El Verde; $n = 4$) and elfin forest (Pico del Este, $n = 6$). Samples were collected October–November 1993. Treatments were control (C), fertilization (F), and debris removal (DR)

	El Verde			Pico del Este	
Component	C	F	DR	C	F
Standing litter					
leaves	166.4 ± 39.5	179.2 ± 37.7	170.6 ± 19.9	113.7 ± 26.9	49.6 ± 4.8
wood	43.9 ± 8.7	45.9 ± 6.9	52.7 ± 7.1	102.7 ± 16.1	152.7 ± 34.8
miscellaneous	19.1 ± 7.9	54.1 ± 4.9	29.4 ± 8.4	44.5 ± 19.01	111.8 ± 32.6
total	229.3 ± 42.7	279.0 ± 47.6	252.8 ± 21.3	260.8 ± 41.5	314.0 ± 49.7
Live biomass					
graminoids	1.8 ± 1.3	0.2 ± 0.1	11.8 ± 10.7	21.4 ± 12.5	197.0 ± 59.0*
bryophytes	0	0	0	145.6 ± 31.9	47.6 ± 12.7*
ferns	4.4 ± 4.1	1.0 ± 0.9	7.1 ± 4.0	18.1 ± 11.2	42.8 ± 10.4
vines	6.8 ± 2.5	8.3 ± 8.2	2.9 ± 1.4	47.3 ± 31.7	37.0 ± 18.8
woody seedlings	11.8 ± 5.9	4.2 ± 2.0	7.0 ± 2.4	35.6 ± 14.7	21.4 ± 7.7
epiphytes	0	0	0	38.1 ± 21.2	0
total	24.8 ± 4.6	13.7 ± 9.0	28.7 ± 19.9	306.1 ± 45.9	345.8 ± 67.2

*$P < 0.05$.

Table 2 Mean tree diameters at El Verde (EV) and Pico del Este (PE) in months following initiation of fertilization or debris removal treatments. Plot means ($n = 4$, EV; $n = 6$, PE) that combine all trees > 5 cm d.b.h. are shown with ± 1 SE There are no debris removal experiments at PE

Site	Control	Fertilization	Debris removal
El Verde			
0 months	16.9 ± 1.0	18.3 ± 2.1	14.3 ± 2.0
12 months	17.2 ± 1.1	18.6 ± 2.1	14.5 ± 2.0
25 months	17.5 ± 1.2	18.9 ± 2.2	14.7 ± 2.0
35 months	17.7 ± 1.3	19.3 ± 2.2	14.8 ± 2.0
47 months	17.9 ± 1.3	19.5 ± 2.2	14.9 ± 2.1
Pico del Este			
0 months	9.3 ± 0.9	9.7 ± 0.7	
12 months	9.3 ± 0.9	9.7 ± 0.7	
25 months	9.3 ± 0.9	9.7 ± 0.7	
37 months	9.4 ± 0.9	9.8 ± 0.7	
48 months	9.4 ± 0.9	9.8 ± 0.7	

among plots, but did change with time ($P < 0.001$); the pattern of change differed between treatments (time by treatment interaction; $P < 0.001$). Graminoids dominated after 2 year in four of the six F plots, but a herb (*Pilea krugii* Urb.) dominated one plot, and little understorey response was found in the sixth plot (L. Walker, personal observation). Bryophyte cover at PE was significantly higher ($P = 0.007$) in C (Fig. 4e) than in F plots (Fig. 4f), and there were also significant time effects ($P < 0.001$) and time by treatment interactions ($P < 0.001$). Cover of ferns at PE (data not shown) did not vary by treatment ($P = 0.82$) or time ($P = 0.093$) but there was a time by treatment interaction ($P = 0{,}002$). Vegetative cover of other measured components of the vegetation was < 25% in at least two thirds of the plots and was not analysed.

