BIOTROPICA 32(2): 262–275 2000

Seedling and Sapling Dynamics of Treefall Pits in Puerto Rico[1]

Lawrence R. Walker[2]

Department of Biological Sciences, University of Nevada, Las Vegas, Box 454004, 4505 Maryland Parkway,
Las Vegas, Nevada 89154-4004, U.S.A.

ABSTRACT

Seedling and sapling dynamics in a Puerto Rican rain forest were compared between forest understory and soil pits created by the uprooting of 27 trees during Hurricane Hugo. Soil N and P, organic matter, and soil moisture were lower and bulk densities were higher in the disturbed mineral soils of the pits than in undisturbed forest soils ten months after the hurricane. No differences in N and P levels were found in pit or forest soils under two trees with N-fixing symbionts *(Inga laurina* and *Ormosia krugii*) compared to soils under a tree species without N-fixing symbionts *(Casearia arborea*), but other soil variables (Al, Fe, K) did vary by tree species. Forest plots had greater species richness of seedlings (<10 cm tall) and saplings (10–100 cm tall) than plots in the soil pits (and greater sapling densities), but seedling densities were similar between plot types. Species richness and seedling densities did not vary among plots associated with the three tree species, but some saplings were more abundant under trees of the same species. Pit size did not affect species richness or seedling and sapling densities. Recruitment of young *Cecropia schreberiana* trees (>5 m tall) 45 months after the hurricane was entirely from the soil pits, with no tree recruitment from forest plots. Larger soil pits had more tree recruitment than smaller pits. Defoliation of the forest by the hurricane created a large but temporary increase in light availability. Recruitment of *C. schreberiana* to the canopy occurred in gaps created by the treefall pits that had lower soil nutrients but provided a longer-term increase in light availability. Treefall pits also significantly altered the recruitment and mortality of many understory species in the Puerto Rican rain forest but did not alter species richness.

Key words: Cecropia schreberiana; Dacryodes excelsa; *hurricane; nitrogen fixation; soil nutrients; tropical rain forest.*

TREEFALLS ARE A MAJOR CONSEQUENCE OF WINDSTORMS IN FORESTS (Brokaw 1985, Foster 1988), and create gaps in the forest canopy that may be critical to the regeneration of forest species (Denslow 1987, 1995). A treefall gap from an uprooted (vs. snapped or dead-standing) tree trunk consists of at least four distinct microsites: the mound, or pile of uprooted soil and roots; the soil pit, or shallow hole left after the major roots and attached soil are uprooted; the horizontal trunk; and the area where the crown of the tree fell (Uhl *et al.* 1988, Peterson *et al.* 1990). Each of these microsites differs from the surrounding forest and may have more light (Denslow 1987, Denslow *et al.* 1990), hotter, wetter, or drier soils (Beatty & Stone 1986, Peterson *et al.* 1990), or either lower or higher nutrient availability (Beatty & Sholes 1988) than the forest floor. Treefall gaps therefore may favor establishment of species not normally found in the understory of shaded forests (Putz 1983, Peterson & Pickett 1990, Peterson *et al.* 1990, Carlton & Bazzaz 1998). Differential species responses to these microsites is one way species diversity can be maintained in a forest (Beatty & Stone 1986, Denslow 1987, Brandani *et al.* 1988, Webb 1999).

Colonization of treefall gaps depends on the pool of available propagules and on an amelioration of the factors that normally limit growth in the understory. In boreal or temperate forests, slow decomposition of forest litter and cold wet soils may limit regeneration; thus exposure of mineral soil by an uprooted tree can be essential in providing the increased nutrients, increased soil temperatures, or decreased soil moisture needed for the establishment of many plant species (Murray & VanVeldhuizen 1980, Thompson 1980, Beatty & Stone 1986). Local responses, however, may vary considerably depending on microclimate, soil type, depth to water table, and disturbance severity (Carlton & Bazzaz 1998, Webb 1999). In tropical forests, light often is considered the resource that most limits the establishment and growth of plants in the understory (Denslow *et al.* 1990). Consequently, most studies of tropical treefall gaps have focused on the trunk and crown portions of the gap where the canopy opening is largest, but where the forest floor is undisturbed. Alternatively, soil nutrients may limit forest regeneration in tropical treefall gaps. Walker *et al.* (1996) noted dramatic species responses to artificial nutrient additions in hurricane-created gaps of Puerto Rican forests. Anderson and Swift (1983) and Zimmerman *et al.* (1995) demonstrated that nutrients can be immobilized in tropical forest gaps by the addition of large amounts of woody de-

---

[1] Received 17 August 1998; revision accepted 5 April 1999.
[2] E-mail address: walker@nevada.edu

bris. Yet Vitousek and Denslow (1986) found lower nutrient levels in the exposed mineral soil pits of treefalls in Costa Rica than along the trunk or under the fallen crown of the tree where woody debris is generally concentrated. Reductions in soil nutrient levels in soil pits compared to undisturbed forest soils therefore may limit plant colonization. Soil N in pits may be increased by the presence of N-fixing symbionts associated with the roots of the fallen tree (J. Lodge, pers. comm.), a factor that (to my knowledge) has not been examined previously. Increased N thus could increase seedling or sapling densities or favor colonization of species responsive to nutrient additions.

In this study, I compared seedling and sapling dynamics in soil pits and undisturbed forest floor, where both environments had experienced a temporary reduction in shade from the defoliation of the canopy during Hurricane Hugo (September 1989) but had soil conditions that were distinct. Soil pits were chosen as the microsite within the treefall gap most likely to differ in soil characteristics from the adjacent forest and most likely to alter plant establishment patterns. Soil mounds, important sites of establishment in some temperate forests (Webb 1999), erode quickly under the high rainfall conditions in Puerto Rico and were not considered in this study. I asked the following questions: (1) how does the soil physical environment differ between the soil pit and the forest floor?; (2) do tree species that have N-fixing symbionts influence soil nutrients or species composition of colonizers?; and (3) what are the consequences of uprooting and defoliation for populations of seedlings and saplings and for tree recruitment?

METHODS

This study was conducted within a 70-ha research forest near the El Verde field station in the Luquillo Experimental Forest (LEF) of eastern Puerto Rico (18°19′N, 65°49′W). The subtropical wet forest (Ewel & Whitmore 1973) is dominated by *Dacryodes excelsa* (tabonuco; Burseraceae) and *Prestoea montana* (sierra palm; Arecaceae). Prior to a recent hurricane (see below), the forest had a closed canopy at 20 to 25 m and generally sparse vegetation on the forest floor. At 350 to 400 m elevation, the forest receives a mean annual precipitation of 3460 mm and the mean monthly temperatures range between 21 and 25°C (Brown *et al.* 1983). 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. Taxonomic nomenclature follows Liogier and Martorell (1982).

