Principes, 38(4), 1994, pp. 182–189

Effects of Hurricane Joan on the Palms of the Caribbean Coast Rainforest of Nicaragua

JOHN VANDERMEER
Department of Biology, University of Michigan, Ann Arbor, Michigan 48109

Hurricane Joan passed over the Caribbean coast city of Bluefields, Nicaragua, on October 22, 1988. In 1971 Hurricane Irene had struck the coast just south of Joan's landfall, indicating that hurricane hits are a relatively common occurrence in the region, at least from an ecological point of view, and it has been calculated that, on average, a hurricane strikes this coast about once per century (Boucher 1992). In the case of Hurricane Joan, approximately 500,000 hectares of tropical rainforest were severely affected, centered on a line between Bluefields and Rama, extending some 50 km inland.

Initial post-hurricane censuses of overstory trees revealed that the forest was as badly damaged as had been indicated in preliminary reports, as we have reported elsewhere (Yih et al. 1991, Vandermeer et al. 1990). In an intensively sampled area of 4,000 m^2, a total of 374 individual trees were encountered, representing 77 different species. Of all individuals encountered, 80.5% were either windthrown (27.3%) or snapped (53.2%), there was no forest canopy at all, and what had been canopy was on the ground as a deep and heterogeneously distributed and constituted layer. Very few individual trees were left standing (19.5%). Also evident was the fact that almost all species were represented by living individuals. Of 77 species of trees encountered in our intensively sampled area (4,000 m^2), all but two were represented by individuals that had already begun to resprout. A vast majority of trees (288 of the 374 individuals encountered) were resprouting.

The literature had suggested that the forest floor, four months after the hurricane, would be a garden of second-growth pioneers. It is well-documented that there are substantial quantities of seeds of pioneers in the seed bank under a tropical forest, and since four months with considerable rainfall had passed between the hurricane and our visit, we anticipated both normal dispersal mechanisms and germination of seed-bank seeds to have created an abundance of pioneers. We expected that the hurricane would have simply created a very large light gap and that the process of secondary succession would have begun, with gardens of seedlings of pioneer species such as *Ochroma, Cecropia, Croton, Heliconia, Heliocarpus, Calathea*, etc.

Our observations turned out to be dramatically at odds with such expectations. What had been forest understory was beneath or interspersed in a deep litter layer, not at all the imagined bare forest floor exposed to the sunlight. Light gaps caused by individual treefalls are characterized by an area in which the forest floor tends to be directly exposed to the incoming light with little debris covering it (the area of the bole), and a separate area with considerable debris covering the soil (the area on which the crown fell) (Orians 1982, Brokaw 1985). In contrast, for the most part the hurricane left almost all of the ground area covered in a deep layer of debris. In sampling seedlings, a total of 46 species were encountered in intensive subquadrats (40 2 × 2 m quadrats, 160 m^2 in total), almost all of which were species encountered as adults in the samples of the forest as a whole. Only one species (*Croton killipianus*) was new and a typical pioneer species; other expected large light gap colonizers, such as *Cecropia, Ochroma, Heliconia, Piper* or *Calathea*, were not encountered at all (although all were seen in surrounding agricultural and fallow fields).

In an attempt to characterize the forest understory, we also sampled the understory monocots, all of which were palms, at the two sites. A total of 13 species was encountered. Understory palms are notable for their ability to withstand physical damage (Rich 1986, Vandermeer et al. 1974, Bodley and Benson 1980), a reputation that was strongly reflected in our data. Of a total of 255 individual palms encountered, only 10 had been killed, despite the fact that many (181) had been severely damaged by falling debris. From our field observations it was quite evident that the understory palm flora, while severely damaged, was certainly not altered permanently. It appeared obvious that the palm flora (and by implication the forest understory in general) was severely damaged, but the majority of individuals were still alive. While epicormic branching (buds borne on trunks) is obviously not a possible strategy for monocots, the palm species seem well-suited to withstand the considerable physical damage exerted by the hurricane, through a variety of their own structural features (e.g., Rich 1986, Bodley and Benson 1980, Chazdon 1986). Whether this initial response of the understory palm flora would persist in future years was the purpose of the present study.

Methods

The study was conducted in three sites distributed as representatively as possible within the area damaged by Hurricane Joan. Based on local features, the sites were referred to as Bodega, Fonseca, and Delicias. Site selection was very much hampered by the primitive means of travel available in the region, made especially difficult by the hurricane with thousands of trunks blocking most waterways, that provided access for automated transportation in the zone. Thus, while we attempted to choose three representative sites, our choices were quite limited to begin with. During the first expedition to the area (described above), only Bodega and Delicias were visited. Thus were established four plots (100 m × 10 m) in February of 1989, two each at Bodega and Delicias.

