

Hurricanes and Mangrove Regeneration: Effects of Hurricane Joan, October 1988, on the Vegetation of Isla del Venado, Bluefields, Nicaragua¹

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ABSTRACT

Based on sampling of a hurricane-damaged Caribbean mangrove forest, stand structure and composition are characterized for both pre- and posthurricane vegetation. Before the storm, stand structure was typical of mangrove forests throughout the region, but poorly developed compared to upland forests in the same life zone, as expressed in a composite index of tree height, basal area, stem density, and species diversity. The hurricane inflicted the most severe damage upon the largest trees and markedly reduced the complexity index of the stand, but it appears to have favored the establishment of abundant regeneration by all of the original mangrove species. Periodic destruction of Caribbean mangrove forests by cyclonic storms is proposed as one explanation for their characteristically low structural complexity as well as the lack of typical "climax" components in the vegetation.

RESUMEN

En base al muestreo de un manglar caribeño afectado por vientos huracanados, se caracterizan la estructura y la composición vegetacionales del rodal antes y después del ciclón. Antes del huracán, este rodal presentaba un desarrollo estructural típico de los manglares caribeños pero pobre en comparación con bosques de tierra firme dentro de la misma zona de vida, según un índice basado en la altura, área basal, densidad y diversidad de los árboles. El huracán provocó los daños más severos entre los árboles más desarrollados y redujo marcadamente el índice de complejidad del rodal, pero parece haber promovido el establecimiento de regeneración abundante de todas las especies de mangle previamente presentes. La destrucción periódica de los manglares caribeños por tormentas ciclónicas se propone como una explicación de su complejidad estructural característicamente baja así como la falta de un típico componente "clímax" en esta vegetación.

Key words: diversity; forest structure; hurricane damage; mangrove; Nicaragua; regeneration; succession.

THEIR DISTRIBUTION ALONG LOW LATITUDE SEACOASTS inevitably places mangrove swamps among the terrestrial ecosystems most prone to experience the passage of hurricanes and other tropical cyclones. Because the frequency of such storms at any one site is commonly well within the potential lifetime of individual trees (Egler 1952, Stoddart 1963, Gentry 1974, Lugo *et al.* 1976, Neumann *et al.* 1981, Boucher, in press), these disturbances predictably influence the selection regimes of mangrove species as well as their community dynamics. An understanding of mangrove responses to hurricane impact should assist in interpreting the distribution and structure of these ecosystems and in designing appropriate management strategies.

Numerous reports of the ecological effects of hurricanes mention damage to mangrove vegetation (Davis 1940, Egler 1952, Wadsworth & Englerth

1959, Craighead & Gilbert 1962, Sauer 1962, Stoddart 1963, Vermeer 1963, Glynn *et al.* 1964, Alexander 1967, Heinsohn & Spain 1974, Bunce & McLean 1990, Wunderle *et al.* 1992), but the accounts are, for the most part, general and qualitative. Virtually complete defoliation by wind and/or waves, shearing of branches and trunks, uprooting of some trees, damage to bark, and the deposition of sediment and organic debris often produce an initial impression of complete devastation. Recuperation of some of the stripped trees may take place through sprouting and refoliation (Craighead & Gilbert 1962, Sauer 1962); failure to recover depends in part on species characteristics (Wadsworth & Englerth 1959), topographic situation (Craighead & Gilbert 1962), sedimentation and drainage patterns (Craighead 1971, Heinsohn & Spain 1974, Cintrón *et al.* 1978), and proximity to the hurricane track (Stoddart 1963). Seedlings and saplings often survive the storm or appear prolifically in subsequent months (Craighead & Gilbert

¹ Received 1 March 1991, revision accepted 25 November 1991.