Hurricane Hugo passed directly over the LEF on 18 September 1989, uprooting 9–39 percent of the trees (depending on distance to the center of the hurricane) and severely defoliating 56 percent of the trees in the LEF (Brokaw & Walker 1991, Walker 1991). Subsequent uprooting of trees damaged by Hurricane Hugo continued for over three years (Walker 1995); but all trees used in this study were uprooted during the hurricane, providing a unique opportunity to compare treefalls of identical age. My study area was in the forest that experienced the least damage (9% of all trees uprooted). A total of 27 uprooted trees ($\bar{x} = 16.5 \pm 2.6$ m tall) were chosen from two tree species with symbiotic N-fixing bacteria (Edmisten 1970), *Inga laurina* (Fabaceae; $N = 4$) and *Ormosia krugii* (Fabaceae; $N = 9$), and one tree species without the symbiont, *Casearia arborea* (Flacourtiaceae; $N = 14$). I observed live nodules on roots of the first two tree species but N fixation was not measured. These three species were among those most susceptible to uprooting (Walker 1991, Zimmerman *et al.* 1994) and represented all uprooted individuals of these three species that were found within easy access to trails within the lower third of the research forest. The trails were narrow footpaths covered by forest canopy and did not appear to alter light levels or species composition.

Length and width of each soil pit was recorded in May 1990 (8 mo after Hurricane Hugo). One plot (0.5 m^2; 50 × 100 cm) was placed in the center of the mineral soil of each pit (“pit plot”), and one plot (of equal size) in the undisturbed forest floor (“forest plot”) 2–5 m from the edge of the soil pit in a haphazardly chosen direction (excluding the area under the uprooted trees). The forest plots were selected to be outside the vertical extension of the canopy gap created by the treefall (Brokaw 1985) but still within the presumed zone of influence of roots and nodules from the target tree. The understory in the forest plots was largely undisturbed by the hurricane.

No light measurements were made in this study, but the effects of Hurricane Hugo on light levels were evaluated carefully by Fernández and Fetcher (1991) in a 32-m transect within the same forest (*ca* 0.1–0.6 km from my plots) that received similar hurricane damage. Their study showed that median values of total daily photosynthetic photon flux density (PPFD) 60 cm above the forest floor were similar to values in large treefall gaps (>400 m^2) for ten months after the hurricane. By 14 months, regrowth of the forest understory and canopy had reestablished a shaded forest environment (Fernández & Fetcher 1991). Although only pit plots in this study were located within the canopy gaps created by each treefall (*sensu* Brokaw 1985), both pit and forest plots were affected by the increased light availability created by defoliation of canopy trees. In addition, forest plots were not removed completely from possible increases in light from the adjacent treefall gap. Light levels between the pit and forest plots in this study were probably similar during the first ten months following the hurricane but stayed higher for a longer time in the pit plots than the forest plots. Therefore, soil and vegetation parameters were initially the principal distinction between pit and forest plots.

One sample of surface mineral soil (6 cm diameter × 5 cm deep) was collected from each 0.5-m^2 plot in July 1990 (10 mo after Hurricane Hugo). Mineral soils were sampled after the removal of the O1 and O2 organic horizons in the forest and any miscellaneous organic debris in the pit. The sampled soils thus represented the rooting medium for new or established seedlings. The fresh samples were weighed, dried for four days at 40°C, and weighed again to determine gravimetric water content (fresh minus dry mass divided by dry mass). Total organic matter was determined by mass loss upon ignition at 490°C for five hours. Bulk density was determined by dividing dry mass by volume, and soil pH was determined on a saturation paste obtained by mixing equal volumes of soil and water. Soils were then passed through a 0.15-mm (100 mesh) sieve and analyzed for total N using a modified Kjeldahl method to include nitrate and nitrite (Page 1982) and for total P (Luh Huang & Schulte 1985). Exchangeable ions were extracted using either 2N KCl (Al, Ca, Mg) or Olsen-EDTA (Fe, Mn, K) and analyzed with a Beckman plasma emission spectrometer (Hunter 1974).

Measurements of saplings, seedlings, and ground cover were made in the 0.5-m^2 plots in pits and adjacent forests seven times between May 1990 and May 1992, at 8, 13, 18, 22, 25, 30, and 32 months after Hurricane Hugo. At each visit, all woody saplings (10–100 cm tall; excluding vines) in each plot were identified and permanently labeled; all woody seedlings (<10 cm tall) were counted and their subsequent survivorship recorded (live = green leaves present). In addition, the cover of graminoids, ferns, vines, litter (leaves, twigs, and roots combined), and bare soil was estimated visually and assigned to one of five cover class categories (absent, <25, 26–50, 51–75, and >75%). To determine potential recruitment to the canopy 45 months after the hurricane (June 1993), the number of young trees that reached >5 m tall after the hurricane was counted in each 0.5 m^2 pit and forest plot. I also determined whether the original uprooted tree was alive (green leaves present) or dead after 45 months because live trees could reduce tree recruitment through competition.

Two-way ANOVAs (SigmaStat 1995) were used to compare soil parameters in pits versus forest plots (habitat effect) for each tree species (species effect). Two-way repeated measures ANOVAs (SigmaStat 1995) were employed to compare the changes in density of the total number of species, seedlings, and saplings between pit and forest plots during the 32-month study period and determine how these temporal patterns varied by the species of uprooted trees. One-way repeated measures ANOVAs were used to compare densities of each species during the study period. Linear regression was utilized to compare tree recruitment and the number of species in each plot versus overall soil pit dimensions, and nonparametric one-way ANOVAs (Kruskal-Wallis) to compare pit size and volume among the three uprooted tree species. Paired *t*-tests were used to compare recruitment and mortality of all species with at least one sapling appearing or dying during the study period. Chi-square analysis was applied to analyze the change in cover class frequencies with time, and tree recruitment as a function of the survival of the uprooted trees. One-way ANOVAs yielded comparisons of new tree recruitment as a function of the species of uprooted trees. All means are presented with standard errors and significance was determined at the 0.05 level.

RESULTS

Soils in the pits under uprooted trees had lower N, lower P, lower organic matter, were drier, had higher bulk densities, and were more acidic than soils from adjacent forest plots (Table 1). Soil concentrations of Al and Fe were higher and Ca was lower in pit soils than forest soils, Mg tended to be higher in forest than pit soils, and K and Mn did not differ between pit and forest soils (Table 2). Most soil parameters did not vary between tree species; however, Al and Fe were higher in *O. krugii* pit soils than *C. arborea* pit soils, and K was higher in forest soils adjacent to *O. krugii* than those adjacent to *C. arborea* (Table 2). Values for soil nutrients from *I. laurina* were generally intermediate between the other two species. Soil N was the only

TABLE 1. *Soil parameters from the pit and forest plots ($\bar{x}$ ± SE). Significant ANOVA results are indicated by *** ($P <$ 0.001). NS = not significant ($P >$ 0.05).*