In February of 1990, all three sites were visited and additional plots established at each, such that a total of 10 plots (100 m × 10 m) were included in the study—three at Bodega, three at Fonseca, and four at Delicias. Subsequent to our initial expedition to the area, a logging road had been built at Delicias in such a way that one of the two original plots had been affected (approximately 20 meters at the origin of the plot was within 10 meters of the new logging road, thus not physically encountering the plot itself, but certainly having at least a small effect). This was the main reason for adding a fourth plot at Delicias. All adult trees in all ten plots were permanently marked and measured, understory palms censused, overstory shade estimated, and seedlings/saplings censused in subplots, all of which is described below.

In February of 1991 all ten plots were recensused, and in February of 1992 the second plot at Delicias was abandoned due to excessive vandalism. In February of 1993, plots 3 and 4 at Delicias had been completely slashed and burned and converted to a cassava/taro plantation, and thus had to be abandoned.

In each of the 10 permanent plots the left-hand side of the plot was censused yearly for understory palms (i.e., a plot 100 m × 5 m). All species of palms whose highest leaf apex was 1 m or more were recorded. While several species are clonal (i.e., *Geonoma congesta*, *G. longevaginata*, *Bactris* sp. 1., *Bactris* sp. 2, *Prestoea decurrens*, *Reinhardtia latisecta*), it is usually a simple matter to distinguish one clone from another, and only individual plants were recorded (i.e., all canes from a single cone were lumped as one individual). Frequently this gives rise to a "rare" species appearing to be much more abundant than it in fact does, as is obviously the case with *Bactris* sp. 1, and *Desmoncus* sp. (the latter because of its viny nature).

Censuses were done visually without marking individual plants for the purpose of recording any large-scale changes that might happen subsequent to the hurricane. Since the purpose was only to record large-scale effects, a variety of error sources enter this data set. A visual judgment was made as to whether each individual entered the >1 m height category. Thus the same individual could possibly be included in one year but not the next because of changes in judgment of the observer. Furthermore it was frequently visually estimated whether an individual was within 5 m of the center transect line, a method similarly affected by observer judgments. Neither of these two effects are likely to be very severe, but they are nevertheless inherent in the data collection technique. Finally, since individual plants were not marked, it is always possible that an individual encountered one year will not be encountered the next, simply because of the problems inherent in searching for plants in a severely damaged forest. Especially during the first two or three years, the understory was filled with dead and dying trees and fallen branches and debris, and some areas were extremely difficult to search. Undoubtedly this is a situation that could easily have contributed to inaccuracies in data collection. On the other hand, for the purposes at hand—to search for large-scale changes in the understory palm flora—I have no reason to doubt that the data collected are adequate to the task.

All individuals were identified by myself, with

Table 1. Number of individuals of each species encountered in all years sampled in each plot. D = Delicias, B = Bodega, and F = Fonseca.

	D1					D2			D3			D4			B1		
Name	89	90	91	92	93	89	90	91	90	91	92	90	91	92	89	90	91
Asterogyne martiana	0	13	12	14	14	1	0	0	0	0	0	0	7	2	0	0	0
Astrocaryum alatum	4	5	10	11	5	5	12	14	15	20	22	36	38	41	0	0	0
Bactris 1	6	5	6	7	2	6	10	12	4	7	11	2	2	2	2	2	3
Bactris 2	0	0	0	2	1	0	0	0	4	0	0	2	0	0	0	0	0
Bactris 3	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0	0	0
Bactris hondurensis	0	0	2	1	2	0	0	2	0	3	1	0	2	3	0	0	1
Calyptrogyne	0	7	2	1	0	0	2	0	0	0	0	0	2	0	26	27	31
Chamaedorea exorrhiza	3	2	3	3	0	0	4	4	0	0	0	0	0	0	0	1	0
Chamaedorea sp.	0	1	7	0	0	0	3	0	15	17	2	7	5	0	0	1	1
Cryosophila albida	8	16	24	23	15	3	2	2	0	2	3	20	27	29	0	1	1
Desmoncus sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
Geonoma congesta	46	41	59	76	51	39	30	26	37	44	63	40	50	61	27	11	12
Geonoma interrupta	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Geonoma longevaginata	2	2	9	13	11	0	0	1	10	7	42	0	0	11	2	2	1
Geonoma sp.	0	0	0	2	0	0	0	0	0	0	2	0	2	4	0	0	0
Prestoea decurrens	2	1	3	2	4	0	5	5	14	13	16	0	0	0	8	1	2
Reinhardtia latisecta	2	3	6	2	3	0	2	2	6	7	6	0	0	0	30	26	25
Reinhardtia simplex	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
Socratea exorrhiza	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Welfia georgii	12	16	24	25	21	11	12	10	4	5	6	2	2	5	3	1	1

