# Mangroves, Hurricanes, and Lightning Strikes

## *Assessment of Hurricane Andrew suggests an interaction across two differing scales of disturbance*

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The track of Hurricane Andrew carried it across one of the most extensive mangrove forests in the New World. Although it is well known that hurricanes affect mangrove forests, surprisingly little quantitative information exists concerning hurricane impact on forest structure, succession, species composition, and dynamics of mangrove-dependent fauna or on rates of ecosystem recovery (see Craighead and Gilbert 1962, Roth 1992, Smith 1992, Smith and Duke 1987, Stoddart 1969).

After Hurricane Andrew's passage across south Florida, we assessed the environmental damage to the natural resources of the Everglades and Biscayne National Parks. Quantitative data collected during subsequent field trips (October 1992 to July 1993) are also provided. We present measurements of initial tree mortality by species and size class, estimates of delayed (or continuing) tree mortality, and observations of geomorphological changes along the coast and in the forests that could influence the course of forest recovery. We discuss a potential interaction across two differing scales of disturbance within mangrove forest systems: hurricanes and lightning strikes.

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**The recovery of Florida's mangrove forests is by no means assured**

### South Florida mangrove landscapes

Along the southwest Florida coast, a vast network of interconnecting waterways, shallow bays, and mangrove forests stretches from Naples southward to Cape Sable, forming the Ten Thousand Islands.[1] The northern portion of this coastline is comprised of hundreds of small islands and interconnected waterways, whereas in the southern half the islands and waterways are much larger. Within this broad estuarine area there are more than 60,000 ha of mangroves.

The coastal forests are tall, with individuals of the red (*Rhizophora mangle*), black (*Avicennia germinans*), and white (*Laguncularia racemosa*) mangroves attaining heights of 25 m. Tree height declines as one moves upstream toward the freshwater Everglades.

Oyster bars are common within the coastal embayments. Bottom environments are largely barren, calcareous and organic muds with limited areas of dense seagrass growth. The coastal mangroves form a continuous band (0.1–15 km in width) and extend landward as fingers along the numerous creeks and rivers that drain the upland Everglades marshes.

Many of the larger coastal islands in the southern Ten Thousand Islands support marshes dominated by the grass *Spartina bakeri*, the rush *Juncus roemerianus*, and the grass *Cladium jamaicense* within their interiors. Small, isolated marshes dominated by *Spartina alterniflora* are found seaward of the mangrove forest. Calcareous and quartz sand beaches are common along the exposed side of the seawardmost islands.

The southeast Florida mangrove forests around Biscayne Bay have a different character than those of the west coast. A band of tall trees (heights of more than 15 m) is found along the shore and may reach 200 m inland. Behind this is a band of dwarf mangroves (heights of less than 1.5 m), primarily of *R. mangle*. This forest ends abruptly at humanmade canals around the agricultural and suburban areas of south Dade County.

A number of keys form the eastern side of Biscayne Bay. The intertidal portions of these keys are domi-

[1]Places named are shown on the map on page 228.

nated by mixed mangrove forests. Several large mangrove overwash islands are found in the southern portion of the bay. The width of mangrove forests adjacent to Biscayne Bay is significantly less than that of the forests along the west coast, and their area (approximately 4000 ha) is much less as well.

## Areal extent of mangrove-forest damage

Our surveys used fixed-wing aircraft and helicopters flying along both north-to-south transects (across the storm's path) and seaward-to-landward gradients in the forest along both coasts. For these surveys, we classified the damage using the following scale: none, partial (less than 25% leaf loss), major (25–50% defoliation, some loss of branches, and scattered fallen trees), severe (more than 75% defoliation, some fallen trees), total (more than 50% trees down), and catastrophic (more than 75% of trees fallen or broken).

Top: Normal appearence of a mangrove forest canopy that has not been struck by a hurricane in more than 30 years. Note the bright green color of the canopy. Photo taken in May 1992. Bottom: Severely damaged mangrove forest at the entrance to Rodger's River. View is to the north toward Highland Beach. Note the large numbers of downed stems. Standing stems have lost most branches and almost all leaves. Photo taken two weeks after Hurricane Andrew. Photos: Stuart Pimm.