Tree species	Plot type	Organic matter (%)	Moisture (%)	Bulk density (g/m^2)	pH
Ormosia	Pit	17.14 ± 0.82	27.91 ± 2.13	0.82 ± 0.02	3.40 ± 0.04
krugii	Forest	28.83 ± 1.61	40.22 ± 3.00	0.59 ± 0.06	3.53 ± 0.06
Casearia	Pit	20.22 ± 0.83	30.64 ± 2.71	0.83 ± 0.02	3.40 ± 0.05
arborea	Forest	25.94 ± 0.75	41.95 ± 2.51	0.65 ± 0.04	3.69 ± 0.08
Inga	Pit	19.22 ± 1.65	25.11 ± 1.91	0.83 ± 0.06	3.20 ± 0.04
laurina	Forest	26.53 ± 1.81	40.82 ± 2.44	0.63 ± 0.07	3.57 ± 0.13
Two-way ANOVA results:					
Species effect		0.785 NS	0.436 NS	0.955 NS	0.399 NS
Plot type effect		<0.001***	<0.001***	<0.001***	<0.002***
Species × plot interaction		0.614 NS	0.864 NS	0.896 NS	0.575 NS

soil factor with a significant interaction between habitat and tree species (Table 2): *O. krugii* soil N varied more between pit (low) and forest (high) plots than soils for *C. arborea* or *I. laurina.*

The number of species (saplings and seedlings combined) was higher ($P < 0.001$) in the forest than in the soil pits under each species of uprooted tree, and there was no difference in number of species among sampling dates within the forest or the pits or between uprooted tree species (Fig. 1a therefore shows all uprooted tree species combined). In contrast, seedling densities did not differ between forest and pit plots but tended ($P = 0.09$) to vary by date (Fig. 1b; all species combined because no differences were found among seedling densities for each of the three uprooted tree species). Seedlings associated with all three tree species had similar patterns of variation in density, with lowest values 18 months after Hurricane Hugo. Sapling densities demonstrated a significant plot type × tree species interaction ($P < 0.001$), due largely to the high mortality of *Cecropia schreberiana* (Moraceae) seedlings in forest plots associated with *I. laurina* trees and the variable relationship between the (higher; $P < 0.001$) densities in the forest and the (lower) densities in the pit plots (Fig. 2). Species of saplings that had significant changes ($P < 0.05$) in density during the study period are shown in Figure 3 (all species of uprooted trees combined to increase sample size because average plot frequency per species was low; Table 3). Two species were included that did not have significant density changes but illustrated plot to plot variability: *D. excelsa* in the forest plots that showed late increases in some plots only ($P = 0.191$), and *Miconia racemosa* (Melastomataceae) in pit plots that had large increases in some plots ($P = 0.06$). Another pioneer species, *Phytolacca rivinoides* (Phytolaccaceae), had a pattern and P value similar to that of *M. racemosa* in the pit plots. *Inga laurina* saplings were abundant in forest plots and had both large recruitment and mortality, but densities did not vary with time (Table 3). Densities of species characteristic of early succession ("pioneer species"; *e.g., Alchornea latifolia* [Euphorbiaceae], *C. schreberiana, Heterotrichum cymosum* [Melastomataceae]) declined significantly over time (Fig. 3); densities of some species characteristic of later successional forests ("primary species") increased significantly (*Matayba domingensis;* Sapindaceae) or tended to increase (*D. excelsa*). A full list of sapling species found in both pit and forest plots (Table 3) indicates that 23 species were found in both plot types, and that there was a total of 27 species in all pit plots combined, with 40 species in all forest plots (Sørensen's coefficient of similarity between pit and forest plots = 69%). Four species increased in density during the study period, four declined, and two showed both increases and declines. Species with the highest frequencies also had the highest maximum densities, but the variable date of highest density among species showed the dynamic nature of the sapling pool in both pit and forest plots. Numbers of species, seedlings, and saplings per 0.5-m^2 plot did not vary by overall pit area ($\bar{x} = 3.3 \pm 0.7$ m^2; $P = 0.67$, 0.15, 0.26, respectively). Pit size ($P = 0.52$) and pit volume ($P = 0.26$) did not vary among the three species of uprooted trees.

The patterns of sapling appearance during the study period had no significant relationship with mortality patterns (Table 3). *Casearia arborea* and *I. laurina* saplings were most abundant under uprooted trees of the same species, with higher mortality than recruitment, probably due to self-thinning of crowded saplings. Some pioneer species (*e.g., A. latifolia, C. schreberiana, Schefflera moro-*

TABLE 2. *Elemental analyses of soils from the pit and forest plots (mg/g;* $\bar{x}$ *± SE). Significant ANOVA results are indicated by * (P < 0.05), ** (P < 0.01), *** (P < 0.001). NS = not significant (P > 0.05).*

Tree species	Plot type	Nitrogen	Phosphorus	Aluminum	Calcium	Iron	Magnesium	Manganese	Potassium
Ormosia krugii	Pit	1.74 ± 0.10	0.22 ± 0.01	83.44 ± 4.03	0.17 ± .10	78.55 ± 3.76	0.99 ± 0.13	0.38 ± 0.14	0.51 ± 0.04
	Forest	6.36 ± 0.53	0.30 ± 0.01	70.11 ± 4.03	0.86 ± 0.10	62.55 ± 3.76	1.30 ± 0.13	0.68 ± 0.14	0.61 ± 0.04
Casearia arborea	Pit	3.06 ± 0.32	0.21 ± 0.01	68.07 ± 3.23	0.36 ± 0.08	62.28 ± 3.01	1.66 ± 0.11	0.35 ± 0.11	0.48 ± 0.03
	Forest	5.41 ± 0.37	0.29 ± 0.01	59.92 ± 3.23	0.79 ± 0.08	54.35 ± 3.01	1.34 ± 0.11	0.52 ± 0.11	0.46 ± 0.03
Inga laurina	Pit	2.71 ± 0.84	0.21 ± 0.02	66.25 ± 6.05	0.24 ± 0.15	64.25 ± 5.64	0.96 ± 0.20	0.25 ± 0.21	0.68 ± 0.07
	Forest	6.03 ± 0.15	0.30 ± 0.02	57.00 ± 6.05	0.60 ± 0.15	50.50 ± 5.64	1.17 ± 0.20	0.35 ± 0.21	0.55 ± 0.07
Two-way ANOVA results:									
Species effect		0.598 NS	0.765 NS	0.002**	0.439 NS	0.002**	0.696 NS	0.416 NS	0.027*
Plot type effect		<0.001***	<0.001***	0.009**	<0.001***	<0.001***	0.042*	0.157 NS	0.674 NS
Species × Plot interaction		0.032*	0.986 NS	0.774 NS	0.283 NS	0.479 NS	0.954 NS	0.809 NS	0.134 NS

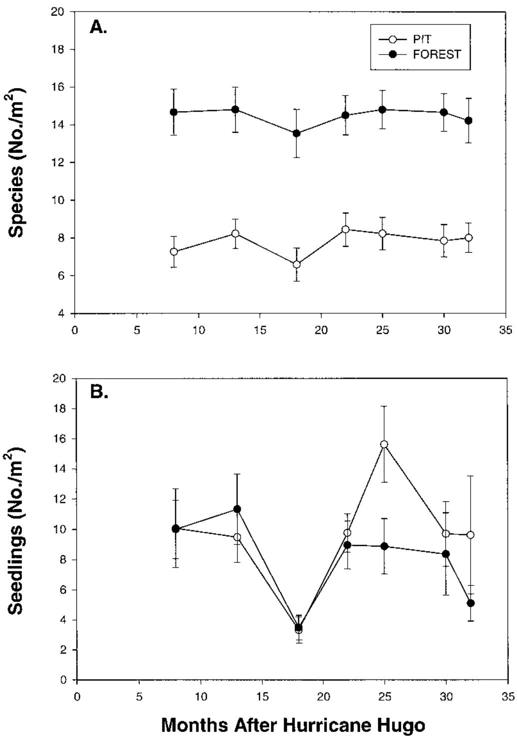

FIGURE 1. Species (Fig. 1a) and seedling (Fig. 1b) densities in pit (open circles) and forest (closed circles) plots under all three tree species combined for seven sampling dates following Hurricane Hugo (September 1989; no./m^2; $\bar{x}$ ± SE; N = 27).

