Wind Damage Effects of Hurricane Andrew on Mangrove Communities Along the Southwest Coast of Florida, USA

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ABSTRACT

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On August 24, 1992, Hurricane Andrew downed and defoliated an extensive swath of mangrove trees across the lower Florida peninsula. Permanent field sites were established to assess the extent of forest damage and to monitor the rate and process of forest recovery. Canopy trees suffered the highest mortality particularly for sites within and immediately north of the storm's eyewall. The type and extent of site damage, windthrow, branch loss, and defoliation generally decreased exponentially with increasing distance from the storm track. Forest damage was greater for sites in the storm's right quadrant than in the left quadrant for the same given distance from the storm center. Stand exposure, both horizontally and vertically, increased the susceptibility and probability of forest damage and accounted for much of the local variability. Slight species differences were found. *Laguncularia racemosa* exceeded *Avicennia germinans* and *Rhizophora mangle* in damage tendency under similar wind conditions. Azimuths of downed trees were strongly correlated with maximum wind speed and vector based on a hurricane simulation of the storm. Lateral branch loss and leaf defoliation on sites without windthrow damage indicated a degree of crown thinning and light penetration equivalent to treefall gaps under normally intact forest conditions. Mangrove species and forests are susceptible to catastrophic disturbance by hurricanes; the impacts of which are significant to changes in forest structure and function.

ADDITIONAL INDEX WORDS: *Mangroves, hurricanes, Florida, tropical cyclones, forest damage, windthrow, disturbance, canopy structure, gap dynamics, defoliation.*

INTRODUCTION

Mangrove forests occupy the intertidal zone at the land-sea interface; at landfall, hurricanes are often most intense and inflict destructive physical forces of wind and surge. Because hurricanes are fueled by warm sea temperatures, they are usually at their greatest overland strength at initial landfall. Mangroves are a prominent and ubiquitous ecosystem throughout the world's tropical coastlines, yet little has been published on their response and resiliency to tropical cyclones. Recent hurricanes, Hugo in 1989 and Andrew in 1992, have spawned numerous scientific studies of storm effects on plant and animal communities (FINKL and PILKEY, 1991; LOOPE *et al.*, 1994; PIMM *et al.*, 1994; WALKER *et al.*, 1991) establishing a baseline of research for comparisons among regions, forest types, and species.

Some of the earliest observations of hurricane effects on south Florida mangroves were reported by CRAIGHEAD (1964), DAVIS (1940), and EGLER (1952). Craighead, in particular, described and photographed hurricane-damaged vegetation, including mangroves, throughout Everglades National Park following the 1947, 1960, and 1965 storms. He also documented a range of damage responses from complete blowdowns, canopy defoliation, and root suffocation following hurricanes Donna in 1960 and Betsy in 1965 (CRAIGHEAD and GILBERT, 1962; CRAIGHEAD, 1971). Follow-up studies by Craighead showed that mangrove trees in some areas were still undergoing delayed mortality as long as ten years after initial impact (CRAIGHEAD, 1971).

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More recently, SMITH *et al.* (1994) reported on initial storm effects of Hurricane Andrew for east and west coast mangroves of south Florida. Their work combined aerial and ground surveys showing the distribution and pattern of mangrove destruction and mortality on a local and regional basis. Six months after initial surveys, SMITH *et al.* (1994) found that tree death was not a static process with the passing of Hurricane Andrew, but rather a dynamic struggle of survivorship (resprouting) and delayed mortality akin to Craighead's findings. Their results also showed that young recruits in pre-existing light gaps proved resilient to impact, indicating a possible interaction between small-scale lightning gap dynamics with less frequent, large-scale hurricane effects.

