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Hurricane Aftermath: Resiliency of an Orchid-Pollinator Interaction in Puerto Rico

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ABSTRACT.— The impact of severe habitat disturbance on plants and animals is often dramatically negative, but across species and guilds there is considerable variance. The effects of hurricane damage exemplify this phenomenon. When most organisms are adversely affected, it is expected that the dynamics of their inter actions will also be altered. The consequences of a direct hit by Hurricane Hugo, a category 4 storm, on a plant-pollinator interaction was investigated by comparing pre-hurricane (1981–1985) with post-hurricane data (1989-1990). The nectarless, self-compatible *Epidendrum ciliare* L. (Orchidaceae) is pollinated by *Pseudosphinx tetrio* (L.) (Sphingidae), a large hawkmoth. Despite severe habitat alteration and some plant damage (uprooting, breakage and sun scorching), flowering phenology was apparently unaltered. Pollinator service was different from that of previous years in that mom flowers were visited (57% vs. 28-41%). The higher number of effective visits increased pollinarium removals, but the number of pollinia depositions remained about the same (11% vs. 11–15%). Fruit fates differed among seasons. Post-hurricane loss of fruits to rat predation was higher than previous years, but the proportion of fruits reaching maturity was similar to prehurricane seasons. Final fruit set after the hurricane (5.3%) fell within the range of previous years. Although details of the plant-pollinator dynamics were altered, the short-term consequences of hurricane induced damages were apparently minimal.

RESUMEN.—El impacto severo causado por disturbios al hábitat de plantas y animales es a menudo dramaticamente negative, pero entre especies y asociaciones hay una variacion considerable. El efecto de los daños por huracanes ejemplifica este fenómeno. Cuando la mayor parte de los organismos son afectados adversamente, es de esperarse que la dinámica de sus interacciones también sea alterada. Las consecuencias directas causadas por el impacto del huracán Hugo, una tormenta con categoría 4, sobre la interacción planta-polinizador fue investigada comparando datos pre-huracán (1981–1985) y post-huracán (1989-1990). *Epidendrum ciliare* L. es una orquídea que produce flores sin néctar y autocompatibles, la cual es polinizada por *Pseudosphinx tetrio* (L.) (Sphingidae} una alevilla grande. Independientemente de la alteración severa del hábitat y algunos daños en las plantas (raíces desaraigadas, hojas quebradas y quemadas por el sol) la fenología del florecimiento spar entemente no fue alterada. La visita de los polinizadores fue diferente en comparación con los años anteriores, porque un mayor número de flores fuerun visitadas (57% vs. 28-41%). El aumento de visitas prudujo un aumento en la remoción de las polinarias. El número de polinizadores se mantuvo más o menos igual (11% vs. 11–15%). **La producción y madurés de los frutos fue distinta entre temporadas. La cantidad de frutos perdidos después del huracán debido a predación por ratas fue más alto que en años anteriores, pero la proporción de frutos maduros fue similar a temporadas antes del huracán. La maduración de frutos después del huracán fue de 5.3%, la cual cayó dentro del rango de años anteriores. Algunos detalles en la dinámica entre polinizador y plantas fueron alterados, pero el daño a corto plazo causado por el huracán fue mínimo.**

INTRODUCTION

Ecological effects of disturbance vary quantitatively and qualitatively depending on the magnitude of the disturbance. The passage of hurricanes is relatively common in certain regions of the world, such as the Caribbean. Severe cyclonic storms affect ecosystems on a broad scale with immediate and sometimes lasting consequences (cf. Bellingham et al., 1995). However, considerable variance occurs in the short and long term effects on plant and animal populations (Schowalter, 1994). Obvious consequences of hurricanes are forest defoliation, branch breakage, and tree falls (Walker et al., 1992). In the more severely disturbed areas, tree species richness may be unaltered (Yih et al., 1991), but epiphyte communities can be virtually eliminated (Migenis and Ackerman, 1993). Less visible changes occur below ground where mycorrhizal activity and nutrient cycling processes are altered (Lodge and McDowell, 1991).

Animal populations are often as affected by hurricanes as plant communities. Some may suffer mortality during the storm, but most animals appear to suffer more from the consequences of habitat destruction in the days, weeks and months afterward (Waide, 1991). Specialists such as frugivores and nectarivores seem most susceptible, largely due to the immediate loss and slow recovery of their food resources (Askins and Ewert, 1991; Lynch, 1991; Wunderle et al., 1992). Nevertheless, populations of some animals actually increase after the passage of a hurricane (Covich et al., 1991; Woolbright, 1991).

