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Notes and Comments

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IMMEDIATE IMPACT OF HURRICANE HUGO ON A PUERTO RICAN RAIN FOREST

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Tropical forests are subject to natural disturbances ranging from falling trees to landslides, forest fires, and hurricanes (Jordan 1986). Hurricane Hugo struck northeastern Puerto Rico on 18 September 1989 (Fig. 1) with maximum sustained winds of over 166 km/h and caused considerable damage to the Luquillo Experimental Forest (LEF). Hurricanes of this magnitude (category 4) pass over LEF at an estimated recurrence interval of 60 yr (Scatena 1989). Hugo was the first hurricane to pass directly over LEF since 1932. The path, wind velocities, and seasonality of this storm were typical of previous hurricanes, but rainfall associated with the storm was unusually low, 100–339 mm (USDC 1990) vs. 500–750 mm for all previous hurricanes since 1876 (Salivia 1972).

Previous research at LEF (Brown et al. 1983) and sampling begun 1 yr prior to Hurricane Hugo have provided us with an exceptional opportunity to measure damage to previously marked trees, to evaluate whether damage to trees can be predicted by wood density, tree diameter, or the presence of buttresses, and to compare light levels before and after the hurricane. Our data on the immediate and short-term (2 mo) effects of Hurricane Hugo should assist later studies to place patterns of damage in the context of recovery.

Methods

We measured the impact of Hurricane Hugo at two study sites in LEF (Fig. 1): Bisley and El Verde. Both sites are located ≈400 m above sea level in the subtropical wet forest life zone (Holdridge 1967), have slopes facing predominantly north and northwest, and had similar closed-canopy vegetation prior to the hurricane. Previous disturbances at both sites included the 1928 and 1932 hurricanes (Crow 1980) and human activities (coffee plantations, charcoal production, and selective cutting of timber species, which ended about 1900, 1940, and 1970, respectively [Scatena 1989]).

At Bisley, the diameters of the stems of all trees >10 cm dbh (diameter at breast height) were measured, and each tree was permanently marked in May 1988 in a 1-ha plot (Bisley Biodiversity Plot) established by the University of Puerto Rico and the Smithsonian Institution/Man and the Biosphere Biological Diversity Program. At El Verde, all trees >10 cm dbh were measured and permanently marked in 20 300-m^2 plots established in April–June 1989; all saplings >1 m tall and <5 cm dbh were marked in 1 400-m^2 plot established in August–November 1988. All plots at El Verde were located in 20 ha of forest on slopes <30°.

After Hurricane Hugo, damage was assessed at Bisley (14 October 1989) and at El Verde (26 September–14 October 1989) by: (1) counting the number of stems of trees and saplings that either snapped or were uprooted; (2) counting the number of trees and saplings

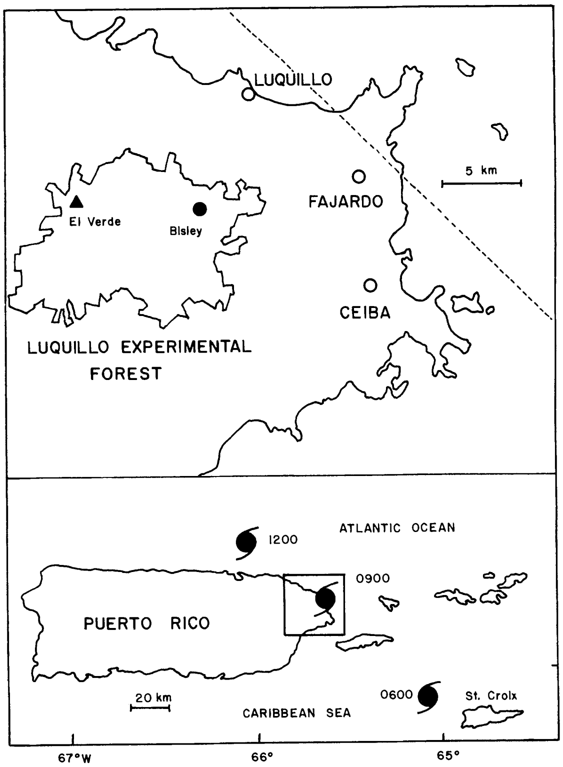

FIG. 1. Track of Hurricane Hugo on 18 September 1989 (Matos 1989, and D. Foster, E. Boose, and M. Fluet, *personal communication*). The upper map shows the approximate path of the center of the eye (– – –), Luquillo Experimental Forest, and the two vegetation study sites in the rain forest, Bisley and El Verde.