Structural impacts from hurricanes have been reported for mangrove systems elsewhere. STODDART (1963) documented the local effects of wind and surge from Hurricane Hattie in 1961 on mangrove and reef structure of Belize. Stoddart described and mapped the general extent and compass orientation of forest damage attributed to direct wind and wave action. In a report on damage caused by cyclone Kathy to mangrove forests in Australia, BARDSLEY (1985) determined that dwarf mangrove species and forests sustained little impact in contrast to tall emergent mangroves. WUNDERLE *et al.* (1992) censused a number of forest types in Jamaica following Hurricane Gilbert in 1988 and found the greatest structural damage in their mangrove plots. They reported that average foliage height was significantly reduced by 4 m or more due to the severe loss of dominant overstory trees. Following Hurricanes Domoina and Imboa in 1984, STEINKE and WARD (1989) conducted mortality counts of mangrove trees by species found in the St. Lucia estuary on the east coast of southern Africa. Their work estimated 33% mortality of white mangrove, *Bruguiera gymnorrhiza*, which made up 92% of the woody stems in near shoreline sites. Observations by ROTH (1992) of Hurricane Joan in 1988 on the Nicaraguan coast also affirm the susceptibility of emergent mangroves to windthrow under hurricane conditions.

Collectively, these studies document the susceptibility and vulnerability of mangrove species and systems to hurricane disturbance. However, it is yet unclear how the physical and biological elements interact to explain the varying degrees of windthrow and mortality relative to hurricane intensity and spatial dynamics. In this study, we investigated wind damage relationships of Hurricane Andrew on mangrove forest structure and sites along the southwest coast of Florida, USA. Important questions that were addressed included the degree and expression of impact in relation to the path and intensity of Andrew as it moved across and exited the peninsula. We also examined differences in tree size and species susceptibility within and between sites under different projected wind conditions. A hurricane simulation model was used to reconstruct predicted wind speeds and vectors for each study site for every 15 minutes of Andrew's course across south Florida. A chronological overview of Andrew's storm track and general meteorology are given in STONE *et al.* (1993).

METHODS

Permanent field plots were established in October 1992 and early 1993 subsequent to Hurricane Andrew. Plots were stratified to include sampling locations within the eyepath and outside the ring of maximum winds in the right and left quadrants in relation to Andrew's path and circulation (Figure 1). Sites impacted by Hurricane Andrew were established in Everglades National Park, Ten Thousand Islands National Wildlife Refuge (NWR), and Rookery Bay National Estuarine Research Reserve (Figure 1). Additional sampling with line transects was conducted to record treefall azimuths and to measure canopy disturbance and closure at control sites and other impacted sites in order to increase the sampling area. Control sites were located north and south of Andrew's path at Ding Darling NWR and National Key Deer NWR, respectively (Figure 1). Species composition for all plots and transects included combinations of black mangrove, *Avicennia germinans* (L.) Stearn, white mangrove, *Laguncularia racemosa* (L.) Gaertn.f., and red mangrove, *Rhizophora mangle* L.

Forest data were gathered from circular 0.05 ha plots, 12.6 m in radius. Plot locations and centers were established randomly and permanently marked with a treated fence post. Every tree stem above breast height (1.4 m) was stem mapped and tagged. Species, diameter at breast height (dbh), crown class, crown ratio, damage type, treefall azimuth, sprouting response, and viability were also recorded. Readings of photo-

