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SHORT COMMUNICATION

Hurricanes need not cause high mortality: the effects of Hurricane Gilbert on forests in Jamaica

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In recent years, increasing attention has been paid to the role of disturbance, both minor and catastrophic, in determining ecosystem structure, species diversity and relative abundance of species (Connell 1978, Grubb 1977, Hubbell & Foster 1986) Windstorms, a well-known type of natural catastrophe, can damage up to 100% of forest canopy trees (Foster 1988, Lugo *et al* 1983, Naka 1982, Weaver 1986, Webb 1958, Whitmore 1974) and favour the establishment of gapdemanding species at frequencies higher than would otherwise be found (Foster 1988, Hartshorn 1978, White 1979, Whitmore 1989) However, the effects on tree mortality have rarely been reported despite their importance for population and community structures We report here the effects of Hurricane Gilbert, one of the most powerful hurricanes ever recorded, on several forest types in Jamaica

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The Caribbean islands have relatively little remaining natural forest (Johnson 1988) The influence of hurricanes on its structure and diversity is clearly very important, although not fully understood (Crow 1980) Infrequent hurricane damage could account for the occurrence of gap-demanding species in the natural montane forests of Jamaica at greater frequencies than can be explained by normal rates of gap formation (Sugden *et al* 1985) Five hurricanes have passed within 20 km of the Blue Mountains since 1870 (Healey 1990) Hurricane Gilbert, which passed over Jamaica from SE to NW (Figure 1) on 12 September 1988, was the most powerful on record (*New Scientist* 1988), pressure at the eye of the storm was 885 mbar, maximum wind speeds were > 255 km h⁻¹, and up to 400 mm of rain fell during the storm (Jamaican Meteorological Service 1988) We report here an assessment of hurricane damage to four widely separated areas of Jamaican native forest (Figure 1)

Blue Mountains A general survey of the Blue Mountains forests above 1000 m was done from subsidiary ridges and light aircraft (Dec 1988-June 1989) Damage was very patchy some areas were devastated, others hardly affected We estimated that 30% of the area was severely damaged (up to 20%, but more usually 10%, of the trees blown down and the remaining trees heavily damaged leaving large areas apparently leafless) Another 30% was moderately damaged (relatively few uprooted trees, but significant crown damage and defoliation visible even three months after the hurricane) The rest of the area, mostly more protected gullies on the lower slopes, showed minor damage (moderate defoliation, but recovery already evident at the time of survey) The damage was concentrated near the crests of the main and spur ridges (Figure 2) However, severe damage occurred in all kinds of topographic positions, including gully heads Plantations of *Pinus caribaea* between 700 and 1000 m were very heavily damaged, with c 80% of the trees broken or uprooted

From January to June 1989 (3-8 months after the hurricane), we evaluated in detail the impact of the hurricane on 2600 permanently marked trees in 49



Figure 1 The approximate path of Hurricane Gilbert over Jamaica on 12 September 1988 Pressure at the eye of the storm was 885 mbar Average windspeeds at the Kingston airport exceeded 205 km h^{-1} for more than 3 hours and maximum winds of > 255 km h⁻¹ were recorded at various locations Up to 400 mm of rain fell on 12 September, and large areas of the island received more than 250 mm (Jamaican Meteorological Service 1988) The sites of the various detailed studies reported here are indicated



Figure 2 (a) Photograph taken looking west along the main ridge of the Blue Mountains from Belle Vue Peak towards John Crow Peak showing patchiness of the damage and defoliated areas (Damage was more severe further east on the main tidge) (b) Sketch of the same view indicating which areas of the photo correspond to each of the three damage classes: Note heavy damage parallel to and south of the main ridge

plots of $10 \text{ m} \times 10 \text{ m}$ along the crest of the main ridge between Morce's Gap and John Crow Peak (1540–1770 m altitude), inventoried in previous studies (Healey 1990, Tanner 1977, Tanner *et al* 1990) Overall, 37°_{10} of the trees were either killed or seriously damaged Mortality since the last recensus (7 1°_{0} in 5 years) was only slightly higher than would have been expected from the long-term

average (Table 1), though the hurricane probably doubled annual mortality for 1988 Species-specific mortality ranged from 0 to 32% On the whole, severe crown breakage was a more common cause of death from the hurricane than uprooting This may have been because the relatively low rainfall before and during the storm did not saturate the soils, leaving them relatively strong and stable Contrary to previous findings (Lugo *et al* 1983, Putz *et al* 1983, Healey 1990), snapped trees did not have smaller dbhs than uprooted trees (Komolgorov-Smirnov 2-sample test, P < 0.5, $n_1 = 359$, $n_2 = 130$) This contrast may be due to the stunted character of the ridge-top forest, where trees are short (canopy height 8–15 m) and mostly small in diameter (mean dbh c 14 cm for trees > 3 cm dbh, Healey 1990) A significant majority of the fallen trees fell towards the NE (X² P < 0.05, 64% fell in directions between 10° and 100°), which suggests that most fell during the first part of the storm

Far fewer trees were killed by the hurricane than were damaged without being killed, although some of the damaged trees may yet die, and apparently dead trees may resprout (56% of all stems in the plots had fresh epicormic resprouts) Relatively few individuals were fully defoliated, most retained leaves in the lower crown, but stripping of twigs as well as leaves contributed to the openness of the canopy In areas with substantial canopy damage, many seedlings of gap-demanding species germinated within three months of the storm There were up to 2000 seedlings m⁻² of the most abundant species (*Alchornea latifolia*) compared with 0 24 m⁻² in undisturbed forest (Healey 1990), and *Bocconia frutescens* was also common