totoni; Araliaceae) experienced high mortality of saplings already established in the plots before this study began eight months following the uprooting of the trees. Some primary forest tree species (*e.g., D. excelsa, Guarea guidonia* [Meliaceae], *M. domingensis, Myrcia splendens* [Myrtaceae], *Ocotea leucoxylon* [Lauraceae], and *O. krugii*) and understory shrub species (*e.g., Palicourea riparia* [Rubiaceae], *Piper glauca* [Piperaceae]) had net increases in sapling numbers (Table 3). Some of these increases represented growth of seedlings present in forest plots prior to the hurricane (advance regeneration). Only increases of *D. excelsa, M. splendens,* and *P. glauca* were statistically significant (Table 3). Interestingly, some species (*e.g., P. riparia, Tabebuia heterophylla* [Bignoniaceae]) had similar relationships between recruitment and mortality in both pit and forest plots, but other species differed (*e.g., C. arborea* and *C. schreberiana* saplings were more likely to die in the forest than the pit plots).

Cover of graminoids (mostly the grass *Ichnanthus pallens* [Poaceae]) declined during the study

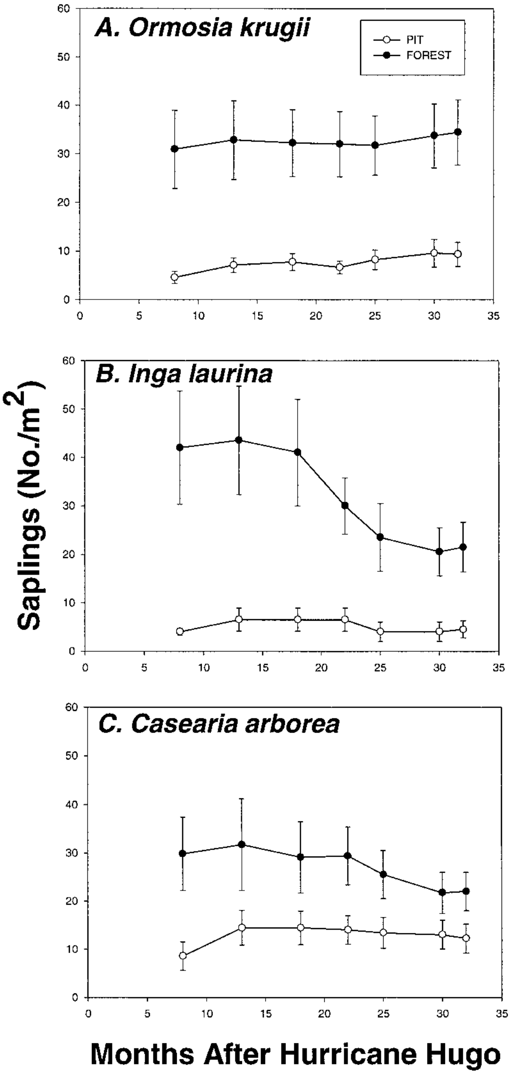

FIGURE 2. Sapling densities in pit and forest plots associated wth three tree species following Hurricane Hugo ($\bar{x}$ ± SE; $N = 9$, 14, and 4 for *Ormosia krugii, Inga laurina,* and *Casearia arborea,* respectively).

period in both the pit ($P = 0.04$) and forest ($P < 0.001$) plots (Fig. 4a,b; all three tree species combined) and was significantly greater in the forest plots ($P < 0.001$) than the pit plots. Cover of bare soil declined ($P = 0.004$) in the pit plots (Fig. 4c) and cover of litter increased in the pit plots (Fig. 4d; $P = 0.005$). Forest plots always had > 75 percent cover of litter, and bare soil was rare. Cover of vines and ferns in both habitats did not change during the study period.

Recruitment of woody plants (>5 m tall) into the forest canopy 45 months after the hurricane occurred in 80 percent of the pit plots but in none of the forest plots ($\bar{x} = 6.4 \pm 0.3$ m tall; $N = 41$ plants >5 m; density = 1.5 plants/plot), despite higher sapling densities in the forest. Pits with a larger overall area had more tree recruitment into the 0.5-m^2 plots than smaller pits ($P = 0.01$). Tree recruitment was not significantly different in pits of uprooted trees that were still alive 45 months after the hurricane versus uprooted trees that were dead ($P = 0.22$; $N = 23$ alive, 18 dead) and did not differ significantly among the three species of uprooted trees. All new trees were *C. schreberiana* ($N = 37$), but the large shrubs or small trees, *Psychotria berteriana* ($N = 1$) and *M. racemosa* ($N = 1$), and the tree fern (*C. arborea;* Cyatheaceae; $N = 2$) also reached heights of > 5 m during the 32-month study period.

DISCUSSION

The uprooting of between 9 and 39 percent of the trees in the LEF of Puerto Rico during Hurricane Hugo in September 1989 (Brokaw & Walker 1991) exposed *ca* 5 percent of the ground surface in one 16-ha plot (Zimmerman *et al.* 1994), but only 0.6 percent of a larger (6474 ha) portion in the LEF (Scatena & Larsen 1991). Background estimates of the percent ground surface exposed by uprooting are generally low in the tropics (*e.g.,* 0.09%; Putz 1983) compared to the temperate zone (6–45%; Beatty & Stone 1986, Webb 1988), perhaps due to the rapid leveling of pit and mound microtopography in the tropics (Putz 1983) and stony soils that allow mounds to persist in some temperate forests (S. Webb, pers. comm.). Despite the relatively small area of ground surface that they impact, treefalls alter the physical environment in ways that affect nutrient availability, light, litterfall, and forest regeneration (Richards & Williamson 1975, Denslow 1987, Uhl *et al.* 1988). In Puerto Rico, treefall pits provided a microhabitat that favored recruitment of *C. schreberiana,* a colonizing tree species, and altered establishment and mortality patterns of understory plants, but not overall species richness.