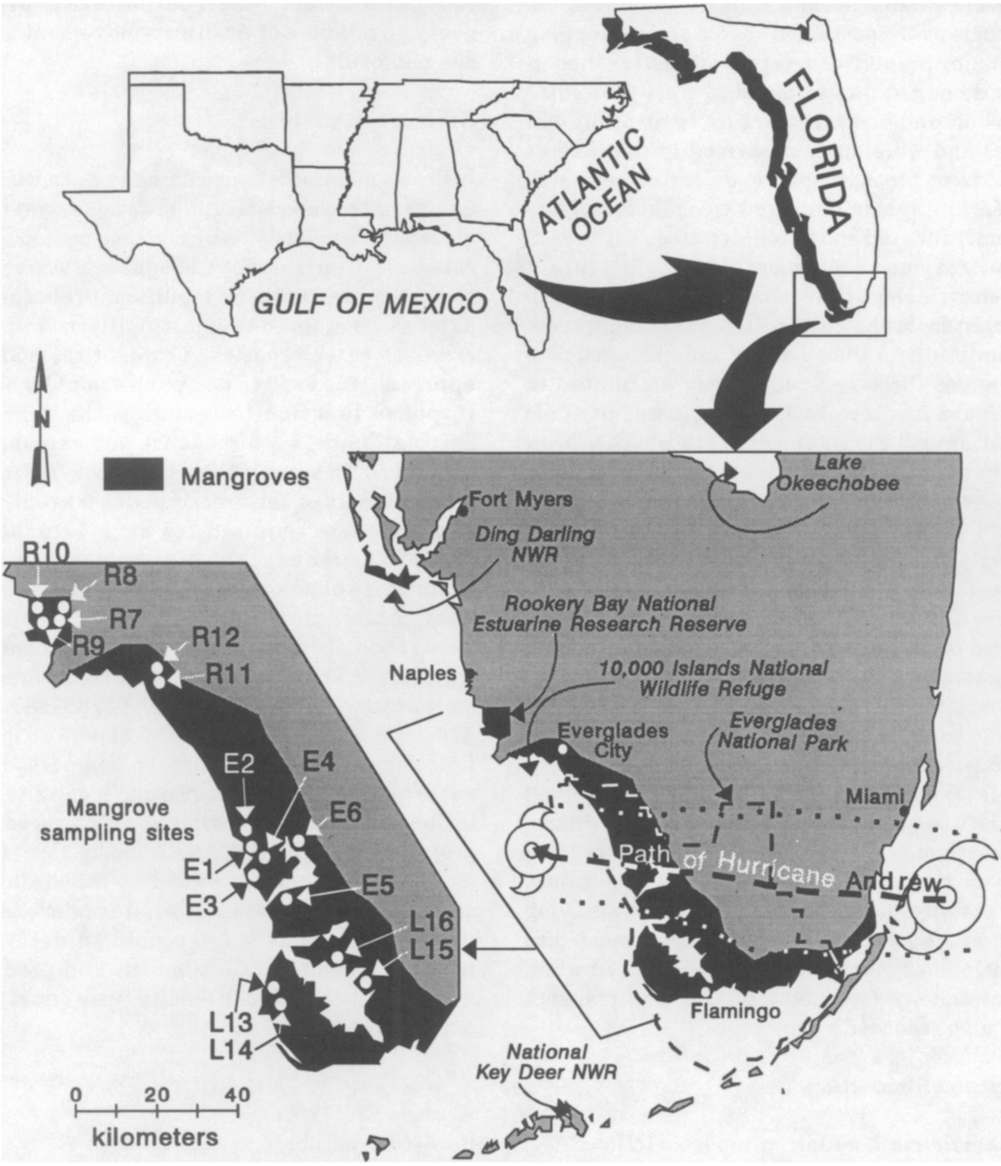

Figure 1. Map of south Florida mangrove distribution, location of permanent forest plots and storm track of Hurricane Andrew.

synthetically active radiation (PAR) were taken with a portable LI-COR, LI-191SA quantum sensor above and beneath the canopy at plot center and the periphery at principal compass positions. Light measurements at ground level were taken at a standardized height of 2 m oriented in both east-west and north-south positions. Global positioning receivers were used to georeference plot locations for mapping and hurricane simulation purposes.

Tree damage classes were established to distinguish damage extent between dead and severely damaged trees, moderately damaged, and lightly damaged. Uprooted individuals and boles snapped below the live crown were categorized as severely damaged and unlikely to survive. Individuals which sustained severe crown cropping and major branch loss were classified as moderately damaged. Many of these trees had sufficient bole and branch structure to resprout new leaves and were aptly described in the field as "chia" trees for their spindly epicormic regrowth and form. Lightly damaged trees included any normally foliated and defoliated trees with residual primary and secondary branch structure.

Prehurricane stand conditions were reconstructed from the composite of surviving trees and individuals whose death and damaged condition was directly or indirectly attributed to Hurricane Andrew. In all cases, it was possible to distinguish the timing of death whether prior to the storm, during the storm, or subsequent to the storm. Trees that were dead prior to storm impact were excluded from any data summaries or analyses. Study sites were assigned to distance class and quadrant from storm center to test for differences in site response. All sites designated in the eyepath were less than 10 km from the central storm track. Right and left quadrant sites sampled in this study ranged in distance from 20 to 40 km outside the storm's ring of maximum winds.