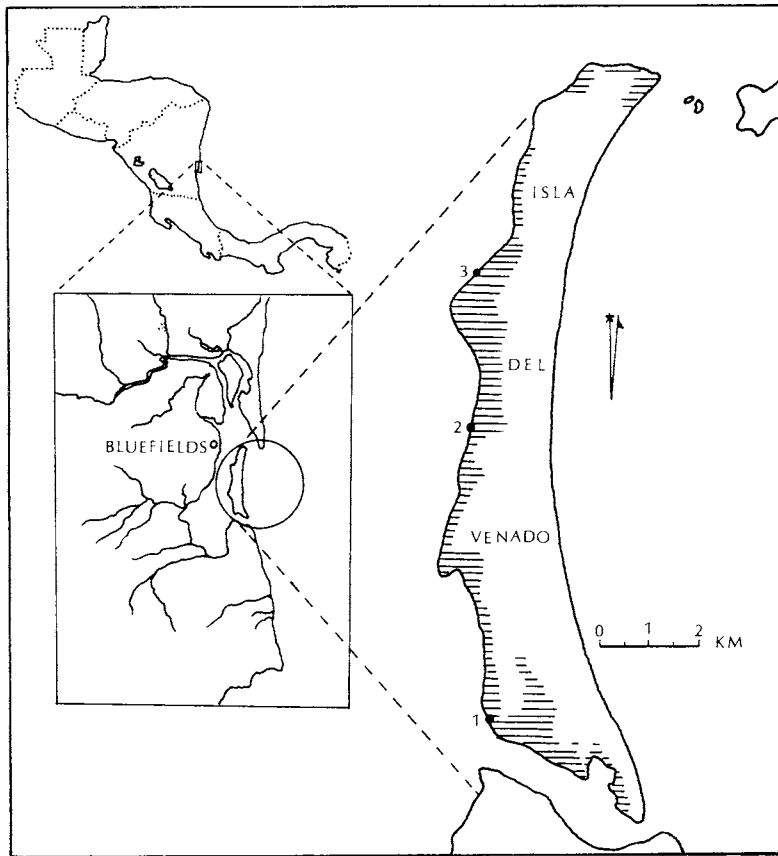


FIGURE 1. Composite map locating Isla del Venado ($11^{\circ}55'N$; $83^{\circ}45'W$) in relation to Bluefields, Nicaragua, and indicating mangrove communities (hatched area) and numbered sampling transects (●).

1962, Sauer 1962, Craighead 1964, Alexander 1967, Wunderle *et al.* 1992), but exceptions occur (Egler 1952, Stoddart 1963). Long-term studies tracing the fate of this regeneration appear to be nonexistent, and although the recovery of mangrove ecosystems after hurricanes is widely recognized (Lugo & Snedaker 1974, Jiménez *et al.* 1985), the process is poorly documented.

The present survey was undertaken 17 months after a Caribbean hurricane swept directly across an extensive stand of mangrove forest. Objectives of the survey were to record damage and early recovery and to leave marked plots for continuing observation, with the intent of exploring the ecological significance of hurricanes for mangrove vegetation.

STUDY SITE AND METHODS

Isla del Venado is an elongated barrier island fronting the Bay of Bluefields on the Caribbean coast of

Nicaragua (Fig. 1). Its climate corresponds to the tropical wet life zone of Holdridge (1967). The island extends 15 km in a broad north-south arc and is close to 2 km wide throughout its length; its bayward side is fringed in a band 0.1 to 1.0 km wide with mangrove vegetation growing on a substrate of fine-grained mineral and organic deposits. Although topographic relief is negligible within the mangrove area and most of the island may be subject to occasional flooding, the surface is not typically overwashed at high tide. The mangroves would be categorized as "fringe forest" in the typology of either Lugo and Snedaker (1974) or Cintrón *et al.* (1985).

Moving westward at $15\text{--}16\text{ km hr}^{-1}$ along parallel $12^{\circ}N$, Hurricane Joan struck Isla del Venado on 22 October 1988. Meteorological data are not available for the island itself, but Bluefields, located directly across the bay, experienced sustained wind speeds of 217 km hr^{-1} near the center of the storm

TABLE 1. Trees (≥ 2.5 cm DBH) encountered in posthurricane strip transects, Isla del Venado, Bluefields, Nicaragua.

Species	Transect 1		Transect 2		Transect 3		Total	
	#	%	#	%	#	%	#	%
<i>Avicennia germinans</i>	6	21	17	65	7	64	30	45
<i>Laguncularia racemosa</i>	10	34	8	31	1	9	19	29
<i>Pelliciera rhizophorae</i>	0	0	0	0	1	9	1	2
<i>Rhizophora mangle</i>	13	45	1	4	2	18	16	24
Total	29	100	26	100	11	100	66	100

with gusts exceeding 250 km hr^{-1} (INETER 1988). Rainfall in Bluefields totaled more than 400 mm for the period of 21–23 October and tidal surge there was substantial (INETER 1988). Immediately following the storm observers reported that the mangrove forests throughout the bay had been killed; seven months later there was no sign of recovery visible from 50 m offshore other than the large green fronds of leather fern (*Acrostichum* sp.) among the apparently leafless trunks of the mangroves (pers. obs.).

On 16–17 March 1990 woody vegetation was sampled along three strip transects crossing the damaged mangrove fringe on Isla del Venado (Fig. 1). The island was chosen as a study site because of its location directly in the path of the hurricane as well as the appearance of rather uniform physical conditions along its length. Originating from randomly located points on the island's west shore, the sampling strips were oriented due magnetic east to detect possible topographic zonation in the vegetation.

Strip transects measured $5 \text{ m} \times 100 \text{ m}$, or 0.05 ha each. All woody vegetation rooted within these areas was recorded, in 2 categories. For individuals ≥ 2.5 cm DBH (bole diameter at breast height, or 1.3 m above ground level), record was made of distance along the transect (dm), species, DBH (cm) measured with diameter tape, approximate height (ocular estimate to nearest meter by experienced forester), condition of main stem (broken vs not), and recovery class (well refoliated vs poorly refoliated vs dead). For smaller individuals only position (as above), species, height (to nearest half-meter), and origin (sprout vs seedling) were noted. Patches of *Acrostichum* fern and accumulations of dead wood were also recorded.

RESULTS

PRE-EXISTING STAND.—There were 66 individuals ≥ 2.5 cm DBH (hereafter referred to as "trees") in the three strip transects. Four mangrove species were represented, as enumerated in Table 1; the presence

of *Pelliciera rhizophorae* is considered unusual for the Caribbean area (Roth & Grijalva 1991).