Numbers of woody seedlings differed among treatments at both sites. At EV there were significant treatment ($P < 0.001$; DR > C > F), time ($P = 0.026$), and time by treatment interactions ($P < 0.001$) for woody seedling densities (Fig. 5a; analysed by repeated measures ANOVA), Woody seedling densities at PE (Fig. 5b) remained constant in the C plots but declined significantly over time in the F plots ($P < 0{,}001$) and trajectories for the two treatments (time-treatment interaction) were significantly different ($P < 0.001$). There was no significant treatment effect.

Recruitment of woody seedlings at EV was greatest in the DR plots (DR > F > C), particularly for species characteristic of early succession (e.g. *Cecropia schreberiana* Miq.). Debris removal had a negative effect on recruitment of some late successional species (e.g. *Dacryodes excelsa* Vahl.). Mortality was generally highest in the F plots (F > DR > C), but again differed by species. Full details are reported in Guzmán-Grajales & Walker (1991) and Guzmán-Grajales (1992).

Recruitment of new woody seedlings was greater in C plots at PE (51.3% of initial pool size of 117 seedlings) than in F plots (18.8% of initial pool of 131 seedlings). Seedling mortality (percentage of initial seedling pool) was greater in F plots (67.9%) at PE than in C plots (21.4%).

The density of new saplings at EV was significantly higher in the F plots than the C or DR plots (Fig. 6; $P = 0.002$; repeated measures ANOVA following log transformation). There were also significant changes in sapling density during the study (time effect; $P = 0.04$) but the temporal pattern of those changes did not vary by treatment (time by treatment interaction; $P = 0.39$). The cohort of saplings in the F plots was dominated by *Cecropia screberiana* individuals (103/133 or 77% of all saplings); 12 other sapling