Line transects were used to supplement fixed plot data to quantify the degree of canopy disturbance at control sites and additional site locations in the storm's right and left quadrants. PAR readings were taken at 10 m intervals along a 150 m transect and averaged for a mean site condition. Azimuths of hurricane-induced windfall of canopy trees intersecting the transect were also recorded.

Hurricane Simulation

A hurricane simulation model, HURACAN, was used to generate a chronology of predicted wind speeds and vectors for each plot location (DOYLE, 1994). This provided important environmental data on hurricane strength and position at each site over the course of Andrew's crossing and exiting the south Florida peninsula. A radius of maximum winds of 18 km (POWELL and HOUSTON, 1993) and an inflow angle of 45 degrees were used to compute surface wind speeds and vectors. National Weather Service tracking data of Andrew's latitude, longitude, date, hour, maximum sustained winds, central pressure, and forward speed were used to parameterize the model. Model output was generated every 15 minutes of Andrew's movement across the peninsula.

Statistical Analysis

Relationships between damage class with site position, tree species, and crown class were analyzed with an analysis of variance procedure for categorical variables. A Chi-square test was used to determine whether a significant relationship existed between damage condition and site, crown class, and species. A categorical modeling approach was used to derive an ordinally scaled response function for gauging the degree of association between response and explanatory variables. To satisfy the asymptotic normality requirements of the procedure, at least 25 to 30 samples were required for each explanatory level; no more than 20% of the categories had a sample size of less than 5. A Chi-square test was used to determine whether treefall azimuths were randomly distributed. Frequency counts of windthrow azimuths by site were assigned to *a priori* wind angle classes at 0–90, 90–180, 180–270, and 270–360 degrees. Damage response functions were established to compare differences between species, crown class, and site in relation to site-specific wind speeds and vectors projected with the HURACAN model. Correlation analyses were used to associate forest-damage statistics with prevailing wind conditions. Regression analysis was applied to determine whether mean treefall azimuths and predicted vectors at peak wind intensity were equal to an expected slope of 1.

RESULTS

Forest Structure

All study sites, except control sites at Ding Darling NWR and National Key Deer NWR, were impacted by Hurricane Andrew to some degree. Stem density and basal area decreased for all 16 permanent study sites subject to hurricane-force winds (Table 1). Sites within the eyepath sustained the highest mortality and overall change in forest structure. Stem density was reduced by 16%–61% of prehurricane condition, while standing basal area was altered as much as 20%–94% (Table 1). Right quadrant

Table 1. *Density and basal area of live stems at mangrove study sites along the southwest coast of Florida prior to and following Hurricane Andrew. Percent reduction in stem density and standing basal area due directly to wind damage are also given.*

		Density (stems/ha)			Basal Area (m^2/ha)		
Site[a] No.	Hurricane Quadrant	Pre Hurricane	Post Hurricane	% Decrease	Pre Hurricane	Post Hurricane	% Decrease
1	Eyepath	4317	3524	18	36.63	27.06	26
2	Eyepath	4091	2773	32	24.10	10.99	54
3	Eyepath	1937	889	54	27.52	6.41	77
4	Eyepath	2508	984	61	32.85	14.56	56
5	Eyepath	6444	5429	16	16.00	12.87	20
6	Eyepath	1700	663	61	21.18	1.36	94
7	Right	2620	2420	8	33.79	31.17	8
8	Right	2900	2800	3	27.37	26.82	2
9	Right	3880	3560	8	27.28	26.95	1
10	Right	2980	2700	9	31.99	28.63	11
11	Right	3040	2180	28	25.92	12.61	51
12	Right	4320	3900	10	17.73	12.08	32
13	Left	4203	3566	15	32.11	21.05	34
14	Left	4840	4713	2	27.87	27.43	2
15	Left	4585	4076	11	26.65	22.72	15
16	Left	4458	4203	6	47.74	40.69	15

[a]All sites represent a 500 m^2 study plot.

sites, located between Everglades City and Naples (Figure 1), were reduced in stem density from 3%-28% and in basal area from 1%-51%; the variability was largely determined by stand condition, exposure, and distance from Andrew's eyepath. Left quadrant sites were relatively unaffected in terms of numbers of downed trees, 2%-16% but showed signs of significant limb loss and defoliation. The reduction in stand basal area was slightly greater for these same plots, ranging between 2% and 34%.