Tree size and density estimates are summarized in Table 2. Stem density and basal area varied considerably among transects as reflected in the large standard errors. This variability is associated in part with the low number of trees in transect 3, nearly one-half of whose surface (233 m^2 of 500 m^2) was occupied by a thick cover of *Acrostichum* sp. Values in Table 2 represent minimum estimates for the pre-existing stand since they exclude trees broken below 1.3 m, of which three sprouting specimens of *Laguncularia* were counted; fallen trees, of which there was one sprouting *Rhizophora*; any individuals uprooted and blown from the sample area, of which no evidence was noted; and dead stems lying across but not appearing to have been rooted within the strips.

To permit comparison with mangrove forests elsewhere, complexity indices (Holdridge 1967) based on these strips are presented in Table 3. The indices, which are composite values proportional to species number, stem density, maximum height, and basal area (total stem cross sectional area at 1.3 m above ground), of stands, are recorded here both for the standard tree component (DBH ≥ 10 cm) and using a smaller minimum diameter (2.5 cm) as adapted for mangrove vegetation by Pool *et al.* (1977). Complexity indices are computed for each strip separately, doubling stem numbers and basal areas to conform to the stipulated 0.10-ha transect. (Although such extrapolation normally would be problematical due to the nonlinear relationship of

TABLE 2. Structural parameters (± 1 SE) of prehurricane mangrove forest, Isla del Venado, Bluefields, Nicaragua.

Average DBH: 14 (± 4) cm
Height of tallest trees: 25 m (incl. 1 broken at this level)
Tree density: 440 (± 111) ha^{-1}
Basal area: 14.88 (± 9.29) $\text{m}^2 \text{ ha}^{-1}$
Tree species: 4

TABLE 3. Complexity indices^a of prehurricane mangrove vegetation, Isla del Venado, Bluefields, Nicaragua, and of fringe (F) and overwash (O) mangroves elsewhere.^b

Mangrove location	Life zone ^c	Type	Complexity index	
			Trees ≥ 2.5 cm DBH	Trees ≥ 10 cm DBH
Isla del Venado, 1	T Wet	F	14.3	6.2
Isla del Venado, 2	T Wet	F	7.9	2.7
Isla del Venado, 3	T Wet	F	0.2	0.1
Florida	ST Moist	O	3.4	0.8
Florida	ST Moist	F	9.6	1.4
Ceiba, Puerto Rico	ST Dry	F	16.2	0.2
Aguirre, Puerto Rico	ST Dry	F	29.9	5.6
Punta Gorda, Puerto Rico	ST Dry	F	0.9	0.0
Isla Roscell, Mexico	ST Dry	O	10.1	5.7
Sta. Rosa, Costa Rica	T Dry	F	4.9	3.6

^a Holdridge (1967).

^b Pool *et al.* (1977).

^c T = tropical; ST = subtropical.

species number to sampling area, it is unlikely within the mangrove community that larger sampling units would have included additional tree species; species totals are consequently left unchanged in the weightings.) Complexity indices reported by Pool *et al.* (1977) for fringe and overwash mangroves not recently disturbed by hurricanes in Florida, Puerto Rico, Mexico, and Costa Rica are tabulated for comparison; their averages closely approximate those of the reconstructions of prehurricane Isla del Venado.

No clear grouping of species into zones or belts parallel to shore was apparent for the prehurricane stand. *Rhizophora*, the mangrove most commonly reported as forming an outermost band, was indeed found in the first 5 m of each transect; but it was also encountered as far from shore (100 m, the inner limit of the transects) as any of the other species

and at a wide range of intermediate points. Locations of *Avicennia* and *Laguncularia* likewise extended from the 5 m point to the inland ends of the transects, with no segregation evident. Variance-ratio tests failed to show significant positive or negative association (presence/absence data) among the three principal mangrove species using a range of quadrat sizes from 25 m² to 75 m² ($\chi^2_{0.05} > W > \chi^2_{0.95}$), except that *Avicennia* and *Rhizophora* were negatively associated at the 25 m² size. Abundance values of *Avicennia* and *Rhizophora* exhibited negative pairwise correlation using 25 m² (Spearman's rank $r = -0.349$, $N = 33$, $0.01 < P < 0.05$) and 75 m² ($r = -0.713$, $N = 11$, $0.01 < P < 0.05$) quadrats. The single adult of *Pelliciera* was found 28.2 m from the water's edge.

DAMAGE TO PRE-EXISTING STAND.—Trees in the sample strips manifested heavy damage inflicted by the hurricane; severed branches and twigs had left most specimens with bare, open crowns. Trees of each species are enumerated by recovery class and condition of main stem in Tables 4 and 5. Forty-five percent of the trees had broken trunks, and only 42 percent of individuals were found to be well refoliated 17 months after the storm. *Rhizophora* in these strips had higher proportions of dead, poorly refoliated, and broken-stemmed individuals than *Avicennia* or *Laguncularia*, but the differences were not statistically significant ($\chi^2 = 7.06$, 4 df, $0.50 > P > 0.10$ for recovery category; $\chi^2 = 2.07$, 2 df, $0.50 > P > 0.10$ for stem condition; *Pelliciera* excluded due to insufficient counts).

