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Hurricane Hugo: Damage to a Tropical Rain Forest in Puerto Rico

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NOTE: At the time of publication, author Frederick N. Scatena was affiliated with the USDA Forest Service. Currently (September 2005), he is a faculty member in the Department of Earth and Environmental Science at the University of Pennsylvania.

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Abstract

Hurricane Hugo of September 1989 caused severe damage to the rain forest in the north-east corner of Puerto Rico. We assessed the severity of damage distributed in space, species, and size-classes of trees in the Bisley Watersheds of the Luquillo Experimental Forest. We analyzed pre- and post-hurricane data for vegetation from transects established in 1987 and 1988. The severity of damage was significantly greater in valleys than on ridges and slopes. All the species except Dacryodes excelsa, Sloanea berteriana, and Guarea guidonia showed 100% severe damage. Large trees (> 70 cm DBH) were highly susceptible to hurricane damage, but there was no clear pattern in the small size-classes. D. excelsa (tabonuco) was the most resistant to damage by the hurricane. Tabonuco which has extensive root-grafts and root anchorage to bedrock and subsurficial rocks, apparently can survive frequent hurricanes and continue as a dominant species in this montane tropical rain forest. The high frequency of hurricanes, which can override other ecological and topographic factors, may largely determine the overall spatial pattern of species in this rain forest.

Comments

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Hurricane Hugo: damage to a tropical rain forest in Puerto Rico

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ABSTRACT. Hurricane Hugo of September 1989 caused severe damage to the rain forest in the north-east corner of Puerto Rico. We assessed the severity of damage distributed in space, species, and size-classes of trees in the Bisley Watersheds of the Luquillo Experimental Forest. We analyzed pre- and post-hurricane data for vegetation from transects established in 1987 and 1988. The severity of damage was significantly greater in valleys than on ridges and slopes. All the species except *Dacryodes excelsa*, *Sloanea berteriana*, and *Guarea guidonia* showed 100% severe damage. Large trees ($>$ 70 cm DBH) were highly susceptible to hurricane damage, but there was no clear pattern in the small size-classes. *D. excelsa* (tabonuco) was the most resistant to damage by the hurricane. Tabonuco which has extensive root-grafts and root anchorage to bedrock and subsurficial rocks, apparently can survive frequent hurricanes and continue as a dominant species in this montane tropical rain forest. The high frequency of hurricanes, which can override other ecological and topographic factors, may largely determine the overall spatial pattern of species in this rain forest.

KEY WORDS: disturbance, dominant species, Hurricane Hugo, Puerto Rico, tabonuco, tropical rain forest.

INTRODUCTION

Disturbance is an important force which contributes to the dynamics, structure, and function of forest ecosystems (Bormann & Likens 1979a,b, Pickett & White 1985). Tropical forests are shaped by natural disturbances of different forces and frequencies (Hartshorn 1978, Pickett & White 1985). Hurricanes, one of the largest types of natural disturbance, are common in the Luquillo Experimental Forest, Puerto Rico (Saliva 1972, Scatena 1989, Wadsworth & Englerth 1959, Weaver 1986). The devastating effects of hurricanes can be a major determinant of distribution patterns of tree species as well as affecting the overall function of the forest ecosystem.

In this paper, we will examine the following questions. (1) How was the severity of damage of Hurricane Hugo distributed in space?, and (2) did this damage vary among species or size-classes of trees?

Hurricane Hugo

Hurricane Hugo hit Puerto Rico on 18 September 1989 with sustained winds of 230 km h^{-1}. The main centre was the north-east corner of the Island (Figure 1). It was the largest hurricane to strike directly the rain forests of the Caribbean National Forest or the Luquillo Experimental Forest (LEF) in Puerto Rico since 1932 (Saliva 1972, Wadsworth & Englerth 1959, Weaver 1986).