the aid of Mr. Nelson Zamora of the Universidad Nacional de Costa Rica, a noted Costa Rican plant taxonomist. All species were relatively easily identified with the exception of several species of *Bactris* and *Chamaedorea.* Because field identification in both of these cases was difficult, strategic lumping was employed. Thus, *Bactris* sp. 1, *Bactris* sp. 3, and *Bactris hondurensis* are quite distinctive and could be identified in the field. However, *Bactris* sp. 2 is a composite of a minimum of four species. *Chamaedorea exorrhiza,* with its distinctive aerial roots, was clearly identifiable, but at least two other species, virtually indistinguishable at small size, were also encountered, and lumped as *Chamaedorea* spp. Thus the list of 20 species presented below is actually a list of a minimum of 24 species. Furthermore, several other species were observed, but no individuals ever entered the >1 m category, including *Geonoma cuneata* and *Chamaedorea geonomiformis.*

Finally, it should be noted that, to my knowledge, this is the first time that the palm flora of this region has been examined at all. Several species seem to represent material that is genetically distinct from what I have seen elsewhere, and ultimately may prove to be distinct species, as could be the case in any newly examined area. For example, specimens of *Astrocaryum alatum* in this area have distinctly smaller seeds, smaller vegetative stature, and smaller and more finely divided leaves than the specimens I have seen in Costa Rica. Detailed systematic studies in this region are clearly warranted.

Results

The results of this five-year study are presented in Table 1. The major and most obvious conclusion to be drawn is that major changes in palm flora as a result of the hurricane did not seem to occur. The general pattern of relative abundance seems to have been maintained in all ten plots, despite significant floral differences among sites and plots. As discussed more fully below, all of these species seem particularly resistant to physical damage, possibly one of the reasons the lowland Central American Caribbean rainforests are so rich in palm species. Photographs of the area near Delicias are presented in Figure 1, illustrating the general aspect of the forest four months and four years after the hurricane.

Each of the three sites could be distinctly characterized with regard to its palm flora. Delicias is rich in *Astrocaryum alatum* and *Geonoma congesta,* with *Welfia georgii* frequently also a common part of the flora. At Bodega *G. congesta*

Table 1. Extended.

B1		B2					B3			F1				F2				F3			
92	93	89	90	91	92	93	90	91	92	90	91	92	93	90	91	92	93	90	91	92	93
0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	68	65	87	87	73	55	78	115	42	40	59	38
5	4	2	4	5	4	4	3	1	1	1	3	6	2	7	3	5	4	0	1	0	1
0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0
1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
38	34	3	3	3	4	2	1	3	2	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0
1	1	0	0	0	0	0	0	0	0	3	3	5	3	0	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	1	0
19	12	13	10	17	17	17	12	9	8	4	3	4	4	3	4	1	2	3	4	13	14
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	3	2	3	0	0	1	11	9	14	23	19	28	29	12	8	15	22	57	40	43	49
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	1	4	2	1	1	1	5	5	4	0	0	0	0	0	1	0	0	8	6	8	7
35	32	4	5	3	5	2	19	19	24	0	0	1	1	21	10	15	16	30	23	41	28
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	2	4	3	2	4	3	2	1	1	0	0	0	0	0	0	1	0	1	0	3	0

dominates, but there is a notable absence of *A. alatum* (although the latter has been seen outside of the sampling plots—it is a rather rare species in the area), and typically with a relatively large abundance of *Reinhardtia latisecta*. Fonseca is characteristically dominated by *A. alatum* and *Geonoma longevaginata*, with *R. latisecta* sometimes abundant also. Occasionally a particular plot is characterized by a particular species, such as D-1 with *Asterogyne martiana*, B-1 with *Calyptrogyne* sp., and D-3 with *Prestoea decurrens*. Despite this arguable uniqueness of each site, and frequently each plot within each site, we see little evidence that there had been a dramatic shift in the nature of the understory palm flora during five post-hurricane years.