Broken trunks had significantly larger basal di-

TABLE 4. Recovery of trees in mangrove samples, Isla del Venado, Bluefields, Nicaragua, 17 months after Hurricane Joan.

Species	Number of individuals per recovery class			Total
	Well refo- liated	Poorly refo- liated	Dead	
<i>A. germinans</i>	14	4	12	30
<i>L. racemosa</i>	11	4	4	19
<i>P. rhizophorae</i>	0	1	0	1
<i>R. mangle</i>	3	5	8	16
Total	28	14	24	66

TABLE 5. Stem condition of trees in mangrove samples, Isla del Venado, Bluefields, Nicaragua, 17 months after Hurricane Joan.

Species	Number of individuals with main stem		
	Broken	Entire	Total
<i>A. germinans</i>	11	19	30
<i>L. racemosa</i>	10	9	19
<i>P. rhizophorae</i>	0	1	1
<i>R. mangle</i>	9	7	16
Total	30	36	66

ameters than unbroken ones (21 cm vs 7 cm; two-sided $\alpha = 0.0011$); by implication it was probably the taller trees of the prehurricane stand that were most likely to suffer breakage. Average height at the time of sampling did not differ between broken and unbroken stems, so the effect of the wind was evidently one of leveling. This effect was augmented by survival, since the mean height of well refoliated individuals was significantly below that of remaining dead trunks (5 m vs 10 m; two-sided $\alpha = 0.0044$). Recovery class for broken trees did not vary significantly by diameter nor by height at which the trunk snapped, but stem breakage itself was strongly associated with mortality ($\chi^2 = 18.43$, 2 df, $P < 0.001$).

Among the unbroken trunks, those with good refoilation had smaller diameters than those which recovered poorly or died (5 cm vs 8 cm vs 16 cm; $F = 11.83$, $\alpha = 0.0001$). They were also of shorter stature than the unbroken trunks which recovered poorly or died (5 m vs 6 m vs 12 m; $F = 4.4$, $\alpha = 0.02$).

Dead trees constituted 36 percent of all stems on sample strips and averaged more than twice the diameter of trees that survived (21 cm vs 10 cm; two-sided $\alpha = 0.0175$), leaving only 32 percent of the basal area in live stems after the hurricane.

SEEDLING REGENERATION.—Seventeen months after Hurricane Joan struck Isla del Venado, seedlings of the three principal mangrove species were found growing plentifully throughout the damaged stand except within aggregations of *Acrostichum* fern, from which they were virtually absent (Table 6). *Avicennia* seedlings were most abundant on all sampling strips and constituted over one-half of this regeneration, followed in total numbers by *Laguncularia* and *Rhizophora*; but population density estimates did not differ significantly among the three species (8583 vs 3943 vs 2054 ha⁻¹ of fern-free area; $F = 3.96$, $\alpha = 0.0801$). Ten seedlings of *Pelliciera rhizophorae* were recorded. "Stump" sprouts were uncommon, largely because most stem breakage had occurred at higher levels on the trunks; the three recorded cases of basal sprouting involved *Laguncularia*.

Like the adults, the seedlings showed little evidence of segregation into zones by species. No significant overall or pairwise association among species occurrences was found in 25 m² sections of the sampling strips, although abundance values for *Laguncularia* and *Avicennia* were positively correlated within these same sections ($0.01 < P < 0.05$). The species of a given seedling was associated with the species of its nearest adult within the same strip ($\chi^2 = 17.37$, 4 df, $P = 0.0016$), but the narrowness of the strips precluded reliable determination of

TABLE 6. Mangrove seedling numbers and densities by species and strip transect, Isla del Venado, Bluefields, Nicaragua, 17 months after Hurricane Joan.

Species	Number of individuals							
	Transect 1		Transect 2		Transect 3		Total	
	#	%	#	%	#	%	#	%
<i>A. germinans</i>	155	42	541	60	235	69	931	57
<i>L. racemosa</i>	141	39	266	29	49	14	456	28
<i>P. rhizophorae</i>	5	1	3	0	2	1	10	1
<i>R. mangle</i>	66	18	99	11	56	16	221	14
Total	367	100	909	100	342	100	1618	100

Averaged over:	Seedling density (individuals m ⁻²)			
	Transect 1	Transect 2	Transect 3	Mean (± 1 SE)
Entire transect	0.73	1.82	0.68	1.08 (± 0.37)
<i>Acrostichum</i> -free area	0.94	2.18	1.28	1.51 (± 0.37)

TABLE 7. Complexity indices of posthurricane mangrove vegetation by strip transect, Isla del Venado, Bluefields, Nicaragua.

Transect	Complexity index ^a	
	Trees ≥2.5 cm DBH	Trees ≥10 cm DBH
1	0.6	0.1
2	0.9	0.3
3	0.0	0.0

^a Holdridge (1967).

nearest adult neighbors. However, the seedling cohort appeared thus far to be reproducing at least the proportions of species in the older stand; the number of seedlings per strip of a given species was significantly correlated with the number of prehurricane adults of that species on the same strip ($r = 0.78$, $N = 12$, $P < 0.01$) and total seedling numbers were positively correlated with overall adult totals for the four species as well ($r = 0.95$, $N = 4$, $P \approx 0.05$).