STUDY SITE

We assessed damage done by Hurricane Hugo in the Bisley Watersheds of the Luquillo Experimental Forest (LEF), Puerto Rico. The LEF is located in the north-east corner of the Island (18°18′N, 65°50′W) (Figure 1). Situated in the Luquillo Mountains, the LEF ranges from about 100 m to 1075 m above msl with an area of 11,330 ha (Brown *et al.* 1983). Some 46% of the mountainous areas are within the 305–610 m range with only 3% above 915 m (Brown *et al.* 1983). The LEF includes four life zones: subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rain forest (Holdridge 1967). The forest has a long history of ecological research (e.g. Brown *et al.* 1983, Odum & Pigeon 1970) and is currently a Long-Term Ecological Research (LTER) site of the National Science Foundation.

The Bisley Watersheds, which range in elevation from 267–450 m, are within the subtropical wet forest (Holdridge 1967). The topography of the watersheds is rugged with steep slopes, ridges, and valleys. The depth to bedrock is less on ridges and slopes than in valleys, and subsurficial boulders are common on ridges and some of the slopes (Basnet 1990). Annual rainfall averages approximately 3300 mm with a high year-to-year variation and little seasonality (Scatena 1989). Mean annual temperature is about 25°C.

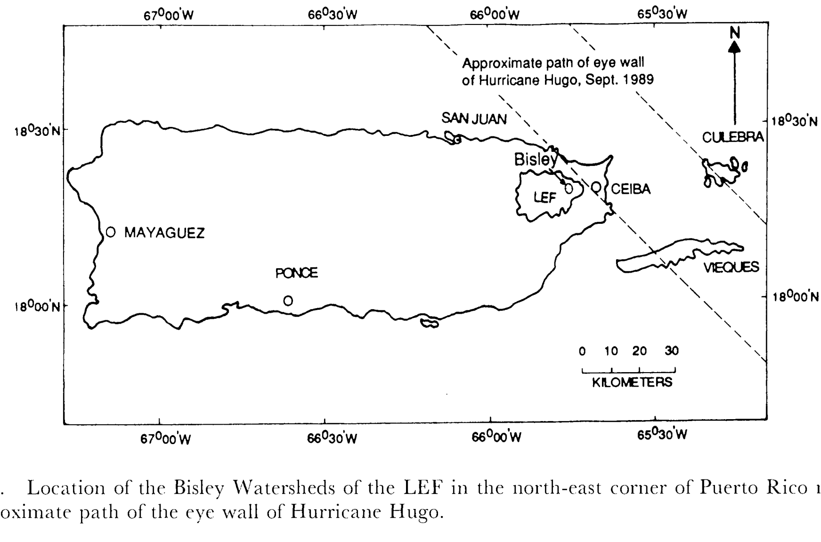

Figure 1. Location of the Bisley Watersheds of the LEF in the north-east corner of Puerto Rico relative to the approximate path of the eye wall of Hurricane Hugo.

This forest is locally called Tabonuco Forest, after the name of a dominant tree species, tabonuco (*Dacryodes excelsa* Vahl) and is characterized by an abundance of large diameter, tall trees with complex canopy stratification (Briscoe & Wadsworth 1970). Tabonuco dominates ridges and slopes and occurs in unions of 2–14 individuals, which are interconnected by extensive root-grafts (Basnet 1990). These roots are often anchored to subsurface rocks.

METHODS

Scales of damage

Damage to the forest from Hurricane Hugo was severe, ranging from defoliation to breakage and overturning of trees. Because damage was so complex we have used an arbitrary categorization to describe the damage observed. Since all trees were damaged in some way, the purpose of this study was to quantify the severity of the damage. The following mutually exclusive categories were used in order of increasing intensity of damage: (1) standing defoliated (DF) — includes trees that remained standing but were completely defoliated, missing twigs and minor branches, (2) branches broken (BB) — includes standing trees that had major branches broken, (3) stem broken (SB) — includes trees that lost all branches and often a small part of bole, and (4) uprooted or broken (UB) — includes trees that were uprooted or broken at the lower part of the bole and lying on the forest floor.