Analyses showed that there was a significant difference in damage extent (*i.e.*, light vs. moderate + severe) between eyepath sites and all other sites outside the ring of maximum winds both in the right and left quadrants ($p < 0.001$). Eyepath sites were significantly more reduced in canopy structure. Damage categories and hurricane quadrant classes were collapsed to meet the minimum class size requirements for the analysis.

Species and Crown Class Response

Species response was not consistent with site location or crown class. *Laguncularia racemosa* exceeded *Avicennia germinans* and *Rhizophora mangle* in damage tendency for right and left quadrant sites ($p < 0.001$), but this relationship failed to hold for sites within the eyepath ($p = 0.0568$) (Figure 2). This result appears to be influenced by the variability in species composition and damage extent on a plot by plot basis. Canopy trees sustained significantly greater direct wind damage than did subcanopy trees ($p < 0.001$) (Figure 2). Damage to subcanopy trees was largely the effect of collateral damage from felled and topped canopy trees. There was no difference in species response with respect to damage by crown class.

Windthrow Patterns

All permanent plots and line transects showed windfall patterns that were non-randomly distributed ($p < 0.05$). Treefall azimuths were generally restricted to a fairly narrow range of less than 90 degrees. Sites within the eyepath of Andrew had the most damaged trees per plot and the widest range of treefall angles. Few trees were felled in a northerly direction, and these were located in the eyepath sites where trees were downed by front and rear side winds of the hurricane.

The spectrum of study sites from north to south captured the full range of treefall angles corresponding with hurricane circulation. Site-