**Everglades National Park.** Results indicate catastrophic disturbance of the entire west-coast mangrove forest from the Chatham River to Shark Point. In the vicinity of Highland Beach, mangroves were 80–95% destroyed by trunk snapping and uprooting. This damage resulted from wind rather than storm surge, because the effect extends well inland from the coast. Areas of greater than 75% tree mortality are commonly in elongate bands less than a few hundred meters wide, corresponding to the report of numerous wind microbursts (Powell and Houston 1993).

Damage appeared to be much less along waterways with low (less than 3 m tall) fringing mangroves and in interior areas where the forest takes on a short, or dwarf, growth form (Odum et al. 1982). The low fringing forests are comprised primarily of *R. mangle*. The dwarf interior stands contain *A. germinans* and *L. racemosa*, in addition to *R. mangle*.

Damage on the west coast decreases rapidly to the south, moving from Shark Point (total to catastrophic damage) to the lower Shark River (severe) and into northern Cape Sable and Whitewater Bay (none to partial). The mangrove forests and interior marshes of Cape Sable and along northern Florida Bay suffered minor defoliation and occasional fine-branch breakage.

The gradient in forest damage to the north decreased much less rapidly than the gradient to the south. This pattern is coincident with the strongest winds extending further to the north than the south in Hurricane Andrew (Powell and Houston 1993).

A band of standing, dead *Rhizophora* extended from the mouth of Lostman's River northward past the Chatham River and into the northern Ten Thousand Islands area. Coastal mangrove forests in the northern Ten Thousand Island region all showed major to severe damage with occasional areas of total to catastrophic impacts. Within the Rookery Bay National Estuarine Research Reserve, well north of the path of the eye, tall forests suffered severe to total damage and even the low fringing forests had defoliation and limb breakage.

The mangrove forests in the southern portion of Naples Bay all had partial defoliation. The interior, shorter forests appeared much less damaged, although major defoliation was observed.

Large numbers of trees along the upstream mangrove marsh interface were either down or were totally defoliated from the upper Shark River to the Chatham River. Large amounts of Brazilian pepper (*Schinus terebinthifolius*), an invasive exotic species, are mixed in with the mangroves in this region. Most of the Brazilian pepper, although knocked over and defoliated by Andrew, showed strong recovery in the following ten months. Unfortunately, Brazilian pepper leafed out much faster than did the surviving mangroves.

Marsh areas in the interior portions of larger coastal islands, dominated by *S. bakeri*, appeared to have escaped major damage from the storm. The numerous small coastal marshes, dominated by *S. alterniflora*, also survived relatively undamaged.

**Biscayne National Park.** We observed a pattern similar to that seen in Everglades National Park on the western shore of Biscayne Bay. Damage to the tall (10–15 m) fringing forests of red and black mangroves was catastrophic from Mangrove Point on the south to Matheson Hammock in the north. The much shorter (less than 1.5 m) dwarf *Rhizophora* immediately landward of the taller mangrove fringe appeared almost unscathed (no damage or partial defoliation) from north of Black Point to south of Mangrove Point. The northern and southern portions of these areas generally had less complete destruction than the areas within the eye path. Many areas of complete windthrow were found within this zone.

On the eastern islands, areas of severe mangrove destruction were found on Elliott and Old Rhodes keys. Much of this damage was the result of an intense south-to-north storm surge generated as Andrew moved inland. The Arsenicker Keys within south Biscayne Bay also suffered catastrophic storm damage. In the southern portion of Biscayne National Park and on the outer keys, the shorter fringing red mangroves appeared relatively healthy. These shorter trees were most likely covered by the storm surge and thus escaped damage from high winds.