Of course subtle effects may exist. In Figure 2a, b and c, I have plotted genet abundances of the three commonest species over time. In all three cases there is a suggestion that populations are increasing in numbers. This suggestion is further enhanced with regressions—in 29 out of 36 cases the regression coefficients (population growth rates) are positive, although attaining statistical significance with such small numbers is difficult and only two examples are significant at the .05 level (see Table 2). On the other hand, looking at all the regression coefficients in Table 2, the probability of getting 29 or more positives out of a sample of 35 (if the real value were 0) by chance is less than .01, and a simple t-test shows a highly significant difference from zero ($t = 4.34$, $df = 34$, $p < .001$). These data may thus indicate that the population densities are generally increasing and a subtle effect of the hurricane was to provide at least a temporary advantage to understory palms. But it could also be a consequence of increasing ease of sampling the flora as the forest regenerates. Indeed, in 1989 it was impossible even to walk through the forest, the plots sampled by climbing through a forest canopy that effectively had been dropped to the ground. By 1993, there was enough of a new canopy and the debris deposited by the hurricane had decayed enough to make it far easier to maneuver through the forest. Thus, each year it may simply be that I see more of what was there in the first place. Such an interpretation is supported by the data on *Asterogyne martiana*. A single individual was encountered in 1989, yet by 1990 13 individuals were encountered in plot D-1. Many of these 13 individuals were already large and robust in 1990, as illustrated in Figure 3, suggesting that the 1989 census had simply overlooked the leafless trunks of these 13 individuals, which were probably buried in a mound of post-hurricane debris.

Discussion

The principal result of this study is that the understory palm flora was not greatly affected by the hurricane. If there was any effect at all it may have been slightly positive in that several species appear to be more common than before the hurricane, although this appearance could be due to sampling error, as discussed above. But even if the subtle increase in population densities is not a sampling artifact, the general result is striking. The hurricane did not have a significant effect on the understory palm flora.

Unfortunately no pre-hurricane data are available for these sites. In our initial surveys we were able to locate what seemed to be all of the understory palms, living or dead, that were underneath the large amount of dead vegetative material deposited by the hurricane. These densities generally correspond to other forests in Central America (e.g., Vandermeer 1993), and it is unlikely that the pre-hurricane forests were any different.

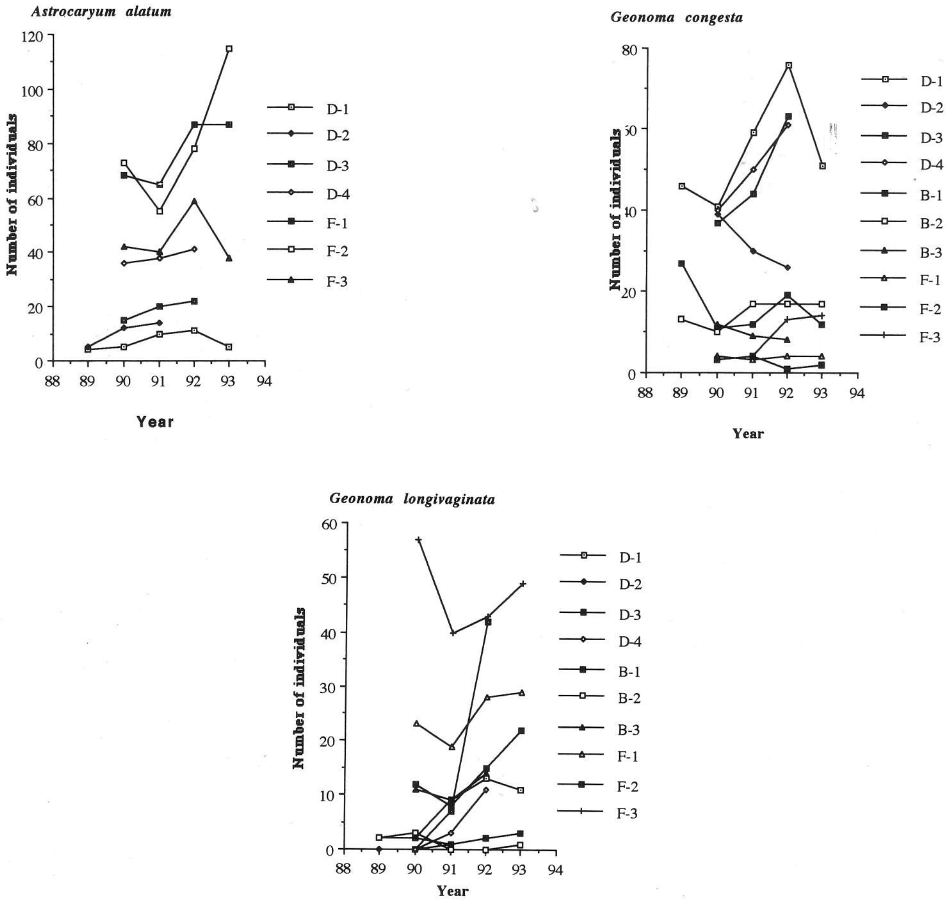
This result is not really surprising given the natural history of the species concerned. Almost all appear to be particularly resistant to physical damage. *Asterogyne martiana* has a single flexible trunk, and it is frequently seen in other forests with the trunk angled strongly or even bent, reflecting the effect of past damage. Several of the species have multiple and flexible canes (*Geonoma congesta*, *G. longevaginata*, *Bactris* spp. 1, 2, and 3) which can be virtually plastered to the ground, yet the meristem simply begins growing upward, resulting in the well-known bent canes of *Geonoma congesta* commonly encountered wherever the species occurs. Others of the species spend all of their life cycle with their meristems under the ground or at ground level (*Calyptrogyne* sp., *Bactris hondurensis*), and thus can withstand whatever physical damage that doesn't disturb the physical integrity of the ground. Others spend their juvenile years with their meristems under the ground (*Cryosophila albida*, *Geonoma interrupta*, *Prestoea decurrens*, *Reinhardtia latisecta*, *Welfia georgii*) such that their age distribution will be altered by the hurricane (since most of the adults will be killed), but all or almost all juveniles will survive. My studies of *W. georgii* in Costa Rica underscore that point (Vandermeer 1977, 1983; Vandermeer et al. 1979). In the case of *W. georgii*, for example, many felled