The soils in 10-month-old treefall pits of Puerto Rico had lower soil nutrient (total N and P) levels, soil organic matter, and soil moisture than soils from adjacent undisturbed forests. These soil conditions, generally unfavorable to plant growth, resulted from the upheaval and removal of surface organic matter and exposure of subsurface mineral soils (Beatty & Stone 1986, Vitousek & Denslow 1986). N availability (not measured in this study)

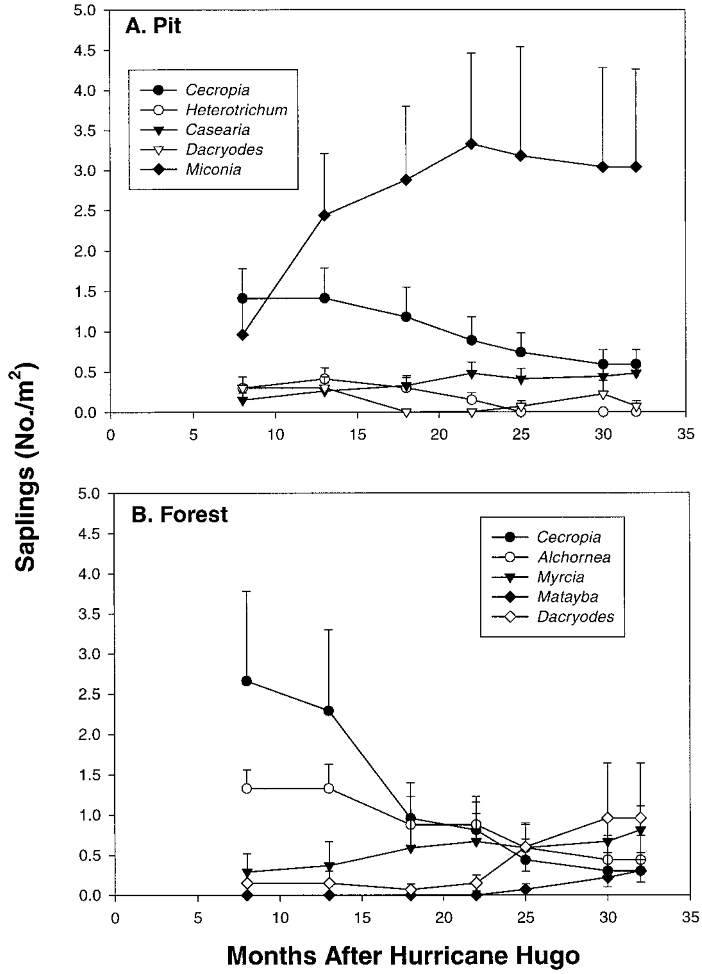

FIGURE 3. Sapling densities ($\bar{x}$ ± SE, $N = 27$) that changed significantly through time ($P < 0.05$, repeated measures ANOVA) following Hurricane Hugo, with the exception of *Dacryodes excelsa* in the forest plots ($P = 0.191$). See Table 3 for full species names.

may not increase initially in a treefall pit as it does below the trunk or crown of a fallen tree (Uhl *et al.* 1988). Vitousek and Denslow (1986) found that pit soils contained less available N and P than forest soils in two- to seven-month-old Costa Rican treefall gaps. Soil nitrate levels, however, may increase immediately following forest disturbances such as clear-cutting (Vitousek & Reiners 1975) or trenching (Silver & Vogt 1993) due to root decay and leaching. Increases in nitrates may trigger germination of colonizing species such as *C. schreberiana* (Everham *et al.* 1996) and the growth of such species is also responsive to nutrients. In several post-hurricane studies in the LEF, artificial fertilization greatly increased density and growth of *C. schreberiana* saplings and trees (Walker *et al.* 1996). The experimental removal of fine leaf litter that fell during Hurricane Hugo (Lodge *et al.* 1991) increased *C. schreberiana* seedling densities initially but reduced seedling and sapling growth, presumably because it removed nutrients made available through decomposition of the litter (Guzmán-Grajales & Walker 1991). Erosion of the mound (Peterson *et al.* 1990) and subsequent additions of litter gradually increase nutrient levels in the pit.

The species of the uprooted tree had no effect on total soil N or P (*cf.* Vitousek & Denslow 1986), with the exception of a greater difference in soil N between forest and pit soils for *O. krugii* than for *C. arborea.* Plot type and/or tree species effects were found for all soil variables except Mn. The higher Al and Fe levels and lower pH in pit

TABLE 3. *Maximum sapling densities ($\bar{x}$ ± SE; N = 27 plots), frequencies, recruitment, and mortality in pit and forest plots, ordered by frequency of occurrence in the 27 pit plots, then decreasing frequency of remaining species found only in the forest plots. Dates of maximum density (first date if several dates have equally high densities) are in months after Hurricane Hugo (1 = 8, 2 = 13, 3 = 18, 4 = 22, 5 = 25, 6 = 30, 7 = 32 mo). Stars following the date indicate significant change in density during the experiment (repeated measures ANOVA; (*) = $P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). Symbols following the star indicate generally positive or negative direction to the changes in density. Frequency is the percentage of 27 plots in which each species was found. Recruitment and mortality are the total numbers of saplings that appeared or died during the 24-month study period.*

Species	Maximum density (Pit)	Date	Frequency	Recruitment	Mortality	Maximum density (Forest)	Date	Frequency	Recruitment	Mortality
1. *Cecropia schreberiana*	1.41 ± 0.37	1**/−	0.48	1	13	2.26 ± 1.12	1**/−	0.29	0	35
2. *Miconia racemosa*	3.33 ± 1.13	4(*)/+	0.44	53	18	0.30 ± 0.17	2	0.11	5	5
3. *Psychotria berteriana*	1.92 ± 0.61	3(*)/+	0.33	15	8	0.59 ± 0.26	4	0.18	2	5
4. *Casearia arborea*	0.48 ± 0.14	4*/+	0.33	12	2	3.85 ± 2.88	2	0.26	24	36
5. *Palicourea riparia*	0.74 ± 0.26	2	0.29	17	7	2.29 ± 0.86	4	0.37	25	11
6. *Heterotrichum cymosum*	0.41 ± 0.14	2***/−	0.29	4	13	0	—	—	—	—
7. *Tabebuia heterophylla*	1.26 ± 0.82	2	0.22	14	12	1.26 ± 0.51	2	0.26	12	11
8. *Schefflera morototoni*	0.51 ± 0.27	6	0.15	3	3	2.51 ± 0.74	2	0.44	8	16
9. *Phytolacca rivinoides*	0.15 ± 0.07	1(*)/−	0.15	0	4	0	—	—	—	—
10. *Dacryodes excelsa*	0.30 ± 0.14	1*/−,+	0.15	3	3	0.96 ± 0.68	6	0.15	15	4
11. *Alchornea latifolia*	0.15 ± 0.07	5	0.07	1	0	1.33 ± 0.35	1***/−	0.44	2	14
12. *Laetia procera*	0.14 ± 0.10	6	0.07	2	1	0.44 ± 0.25	2	0.18	4	5
13. *Guarea guidonia*	0.07 ± 0.07	3	0.04	2	0	1.26 ± 0.51	7	0.33	10	2
14. *Ocotea leucoxylon*	0.07 ± 0.07	1	0.04	0	0	1.55 ± 0.62	1	0.33	4	4
15. *Piper glauca*	0.07 ± 0.07	1	0.04	0	1	1.63 ± 0.60	5(*)+,−	0.33	20	10
16. *Byrsonima coriacea*	0.22 ± 0.22	5	0.04	4	1	1.63 ± 1.18	1	0.29	8	7