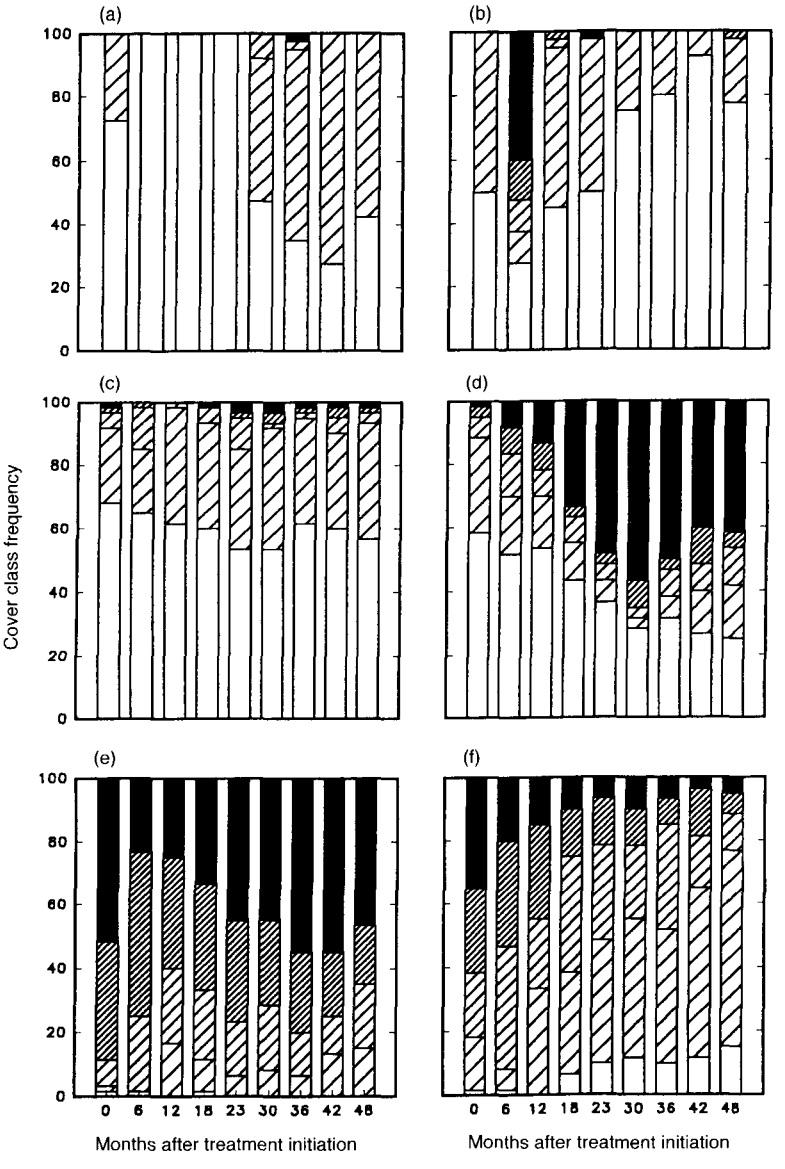

Fig. 4 Frequency distribution of understorey biomass. (a) graminoids in EV control plots; (b) graminoids in EV fertilizer plots; (c) graminoids in PE control plots; (d) graminoids in PE fertilizer plots; (e) bryophytes in PE control plots; and (f) bryophytes in PE fertilizer plots. Five cover classes are indicated as open (0% cover); open diagonal (1–25%); medium diagonal (26–50%); dense diagonal (51–75%); and solid (76–100%).

species were also recorded. Most recruitment of *Cecropia* saplings occurred earlier (within 11 months) than recruitment of other species (> 11 months after treatment initiation). A sharp decline in sapling densities between 35 and 48 months after treatment initiation resulted from high mortality of *Cecropia* saplings (Fig. 6).

Discussion

Our study indicated that Puerto Rican forests respond to hurricane disturbance in ways that are mediated by overall productivity as well as by the range of growth habits exhibited by the species assemblages. As predicted, leaf litter production was less responsive to nutrient additions in the elfin forest (Pico del Este, PE) than in the more productive lowland forest (El Verde, EV). However, understorey biomass was both greater and more responsive to nutrient additions at PE than at EV. Growth of graminoids at both sites and of a pioneer tree *(Cecropia)* at EV were much more responsive to nutrient additions than growth of mature forest trees, suggesting a partitioning of responses among understorey, pioneer and mature forest species.

LITTER FALL

Leaf litter production has been used as a convenient measure of forest productivity and nutrient cycling in the tropics (Vitousek & Sanford 1986) where high species richness confounds species-based approaches to measuring productivity. Rates of recovery of pre-disturbance levels of litterfall after defoliation by hur-

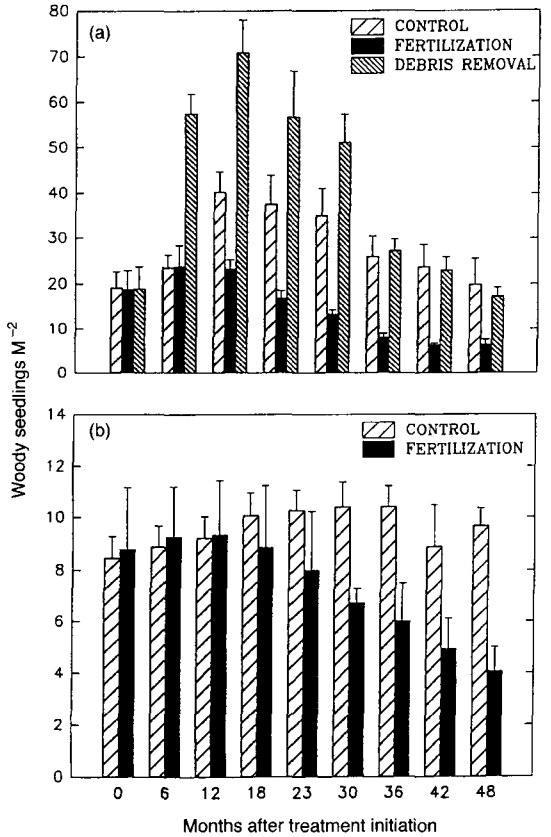

Fig. 5 Density of woody seedlings < 200 cm tall. (a) EV (n = 4 plots; (b) PE (n = 6 plots) (mean ± SE).