Table 2. Regression coefficients (estimates of crude population growth rate) and their significances for selected examples. All cases in which 10 or more individuals were encountered at some time during the study are included in this table. Asterisks indicate significance at the .05 level.

Species	Plot	Regression Coefficient	Significance
Asterogyne martiana	D1	2.9	.13
Astrocaryum alatum	D1	1.1	.52
Astrocaryum alatum	D2	1.4	.20
Astrocaryum alatum	D3	3.5	.15
Astrocaryum alatum	D4	2.5	.07
Astrocaryum alatum	F1	7.9	.14
Astrocaryum alatum	F2	8.9	.24
Astrocaryum alatum	F3	5.2	.91
Bactris 1	D2	3.0	.12
Bactris 1	D3	3.5	.05
Calyptrogyne sp.	B1	2.7	.06
Cryosophila albida	D1	2.1	.38
Cryosophila albida	D4	4.5	.2
Geonoma congesta	D1	4.5	.37
Geonoma congesta	D2	−6.5	.14
Geonoma congesta	D3	13.0	.17
Geonoma congesta	D4	10.5	.02*
Geonoma congesta	B1	−2.2	.38
Geonoma congesta	B2	1.5	.15
Geonoma congesta	B3	−2.0	.18
Geonoma congesta	F3	4.2	.07
Geonoma longevaginata	D1	2.9	.04*
Geonoma longevaginata	D3	16.0	.38
Geonoma longevaginata	D4	5.5	.33
Geonoma longevaginata	B3	1.5	.59
Geonoma longevaginata	F1	2.7	.25
Geonoma longevaginata	F2	3.7	.19
Geonoma longevaginata	F3	−2.1	.64
Prestoea decurrens	D3	1.0	.55
Reinhardtia latisecta	B1	1.3	.40
Reinhardtia latisecta	B3	2.5	.33
Reinhardtia latisecta	F2	−1.0	.71
Reinhardtia latisecta	F3	1.2	.80
Welfia georgii	D1	2.7	.12
Welfia georgii	D2	−0.5	.67

←

1. Photos of the area immediately after and four years after the hurricane. Top photo is near Delicias in February of 1989, four months after the hurricane. Note the individuals of *Geonoma congesta* clearly visible, and the damaged *Welfia georgii* to the left. Bottom right is an individual of *Geonoma congesta* in the understory of the same forest in February of 1993. Bottom left is an individual of *Welfia georgii* in the understory of the same forest in February of 1993.