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TABLE 1. Hurricane damage to trees (>10 cm dbh) and saplings (>1 m tall and <5 cm dbh) at two sites in the Luquillo Experimental Forest.

				Percent of individuals			
Species	Site	N*	(N)†	Snapped stems	Uprooted stems	>66% defoliated‡	>66% of branches damaged§
Dacryodes excelsa Vahl (2/1)‖	Bisley	38	(30)	13	8	97	40
	El Verde	73	(59)	5	5	47	3
Manilkara bidentata (A. DC.) Cher (9/9)	Bisley	12	(9)	8	17	89	33
	El Verde	22	(18)	14	5	11	5
Prestoea montana (R. Grah.) Nichols (1/2)	Bisley	128	(96)	15	10	89	NA¶
	El Verde	91	(71)	21	1	65	NA
Sloanea berteriana Choisy (3/6)	Bisley	76	(27)	16	45	96	44
	El Verde	23	(13)	30	13	69	23
All trees	Bisley	423	(237)	21	23	93	48
	El Verde	510	(393)	13	10	62	13
All saplings	El Verde	222	(190)	14	<1	75	ND#

* N = total number of individuals.
† (N) = all standing individuals (not snapped or uprooted and used to calculate defoliation and branch damage).
‡ % of standing individuals with extensive defoliation (>66% leaf loss).
§ % of standing individuals with extensive damage (>66% of branches with a diameter > 1 cm broken); this category does not include the palm *Prestoea montana.*
‖ Basal area rank of each species from the forest plots (Bisley/El Verde). Total number of species was 34 (Bisley trees), 42 (El Verde trees), and 28 (El Verde saplings).
¶ NA = not applicable.
# ND = no data available.

that had lost two-thirds of their prehurricane foliage; and (3) counting the number of trees that had lost two-thirds of their branches (>1 cm diameter). Iterative fitting of log-linear models (Sokal and Rohlf 1981) was used to detect differences in amount of damage as affected by site and species to the six most abundant species found at both sites. The model rejection level was set at $P > .90$ (Edwards 1989). To assess the influence of the specific gravity of wood on the probability of stem breakage or uprooting, values for the most common tree species were taken from the literature (Wellwood 1946, Chudnoff 1984). No data were found for the palm *Prestoea montana* (R. Grah.) Nichols, so this species was not included in this portion of the analysis. In addition, at Bisley the presence or absence of buttresses was recorded. At El Verde the presence of new leaves was recorded on 6–12 November 1989 for all species except *Prestoea montana.*

Photosynthetic photon flux density (PPFD) was measured on 17–18 March 1988 (under a closed canopy) and 23–24 November 1989 (after the hurricane) at a location next to the site previously used by Odum and Jordan (1970) for measurements of canopy gas exchange. In 1988, 10 gallium-arsenide-phosphide sensors were located haphazardly within an area of $\approx$100 m^2. In 1989, we laid out a transect with 12 sensors that crossed the original site. In both years, sensors were placed 30–50 cm above the ground. The sensors were calibrated under clear sky conditions with neutral density filters and a quantum sensor (LI-COR). Each year, on both measurement days, readings were taken every 5 s between 1100 and 1300 local time using a data logger. Solar altitude at midday was 72° in March 1988 and 52° in November 1989. Sky conditions were similar for both sets of measurements (sunny with scattered clouds).

Results and Discussion

Hurricane damage to the vegetation was not uniform throughout LEF. At Bisley, more trees were severely defoliated ($\chi^2 = 71.99$, df = 1, $P < .0001$) and more had severe branch damage ($\chi^2 = 94.35$, df = 1, $P < .0001$) than trees at El Verde (Table 1). Possible explanations for these differences include: (1) a significant difference in the relative abundance of tree species found in both sites (Spearman's $r_s = 0.02$, $N = 55$, $P > .05$); and (2) the greater proximity of the Bisley plot to the center of the eye of the hurricane (cf. Wadsworth and Englerth 1959). The Bisley and El Verde trees did not differ significantly ($\chi^2 = 2.11$, df = 1, $P > .05$) in the proportion of damaged stems (snapped or uprooted; Table 1). At El Verde, as many saplings as trees were severely defoliated and had severe stem breakage (Table 1); uprooting, however, was mostly limited to trees.