TABLE 3. *Continued.*

Species	Maximum density (Pit)	Date	Frequency	Recruitment	Mortality	Maximum density (Forest)	Date	Frequency	Recruitment	Mortality
17. *Myrcia splendens*	0.07 ± 0.07	7	0.04	1	0	0.81 ± 0.30	7*/+	0.26	10	2
18. *Nectandra sintenisii*	0.07 ± 0.07	7	0.04	0	1	1.33 ± 0.97	1	0.26	5	12
19. *Prestoea montana*	0.37 ± 0.30	6	0.04	6	1	0.59 ± 0.24	4	0.22	2	3
20. *Chionanthus domingensis*	0.07 ± 0.07	2	0.04	1	1	2.37 ± 1.33	2	0.22	8	18
21. *Ormosia krugii*	0.07 ± 0.07	2	0.04	1	0	0.74 ± 0.47	3	0.22	7	4
22. *Matayba domingensis*	0.07 ± 0.07	6	0.04	2	0	0.30 ± 0.14	7	0.15	5	0
23. *Psychotria patens*	0.07 ± 0.07	1	0.04	1	0	0.07 ± 0.07	2	0.07	1	0
24. *Casearia sylvestris*	0.07 ± 0.07	4	0.04	1	1	0	—	—	—	—
25. *Tetragastris balsaminifera*	0.07 ± 0.07	4	0.04	1	0	0.51 ± 0.27	4	0.15	2	0
26. *Hirtella rugosa*	0.07 ± 0.07	2	0.04	0	1	0.15 ± 0.15	7	0.04	2	0
27. *Trema micranthum*	0.07 ± 0.07	1	0.04	0	1	0	—	—	—	—
28. *Inga laurina*	0	—	—	—	—	5.85 ± 2.59	3	0.48	21	35
29. *Andira inermis*	0	—	—	—	—	0.07 ± 0.07	4	0.15	1	0
30. *Manilkara bidentata*	0	—	—	—	—	0.29 ± 0.23	1	0.07	0	0
31. *Psychotria brachiata*	0	—	—	—	—	0.15 ± 0.10	1	0.07	0	0
32. *Homalium racemosum*	0	—	—	—	—	0.15 ± 0.10	5	0.07	1	0
33. *Nectandra antillana*	0	—	—	—	—	0.29 ± 0.29	1	0.04	0	2
34. *Swietenia macrophylla*	0	—	—	—	—	0.15 ± 0.15	1	0.04	0	0

TABLE 3. *Continued.*

Species	Maximum density (Pit)	Date	Frequency	Recruitment	Mortality	Maximum density (Forest)	Date	Frequency	Recruitment	Mortality
35. *Alchorneopsis portoricensis*	0	—	—	—	—	0.07 ± 0.07	1	0.04	0	1
36. *Ocotea floribunda*	0	—	—	—	—	0.07 ± 0.07	1	0.04	0	0
37. *Inga vera*	0	—	—	—	—	0.07 ± 0.07	6	0.04	1	0
38. *Ixora ferrea*	0	—	—	—	—	0.81 ± 0.81	4	0.04	3	9
39. *Piper amalago*	0	—	—	—	—	0.07 ± 0.07	1	0.04	1	2
40. *Samyda dodecandra*	0	—	—	—	—	0.07 ± 0.07	1	0.04	0	0
41. *Buchenavia capitata*	0	—	—	—	—	0.07 ± 0.07	1	0.04	0	0
42. *Solanum rugosum*	0	—	—	—	—	0.07 ± 0.07	1	0.04	0	0
43. *Trichilia pallida*	0	—	—	—	—	0.07 ± 0.07	5	0.04	1	0
44. *Myrcia leptoclada*	0	—	—	—	—	0.07 ± 0.07	1	0.04	0	0

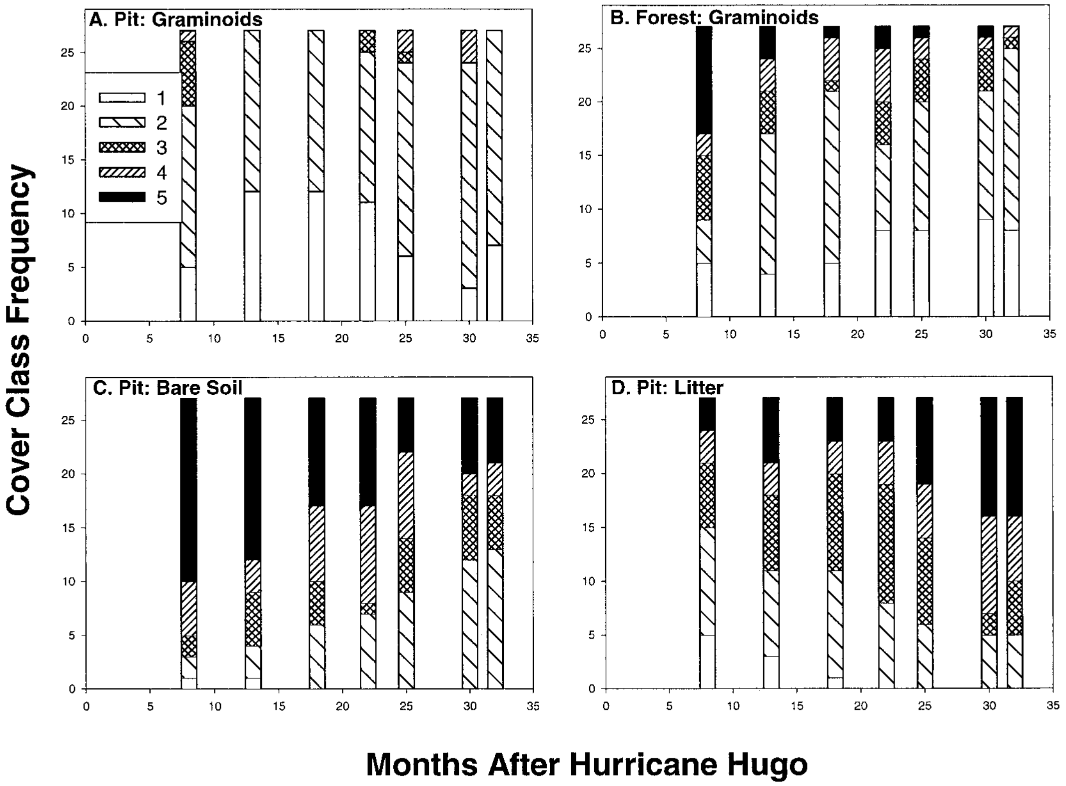

FIGURE 4. Cover class frequencies of four variables that changed significantly during the 32-month study period (graminoids in the pit and forest plots, bare soil and litter in the pit plots). Cover classes are: 1 = absent; 2 = <25; 3 = 26–50; 4 = 51–75; 5 = >75 percent (*N* = 27 plots).

versus forest soils and the higher Al and Fe levels under *O. krugii* than under *C. arborea* trees may be due to leaching of cations by increased nitrate levels (Silver & Vogt 1993; J. Lodge, pers. comm.). There were few effects of tree species on understory plant dynamics, suggesting that the N-fixing bacteria associated with *O. krugii* and *I. laurina,* although influencing some aspects of soil chemistry, were not important determinants of species composition or density. Two effects of tree species that did occur were the abundance of *I. laurina* seedlings under *I. laurina* trees and *C. arborea* seedlings under *C. arborea* trees, presumably more a matter of dispersal than nutrient dynamics.