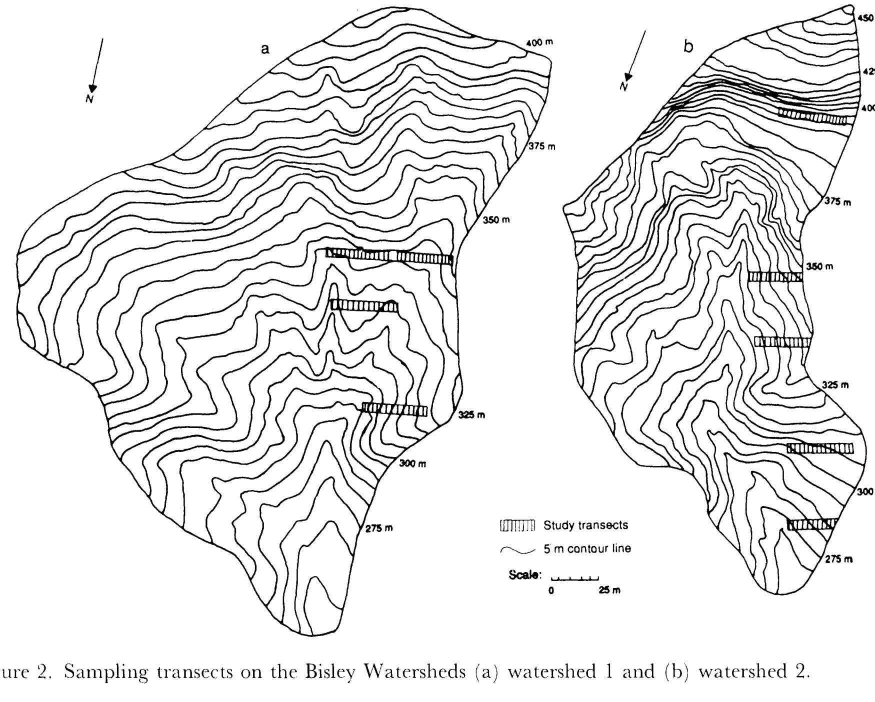

Figure 2. Sampling transects on the Bisley Watersheds (a) watershed 1 and (b) watershed 2.

Damage assessment

Damage was assessed six weeks after Hurricane Hugo hit the Island. Sampling of the vegetation was done using permanent transects that had been established in 1987 and 1988 in watersheds 1 and 2 (Figure 2; Basnet 1990). Along the altitudinal gradients of each watershed, six strip transects (divided into ridges, valleys, and slopes) each 5 m wide by 60–70 m long were established from one valley to an adjacent valley across a ridge. Within each transect all the trees with > 2.5 cm diameter at breast height (DBH) had been recorded before the hurricane. We relocated nine of the twelve transects (Figure 2) and all standing trees (> 10 cm dbh, $N = 181$) within them which had been recorded previously. Locating individual trees in these transects was possible because the trees had been mapped and recorded in detail prior to the hurricane (Basnet 1990).

The species, height, and DBH (diameter at 1.4 m above the ground) of all trees were recorded. We classified each tree according to the damage categories described above. We calculated the density and basal area of each species for the standing defoliated, branch broken, and stem broken categories in all three topographic positions. We then calculated uprooted or broken (UB) as the difference between the pre-hurricane density or basal area and the density or basal area of standing defoliated, branch broken, stem broken trees ($UB = BD - (DF + BB + SB)$), where BD is pre-hurricane density or basal area. Severe damage (SD) was calculated as: $SD = BB + SB + UB$. The same procedure was used to estimate damage for different size-classes of trees. The density of trees was calculated as the number per hectare for each topographic position.

For statistical analyses, tests of independence (G-test), and a chi-square criterion (Sokal & Rohlf 1981), were used to determine if the damage categories were independent of topography, species, and size-classes of trees.