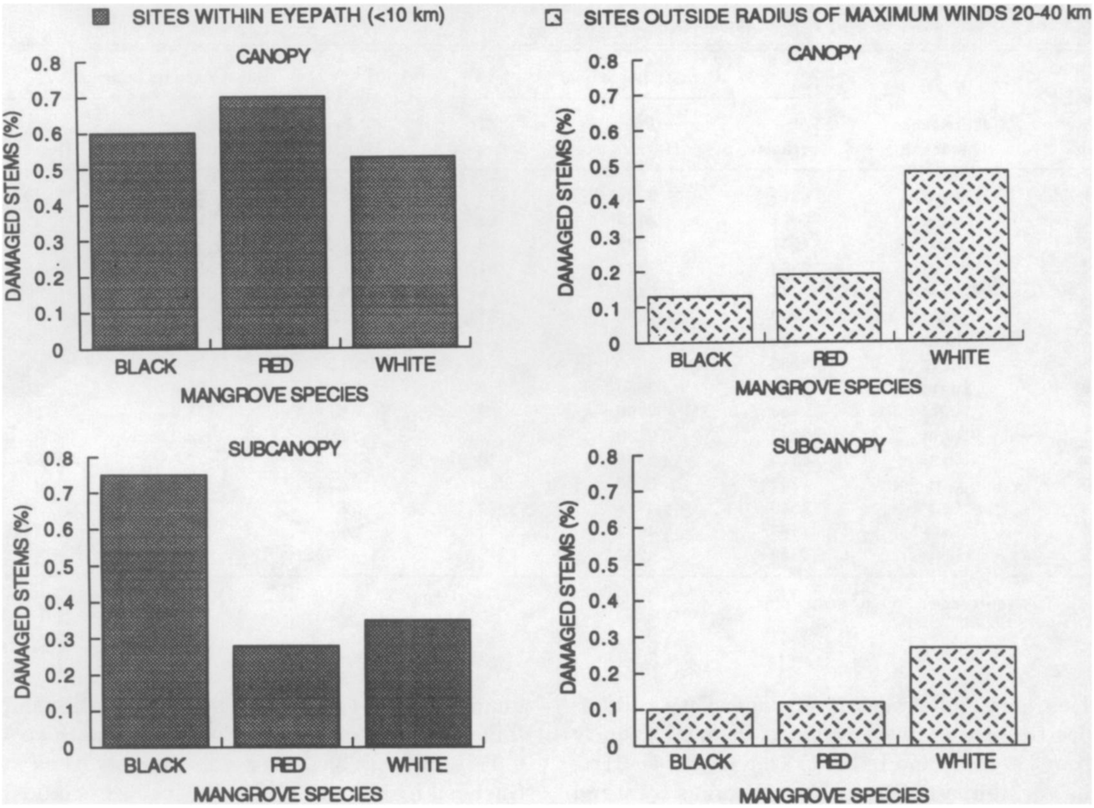

Figure 2. Proportion of severely damaged stems by species and crown class for sites within the eyepath and outside the radius of maximum winds.

specific wind vectors at maximum wind intensity were estimated from the HURACAN model and correlated with the actual mean treefall directions for all sampling locations (Figure 3). A Pearson correlation of 0.93 indicated a strong association between hurricane position, strength, and circulation with the resulting damage expression (*i.e.*, compass orientation) on the landscape (Figure 3). Regression analysis and confidence interval tests of the predicted slope without an intercept was not different from 1 ($p < 0.10$).

Leaf Defoliation

Leaf defoliation was apparent at all sites except control sites at Ding Darling NWR and National Key Deer NWR. Percent PAR of full sunlight reaching the forest floor decreased exponentially with increasing distance from the hurricane track (Figure 4). Local variability was evident during field excursions where taller, more developed stands, islands, and forest edges absorbed the brunt of Andrew's wind; young, low stature stands often escaped major blowdown impacts. Conversely, canopy damage and PAR penetration increased exponentially with increasing wind speed at maximum hurricane force determined from the HURACAN model (Figure 5). Predicted wind speed takes into account both the storm's strength, proximity, quadrant, and forward speed.

DISCUSSION

The degree and expression of forest damage at a regional scale was clearly related to Andrew's course and circulation. Sites within Hurricane Andrew's eyepath were severely impacted with blowdowns of 50–100% of the standing biomass.

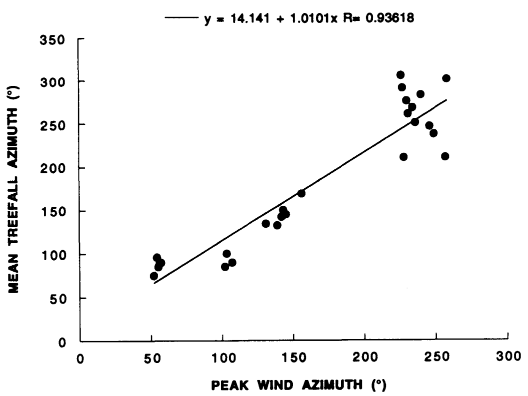

Figure 3. Scatter diagram and regression of actual mean treefall azimuths by site and predicted wind angle at peak hurricane wind speeds from the HURACAN simulation for all sample sites.

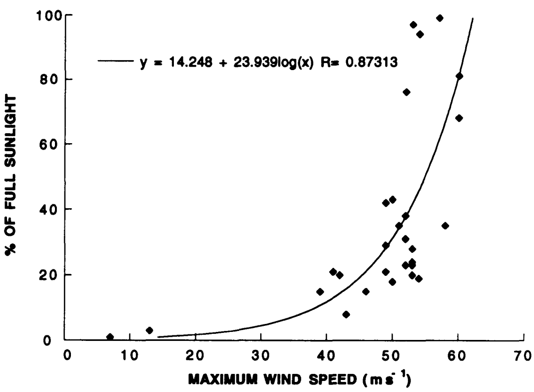

Figure 5. Scatter diagram and curvilinear fit of percent light (PAR) penetrating the residual forest canopy and maximum predicted wind speed from the HURACAN simulation for all sample sites.