2A. Line graph of number of individuals of *Astrocaryum* over time. 2B. Line graph of *Geonoma congesta* over time. 2C. Line graph of *Geonoma longevaginata* showing number of individuals and time scale.

adults were seen in 1989, and it was not until 1993 that a single individual (at Fonseca) was seen fruiting, probably indicating a dramatic change in the demography of the species. Also, Chazdon (personal communication) reports that large individuals of *W. georgii* can be found in secondary forests in Costa Rica, presumably evading the teeth of the chain saw by keeping their meristems under the ground.

The very long term effects of periodic hurricanes are difficult to judge from the data available. While it can be said with some confidence that the hurricane does not significantly affect the palm flora over the short term, many long term effects could exist. For example, the same periodic resetting of population densities thought to prevent competitive exclusions of canopy trees (Vandermeer et al. 1993) might be very important here in that subcanopy and canopy dicot trees may eventually outcompete the palm understory, but with a hurricane every century or so (Boucher 1992) a short advantage is given to local populations, at least those that have some sort of mechanism to withstand the physical damage of the hurricane.

A particularly interesting case is that of *Socratea exorrhiza*. Three adult individuals of this species were encountered in 1989, but none since. Since this species is so obvious and striking because of its large stilt roots, it is easy to spot in the forest. Subsequent to the detection of these three individuals in 1989 (all of which died during the following year), successive expeditions have been unable to spot a single individual of the species. Each year all participants in the expedition (typically between 20 and 30 people) are instructed

3. Photo in plot D-1 of large specimen of *Asterogyne martiana.*

to "find" *S. exorrhiza,* and during the two-week stay in the area, traversing not only the 10 permanent plots but also surrounding logging roads and hunters' trails. As of 1993 none had been encountered. This species is well-known to resist physical damage by rerooting along its trunk (Bodley and Benson 1980), and it seems likely that the only reason this was not possible was due to the large size of the damaged individuals encountered in 1989. Apparently unlike other arborescent species (e.g., *Welfia georgii, Prestoea decurrens, Cryosophila albida*), a significant reservoir of juveniles with protected meristems did not exist in the area, possibly due to a failure in the seed dispersal mechanism of this species. The lack of abundant juveniles seems to have caused a local extinction in the case of this formerly rare but extant species.

Finally it is worth emphasizing that all the species encountered in this study appear to have some mechanism for withstanding physical damage, as noted earlier. It could be that species lacking such mechanisms simply do not exist in the area precisely because of periodic hurricane damage.

Literature Cited

BODLEY, J. H. AND F. C. BENSON. 1980. Stilt-root walking by an Iriartoid palm in the Peruvian Amazon. Biotropica 12: 67–71.

BOUCHER, D. 1992. En la Costa, un huracán cada siglo. Wani (Managua) 12: 32–34.

BROKAW, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66: 682–687.

CHAZDON, R. L. 1986. The costs of leaf support in understory palms: economy versus safety. Am. Nat. 129: 9–30.

ORIANS, G. H. 1982. The influence of tree falls in tropical forests on tree species richness. Trop. Ecol. 23: 255–279.

RICH, P. 1986. Mechanical architecture of arborescent rain forest palms. Principes 30: 117–131.

VANDERMEER, J. H. 1977. Notes on density dependence in *Welfia georgii*, a lowland rainforest palm from Costa Rica. Brenesia 10/11: 1–15.

———. 1983. *Welfia georgii. In:* D. Janzen (ed.). Costa Rican natural history. University of Chicago Press, Chicago, pp. 346–349.

———. 1993. Successional patterns of understory palms in an old cacao plantation on the Caribbean coast of Costa Rica. Principes 37: 73–79.

———, J. STOUT, AND G. MILLER. 1975. Growth rates of *Welfia georgii, Socratea durissima,* and *Iriartea gigantea* under various conditions in a natural rain forest in Costa Rica. Principes 18: 148–154.

———, N. ZAMORA, K. YIH, AND D. BOUCHER. 1990. Regeneración inicial en una selva tropical en la costa caribeña de Nicaragua después del huracán Juana. Rev. Biol. Trop. 38: 347–359.

———, D. BOUCHER, I. PERFECTO, M. MALLONA, AND N. ZAMORA. 1993. Disturbance as a promoter of tropical forest diversity: support of a key assumption in the aftermath of Hurricane Joan in Nicaragua. Submitted to Nature.

———, J. STOUT AND S. RISCH. 1979. Seed dispersal of a common Costa Rican rainforest palm (*Welfia georgii*). Trop. Ecol. 20: 17–26.

YIH, K., D. BOUCHER, J. H. VANDERMEER, AND N. ZAMORA. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. Biotropica 23: 106–113.