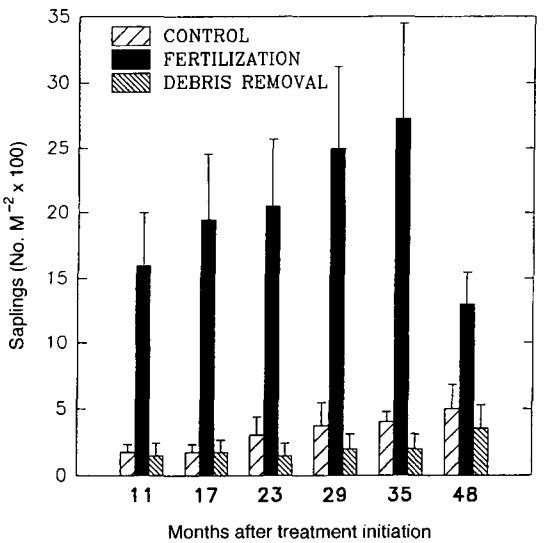

Fig. 6 Density of newly recruited saplings (> 2 cm d.b.h.) at EV (mean ± SE, n = 4 plots).

ricanes have not often been examined in tropical lowland forests (but see Whigham *et al.* 1991). Litterfall recovery may be influenced by the severity of defoliation (e.g. a seven-fold reduction in leaf litterfall by the hurricane at PE compared to a 2.5-fold reduction at EV), the degree and rate of resprouting of mature forest trees (Walker 1991; Yih *et al.* 1991; Bellingham *et al.* 1994) or the effects of significant nutrient inputs from litter additions during the hurricane (Lodge *et al.* 1991; Whigham *et al.* 1991; Zimmerman *et al.* 1995a) on nutrient cycling, nutrient immobilization, recruitment of pioneer trees, and growth of mature forest trees,

At EV, > 50% defoliation of the mature forest trees was followed by rapid recovery of the canopy, primarily by resprouting from the damaged branches of surviving trees (Walker 1991; Zimmerman *et al.* 1994). Where damage to the canopy is more severe, pioneer species may grow into the canopy, thereby altering its composition (Crow 1980; Brokaw & Walker 1991; Bellingham *et al.* 1995) and subsequent rates of leaf litter production. At PE, despite severe defoliation during Hurricane Hugo. total litter inputs were small compared to EV and woody debris was nearly absent (Brokaw & Grear 1991; Lodge *et al.* 1991). Recovery of litter production was much slower than at EV, as mature forest trees damaged by the hurricane replaced their foliage only slowly. Because pioneer species were largely absent from the forest at PE, much of the response to defoliation occurred in the understorey (see below).

We have demonstrated the importance of nutrients in re-establishing leaf production in this study (Figs 2 and 3). However, massive inputs of debris during a hurricane may result in net nutrient immobilization by microbial populations in the woody debris (Lodge *et al.* 1994; Zimmerman *et al.* 1995a) and a delay in recovery of leaf litter production (Fig. 2). Increased nutrient availability augmented production of leaf litter in both our lowland and elfin forests, but the mechanisms may differ. Litterfall nutrient concentrations (and biomass) are generally higher at low altitudes than in elfin forests (Proctor *et al.* 1983; Weaver *et al.* 1986; Veneklaas 1991; Lodge *et al.* 1991; Vitousek *et al.* 1995; but see Medina *et al.* 1981) and immobilization may be an important Factor limiting leaf litter production at lower altitudes. Nutrient immobilization by decaying wood at EV may suppress net primary productivity for 13 years (Sanford *et al.* 1991; Zimmerman *et al*, 1995a) following the hurricane. Higher available nitrogen levels in the DR and F plots (Zimmerman *et al.* 1995a) may explain our results showing higher leaf production in those treatments.