Mean height of *Rhizophora* and *Laguncularia* seedlings was 1.5 m (to nearest half-meter), with *Laguncularia* regeneration differing from the other species in averaging 2 m tall ($F = 44.3$, $\alpha < 0.0001$). If all seedlings became established after the hurricane, their heights represent an average growth of at least 1 m yr⁻¹. Seedling growth rate may be somewhat lower than heights indicate in the case of *Rhizophora*, whose propagules are already typically a few decimeters "tall" before becoming rooted. Field observations did not distinguish whether any rooted seedlings might have weathered the storm, but it is curious that histograms of seedling heights for all of the three principal species appear bimodal with the small second peak at 3 m; if these less numerous taller individuals were not established prior to the hurricane, then their height growth had exceeded 2 m yr⁻¹.

Complexity indices calculated for the posthurricane stand are shown in Table 7. On the average, these are more than an order of magnitude lower than their prehurricane counterparts in Table 3.

DISCUSSION

As reconstructed using Holdridge's index, the structural complexity of the mangrove forest existing on Isla del Venado prior to Hurricane Joan was comparable to that of fringe mangroves elsewhere in the hemisphere, with no differentiation evident in complexity index according to climatic life zone (Table

3). Instead, mangrove communities as a group present substantially lower indices than typical upland forests within their same life zones (Holdridge 1967, Pool *et al.* 1977). Low species diversity, reflecting the physiological challenges of the mangrove habitat, accounts in part for this; but the trees of mangrove swamps are also generally smaller in height and average girth than their upland counterparts. There would be no inherent reason to expect mangrove stands, given sufficient time, to develop smaller trees than other forests even if their growth were slower; but a greater frequency of perturbation of mangrove forests could account for such a discrepancy. Periodic tropical cyclones characterize the area occupied by mangrove ecosystems and have long been proposed as a limitation to these forests' development (Egler 1952). To the extent that storm winds lose force crossing land, one would expect their overall influence upon upland ecosystems to be less pronounced.

Hurricane Joan set back stand development on Isla del Venado by selectively breaking and disproportionately killing the larger trees. Thirty-six percent of the trees on the sample area had died, representing fully 68 percent of the basal area of the pre-existing stand. Trees showing best recovery 17 months after the storm were those of short stature and small diameter. These patterns contributed to the sharply diminished complexity index for these forests after the hurricane.

Similar results are reported elsewhere. Wadsworth (1959) found that sapling stands of white and black mangrove suffered negligible damage from a hurricane which killed 59 percent of the trees in neighboring pole stands. Craighead (1971) noted that individuals less than 2 m tall were the only mangroves to escape complete initial defoliation by hurricanes in Florida. Wunderle *et al.* (1992) found that damage to mangroves in Jamaica from Hurricane Gilbert was proportionately greater in the larger-diameter trees.

The implicit assumption that any dead trees found on Isla del Venado had succumbed to the hurricane warrants scrutiny. It was not possible at the time of sampling to distinguish between stems killed by the storm and dead trunks which may have existed within the stand prior to Hurricane Joan. Data compiled by Jiménez *et al.* (1985) from numerous mangrove stands show a highly variable percentage of standing dead trunks, averaging 26 percent, attributed to "normal mortality." The value of 36 percent of stems found dead in the present study is well within the cited range ($z = 0.60$); however, the diameter classes most affected differ

considerably. As Jiménez and coworkers (1985) point out, mortality from competitive interactions, herbivory, and disease tends to be concentrated in the smaller suppressed stems of a given assemblage, so that standing dead trees from such "normal" causes average only 19 percent of the basal area of the stands they list. The fact that dead stems on Isla del Venado had an average girth more than double that of live ones and made up 68 percent of basal area on sample strips suggests strongly that tree mortality there was primarily catastrophic in origin. Chronic mortality appears more typical of basin mangroves (Jiménez *et al.* 1985) and ones in arid environments (Cintrón *et al.* 1978) where salt stress is likely to be more acute.

Despite the severe blow dealt the former forest, these mangroves evidently are not threatened as a community, given that established seedling densities already appear ample to restock the stand. Silvicultural experience with American mangroves is limited, but natural regeneration has proven effective in replacing harvested portions of stands in Puerto Rico (Wadsworth 1959) and Venezuela (Luna Lugo 1976). Data from several countries in South Asia indicate the densities considered adequate to repopulate mangrove forests; there the regeneration in naturally restocked mangroves is considered "abundant" if seedling densities are anywhere from 605 to over 50,000 individuals ha^{-1} (Liew *et al.* 1977, FAO 1985). Three countries' laws requiring replanting of inadequately regenerated postharvest mangrove stands stipulate densities of 1667 to 10,000 plants ha^{-1} (FAO 1985). If Caribbean mangroves are comparable in this respect, then the range of 9400 to 21,800 seedlings ha^{-1} over most of the area should be more than sufficient for the stand on Isla del Venado to recover. The only apparent obstacle to this is *Acrostichum* fern, which covered 28 percent of the sample area; *Acrostichum* spp. become established in open areas of mangrove forests and are considered intractable weeds by foresters worldwide (FAO 1985).