Top: Sapling-sized mangroves regenerating in a light gap in a mangrove forest located in Missionary Bay, northeast Queensland, Australia. The intact canopy surrounding the gap is approximately 17 m tall. This type of gap is common in mangrove forests the world over, and they were abundant along the southwest Florida coast. Bottom: A former gap without a canopy. Hurricane Andrew destroyed the canopy that had surrounded the saplings. Most saplings in this gap at Mangrove Point in Biscayne National Park survived the hurricane. Photos: Thomas J. Smith III.

## Impacts on coastal geomorphology and forest soil

The brief storm surge caused little shore erosion to the mangrove-dominated peat and marl coastlines or channel margins. Storm winds and surge uprooted some trees at the shoreline, but mangroves along the channel margins generally survived much better, at least initially, than those more inland. Downed mangroves in a leeward setting commonly lay in the water and remained green after the storm. These downed trees created a rough and unstable shoreline that waves and currents will continue to re-profile. We expect this breaking up and washing away of peat, over time, to release large volumes of organic material into the coastal bays.

The surface of the extensive mangrove forest between Lostman's River and Broad River on the west coast was covered by a gray mud layer 1–10 cm thick. This surface is sandy within 100 m of the coastline but is predominantly mud further inland. Quartz and carbonate are the predominant sand components. Organic matter forms 30% of the muddy layers. This layer is exposed at low tide and has become firm and somewhat resistant to erosion. Inland, adjacent to the Harney and Shark rivers, this layer rapidly decreased in thickness, and it was not present on the swamp surface adjacent to Tarpon Bay.

The mangrove wetlands that were severely damaged contained large volumes of dead leaves, twigs, and tree stems. There was commonly a layer of decomposing mangrove leaves beneath the storm-surge mud layer. In addition, the uprooted trees created a highly irregular topography and exposed the substrate to erosion. Uprooting created approximately 1–2 m of relief in the forest floor in some areas. Both native and exotic grasses and sedges have colonized these tip-up mounds in the months since the storm's passage.

## Estimates of tree mortality

After the aerial surveys, 43 plots were sampled throughout damaged forests on both coasts. In each plot, quantitative measurements included species composition, including size (diameter at breast height; DBH); presence or absence of regrowth; presence of seedlings or saplings that had survived the storm; and whether sediment had been deposited at the site.

Our data show that individuals more than 5 cm DBH of all three mangrove species suffered significant initial mortality (Figure 1). Mangroves less than 5 cm DBH had less than 10% mortality. Mortality did not, however, increase linearly with increasing DBH. Maximal mortality was recorded in the 20–25 cm DBH class for *R. mangle* and *A. germinans* and in the 15–20 cm DBH class for *L. racemosa*. Mortality decreased for trees more than 30 cm DBH. Comparisons among species reveal that *A. germinans* had significantly less mortality than either *L. racemosa* or *R. mangle* ($F_{2,59} = 4.27$, $p < 0.05$; Figure 2).

These initial estimates of tree mortality do not reflect the full impact of Hurricane Andrew on the forest, however. During the September 1992 assessment, we found many red mangroves with obvious hurricane damage (e.g., cracked stems and missing bark) that were still bearing green leaves and thus still alive. Numerous individuals of *A. germinans* and *L. racemosa* were observed to be resprouting after complete defoliation from the storm. Although these trees appeared to have survived the hurricane, subsequent remeasurements of marked individuals indicated that they eventually succumbed to hurricane damage. This delayed mortality is particularly pronounced for *L. racemosa*, larger individuals of *A. germinans*, and the smallest size class for all three species (Figure 1). For certain species and size classes, such delayed or continuing mortality has added 50% to our initial estimates of tree death (Figure 1).