Leaf litter production in elfin forests is relatively slow to respond to fertilization (2 years in this study, 4 years in a fertilization experiment in Venezuela, Tanner *et al.* 1992), suggesting other factors besides microbial immobilization of nutrients may limit leaf litter production. Leaching or immobilization of nutrients in bryophytes or organic matter may limit leaf litter production by mature forest species in elfin forests (Proctor *et al.* 1983; Weaver *et al.* 1986; Veneklaas 1991; Weaver 1995). Low soil oxygen due to saturated soil conditions may limit the functioning of roots in nutrient uptake (W. Silver, personal communication). Additional environmental constraints on tree growth, including wind stress, low soil and

air temperatures, or lower mean irradiance (Byer & Weaver 1977; Lawton 1982; Weaver *et al.* 1986; Weaver 1990, 1995; Tanner *et al.* 1992) may also limit leaf litter production. Genetic constraints on leaf litter production are also a possibility (Chapin *et al.* 1986). Slow growth rates often lead to long-lived leaves resulting in slow leaf turnover (Chapin 1980). Thus, one might expect a slower response of litter production to nutrient additions at PE than at EV. At PE, there was actually a net loss of leaf production for one species *(Tabebuia rigida* Urban; Zimmerman, Ackerman & Walker, unpublished data) for several months following Hurricane Hugo.

Despite greater litter production at EV than at PE, total standing litter was similar (EV) or perhaps lower (PE) in F than in C plots, suggesting more rapid decomposition of litter at EV and in F plots (cf. Anderson & Swift 1983; Vogt *et al.* 1986). Factors that limit decomposition at PE (e.g. cold temperatures, saturated soils, a high degree of sclerophylly, and low nutrient to carbon ratios) may also limit above-ground primary production.

TREE GROWTH

Elfin forests are known to be shorter and grow more slowly than lower altitude forests (Grubb 1977; Tanner *et al,* 1992), yet the mechanisms causing these differences are not understood. Several studies have found that fertilization increased above-ground tree diameter growth in high altitude forests in Venezuela (N + P: Tanner *et al.* 1992), Jamaica (N or P: Tanner *et al.* 1990), and Hawaii (complete fertilizer: Gerrish *et al.* 1988; N: Vitousek *et al.* 1993). We tested the hypothesis that soil nutrients limit above-ground tree growth in the elfin forest. Our results confirmed that diameter growth was greater at EV than at PE, but, unlike the increases we found in litter production with fertilization, tree diameter growth did not increase with fertilization at either site. These results suggest that allocation of reserves in trees that were defoliated during the hurricane preferentially directed growth to the canopy rather than to the trunks (D. Whigham, personal communication). No changes in fine root biomass (< 3 mm diameter) were found during the first two years of our treatments at EV (Parrotta & Lodge 1991) or PE (Parrotta, Zimmerman & Lodge, unpublished data). The slower rate of tree diameter increase in the DR treatment at EV contrasts with increases in leaf litter production in DR plots. Drier soils (Lodge 1993) or greater branch damage during Hurricane Hugo in the DR plots may have reduced tree diameter growth. Our tree diameter growth data in unfertilized plots at EV (0.3 cm $year^{-1}$) and PE (0.025 cm $year^{-1}$) were similar to studies done prior to Hurricane Hugo at EV (0.15 cm $year^{-1}$, Wadsworth 1951; 0.18-0.36 cm $year^{-1}$, Murphy 1970) and PE (0-0.04cm $year^{-1}$, Weaver 1983; Weaver *et al.* 1986), indicating that growth of trunks may not be a very sensitive index of responses to disturbance.

UNDERSTOREY

Live understorey biomass (excluding saplings) was more than 10-fold greater at PE than at EV, largely because of the predominance of bryophytes at PE. However, graminoids, ferns, vines, epiphytes, and woody seedlings also had more biomass at PE. New saplings were only found at EV. The responses of understorey species to our treatments depended on changes in light and nutrient availability, often as mediated by canopy responses to the hurricane and the treatments. At EV, light, litter depth and nutrients all were important in explaining understorey responses. At PE, nutrients provide a partial explanation, but lack of sexual regeneration (seed and seedling pools) might also be important.