Levels of snapping plus uprooting were different between species and between sites according to the analysis by log-linear models. Mean stem diameter was not significantly different for trees that were intact, snapped, or uprooted at Bisley (ANOVA on log-transformed diameters, $F_{2,398} = 0.60$, $P > .05$) or at El Verde ($F_{2,511} = 1.49$, $P > .05$). The proportion of trees that were snapped was significantly negatively correlated with published values of the specific gravity of the wood at Bisley (Spearman's $r_s = -0.85$, $N = 7$, $P < .05$) but not at El Verde (Spearman's $r_s = -0.51$, $N = 9$, $P > .05$). Other studies of damage caused by high winds report greater snapping of trees with wood of low specific gravity and greater (Lugo et al. 1983, Putz et al. 1983) or lesser (Lodge et al. 1989) uprooting of trees with large diameters. Estimates of snapping and uprooting by size class can be dependent on the range of diameters measured (Walker 1991).

Buttressing has also been suggested as a deterrent to uprooting (for review see Smith 1972). Yet, with *Prestoea montana* excluded, trees at Bisley with buttresses ($N = 113$) uprooted as frequently as those without them ($N = 179$; $\chi^2 = 0.44$, df = 1, $P > .05$). *Sloanea berteriana* Choisy, for example, is characterized by "pronounced buttresses at the base of the trunk" (Little and Wadsworth 1989). Of the 76 individuals of *S. berteriana* at the Bisley site, 62 had buttresses, but the presence of buttresses had no effect on whether individuals of this species snapped, uprooted, or remained intact ($\chi^2 = 0.97$, df = 2, $P > .10$). Better predictors of snapping or uprooting in LEF may be the presence or absence of interconnecting root systems, as in the dominant tree, *Dacryodes excelsa* Vahl. (Odum 1970), or soil moisture, soil depth, or topography (Wadsworth and Englerth 1959, Weaver 1989).

As a result of the damage to trees and the removal of the canopy, light levels at the forest floor increased dramatically. Median PPFD at midday rose from 23 $\mu mol \cdot m^{-2} \cdot s^{-1}$ before the hurricane to 404 $\mu mol \cdot m^{-2} \cdot s^{-1}$ afterwards, despite the fact that solar altitude was lower. The distribution of PPFD after the hurricane showed a high proportion of observations >1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 2), indicating that much of the transect was exposed to direct beam solar radiation. The light levels after the hurricane were similar to those found in large gaps and multiple treefalls in closed forest (Chazdon and Fetcher 1984).

Recovery is as variable as damage among tree species (e.g., Walker 1991) and may be more important for survival than resistance to damage (Putz and Brokaw 1989, Boucher et al. 1990). Seven weeks after the hurricane, 70% of the trees at El Verde had produced new leaves. Yet some severely defoliated species (e.g., *Buchenavia capitata* [Vahl.] Eichl. and *Casearia arborea* [L. C. Rich] Urban) rapidly regained their prehurricane foliage, while other severely defoliated species (e.g., *Didymopanax morototoni* [Aubl.] Dcne.) did not.

In this study, we did not find substantial support for various hypotheses that suggest morphological characters of trees can be used to predict the degree of damage a forest will experience during a hurricane. We suggest, instead, that the differential abilities of species to regrow in the disturbed sites may be more important determinants in structuring posthurricane communities in Puerto Rico than their abilities to survive the immediate impacts of hurricane-force winds. For example, pioneer species (*sensu* Swaine and Whitmore 1988) that are able to germinate and grow quickly in high light environments should be favored until the canopy is reestablished.

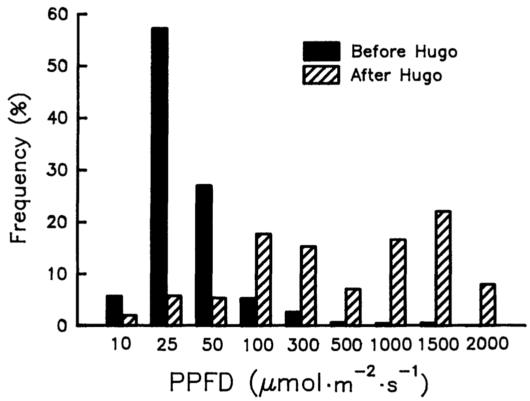

FIG. 2. Frequency distribution of photosynthetic photon flux densities (PPFD; 1100–1300 local time) at Luquillo Experimental Forest before (N = 21 660 records) and after (N = 34 548 records) Hurricane Hugo.

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ON CHOOSING MODELS FOR DESCRIBING AND ANALYZING ECOLOGICAL TIME SERIES

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Morris (1990) concluded that there are three major problems with using simple theoretical models to describe the dynamics of field populations and, specifically, to detect the qualitative stability of emergent equilibria; i.e., to distinguish between stable points, periodic or quasiperiodic cycles, and chaos. These problems are: (1) the parameters that determine the

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