RESULTS

Damage associated with topography

All trees in valleys were severely damaged (SD) whereas severe damage on ridges and slopes was 76% and 78%, respectively (Table 1). Although there was no significant difference between the density of trees damaged on ridges and slopes, ridges received more damage than slopes in terms of basal area (Table 1). The density of uprooted or broken trees was significantly higher in valleys than on ridges or slopes. Trees with broken branches were more abundant in valleys than on ridges and slopes, but this difference was not statistically significant. Trees with broken stems were comparatively less abundant than trees in other categories, and did not differ among topographic positions.

Damage by species

Prior to Hurricane Hugo there were more than 36 tree species recorded in the Bisley Watersheds. After the hurricane we located standing individuals of only

Table 1. Occurrence of damage (% of trees in damage categories) in relation to topography after Hurricane Hugo. Severe damage (SD) equals the sum of branch broken (BB), stem broken (SB), and uprooted or broken (UB). G-test for the severity of damage and locations was significant at $P < 0.01$. Values in parentheses are standard errors of means. All values are rounded. N = number of ridges, valleys, and slopes in transects, Density = number of trees ha^{-1}, BA = basal area (m^2 ha^{-1}), DF = standing defoliated.

				After Hugo									
		Before Hugo		Severe damage		% Density damaged				% BA damaged			
Locations	N	Density	BA	Density	BA	DF	BB	SB	UB	DF	BB	SB	UB
Ridges	7	738 (64)	64 (23)	562 (86)	53 (11)	22	32	6	40	17	28	3	51
Valleys	14	479 (51)	28 (8)	479 (51)	28 (8)	0	38	6	57	0	56	9	34
Slopes	6	833 (90)	53 (18)	650 (98)	32 (13)	22	34	6	38	39	37	15	9

eight species and about half of them occurred only once or twice in all of the transects.

The severity of damage varied significantly among species (G-test, $P < 0.01$). Severe damage was 100% in all but 3 species (Table 2). Tabonuco (*Dacryodes excelsa*) was the only species which showed significant resistance to damage by the hurricane. For instance, 44% of tabonuco was only defoliated (Table 2). Two other species, *Sloanea berteriana* and *Guarea guidonia* also were somewhat resistant but not significantly so (species names follow Brown *et al.* 1983). A high percentage of *Inga fagifolia* trees occurred in the branch broken category. All trees of *Swietenia macrophylla*, *Manilkara bidentata* and *Ocotea leucoxylon* in our

Table 2. Composition of major tree species in the Bisley Watersheds before Hurricane Hugo and the severity of damage (kinds of damage) associated with the species. G-test for the differences in severity of damage between species was significant at $P < 0.01$. Abbreviations as in Table 1.

			After Hugo					
	Before Hugo		% Severe damage		% Tree damage categories			
	% Relative							
Species	Density	BA	Density	BA	DF	BB	SB	UB
Prestoea montana	28	6	100	100	0	46*	0	54
Dacryodes excelsa	26	46	56	66	44	23	8	25
Sloanea berteriana	22	10	98	95	2	28	5	65
Guarea guidonia	6	17	91	97	9	54	9	27
Casearia arborea	3	2	100	100	0	40	0	60
Inga fagifolia	3	2	100	100	0	80	0	20
Alchorneopsis portoricensis	2	5	100	100	0	25	25	50
Manilkara bidentata	2	3	100	100	0	0	0	100
Ocotea leucoxylon	1		100	100	0	0	0	100
Swietenia macrophylla	1	3	100	100	0	0	0	100
Khaya nyasica	1	2	100	100	0	0	50	50
Other species**	5	4	100	100	6	4	11	79

*All defoliated palms were assigned BB category.

**Other species include *Buchenavia capitata*, *Andira inermis*, *Alchornea latifolia*, *Inga vera*, *Cordia borinquensis*, *Cordia sulcata*, *Sapium laurocerasus*, *Magnolia splendens*, and *Cyathea arborea*. (Scientific names of tree species and authorities are found in Brown *et al.* 1983).

transects were uprooted or broken. The other species ranged from 50–65% of trees in the uprooted or broken category. The stem broken category was infrequent for all species (Table 2).