Predictably, plant-animal interactions are affected by hurricanes and sometimes very dramatically because some resources become scarce whereas others become abundant. Facultative frugivores change diets, plants flower en masse, insect outbreaks occur, and herbivory may become rampant (Odum and Ruiz, 1970; Torres, 1992). Mutualistic interactions may be slow to recover with marked consequences when partners asynchronously respond to large scale disturbances (Ferguson et al., 1995). In one case of an obligate fig pollination mutualism, post-hurricane recovery was remarkably rapid (Bronstein and Hossaert-McKey, 1995).

We report on the resiliency of one plant-pollinator interaction at a site that suffered a direct hit by Hurricane Hugo on 18 September 1989. The eye of the storm passed over the northeast corner of the island, where a large population of *Epidendrum ciliare* L. (Orchidaceae) exists. The nectarless, self-compatible flowers are pollinated by the hawkmoth *Pseudosphinx tetrio* (L.) (Sphingidae), and reproductive success is strongly pollination limited (Ackerman and Montalvo, 1990). The moths are attracted to the flowers by their strong but variable floral fragrance (Moya and Ackerman, 1993). Data on plant size, reproductive effort, flowering phenology, pollinator visitation and fruit set were obtained from this population from 1981 to 1984 (Ackerman and Montalvo, 1990). We monitored reproductive effort and success during the flowering season immediately following the passage of the hurricane (1989–1990) and asked whether successful pollinator visits to *E. ciliare* and subsequent fruit maturation were dramatically different from previous years.

METHODS

Our study site was in Puerto Rico, where hurricanes pass over land with an average frequency of every 21 yr (Salivia, 1972). The population of *E. ciliare* was located at the Municipality of Río Grande, Barrio Zarzal, near Ensenada Comezón which was the same site that Ackerman and Montalvo (1990) studied. Most plants occurred on large boulders at the edge of a mangrove forest but a few grew on tree trunks among the rocks. In this population inflorescences begin development soon after shoot maturation, sometime during late summer and early fall. Flowering begins in November and extends into January. Plants form clonal clumps and each shoot produces 1–3 new shoots each year. Each shoot consists of a swollen stem (pseudobulb) and 1–3, thick, coriaceous leaves. Shoots that flower produce from the apex a single, racemose inflorescence of 2–8 flowers.

Hurricane Hugo, a category 4 storm with maximum sustained winds of 166–227 km/h, passed over this site on the morning of 18 September 1989 (Scatena and Larsen, 1991). No quantitative assessment of storm damage was conducted at the site, but many trees were knocked down, a number of *E. ciliare* plants were partially dislodged from their rock and tree substrates, some were crushed by falling trees, and others were damaged by flying debris. Some plants were no doubt submerged in brackish water from the storm surge. The forest canopy was defoliated and most orchids were exposed to direct sunlight which caused some leaf scorching. We recorded the nature of damage to each of the flowering shoots.

Pseudosphinx tetrio is the only reported pollinator of *E. ciliare* and one of the largest sphingids in Puerto Rico. Locally, its larvae specialize on native *Plurneria alba* L., *P. ob-*

tusa L., and introduced *P. rubra* L. (Apocynaceae; Martorell, 1975), but in captivity they will feed on other members of the family when given no options (Santiago-Bay, 1985). Elsewhere, *P. tetrio* larvae have been reported to feed on Oleaceae as well as Apocynaceae (Hodges, 1971). We attempted to census adults at light traps but we were unsuccessful even on moonless nights. Thus, we inferred their activity by evidence of visitation at *E. ciliare* flowers.

Beginning 10 November 1989, we began monitoring flower production and reproductive success about once a week until mid-January. Flowering shoots were measured from rhizome to apex and were used as a measure of plant size. The number of flowers open on each inflorescence and the reproductive status of each flower were recorded during each census. The flowers are large so pollinarium removals and depositions were clearly visible (these were our indicators of effective pollinator activity). At the end of the flowering season we checked the status of developing fruits once a month until dehiscence occurred in June, 1990. Our measures of reproductive success were matured fruits (female success) and pollinarium removals (male success). Both measures represent good, but relative indicators of orchid reproductive success (Nilsson et al., 1992; Ackerman et al., 1996). These methods are the same as those used at this population in previous years (Ackerman and Montalvo, 1990).