If nutrients limit plant establishment, one would expect lower densities of seedlings and saplings in soil pits than in the forest, with increases in density as soil nutrients in pits accumulated. Species richness and sapling densities, but not seedling densities, were lower in pits than forests, probably reflecting not only soil nutrient differences but also the lack of disruption of pre-hurricane sapling populations in the forest understory or rapid germination from buried seed pools (Guariguata 1990). Seedling densities were highly variable in both habitat types and had similar temporal patterns. The distinct drop in seedling densities between 15 and 18 months after Hurricane Hugo (October 1990–March 1991) did not coincide with any increase in sapling densities but did coincide with a period of low rainfall (Scatena *et al.* 1996), suggesting drought as a probable cause of increased seedling mortality in both pit and forest plots. There was no increase in species richness during the study, but densities of several species of saplings varied significantly through time despite high variability among plots. The densities of sapling species typical of early succession generally declined and some species typical of later succession increased during the study period. For some species, recruitment and mortality were similar in pit and forest plots, but *C. schreberiana* and *C. arborea* saplings were more likely to die in the forest than the pit plots. There was no pronounced mortality of saplings between 13 and 18 months following the hurricane.

Treefalls may have their greatest effect on tropical forest regeneration through altering light levels at the forest floor rather than by altering soil nutrients (Vitousek & Denslow 1986, Denslow *et al.* 1990). *Cecropia schreberiana* and other early successional species often have viable seeds in the soil, germinate in response to an increase in red:far-red ratios or soil temperature, and grow rapidly in high light environments (Silander 1979, Vásquez-Yanes & Smith 1982, Denslow 1987). During Hurricane Hugo, defoliation resulted in increased light levels at the forest floor (Fernández & Fetcher 1991). Defoliation, however, was variable throughout the LEF, and stands of *C. schreberiana* trees established after the hurricane in areas of the forest where defoliation approached 100 percent (Scatena & Lugo 1995). In my study area, defoliation was less (56% of the trees were >75% defoliated) and although seedlings of *C. schreberiana* established on the forest floor (initially denser than in the pits), mortality was high because the canopy closed above the seedlings. *Cecropia schreberiana* seedlings grew into canopy trees only in the treefall pits, presumably as a consequence of both the temporary (*ca* 1 yr) increase in light from defoliation of the surrounding canopy and the longer (*ca* 2–4 yr) increase in light from the uprooting of the tree. The longer period of time allowed some individuals to reach the canopy before the gap closed from lateral expansion of canopy trees (Putz 1983, Putz *et al.* 1983, Walker 1991). Such rapid growth (>4 m/yr) has been noted before in the LEF (Odum 1970). Gap size influences light availability and subsequent plant responses (Chazdon & Fetcher 1984, Denslow 1987), including three-fold faster growth of saplings in multiple treefall gaps than in single treefall gaps of Venezuela (Uhl *et al.* 1988). Pioneer species such as *Cecropia* are also more likely to survive in larger than in smaller gaps (Putz 1983). Brokaw (1987) observed that background (non-hurricane) treefall gaps of at least 150 to 250 m^2 are best for establishment and growth of pioneers such as *C. schreberiana.* Such gap sizes are not common in the LEF except following hurricanes; thus widespread hurricane damage may be necessary to explain the current densities of *C. schreberiana* in the LEF (Brokaw 1998). In this study, the local treefall gaps were rarely >50m^2, so the extended gap duration provided by the uprooting of trees and subsequent delay in canopy closure was apparently critical for establishment of *C. schreberiana* trees. Pit size also was important, as more *C. schreberiana* established in larger pits; there were no size effects on other plant species.

Litterfall is another factor that affects forest regeneration (Beatty & Sholes 1988, Facelli & Pickett 1991, Guzmán-Grajales & Walker 1991, Molofsky & Augspurger 1992). Treefalls may increase litterfall under the fallen crown locally and litter may accumulate gradually in the depression formed by soil pits (Beatty & Stone 1986). Defoliation in the LEF during Hurricane Hugo deposited a thick layer of litter equivalent to more than one year of normal litterfall (Lodge *et al.* 1991). Seedling and sapling responses to the hurricane litterfall in the forest varied, but litter generally increased species richness and reduced seedling and sapling density (Guzmán-Grajales & Walker 1991). In contrast to the forest, the mineral soil exposed at the base of uprooted trees was generally litter-free, suggesting general forest leaf loss during the hurricane occurred prior to treefall in most cases; however, post-hurricane litterfall rapidly covered the pit plots with litter. The consistently higher seedling and sapling species richness and sapling density in the forest plots in this study were probably more a function of establishment dynamics than of differential litter depth. Establishment of seedlings in the pits occurred during the litter-free period within several months after the hurricane (Guzmán-Grajales & Walker 1991). Seedling recruitment then slowed, resulting in the stable populations seen during this study. Seedling and sapling populations in the forest were largely undamaged by the hurricane (Guzmán-Grajales & Walker 1991) and further establishment, when light levels were raised, may have been inhibited by the new hurricane litter, or by the initially rapid growth of graminoids (particularly *I. pallens).*

Treefall pits in Puerto Rico created small islands of infertile soil that were nevertheless colonized by such pioneers as *C. schreberiana*, *M. racemosa*, and *C. arborea.* These species are also typical colonists of larger infertile gaps such as landslides (Guariguata 1990, Walker & Neris 1993). Perhaps soil infertility in the mineral soil of the pit was only limiting to growth of colonizers until their roots could tap the higher nutrient levels in the adjacent forest floor (*C. schreberiana* recruitment was denser at the edge than at the center of the pits; L. Walker, pers. obs.). Alternatively, reduced root competition may favor seedling establishment. With the additional light following the defoliation of the LEF by Hurricane Hugo, these treefall pits provided an opportunity for *C. schreberiana* saplings to reach the canopy, many of which survived to reproduce and reestablish the seed bank (Brokaw 1998). In this sense, the net effect of the hurricane and treefall combination resembled multiple or large treefall gaps (*cf.* Uhl *et al.* 1988). In contrast, the temporarily higher light conditions in the forest plots due to leaf loss during the hurricane were not sufficient to allow establishment of *C. schreberiana* trees or the growth of understory seedlings of other species into the canopy. Instead, existing canopy trees closed the gaps with lateral growth. Therefore, the net effect of the treefall gaps on the species composition of the forest was an increase in the numbers of *C. schreberiana* trees during the first 45 months following Hurricane Hugo. The treefall pits also substantially altered the relative abundances, but not the overall species richness, of populations of other forest canopy and understory species.

ACKNOWLEDGMENTS

I thank M. Aponte, W. Boneta, C. Cancel, M. Cruz, S. Guzmán-Grajales, A. Horowitz, M. Milian, L. Neris, and G. Rivera for assistance with fieldwork. Soils analyses kindly were performed by M. Sánchez at the International Institute of Tropical Forestry. Comments by N. Brokaw, D. Clark, J. Lodge, C. Peterson, E. Powell, S. Webb, J. Zimmerman, and an anonymous reviewer improved the manuscript. This project was funded by NSF grant BSR-8811902 to the Terrestrial Ecology Division, University of Puerto Rico, and to the International Institute of Tropical Forestry (USDA Forest Service) as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by NSF grant RII-8903827 to the University of Puerto Rico.