Structural impact to left and right quadrant sites outside the ring of maximum winds was much less (<50% reduction in basal area) and more variable with distance. This geographic pattern of spatially-distributed wind damage about the hurricane path has been documented for other forest types and regions, including temperate hardwood forest (FOSTER and BOOSE, 1992), montane rain forest (LUGO *et al.*, 1983; WALKER, 1991), and other mangrove systems (BARDSLEY, 1985; STODDART, 1963, 1969).

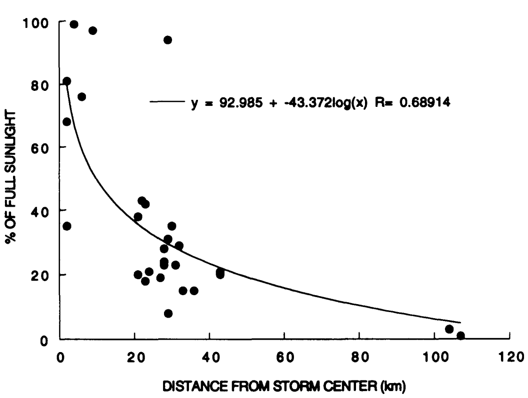

Figure 4. Scatter diagram and curvilinear fit of percent light (PAR) penetrating the residual forest canopy and shortest distance to storm track for all sample sites.

Landform may play a role in the uniformity of this pattern (BELLINGHAM, 1991; FOSTER and BOOSE, 1992). The flat terrain and homogeneous tract of intact mangrove along the southwest coast of Florida contributed to a fairly distinct pattern of large-scale spatial effects (*e.g.*, blowdown swath vs. standing forest and foliated vs. defoliated stands) of Andrew (SMITH *et al.*, 1994) and past hurricane disturbances (CRAIGHEAD and GILBERT, 1962; CRAIGHEAD, 1971). STODDART (1963, 1969) also noted sharp boundaries of downed, defoliated, and undamaged trees from surveys of initial damage effects and recovery of mangrove along the low relief coast of Belize.

Differences in species response indicated that *Laguncularia racemosa* may be more susceptible to wind damage than *Avicennia germinans* and *Rhizophora mangle* at wind speeds around 40 ms^{-1}. Sites in the eyepath showed no differences between species, but these also endured the highest winds in excess of 50 ms^{-1}. These findings suggest that white mangrove may have a lower threshold or tolerance to windthrow under hurricane conditions than red and black mangrove, but all are susceptible to damage above some critical wind force surpassed by Hurricane Andrew. Local site characteristics, tree health, and the dynamic nature of hurricanes play a major role in the local variation of species and stand response to wind disturbance on the landscape.

At a local level, site exposure and forest stature appear to account for much of the variability in site response within given damage zones and wind fields. Taller dominant trees and stands incurred greater damage than did less prominent, less developed stands. BARDSLEY (1985) demonstrated similar results from transect studies of hurricane impact across dwarf and tall mangrove associations in Australia. Within a given site, canopy trees sustained significantly greater damage than did subcanopy trees on a proportional basis. Windthrow of canopy trees were primarily caused by direct wind effects, whereas damaged subcanopy trees were impacted by felled and topped canopy trees. Similar findings have been shown for other temperate and tropical forest systems subject to hurricane disturbance (BROKAW and GREAR, 1991; FOSTER, 1988; FOSTER and BOOSE, 1992; GRESHAM *et al.*, 1991; PUTZ *et al.*, 1983; REILLY, 1991; ROTH, 1992; WUNDERLE *et al.*, 1992).

Coastal and inland islands with open water corridors to direct wind showed greater susceptibility to wind damage particularly on the windward side. This effect was most evident in the variability of mean treefall angles in the Ten Thousand Islands NWR and left quadrant sites along the coast. Stand exposure and changes in the inflow angle of hurricane winds overland and over water may account for differences between actual treefall azimuths and predicted wind direction from the HURACAN model. Island sites in the right quadrant tended to show a pattern of windthrow orientation that aligned with exposure to adjoining water corridors during peak hurricane winds. Coastal sites in the hurricane's left quadrant demonstrated treefall directions that more closely corresponded with adjusted inflow angles of hurricane winds of 20–30 degrees that would otherwise be expected with over water conditions.

