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CONTRASTING HURRICANE DAMAGE IN TROPICAL RAIN FOREST AND PINE FOREST

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When Hurricane Joan struck the southeastern coast of Nicaragua on 22 October 1988, with winds exceeding 250 km/h (Cortes and Fonseca 1988), it severely damaged several different kinds of tropical forest. These included the *Pinus caribaea* forest typical of eastern Honduras and Nicaragua (Clewell 1986) as well as the broad-leaved rain forest found along the Caribbean coast of most of Central America. Although occurring in similar climates, these forests are quite different in structure: the pine forest has a single dominant coniferous species, while the rain forest has hundreds of angiosperm tree species sharing dominance. In this note we describe the differing effects of Hurricane Joan on the physical structures of two kinds of tropical forest.

Study Areas and Methods

The hurricane hit the Nicaraguan coast, which is oriented north-south, almost directly from the east, with its eye following the 12° N parallel (Cortes and Fonseca 1988). As a consequence, its northern flank first hit the thin (1–5 km wide) strip of pine forest close to the coast and then passed into the rain forest area. We studied pine and rain forest sites at nearly the same latitude: El Pinar at 12°12′ N, 83°41′ W, and Las Delicias at 12°16′ N, 83°53′ W. While detailed measurements of wind speeds at the two sites were of course impossible, it is likely that the hurricane struck these two areas with almost exactly the same force, since they are only 23 km apart. It may have been slightly weaker at Las Delicias, the rain forest site, since this area is slightly farther north and inland of El Pinar.

In February 1989, 4 mo after the hurricane, we mapped three transects at El Pinar and two at Las Delicias, each measuring 10 by 100 m (0.1 ha). In each,

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⁴ Escuela de Ciencias Ambientales, Universidad Nacional Autonoma, Heredia, Costa Rica. we located, identified, and measured the diameter of all trees of 5 cm dbh or larger, and noted whether each tree was standing, snapped off, or fallen, and whether or not it was alive, as indicated by the presence of green leaves and/or shoots. We also noted when trees were bent, pinned, or covered with debris.

We calculated rates of damage and recovery using the percentage of trees still alive in February, by site, condition of the tree (standing, snapped, or fallen) and size class. Four size classes were defined by dbh intervals: saplings (1–15 cm), small trees (16–30 cm), medium trees (31–45 cm), and big trees (>45 cm). A fourway log-linear model (Sokal and Rohlf 1981) was used to analyze the interactions among survivorship, tree condition, size class, and site.

Results

A total of 188 trees were located in the five transects: 48 *Pinus caribaea* at El Pinar, and 140 individuals of 38 different species at Las Delicias (Table 1).

The log-linear model indicated no significant threeor four-way interactions, and four significant two-way interactions. These were: site × tree condition, site × survivorship, site × size class and tree condition × survivorship ($\chi^2 = 39.6$, 32 df for the model; $P \leq .005$ for each interaction).

The percentage of trees still standing in the pine forest was over twice that in the rain forest (56 vs. 25%; $\chi^2 = 43.1, 2 \text{ df}, P < .0001$). Damaged trees were somewhat more likely to be uprooted than snapped off in the pine forest (38 vs. 62%), a result different from the rain forest (58 vs. 42%).

Tree survivorship, however, showed the opposite trend, with twice the percentage of trees still alive in rain forest compared to pine forest (87 vs. 42%; $\chi^2 = 61.7$, 1 df, P < .0001). This difference was produced by the high rate of resprouting of snapped and fallen rain forest trees (87 and 79%, respectively). Resprouting was practically nil (5%) in damaged pines.

The site \times size class interaction ($\chi^2 = 13.49$, 3 df, P = .004) indicated significant differences in size structure between the two forests. The rain forest had a size distribution highly skewed to the right (skewness coefficient $g_1 = 4.08$), with a predominance of saplings. On the other hand the pine forest had a fairly symmetrical size distribution ($g_1 = 0.36$) with small trees being the most common class, and no big trees. The rain forest had relatively more trees in the largest and smallest size classes, and the pine forest had more in the middle size classes.

Given this difference in size distribution between the two sites, it is possible that the difference in survivorship might be caused by their size structures. However size differences explained very little of the difference in survivorship between pine forest and rain forest:

				Pine for	rest				
	Sapling		Small tree		Medium tree		Big tree		
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Tota
Standing	9	3	6	4	4	1	0	0	27
Snapped	0	4	0	3	1	0	0	0	8
Fallen	0	0	0	7	0	6	0	0	13
Total	9	7	6	14	5	7	0	0	48
				Rain fo	rest				
	Sapling		Small tree		Medium tree		Big tree		
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Total
Standing	23	0	6	0	2	0	4	0	35
Snapped	26	5	22	2	4	1	1	0	61
Fallen	19	2	10	4	4	3	1	1	44
Total	68	7	38	6	10	4	6	1	140

TABLE 1. Observed frequencies of trees by condition and size class in rain forest and pine forest, February 1989 (Yih et al. 1989). Saplings = 1-15 cm dbh, small trees = 16-30 cm dbh, medium trees = 31-45 cm dbh, big trees = >45 cm dbh.

survivorship was considerably higher in rain forest than pine forest *within* each of the size classes (91 vs. 56% for saplings, 86 vs. 30% for small trees, and 71 vs. 42% for medium trees).