A detailed examination of understorey dynamics at EV during the first year after Hurricane Hugo (Guzmán-Grajales & Walker 1991) found highest woody seedling densities where the hurricane litter was removed (our DR plots). Our study extended this initial data set to 4 years and found the positive effect of the initial debris removal on woody seedling densities disappeared after 28 months (Fig. 5a). Fertilization at EV had a negative effect on woody seedling densities, One possibility is that seedlings were stressed by the repeated additions of fertilizer (Avvere & Shurtleff, personal communication). Alternatively, seedlings in the F plots at EV may have received more shade from the stands of developing *Cecropia* saplings (Fernández & Fetcher 1991), as suggested by higher LAI values in the F plots than the C plots (Zimmerman *et al.* 1995a). Standing litter was not greater in the F than the C plots, so inhibition by litter (Facelli & Pickett 1991) is not a likely explanation. Woody seedling densities in our C plots at EV (20–40 seedlings m^{-2}) were greater than densities of seedlings in nearby plots that were measured in 1965 (1–3 m^{-2}; Taylor *et al.* 1995), suggesting that the hurricane created conditions favorable to an overall increase in seedling densities. A combination of increased light after the hurricane (Fernández & Fetcher 1991) and increased nutrients may have been the cause of the rapid expansion, then decline of the grins, *Ichnanthus pallens,* in the EV F plots (Fig. 4b).

Cecropia schreberiana is a common pioneer at EV (Silander 1979) and is found in scattered locations at higher altitudes, including PE (Weaver 1990), Its seeds are dispersed widely by birds and bats (Holthuijzen & Boerboom 1982), and germinate in response to an increase in the ratio of red/far-red light such as occurs in a gap in the canopy (Silander 1979). Germination may also be triggered by increases in soil nitrogen (Everham 1993). Consequently, *Cecropia* saplings dominated many areas of LEF that were heavily damaged by Hurricane Hugo in 1989 and the declining

density of *Cecropia* trees has been used as an indicator of forest succession and recovery from the 1928 and 1932 hurricanes that also damaged the LEF (Crow 1980; Weaver 1989). Our results indicate that in addition to light availability, *Cecropia* recruitment is also strongly nutrient-limited at EV; fertilizer plots had approximately five fold more recruitment of *Cecropia* saplings than either control or debris removal plots at EV, At PE, no *Cecropia* were found near the plots, but several *Alchornia latifolia* Sw, (another pioneer species common at low altitudes) colonized fertilized plots.

High bryophyte and epiphyte biomass has been recorded for PE (Byer & Weaver 1977) and for other high altitude forests (Nadkarni 1984) and is probably sustained by the nearly constant high humidity. Graminoids and herbs at PE were the only understorey vegetation to respond positively to fertilization, perhaps because of the slow response of the trees, Two species (a sedge, *Scleria* and a grass, *Panicum)* that were present but relatively uncommon in the pre-hurricane understorey, expanded, perhaps vegetatively, into the F plots at PE, One F plot was dominated by a nonmycorrhizal, nutrient-responsive herb, *Piles.* Succession at PE in a nearby clearing made by a plane wreck was also dominated by ferns and grasses for > 18 year (Byer & Weaver 1977; Weaver 1990), although woody seedlings of mature forest species did invade after 6 years (Weaver 1990). Suggested reasons for the delay in reforestation included formation of a hardpan 60 cm below the soil surface (Odum 1970), low rates of sexual reproduction (Howard 1970; Nevling 1971), or leaching of nutrients (Weaver 1990). In contrast, Lawton & Putz (1988) found abundant regeneration of forest trees in natural gaps in an elfin forest in Costa Rica, particularly from buried seeds and epiphytic seedlings. Understorey woody seedlings at PE were dominated by *Wallenia yunquensis* (Urban) Mez that was not represented in the canopy. Stem sprouts of trees found in the canopy (particularly *Calycogonium squamulosum)* were also common. Biomass of woody seedlings was three- to four-fold greater at PE than at EV, despite two- to five-fold lower seedling densities, because both root sprouts and seedlings were larger at PE. Control plots at PE were dominated by bryophytes, not graminoids. Bryophytes are particularly sensitive to high salt concentrations (Avvere & Shurtleff, personal communication) and may have been stressed by application of the fertilizer. Alternatively, the graminoids may have out-competed any bryophytes present in the fertilizer plots.