Heavy fruit set in *E. ciliare* affects future growth and reproduction (Ackerman and Montalvo, 1990) To exacerbate the presumably stressful post-hurricane conditions and to assure that we had sufficient numbers of maturing fruits to assess maturation success, we cross-pollinated 222 of 402 flowers on 99 randomly selected inflorescences. The total of 108 unmanipulated inflorescences produced 417 flowers.

RESULTS

The Zarzal population of *E. ciliare* in the 1989–1990 flowering season produced 209 inflorescences on 87 clumps (probably genets). Flowering began in early November, peaked on 30 November with 375 flowers, and continued through mid-January. This phonological pattern was virtually the same as that of the prehurricane seasons 1982–1983 and 1983–1984 (Ackerman and Montalvo, 1990:fig. 2). The average post-hurricane inflorescence produced 4.0 flowers, which was better than the seasons 1981–1985 (range 3.2–3.7). As in previous years, there was a significant, positive relationship between average stem size of clumps and a square root transformation of the average number of flowers produced per inflorescence (Pearson's correlation: $r = 0.24$, $t = 12.49$, df = 72, $P < 0.001$).

We observed monarch butterflies (Danaidae) several times visiting *E. ciliare* during the day but none were captured. After checking the visited flowers, there was no evidence that the butterflies removed or deposited pollinia.

The proportion of flowers pollinated after the hurricane was about the same as in preceding years (Table 1). The percentage of pollinated flowers that matured fruits was also similar. Final fruit set (after abortion and predation) for prehurricane seasons ranged from 4.5-15% and that of the post-hurricane season was 5.3%

Pollinators made more visits to *E. ciliare* in the flowering season following the hurricane than in the 1982–1983 or 1983–1984 seasons. The higher number of visits produced a greater frequency of pollinarium removals (Table 1). After the hurricane, the pollinaria of more than half the flowers had been removed. The ratios of pollinarium removals to pollinia depositions were 2.55 and 2.37 for the 1982–1983 and 1983–1984 seasons, respectively, whereas that of the post-hurricane season was 4.74. The frequencies of successful and unsuccessful pollinaria among the three seasons were quite different (G-test of independence, 2 df, $P \ll 0.005$).

Hand pollinations during the post-hurricane season substantially increased fruit set, as they had in previous years. Inflorescences of the hand-pollinated group yielded 247 pollinia depositions of which 25 were from natural pollinations. Not all pollinations resulted in matured fruits. Fruit predation by rats (inferred by incisor tooth marks on damaged fruits) accounted for the loss of 103 fruits and 41 others were

TABLE 1. Frequency of pollinarium transfers from flowers of the Zarzal unmanipulated group during the pre-hurricane seasons of 1982–1983 and 1983–1984 (Ackerman and Montalvo, 1990), and the post-hurricane season 1989–1990 of *Epidendrum ciliare.*

Season	Total flowers	Class of visit: Pollinaria removed	Pollinia deposited	Removed & deposited	% poll[1] removed	% flowers visited	% flowers pollinated	% fruits set
Pre-hurricane								
1981–1982	856	—[2]	—	—	—	—		7.0
1982–1983	912	243	32	104	38.0	41.5	14.9	8.3
1983–1984	995	151	24	69	24.9	27.6	10.5	4.5
1984–1985	801		–	–	—		—	15.0
Post-hurricane								
1989-1990	417	190	18	28	52.3	56.6	11.0	5.3

[1] Pollinaria.

[2] Dashes indicate that no data were taken

aborted or lost for unknown reasons. Final fruit set was 25.6% of flowers produced. By contrast, 108 unmanipulated plants produced 417 flowers. Only 46 flowers (8.6%) were naturally pollinated and 22 matured fruits (5.3%). Predation accounted for the loss of 14 fruits, and abortions and unknown causes cost another 10 fruits. Final fruit set for the unmanipulated group was 5.3%, comparable to the pre-hurricane data of 1983–1984 (Table 1).

If stressful conditions affect the fate of pollinations, then we expected to detect a difference between unmanipulated and pollination-enhanced groups in the post-hurricane season. The proportion of damaged shoots caused by the hurricane among the two groups was very similar (unmanipulated: 57% damaged; manipulated: 54%). There were no treatment effects with regard to fruit fate among the hand-pollinated and naturally pollinated groups (maturation, predation, abortion; test of independence; G = 2.4, 2 df, $P > 0.1$). Thus, we combined the data of the two groups to test specifically for damage effects. Frequencies of the three different fruit fates were nearly dependent on plant condition (test of independence; G = 5.28, 2 df, $0.1 > P > 0.05$), but not in the direction expected. Damaged plants had a tendency to mature proportionately more fruits than undamaged plants.