The process of regeneration evident in these mangroves differs thus far from the conventional portrayal of secondary succession. Seedlings established in the first 17 months after the storm were of the same species and in nearly the same proportions as the trees of the previous stand; no new "pioneers" had appeared and no "later-successional" species from the former stand had yet been eliminated in the emerging generation. Given that Caribbean mangrove communities of whatever age are limited to these and a few closely related species (Chapman 1976), if unchanging species composi-

tion in the regrowth implies that the prehurricane stand was itself early-successional, then so must be all mangrove forests in the region, and true successional change would depend upon the mangroves eventually altering their habitats in such a way as to permit establishment of a different set of (non-mangrove) species. Indeed, most discussion of mangrove succession has focused on protracted primary succession in the context of hypothesized land building and spatial zones interpreted as seres, not response to canopy removal by disturbance; but the time scale of storm effects may tend to eclipse the influence of more gradual geologic processes as well as rendering maladaptive for vegetation of tropical coasts the traits typical of "climax" species.

One would expect frequent storm disturbance to favor species capable of constant or timely flowering, abundant seeding or sprouting, fast growth in open conditions, and early reproductive maturity. The three principal Caribbean mangrove species share these "early-successional" traits. Intolerant of shade, they grow quickly as seedlings, as demonstrated in silvicultural studies (Marshall 1939, Wadsworth 1959). Their flowering is precocious and all three flower year-round (Marshall 1939, Little & Wadsworth 1964), but with peaks which in Florida and Panama produce copious propagules between August and October (Craighead 1971, Rabinowitz 1978a, Tomlinson 1980)—precisely the season of greatest hurricane probability (Neumann *et al.* 1981).

From the little comparative evidence available, adaptations to wind disturbance seem to be distributed among the species in an uneven but rather compensatory fashion (Table 8). Thus *Rhizophora mangle* has proven in some cases the most resistant to wind damage (Wadsworth & Englerth 1959, Wunderle *et al.*, 1992), but its older branches are incapable of sprouting once broken (Noakes 1955, Wadsworth 1959, Tomlinson 1980); the other mangrove species coppice well (Marshall 1939, Wadsworth 1959). *Laguncularia racemosa*, on the other hand, is considered least wind-resistant (Wadsworth & Englerth 1959) but is the superior sprouter (Wadsworth 1959). *L. racemosa* seedlings appear to grow faster in the open than those of the other species (Marshall 1939, Ball 1980), but they also have been found the most intolerant of shade (Egler 1952, Wadsworth 1959, Ball 1980) and therefore the least likely to exist beneath a canopy at the time of a disturbance. *Laguncularia* also tends to suffer the highest percent seedling mortality (Davis 1940, Rabinowitz 1978c, Ball 1980). *Avicennia germinans* is thought to be the least shade-

TABLE 8. Summary of reported relative attributes of three Caribbean mangrove species related to persistence following hurricanes (references in text). Plus sign (+) indicates that data from the present study accord with the generalization; minus sign (-) indicates apparent disagreement; asterisk (*) indicates statistical significance ($P < 0.05$) of results in either case.

Attribute	<i>R. mangle</i>	<i>A. germinans</i>	<i>L. racemosa</i>
Resistance to windthrow	highest (-)	intermediate	lowest
Resistance to breakage	highest (-)	intermediate	lowest
Sprouting from damaged trunk	lowest (+)	intermediate (+)	highest (+)
Initial seedling density	lowest (+)	highest (+)	intermediate (+)
Shade tolerance	intermediate	highest (+)	lowest
Seedling growth rate	intermediate (+)	lowest (+)	highest (+ *)
Seedling survival rate	highest (+)	intermediate	lowest (-)

intolerant of the three (Egler 1952) and to produce typically high initial seedling densities (Jiménez *et al.* 1985) but to show the slowest seedling growth (Marshall 1939). Such patterns can be interpreted as illustrating a range of niches all compatible with periodic hurricane disturbance, but oriented toward somewhat different facets and stages of the recovery process.

Sample averages from the present study accorded with most of these patterns, although sample sizes were inadequate in most cases to project the relationships reliably to any larger population (Table 8). Sprouting capacity (based on percent refoliation of broken trunks), "initial" seedling density (17 months after the hurricane), and seedling growth rate (height 17 months after the hurricane assuming simultaneous establishment) followed most closely the predicted order by species. Densities observed during a March 1991 reconnaissance indicated that *Rhizophora* seedlings were surviving considerably better than those of *Laguncularia* and *Avicennia*. Superior shade tolerance of *Avicennia* seedlings was suggested, albeit weakly, by its larger initial number of seedlings ≥ 3 m tall relative to the other species, which could be due to a greater density of *Avicennia* seedlings having grown in beneath the former canopy. Adult *Rhizophora* did not show the lowest proportion of broken stems; and examples of windthrow were scant for all species. Species attributes and availability of propagules undoubtedly interact with other factors such as severity of storm and type of substrate in producing posthurricane regeneration patterns (Cintrón *et al.* 1978), so that

carefully designed future studies could lend additional dimensions to Table 8 as well as providing more rigorous tests for its claims.