LITERATURE CITED

Anderson, J. M., and M. J. Swift. 1983. Decomposition in tropical forests. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). Tropical rain forest ecology and management, pp. 287–309. Blackwell Scientific, London, England.

Beatty, S. W., and O. D. V. Sholes. 1988. Leaf litter effect on plant species composition of deciduous forest treefall pits. Can. J. For. Res. 18: 553–559.

———, and E. L. Stone. 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. 16: 539–548.

Brandani, A., G. S. Hartshorn, and G. H. Orians. 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. J. Trop. Ecol. 4: 99–119.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66: 682–687.

———. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. J. Ecol. 75: 9–19.

———. 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. Bot. Rev. 64: 91–120.

———, and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23: 442–447.

Brown, S., A. E. Lugo, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo Experimental Forest. U.S. For. Serv. Gen. Tech. Rep. SO-44.

Carlton, G. C., and F. A. Bazzaz. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecol. Monogr. 68: 99–120.

Chazdon, R. L., and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. J. Ecol. 72: 553–564.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annu. Rev. Ecol. Syst. 18: 431–451.

——— 1995. Disturbance and diversity in tropical rain forests: the density effect. Ecol. Appl. 5: 962–968.

———, J. C. Schultz, P. M. Vitousek, and B. R. Strain. 1990. Growth responses of tropical shrubs to treefall gap environments. Ecology 71: 165–179.

Edmisten, J. 1970. Survey of mycorrhiza and nodules in the El Verde Forest. *In* H. T. Odum and R. F. Pigeon (Eds.). A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico, pp. F15–F20. N.T.I.S., Springfield, Virginia.

Everham, E. M., III, R. W. Myster, and E. VanDeGenachte. 1996. Effects of light, moisture, temperature, and litter on the germination of five tree species in the tropical montane wet forest of Puerto Rico. Am. J. Bot. 83: 1063–1068.

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

Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. 57: 1–32.

Fernández, D. S., and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. Biotropica 23: 393–399.

Foster, D. R. 1988. Disturbance history, community organization, and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, U.S.A. J. Ecol. 76: 105–134.

Guariguata, M. R. 1990. Landslide natural disturbances and forest regeneration in the Luquillo Mountains of Puerto Rico. J. Ecol. 78: 814–832.

Guzmán-Grajales, S. M., and L. R. Walker. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 407–413.

Hunter, A. H. 1974. International soil fertility evaluation and improvement. Laboratory procedures. Department of Soil Science, North Carolina State University, Raleigh, North Carolina.

LIOGIER, H. A., AND L. F. MARTORELL. 1982. Flora of Puerto Rico and adjacent islands: a systematic synopsis. Editorial Universidad de Puerto Rico, San Juan, Puerto Rico.

LODGE, D. J., F. N. SCATENA, C. E. ASBURY, AND M. J. SÁNCHEZ. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. Biotropica 23: 336–342.

LUH HUANG, C. Y., AND E. E. SCHULTE. 1985. Digestion of plant tissue for analysis by ICP emission spectroscopy. Comm. Soil Sci. Plant Anal. 16: 943–958.

MOLOFSKY, J., AND C. K. AUGSPURGER. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73: 68–77.

MURRAY, M., AND R. M. VANVELDHUIZEN (EDS.). 1980. Forest regeneration at high latitudes. USDA For. Serv. Gen. Tech. Rep. PNW-107, Portland, Oregon.

ODUM, H. T. 1970. Summary: an emerging view of the ecological system and El Verde. *In*: H. T. Odum and R. F. Pigeon (Eds.). A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico, pp. I191–I289. National Technical Information Service, Springfield, Virginia.

PAGE, A. E. 1982. Methods of soil analysis, part 2. American Society of Agronomy, Madison, Wisconsin.

PETERSON, C. J., W. P. CARSON, B. C. MCCARTHY, AND S. T. A. PICKETT. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58: 39–46.

———, AND S. T. A. PICKETT. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. J. Veg. Sci. 1: 657–662.

PUTZ, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64: 1069–1074.

———, P. D. COLEY, K. LU, A. MONTALVO, AND A. AIELLO. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Can. J. For. Res. 13: 1011–1020.

RICHARDS, P., AND G. B. WILLIAMSON. 1975. Treefalls and patterns of understory species in a wet lowland tropical forest. Ecology 56: 1226–1229.

SCATENA, F. N., AND M. C. LARSEN. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23: 317–323.

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

———, S. MOYA, C. ESTRADA, AND J. D. CHINEA. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28: 424–440.

SIGMASTAT 1995. Statistical software, Version 2.0. Jandel Corporation, San Rafael, California.

SILANDER, S. R. 1979. A study of the ecological life history of *Cecropia peltata* L., an early successional species in the rain forest of Puerto Rico. M.S. thesis, University of Tennessee, Knoxville, Tennessee.

SILVER, W., AND K. A. VOGT. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. J. Ecol. 81: 729–738.

SOIL SURVEY STAFF. 1995. Order 1 soil survey of the Luquillo Long-Term Ecological Research grid, Puerto Rico. USDA, Natural Resources Conservation Service.

THOMPSON, J. N. 1980. Treefalls and colonization patterns of temperate forest herbs. Am. Midl. Nat. 104: 176–184.

UHL, C., K. CLARK, N. DEZZEO, AND P. MAQUIRINO. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology 69: 751–763.

VÁSQUEZ-YANES, C., AND H. SMITH. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance. New Phytol. 92: 477–485.

VITOUSEK, P. M., AND J. S. DENSLOW. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. J. Ecol. 74: 1167–1178.

———, AND W. REINERS. 1975. Ecosystem succession and nutrient retention: a hypothesis. BioScience 25: 376–381.

WALKER, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 379–385.

———. 1995. Timing of post-hurricane tree mortality in Puerto Rico. J. Trop. Ecol. 11: 315–320.

———, AND L. NERIS. 1993. Post-hurricane seed rain dynamics in Puerto Rico. Biotropica 25: 408–418.

———, J. K. ZIMMERMAN, D. J. LODGE, AND S. GUZMÁN-GRAJALES. 1996. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. J. Ecol. 84: 877–889.

WEBB, S. L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. Can. J. For. Res. 18: 1186–1195.

———. 1999. Disturbance by wind in temperate-zone forests. *In* L. R. Walker (Ed.). Ecosystems of disturbed ground, pp. 201–236. Elsevier, Amsterdam, The Netherlands.

ZIMMERMAN, J. K., E. M. EVERHAM III, R. B. WAIDE, D. J. LODGE, C. M. TAYLOR, AND N. V. L. BROKAW. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. J. Ecol. 82: 911–922.

———, W. M. PULLIAM, D. J. LODGE, V. QUIÑONES-ORFILA, N. FETCHER, S. GUZMÁN- GRAJALES, J. A. PARROTTA, C. E. ASBURY, L. R. WALKER, AND R. B. WAIDE. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. Oikos 72: 314–322.