We also compared the fate of all post-hurricane pollinations (natural and hand-pollinations) with that of previous years. The pre-hurricane manipulated groups were combined with the unmanipulated groups for the same reasons given above for combining the post-hurricane data (Ackerman and Montalvo 1990:table 4). Of the pre-hurricane seasons, we used only data from 1983–1984 because fruit loss was greater than the previous season and we wished to be conservative in our comparison with fruit maturations of the post-hurricane season (Table 2). We found that fruit maturation frequency was similar between the pre- and post-hurricane seasons (test of independence, G = 0.5, 1 df, $P > 0.1$) but the similarities between the two seasons were derived by different pathways: abortions were more frequent before the hurricane, whereas fruit predation was more frequent afterwards.

DISCUSSION

The habitat and plant damage caused by Hurricane Hugo affected reproductive effort only slightly. We expected some flower bud abortion, but the average number of flowers per inflorescence was higher after the hurricane than in previous seasons. This was not likely a consequence of the hurricane. Flower buds would have been formed by the time the hurricane hit. Remarkably, although more than half of the plants suffered damage (uprooting, sun

TABLE 2. Fruit set and frequencies of fruit abortions, predation, and maturations for *Epidendrum ciliare* manipulated and unmanipulated groups combined at Zarzal for two pre-hurricane seasons (1982–1983, 1983–1984) and one post-hurricane season (1989–1990). Pre-hurricane data are from Ackerman and Montalvo (1990).

Season	Pollinations	Abortions		Predation		Maturations	
		No.	%	No.	%	No.	%
Pre-hurricane							
1982-1983	1019	143	14.0	296	29.0	580	56.9
1983-1984	778	223	28.7	240	30.8	315	40.5
Post-hurricane							
1989-1990	293	51	17.4	117	39.9	125	42.7

[1] Includes data for abortions as well as unknown causes of fruit loss.

scorching, and leaf and stem breakage), flower buds were retained and continued to develop normally. We also expected a more negative response to heavy fruiting by damaged plants than by unscathed ones. However, *E. ciliare* plants were quite resilient on this account as well. Fruit abortions did not increase and final fruit set was similar to pre-hurricane years (Table 2). These measures of reproductive effort and success are indicative of short-term effects. Long-term responses may exist because *E. ciliare* does show a cost to reproduction in response to heavy fruit loads, but only in growth and reproduction in subsequent flowering seasons (Ackerman and Montalvo, 1990).

Pollinator activity was higher after the hurricane than in any of the previous years monitored. However, the number of pollinia depositions was much the same as in previous years. The discrepancy may be attributed to a higher number of pollinarium removals. Pollination in most orchids requires two successive visits: first a pollinarium is removed and then pollinia are deposited, which may be accompanied by another removal. We often assume that if a pollinator is capable of removing a pollinarium, then it should also be able to deposit pollinia on the stigma (Dressier, 1976; Ackerman, 1983). An increase in pollinarium removals without a proportional increase in pollinations has several possible explanations. First, our assumption may be wrong and other less efficient pollinators are involved. Secondly, resources of *P. tetrio* were reduced by the widespread destruction caused by the hurricane, so that the pollinators were migrating in search of food resources for either themselves or their brood. Pollinia depositions may thus have been higher elsewhere, enhancing gene flow. Interpopulation variation in floral fragrance composition is high (Moya and Ackerman 1983), suggesting that under normal circumstances gene flow is restricted. Finally, the second visit often did not happen. *Epidendrum ciliare* offers no pollinator reward, but under such circumstances pollinators still usually visit more than one flower (Heinrich, 1975). If *P. tetrio* were stressed and migrating, they may have been less inclined to explore flowers without immediate and positive feedback.

The aftermath of a hurricane has dramatic visual effects. Habitat destruction is widespread and has been documented in a number of recent studies. Short-term plant and animal responses are varied and sometimes dramatic. In the *E. ciliare-P. tetrio* interaction, the consequences of pollinator service provided by the hawkmoth changed very little. The moth populations were either largely unaffected by hurricane destruction or were very much on the move with immigration approximating emigration. The plants showed almost no change, at least in terms of fruit production, in either their reproductive effort or their reproductive success. Such short-term resiliency was not expected, although the results were consistent with the resiliency shown by a fig pollination mutualism (Bronstein and Hossaert-McKey, 1995). Long-term negative effects may yet occur in the *E. ciliare*- pollinator interaction, but we do not expect that they would be severe nor do we expect that they would persist for organisms that occur in regions where such storms are common.

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