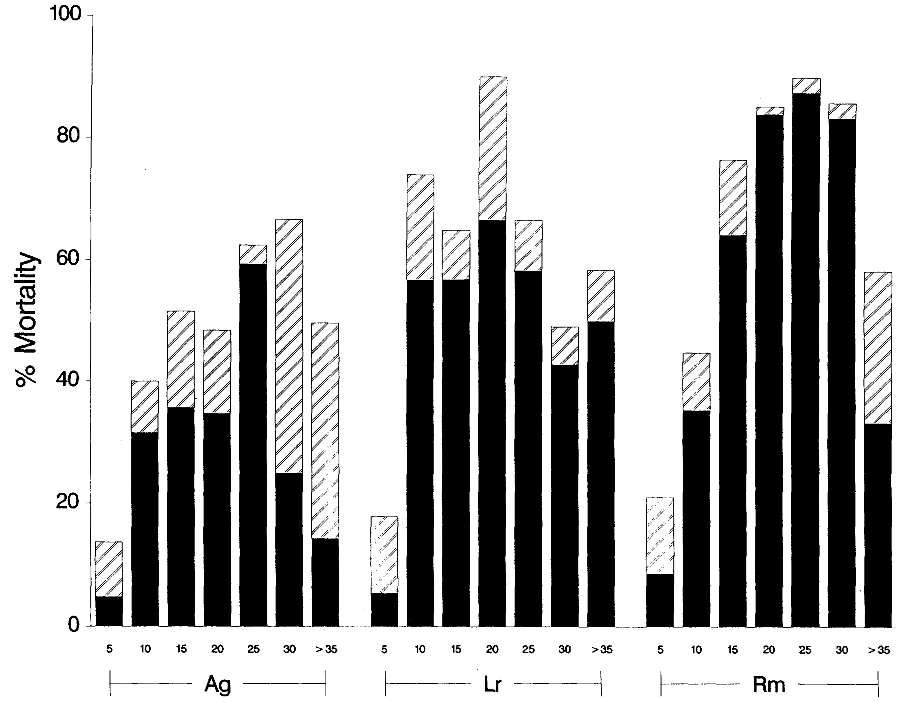


**Figure 1.** Mortality by diameter at breast height class for *Avicennia germinans* (Ag), *Laguncularia racemosa* (Lr), and *Rhizophora mangle* (Rm), measured in September–October 1992 (solid) and in May–July 1993 (cross-hatched). The figure is based on measurements taken on more than 4000 individuals. The diameters are given in centimeters.

The delayed mortality is continuing. More than two years after Hurricane Donna, trees were still dying from the storm's damage (Craighead and Gilbert 1962). Additionally, this continuing mortality is not restricted to sapling and tree-sized individuals. We encountered large numbers of mangrove propagules throughout the affected forests, often more than ten per square meter. The hurricane dispersed a large proportion of these propagules. Many of these seedlings have subsequently perished, especially in regions of sediment deposition and areas subjected to increased concentrations of pore water sulfide.

## Interactions across scales of disturbance

During our overflights, we observed a number of small circular patches of bright green, living mangroves. These patches were embedded in the background of gray, dead trees. The individuals growing in these patches were of smaller stature than the individuals that had comprised the surrounding forest matrix. One of the researchers (TJS) present during the overflights hypothesized that these patches were remnant light gaps in which sapling-sized individuals had survived the impacts of Hurricane Andrew. From earlier reports, we know these gaps are caused by lightning (Craighead 1971). It is interesting to note that southwest Florida has one of the highest incidences of lightning in the United States (Michaels et al. 1987). We hypothesized that survival of individuals that had been growing in these pre-existing light gaps was higher than for individuals growing in the surrounding canopy.

We used color infrared aerial photos from 1990, remaining landmarks (e.g., river bends and islands), and the ground positioning system to locate 14 canopy gaps that existed before Hurricane Andrew. We recorded data on survival in the gaps and in the nearby canopy, or what remains of it.

Mortality of individuals that had been growing in gaps was significantly lower than for individuals growing in the surrounding canopy ($F_{1,59} = 25.68$, $p < 0.001$; Figure 2). Thus, the regenerators from small-scale disturbance in the forest constituted the majority of the survivors of the large-scale catastrophic disturbance. Observations similar to ours were made in the tropical forests of Puerto Rico after Hurricane Hugo (Brokaw and Grear 1991). Given that all three Florida mangroves can reproduce precociously (i.e., individuals less than 1 m in height will produce viable propagules), these sapling-sized survivors may provide the source for recolonization of destroyed forests.