Damage by size-class

Hurricane damage varied significantly among size-classes (G-test, $P < 0.01$). Trees > 60 cm in diameter were highly susceptible to hurricane damage (Figure 3), probably because of their prominence and possibly due to the advanced age of the trees. In trees < 50 cm DBH, there was no clear pattern of damage across the size-classes. There was a weak relationship between the undamaged trees and their sizes ($r^2 = 0.28$, $P < 0.05$). However, trees in the 50–60 cm DBH size-class were the most resistant to damage (Figure 3).

DISCUSSION AND CONCLUSION

Hurricane Hugo caused severe damage in the Bisley Watershed. More than 85% of the trees were severely damaged (e.g. BB, SB, and UB categories) affecting

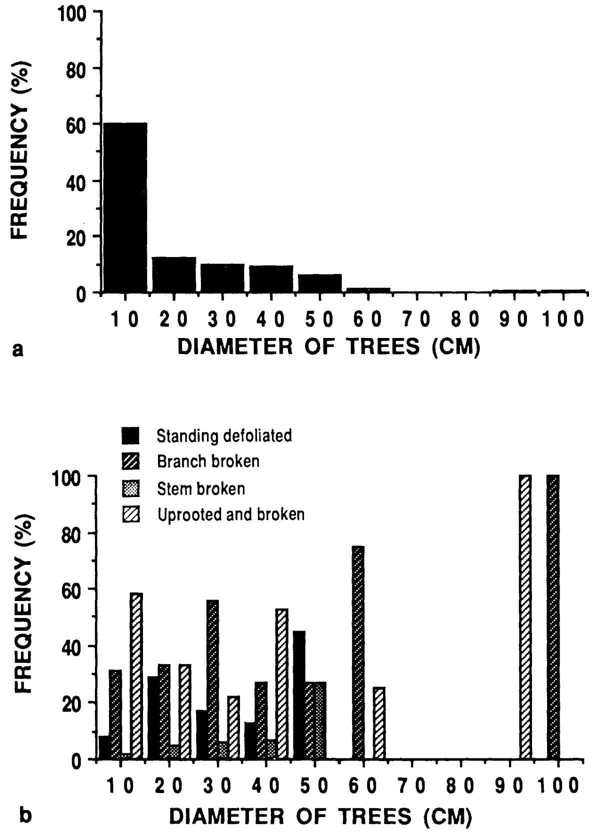

Figure 3. Frequency distribution of intact trees before (a) and severity of damage associated with the diameter size-class of trees after (b) Hurricane Hugo.

81% of the basal area ha^{-1}. Our results indicated that: (1) Every tree was damaged in one way or another, from defoliation to being uprooted or broken (Table 1). (2) The density of uprooted or broken, i.e. the most severe damage category, was significantly higher in valleys than on ridges or slopes. Possible reasons for this are: (a) valleys are inherently unstable because their deep soil and poor drainage (Basnet 1990, Wadsworth 1951, 1953) can promote uprooting (Day 1950, Putz *et al.* 1983, Schaetzl *et al.* 1989), (b) trees in valleys also may be damaged by big trees and branches falling from the adjacent ridges and slopes, and (c) bedrock and subsurficial rocks on ridges and slopes increase the stability of trees by providing anchorage for their roots (Basnet 1989, Hubert 1918, Jane 1986, Wadsworth 1953). (3) All but three tree species (*D. excelsa, S. berteriana*, and *G. guidonia*) suffered 100% severe damage. (4) Tabonuco showed the most resistance to hurricane damage. In an assessment of widespread damage from Hurricane David on forests of Dominica in 1979, Lugo *et al.* (1983) also found that the tabonuco-dominated association was the least affected by the hurricane. Our results provide strong evidence that ridges and slopes are stable sites for tabonuco trees in the LEF. (5) Most of the introduced species (e.g. mahogany) and some local species specially associated with valleys (e.g. *O. leucoxylon*), suffered 100% severe damage. The introduced species were found mainly in valleys where they grew tall, possibly without sufficient root support (e.g. subsurficial rocks and bedrock for root anchorage, see Basnet 1990). (6) Severe damage of palms was different from other sites struck by hurricanes (e.g. Lugo *et al.* 1983). All palms were defoliated in Bisley but many (46%) were still standing (Table 2). (7) Large trees were highly susceptible. This result was expected because the big and old trees are affected by their own weight and by the decaying of roots (Bormann & Likens 1979a,b, Dunn *et al.* 1983, Hubert 1918, Jane 1986, Putz *et al.* 1983). (8) There was no clear pattern of damage across the size-classes of trees < 50 cm in diameter. Lugo *et al.* (1983) found the same result in the forests of Dominica following Hurricane David.