Discussion

Rain forest and pine forest suffered very different sorts of damage from Hurricane Joan. While most of the trees in the rain forest were heavily damaged, resprouting was very common, so that most trees survived. In contrast, in the pine forest the majority of the trees remained standing after the hurricane, but there was much less resprouting than in the rain forest. Although the size structures of the two forests differed, this does not explain the difference in survivorship. Rather, the difference in sprouting ability between conifers and dicots appears to be responsible.

All our sampling was done after the hurricane, and we lack confirmation that wind strengths at the two sites were equal. Nor can our study areas be considered random samples of the vegetation types of the region, although they subjectively appeared to be quite representative. These considerations necessarily limit the degree of confidence we can place in our results.

However, several other studies of hurricane damage to forests show similar differences between conifers and dicots. Foster (1988), Hemond et al. (1983), and Spurr (1956) found that coniferous forests in New England were more susceptible to damage from the 1938 hurricane than those dominated by hardwoods. Although detailed data are not yet available, the same seems to have been true of Hurricane Gilbert in 1988 and Hurricane Hugo in 1989 (Boucher 1990). In the Gulf States, hardwoods survived Hurricane Camille better than pines (Touliatos and Roth 1971). However, in the Flor-

ida Everglades, *Pinus elliottii* was one of the most resistant species during Hurricane Donna (Craighead and Gilbert 1962).

The tendency for dicots to survive damage better than conifers is also evident in responses to other kinds of windstorms. Webb (1989) found that two *Pinus* spp. had heavier mortality than most dicot species after a windstorm in *Pinus–Acer* forests in Minnesota, and that the species' differences were not explained by size differences. A 1983 tornado in Texas (Glitzenstein and Harcombe 1988) caused a substantial decline in the dominant pines, due both to higher mortality of taller trees and lack of subsequent sprouting. A 1985 tornado in beech–hemlock forest in Pennsylvania apparently had similar results (B. McCarthy, *personal communication*). Hardwoods replaced hemlock as the dominants after severe damage due to thunderstorm downbursts in Wisconsin (Dunn et al. 1983).

Our results confirm the importance of sprouting in tropical forests, as pointed out by Putz and co-workers (Putz et al. 1983, Putz and Brokaw 1989). Subsequent mortality, both of sprouts and standing trees, may change the picture in future years. So may the growth of seedlings, which were abundant in the rain forest and practically absent in pine forest. However, the differences that we and other authors have noted, suggest that forests with angiosperm and gymnosperm dominants may have fundamentally different responses to catastrophic disturbance.

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THE IMPORTANCE OF REPORTING STATISTICAL POWER: THE FOREST DECLINE AND ACIDIC DEPOSITION EXAMPLE

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I read the "Special Feature on Forest Decline and Acidic Deposition" (*Ecology* 70:1–15) with considerable disappointment, not because of what was said, but because of what was omitted. None of the authors mentioned β , the probability of making a type II error (not rejecting a null hypothesis of no effect of acidic deposition on forests when in fact there is an effect). Neither did they mention statistical power $(1 - \beta)$, the probability of rejecting the null hypothesis when there is an effect present. Researchers clearly want β to be low and power high in their experiments. These con-

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cepts are well established in the statistical literature (Dixon and Massey 1969, Green 1979, 1989, Sokal and Rohlf 1981, Cohen 1988), and they are extremely relevant to environmental issues such as forest decline (e.g., Peterson et al. 1989). However, these concepts of statistical power analysis have rarely been considered by ecologists, let alone decision makers (Toft and Shea 1983, Peterman 1990).

The purpose of this comment is not to criticize specifically the papers of the "Special Feature on Forest Decline and Acidic Deposition," but rather to use them to highlight a ubiquitous problem with statistical reporting practices in ecology.

To illustrate the utility of statistical power concepts, take the example of decline in growth rate of red spruce (*Picea rubens*) in the eastern United States and Canada. The research reviewed by Pitelka and Raynal (1989) does not show clear evidence of a causal link between acidic deposition and decreased growth rate of red spruce; in essence, most researchers have failed to reject the null hypothesis (H_0) of no effect. However, given the sample size, sampling variability, and parameter estimate from each of the original experiments, one could calculate statistical power, i.e., the probability of correctly rejecting the H_0 of no effect if a real effect (of specified magnitude) of acidic deposi-