Timing of observations is likely to influence perceived patterns as well: "poorly refoliated" individuals may die or continue sprouting, while "well refoliated" trees may later succumb. Relative seedling density will presumably shift at some point in response to differential growth rates and survival of initial populations; from Table 8 one might predict that *Avicennia* will be surpassed in density first by *Laguncularia* and then by *Rhizophora*. Later on, relative growth rates of the different species can continue to change (Ball 1980), in ways which long-term monitoring will help to clarify. Although the component species remain the same, competitive interactions on a given substrate may eventually lead to predominance of one species, as Ball (1980) posits of *R. mangle* in intertidal zones of Florida, until further disturbance restores the earlier diversity. These interactions are little studied and deserve closer attention.

Posthurricane stand development in mangroves is doubtless more relevant to their management than changes which may occur on a geologic time scale. The communities around Bluefields have made use of all four local mangrove species to varying extents for fuel, carved objects, construction materials, and tanning, and evidence persists on Isla del Venado of sporadic past cutting of selected trees. From the initial results presented here it would appear that periodic small harvests, if adjusted in size, position, and timing to encourage patches or strips of regen-

eration of preferred species, represent a "disturbance" from which mangrove stands might readily recover while offering a desirable combination of protection and productive use where hurricanes are frequent. Limiting the size of the cut patches and avoiding *Acrostichum* aggregations should help prevent spread of the fern, and the periodically replenished groupings of seedlings and saplings would presumably speed stand recovery after future hurricanes. Research on the community ecology and management of mangroves would undoubtedly profit from the experience of local resource users, who in turn might benefit from collaboration in testing and refining possible silvicultural treatments and monitoring erosion hazards.

In a classic study, Rabinowitz (1978b) compared seedling survival and growth of American mangrove species beneath the canopies of different species of adults; but she suggested that a logical next step should be to examine their growth in treefall gaps. Given the shade intolerance of these

trees, the results of such inquiry would seem more pertinent to the conditions in which they actually regenerate. The west coast of Isla del Venado is presently an enormous light gap of a sort which these mangroves appear well adapted to recolonize, and the development of its stands will provide a continuing demonstration of their postdisturbance successional processes.

ACKNOWLEDGMENTS

Jorge Brooks of the Nicaraguan Dirección de Recursos Naturales y del Ambiente lent this project many forms of valuable cooperation. Maribel Pizzi, Laureana Rivera, and Manuel Romero of the Escuela de Ecología y Recursos Naturales, Universidad Centroamericana, participated in all aspects of the sampling process. Staff of the Centro de Investigaciones y Documentación de la Costa Atlántica provided generous logistical support in Bluefields. Thanks are due also to D. Jean Lodge and an anonymous reviewer for very helpful comments on a draft of this paper. The fieldwork was supported by NSF grant #BSR-8917680 to John Vandermeer.

LITERATURE CITED

- ALEXANDER, T. R. 1967. Effect of Hurricane Betsy on the southeastern Everglades. *Q. J. Fla. Acad. Sci.* 30(1): 10-24.
- BALL, M. C. 1980. Patterns of secondary succession in a mangrove forest of southern Florida. *Oecologia (Berl.)* 44: 226-235.
- BOUCHER, D. H. In press. Frecuencia de perturbación de la selva de la costa atlántica nicaragüense por huracanes: una vez en el siglo. Wani (Managua, Nicaragua).
- BUNCE, H. W. F., AND J. A. McLEAN. 1990. Hurricane Gilbert's impact on the natural forests and *Pinus caribaea* plantations of Jamaica. *Commonw. For. Rev.* 69(2): 147-155.
- CHAPMAN, V. J. 1976. Mangrove vegetation. J. Cramer, Vaduz, Germany.
- CINTRÓN, G., A. E. LUGO, AND R. MARTÍNEZ. 1985. Structural and functional properties of mangrove forests. In W. G. D'Arcy and M. D. Correa A. (Eds.). *The botany and natural history of Panama. IV series: monographs in systematic botany*, Vol. 10, pp. 53-66. Missouri Botanical Garden, St. Louis, Missouri.
- _____, _____, D. J. POOL, AND G. MORRIS. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10(2): 110-121.
- CRAIGHEAD, F. C. 1964. Land, mangroves, and hurricanes. *Fairchild Tropical Garden Bulletin* 19(4): 1-28.
- _____. 1971. *The trees of South Florida. I. The natural environments and their succession.* University of Miami Press, Coral Gables, Florida.
- _____, AND V. C. GILBERT. 1962. The effects of Hurricane Donna on the vegetation of southern Florida. *Q. J. Fla. Acad. Sci.* 25(1): 1-28.
- DAVIS, J. H., JR. 1940. The ecology and geologic role of mangroves in Florida. *Papers from Tortugas Lab* 32. Carnegie Inst. Washington Publ. 517: 305-412. Washington, D. C.
- EGLER, F. E. 1952. Southeast saline everglades vegetation, Florida, and its management. *Vegetatio* 3(4/5): 213-265.
- FAO. 1985. Mangrove management in Thailand, Malaysia, and Indonesia. *Environment Paper #4*, Food and Agriculture Organization of the United Nations, Rome, Italy.
- GENTRY, R. C. 1974. Hurricanes in South Florida. In P. J. Gleason (Ed.). *Environments of South Florida: present and past*, pp. 73-81. *Memoir No. 2*, Miami Geological Society, Miami, Florida.
- GLYNN, P. W., L. R. ALMODÓVAR, AND J. G. GONZÁLEZ. 1964. Effects of hurricane Edith on marine life in La Parguera, Puerto Rico. *Caribb. J. Sci.* 4(2 & 3): 335-345.
- HEINSOHN, G. E., AND A. V. SPAIN. 1974. Effects of a tropical cyclone on littoral and sub-littoral biotic communities and on a population of dugongs (*Dugong dugon* (Müller)). *Biol. Conserv.* 6(2): 143-152.
- HOLDRIDGE, L. R. 1967. *Life zone ecology.* Tropical Science Center, San Jose, Costa Rica.
- INETER (Instituto Nicaragüense de Estudios Territoriales). 1988. Ciclones tropicales y sus efectos en Nicaragua. In G. Cortés Domínguez and R. Fonseca López (Eds.). *El ojo maldito*, pp. 193-214. Editorial Nueva Nicaragua, Managua, Nicaragua.