Other Jamaican forests Other forested areas in Jamaica also suffered significant damage from Hurricane Gilbert (Table 2), though it is clear that damage was very variable The Blue Mountains (BM) forests were the least damaged, and the difference between the two BM data sets is due to the inclusion of severely

Mortality over 5 year Hurricane Gilbert (7 1		
Previous long-term ave with no serious hurr	1.11		
Visible damage to dea	d trees or apparent cause of death toppled ² trunk or crown broken unknown	(°′₀) (°′₀) (°′₀)	10 38 21
Non-fatal damage ³	toppled ² trunk or crown totally broken crown partly broken crown fully defoliated	(%) (%) (%) (%)	3 8 3 3 4 8 18 2 (range among plots: 0-75%)

Table 1 Mortality and damage patterns in the Blue Mountains forests after Hurricane Gilbert Data are from 49 pre existing plots covering 0 49 ha and comprising 2600 permanently marked trees

'Tanner, unpublished data

²Blown over $\geq 40^{\circ}$ from vertical, trunk not broken

³ Most of the remaining 63% of trees suffered slight damage, mostly partial defoliation

	Mortality	Breakage	Uprooting	
	Mortality of previously enumerated stems during period including Hurricane Gilbert [% (SEM)]	Stems with trunks or crowns completely or partly broken (both alive and dead) [% (SEM)]	Stems toppled (≥ 40°) or fallen (both alive and dead) [% (SEM)]	
Blue Mountains				
1	7 1 (0 7) over 5 years	12 3 (1 0)	43 (06)	
2	N/Á	23 1 (14)	92(10)	
John Crow Mountains				
3	13 5 over 4 vears	21 8	15 0	
4	N/A	147 (11)	28 1 (1 7)	
Cockpit Country 5	N/A	177(21)	199 (27)	
Westmoreland				
6	17 7 over 3 3 years	20 6	18 9	

Table 2 Hurricane Gilbert-related mortality and damage of trees at selected sites in Jamaica (locations of sites shown in Figure 1; damage definitions as in Table 1)

1) Bellingham: $n = 49 \times 100 \text{ m}^2$ plots in Tanner (1977), Tanner *et al* (1990) & Healey (1990) sites, along western crest of range, c 1550 m altitude Tree density c 5300 stems ha⁻¹ (\geq 3 cm dbh); canopy height 5-18 m Resurveyed Jan -June 1989

2) Varty: $n = 64 \times 785 \text{ m}^2$ plots in transects along crest and to N and S of western end of the range, 1300-1600 m Tree density c 4400 stems ha⁻¹ (≥ 5 cm dbh) Surveyed April-June 1989

3) Kelly: $n = 1 \times 900 \text{ m}^2$ plot in Hog House Hill site, 400-500 m (Kelly et al 1988) Tree density c 1500 stems ha⁻¹ (≥ 4 cm dbh); canopy height c 26 m Resurveyed July 1989

4) Varty: n = 70 × 78 5 m² plots in transects at Hog House Hill & Ecclesdown, 300-500 m Tree density c 3200 stems ha⁻¹ (≥ 5 cm dbh) Surveyed June-July 1989

5) Varty: $n = 56 \times 785 \text{ m}^2$ plots in transects at Barbecue Bottom, Pantrepant and Windsor, 150-350 m 6) Kelly: 1100 m² in 2 plots at Copse Mountain, c 300 m Tree density c 1600 stems ha⁻¹ (≥ 3 cm dbh);

canopy height 17-30 m Resurveyed June 1989

damaged plots in the Varty data set while none of the previously enumerated (Bellingham) plots was in the most damaged areas The ridge-top forest suffered the least crown breakage of any site and low tree uprooting One explanation for its apparent resistance is that its exposed topographic position may have caused the ridge top forest to develop its characteristic more aerodynamically streamlined, even canopy and may also have selected species and individuals resistant to high winds (Lawton 1982) The importance of this degree of disturbance for slow-growing (average diameter increment $< 0.2 \text{ mm y}^{-1}$, Tanner et al 1990) montane forest is not yet clear Because of low mortality, Hurricane Gilbert has changed BM forest composition little in the short term

The John Crow Mountains (JCM) plot evaluated by Kelly is in a sheltered hollow and at the low end of the damage range in JCM plots evaluated by Varty The trees in the JCM were more susceptible to uprooting than in other sites, which may reflect the stronger impact of the hurricane in this region as well as the greater average height of the trees (26-28 m, Kelly et al 1988), and

indicates that the limestone substrate did not provide the greater anchoring predicted by other authors (Howard & Proctor 1957) Within-region variability was particularly high in the Cockpit country, where the topographic differences between the ridge tops and slopes and the very sheltered 'cockpit' bottoms account for the larger standard errors Westmoreland was quite strongly affected with the highest mortality of any site

The highest incidence of serious damage to trees in the Jamaican forests was comparable to the average found by Lugo *et al* (1983) in Dominican forests after Hurricane David Their results and reports from other authors (Boucher 1990, Foster 1988, Whitmore 1974, 1989) imply much higher mortality than we have recorded The low mortality has significant implications for the long term effect of the hurricane, which will depend on the relative success of seedlings of gap demanding species that have germinated and the regrowth of damaged adult trees Where substantial numbers of seedlings become established the hurricane will have measurable effects for several centuries, where resprouting is more important the effect will disappear in a few years or decades All the forests probably consist of patches where one or the other means of recovery is stronger, the overall effect of each hurricane depending on the proportions of patches

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