Sites within the eyepath showed a tendency for windfall over a wider range of wind angles than did peripheral sites. This finding demonstrates that peak winds were sustained over a wider range of wind angles in the eyepath than at the storm's periphery as might be expected. Our study indicates that the vulnerability of individual trees to windthrow changed throughout the course of hurricane movement, perhaps depending on the timing and fate of neighboring trees which may have provided some degree of wind sheltering. This was most prevalent for sites within the eyepath where trees of equal size and stature apparently fell on the front and rear passing of the storm. In most cases, the initial burst of critical winds usually did the most damage and accounted for the nonrandom windthrow patterns. Plots within the eyepath showed a skewed effect of treefall in two directions due to front and rearside wind near maximum storm strength. STODDART (1963) also observed opposing windfall angles in the eyepath attributed largely to differential site exposure and sheltering. All other sites outside the radius of maximum winds demonstrated a very narrow range of downed tree azimuths associated with the restricted period and angle of peak winds.

Defoliation was evident at every site except the farthest ones at Ding Darling NWR and National Key Deer NWR. A review of hurricane papers by BROKAW and WALKER (1991) determined that defoliation was the most commonly observed impact across all studies and all vegetation types. PAR readings showed that even sites without windthrows were disturbed by significant removal of lateral branches and leaves. These sites exhibited the same degree of light penetration that may be found in treefall gaps under normal forest conditions (*i.e.*, 20%–40% of full sunlight). Sites within the eyepath of Andrew were completely defoliated by the storm, while the right and left quadrant sites varied greatly depending on the condition and density of survivors.

The extent of canopy disturbance by stem, branch, and leaf stripping was greatest in the eyepath sites and at the highest projected wind speeds. PAR penetration through the residual canopies for all sites indicated a curvilinear relationship of increasing disturbance with increasing wind speed. These results indicate that there are thresholds of wind speed under which leaf detachment and stem breakage occur. Given the range of observed conditions, it appears that critical wind damage appears to take place as wind speed exceeds 40 ms^{-1} and thereafter have an exponential effect with increasing wind speed.

CONCLUSION

Hurricane Andrew had a significant impact on mangrove community structure of south Florida. Forest damage was greatest about the eyepath of the storm decreasing with increasing distance from the storm's track. Sites in the storm's right quadrant showed greater propensity for damage for the same approximate distance from the eye compared with sites in the left quadrant outside the ring of maximum winds. Sites adjacent to open water corridors in the direct windpath of Andrew sustained higher impacts than interior sites with a higher degree of wind sheltering. Species susceptibility to windthrow demonstrated different tendencies such that white > red = black in order of damage and mortality impact. Taller canopy trees demonstrated a greater likelihood to snap and tip-up due to direct wind effects than did smaller subcanopy individuals. Leaf defoliation and lateral branch damage was evident at all sites except control sites where maximum winds failed to reach hurricane force. Defoliated sites without windthrown trees exhibited light (PAR) penetration equivalent to normal canopy gaps prior to the storm. Canopy disturbance was shown to increase exponentially with increasing wind speed. These results have direct implications concerning the role and history of hurricanes on the structure and function of mangroves in south Florida.

Overall, turnover of plant biomass was significant particularly along the immediate eyepath of the storm. This finding suggests that actual forest turnover for mangrove forests of south Florida may be subject to the frequency and trajectory of recurring hurricanes. A hurricane simulation model was used to correlate actual wind abiotics of Hurricane Andrew with the extent of canopy disturbance and orientation of downed trees. Predicted wind speeds and vectors were highly correlated with the expression of wind damage. These relationships can be used to calculate the fate of other historic storms and to predict the impact of future climate.

Global warming is projected to increase the intensity of hurricanes by 50% (EMANUEL, 1987). Under such climate conditions, mangroves may persist but likely undergo further structural changes where the relative age and size of these forests will decrease. The magnitude of such changes could lead to other functional and compositional shifts in plant and animal associations and the local extirpation of mangroves in south Florida.

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