SITE HISTORY

In addition to the recent impacts of Hurricane Hugo, historical disturbances are also important determinants of the present vegetation at each site. At EV, charcoal production, coffee plantations, and selective logging have had an impact on tree species distributions (Garcia-Montiel & Scatena 1994; Zimmerman *et al.* 1994; Zimmerman *et al.* 1995b) and subsequent regeneration processes. At PE, the access road to our site, built in 1965 (Howard 1968) may have increased the density of the graminoids and pioneer species. Weaver (1990) noted that the paucity of pioneer species at PE may be related to the relative lack of historical disturbances. Past hurricanes and tree-falls at both sites have also certainly influenced the distribution of species and therefore the likely sources of propagules available for posthurricane colonization.

CONCLUSIONS

We confirmed the presence of the broad aptitudinal differences in above-ground productivity and response to hurricane damage that we had expected to see in forests of the LEF: lower above-ground productivity and less responsiveness to disturbance and nutrient addition at PE, but nutrient limitation to productivity at both altitudes. These results suggest that the nature of recovery from a disturbance may differ depending on site productivity. Although disturbance history and soil fertility may be important in determining overall site productivity and long-term responses to disturbance, 'transient dynamics' (Tilman 1988) including growth rates, allocation patterns and propagule availability help explain the differences in short-term responses at our sites. The short-term responses of the above-ground vegetation to the hurricane at each site were mediated by interactions between canopy and understorey species. For example, the presence of fast-growing saplings at EV such as *Cecropia* and of mature forest trees that resprouted soon after the hurricane shortened the window of response of understorey species. Previous studies (e.g. Guzmán-Grajales & Walker 1991) suggest that regeneration of mature forest trees from seedlings was delayed and relatively minor. At PE, the absence of seedlings or saplings of fast-growing pioneer tree species, combined with the slower growth response of the mature forest trees allowed the graminoids (F plots) or bryophytes (C plots) to maintain high cover values for longer. Any shifts in species composition that did occur were minor because mature forest tree mortality was low at both sites. However, substantial shifts occurred in relative biomass found in different life forms,

Reproductive strategies clearly also had an effect on community responses to disturbance and nutrient additions. Species such as *Cecropia* may rely on widespread seed banks and germination cues that favour growth in gaps (changes in the light spectrum or nitrate levels). Other responses to disturbance include rapid vegetative expansion from existing populations (recovery of leaves of mature forest trees or the spread of graminoids or bryophytes). Light levels and pre-

disturbance density will determine which of these life forms is successful (e.g. canopy closure will reduce graminoid expansion). Slower responses to disturbance and/or nutrient pulses are demonstrated by the slow canopy recovery and stem and root sprouting of mature forest trees at PE. Recovery of mature forest tree species at PE can thus be delayed for decades by competition from faster-growing graminoids (Weaver 1990).

Competitive interactions may be more intense or prevalent in fertile sites with high productivity (Grime 1979; Keddy 1989) or may be equally important across ranges of productivity, although competition is likely to be for below-ground resources in less fertile sites and for above-ground resources in more fertile sites (Tilman 1988) .Apparent contradictions between these two viewpoints may actually hinge on whether one is considering absolute or relative competition intensity (Grace 1993). Although we did not measure the intensity of competition, our study supports both scenarios, Competition for light and the rapid closure of the canopy at EV had a major impact on responses both to the hurricane and to nutrient addition. However, nutrient immobilization by litter and therefore soil nutrient availability were also important at EV. At PE, canopy closure was not as critical as soil fertility or other soil factors (e.g. aeration, temperature) affecting soil nutrient availability. Our study also suggests that competition, often between different life forms, can be an important variable in recovery of sites of both high and low productivity.

The causes of lower primary productivity with increasing altitude in the tropics are best addressed experimentally. Our additions of a complete fertilizer indicate that responses depend not only on aptitudinal differences in plant communities, but also on plant size (canopy tree vs. sapling vs. understorey), species type (pioneer vs. nonpioneer), reproductive strategy, and disturbance history. Generalizations about controls over primary productivity must consider the relative importance of each of these variables.

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