Hurricanes strike Puerto Rico every 10–30 years (Wadsworth & Englerth 1959, Weaver 1986) and at least one hurricane strikes the LEF every 60 years (Scatena 1989). Such a high frequency of hurricanes overrides other ecological factors and creates a cyclic steady state in the forest ecosystem (Lugo 1980, Lugo *et al.* 1976, 1983). A stable, steady state ecosystem in which there is no net change in total biomass over time, is not possible (see Bormann & Likens 1979a, Lugo *et al.* 1983) particularly in forests that are affected by frequent hurricanes (Crow 1980, Lugo & Battle 1987, Weaver 1986, Whitmore 1974).

Will the tabonuco remain as a dominant species in these Puerto Rican rain forests? In such highly disturbed areas where physical factors are very important in affecting the forest pattern, tabonuco is well adapted to the steep slopes and ridges of the forest (Basnet 1990, Wadsworth 1951, 1953, 1970). The results of this study also suggest that tabonuco was the most resistant to a major hurricane. This is strong evidence that tabonuco will remain as a dominant species in spite of major disturbances, such as frequent hurricanes. In fact most of the tabonuco trees that we recorded before Hurricane Hugo were older than 57 years (60–400 years). The last severe hurricane was in 1932, and tabonuco must have survived many such hurricanes (Wadsworth 1951, 1953). Most tabonuco reach advanced age, whereas other species, especially in valleys, start growing again after every major hurricane event.

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Book review

BENZING, D. H. 1990. *Vascular epiphytes. General biology and related biota.* Cambridge University Press, Cambridge. xvii + 354 pages. ISBN 0-521-26630-0. Price: £40.00/$59.95 (hardback).

Vascular epiphytes constitute perhaps the most characteristic sinusia of tropical moist forests, and have attracted the attention of botanists and ecologists since the first scientific expeditions to the tropics. It was the work of Schimper in South America and the Caribbean (*Botanische Mittheilungen aus den Tropen. Heft 2.* Gustav Fischer Verlag. Jena, 1888) that focussed scientific research on the problems of the morphology and physiological adaptations of vascular epiphytes. David Benzing is responsible for numerous contributions on the biology of epiphytes on many different aspects of habitat selection, morphology and nutrition, particularly with bromeliads and orchids. The present book represents a remarkable effort to undertake a comprehensive review of the physiology, reproductive biology, ecology and biogeography of vascular epiphytes based on a thorough analysis of the available literature and the author's extensive experience with Neotropical epiphytes.

The book includes the whole spectra of vascular epiphytes, from the hemi-epiphytes to the epiphytic hemi-parasites (mistletoes), in an attempt to understand how the epiphytic habit evolved. The author adopts a strong evolutionary viewpoint throughout the book and provides explanations and hypotheses for the sometimes puzzling facts associated with epiphyte frequency in Old and New World forests, or the overrepresentation of monocots compared with dicots in the canopy flora of tropical forests. Each of the chapters is also rich in suggestions for further research, a fact which makes the book not only a source of information, but also a guideline for in-depth research on problems of epiphyte biology. Examples are the suggested approaches to the study of pigmentation patterns in bromeliads, and the hypotheses to explain mimicry and lack of taxonomic diversity in mistletoes. of particular interest is the conceptual model of the convergence of adaptations to drought and nutrient scarcity in epiphytes as was proposed by Small many years ago for bog plants (*Canadian Journal of Botany* 50 : 2227, 1972).