- JIMÉNEZ, J. A., A. E. LUGO, AND G. CINTRÓN. 1985. Tree mortality in mangrove forests. *Biotropica* 17(3): 177-185.
- LIEW, T. C., M. N. DIAH, AND Y. C. WONG. 1977. Mangrove exploitation and regeneration in Sabah. *In* C. B. Sastry, P. B. L. Srivastava, and A. M. Ahman (Eds.). *A new era in Malaysian forestry*, pp. 95-109. Universiti Peranian Malaysia Press, Serdang, Malaysia.
- LITTLE, E. L., JR., AND F. H. WADSWORTH. 1964. Common trees of Puerto Rico and the Virgin Islands. *Agriculture Handbook #249*. U.S. Department of Agriculture, Forest Service, Washington, D.C.
- LUGO, A. E., AND S. C. SNEDAKER. 1974. The ecology of mangroves. *Annu. Rev. Ecol. Syst.* 5: 39-64.
- , M. SELL, AND S. C. SNEDAKER. 1976. Mangrove ecosystem analysis. *In* B. C. Patten (Ed.). *Systems analysis and simulation in ecology*, Vol. III, pp. 113-145. Academic Press, New York, New York.
- LUNA LUGO, A. 1976. Manejo de manglares en Venezuela. *Boletín del Instituto Forestal Latino-Americano* 50: 41-56.
- MARSHALL, R. C. 1939. *Silviculture of the trees of Trinidad and Tobago, British West Indies*. Oxford University Press, London, England.
- NEUMANN, C. J., G. W. CRY, E. L. CASO, AND B. R. JARVINEN. 1981. *Tropical cyclones of the North Atlantic Ocean, 1871-1980*. U.S. National Oceanic and Atmospheric Administration, National Weather Service, Washington, D.C.
- NOAKES, D. S. P. 1955. Methods of increasing growth and obtaining natural regeneration of the mangrove type in Malaya. *Malay. For.* 18: 23-30.
- POOL, D. J., S. C. SNEDAKER, AND A. E. LUGO. 1977. Structure of mangrove forests in Florida, Puerto Rico, México, and Costa Rica. *Biotropica* 9(3): 195-212.
- RABINOWITZ, D. 1978a. Dispersal properties of mangrove propagules. *Biotropica* 10(1): 47-57.
- . 1978b. Early growth of mangrove seedlings in Panamá, and an hypothesis concerning the relationship of dispersal and zonation. *J. Biogeogr.* 5: 113-133.
- . 1978c. Mortality and initial propagule size in mangrove seedlings in Panamá. *J. Ecol.* 66: 45-51.
- ROTH, L. C., AND A. GRIJALVA. 1991. New record of the mangrove, *Pelluciera rhizophorae*, on the Caribbean coast of Nicaragua. *Rhodora* 93(874): 183-186.
- SAUER, J. D. 1962. Effects of recent tropical cyclones on the coastal vegetation of Mauritius. *J. Ecol.* 50: 275-290.
- STODDART, D. R. 1963. Effects of Hurricane Hattie on the British Honduras reefs and cays, Oct. 30-31, 1961. *Atoll Res. Bull.* 95.
- TOMLINSON, P. B. 1980. *The biology of trees native to tropical Florida*. Harvard University Printing Office, Allston, Massachusetts.
- VERMEER, D. E. 1963. Effects of Hurricane Hattie, 1961, on the cays of British Honduras. *Z. Geomorphol.* 7(4): 332-354.
- WADSWORTH, F. H. 1959. Growth and regeneration of white mangrove in Puerto Rico. *Caribb. For.* 20(3/4): 59-71.
- , AND G. H. ENGLERTH. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. *Caribb. For.* 20(1/2): 38-51.
- WUNDERLE, J. M., JR., D. J. LODGE, AND R. B. WAIDE. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. *Auk* 109: 148-166.