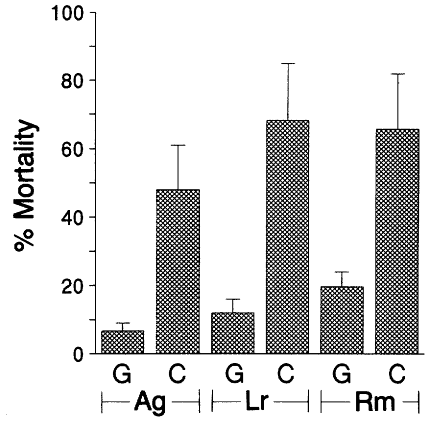


**Figure 2.** Differential mortality for individuals growing in the canopy (C) and in pre-existing canopy gaps (G) for the three species of mangrove trees. Standard error is indicated.

## Andrew's impact on forest nutrient cycles

A considerable mass of leaves, branches, trunks, and roots died as a result of Hurricane Andrew. As this material decomposes, it releases nitrogen and phosphorus both within the forest and into the nearshore zones of Biscayne Bay and the southwest Florida coastline. Based on allometric equations relating biomass to measures of tree height and stem diameter and on published measurements of nitrogen and phosphorus contents of various mangrove tissues, we have calculated a first approximation of the amount of nutrients that have entered the detrital pool (Table 1).

Depending on the species composition of the forest and degree of damage, total dead biomass per hectare may exceed 150 metric tons, including 0.57 metric tons of nitrogen and 0.18 metric tons of phosphorus. The influence of the release of these nutrients on nearshore systems could be substantial. The material is in pools that decompose at vastly different rates, with leaves being fastest, large woody material slowest, and roots intermediate.

Immediately before Hurricane Andrew, we had discovered the remains of tree trunks that had been blown down by Hurricane Donna in 1960. This finding indicates that mangrove wood is extremely persistent. Robertson and Daniel (1989) reported that decomposing mangrove wood was a sink for nitrogen. Within the first few months after decomposition began, *Rhizophora* trunks increased their nitrogen concentration to approximately 2.5 times the level in live trunks, and they maintained high nitrogen concentrations for more than 15 years (the length of the study).

Understanding of phosphorus cycling in mangroves is much less complete than knowledge of nitrogen dynamics (Alongi et al. 1992). Given that in heavily affected areas no plants are left alive, no plants take up nutrients released by decomposing mangrove tissues. Immediately after the storm, an algal mat developed in areas of major canopy loss. By December 1993, even this algal mat had died. Phytoplankton blooms were reported in the second half of 1993 along the southwest Florida coastline and have been attributed to nutrients being released from the affected mangrove forests.[2]

**Table 1.** First-order approximations for mass of dead biomass and associated nutrients from mangroves killed by Hurricane Andrew. Units are metric tons/ha for biomass and nitrogen and kg/ha for phosphorus. Calculations are based on information in Onuf et al. (1977), Twilley et al. (1986), Robertson and Daniel (1989), and van der Valk and Attiwill (1984).

| | Biomass | Nitrogen | Phosphorus |
|---|---|---|---|
| **Leaves** | | | |
| *Avicennia* | 36 ± 15 | 0.38 ± 0.16 | 198 ± 82 |
| *Laguncularia* | 25 ± 6 | 0.10 ± 0.02 | 50 ± 10 |
| *Rhizophora* | 3 ± 3 | 0.02 ± 0.02 | 11 ± 11 |
| **Branches** | | | |
| *Avicennia* | 7 ± 3 | 0.04 ± 0.02 | 19 ± 8 |
| *Laguncularia* | 5 ± 1 | 0.01 ± 0.006 | 5 ± 1 |
| *Rhizophora* | 7 ± 1 | 0.02 ± 0.008 | 13 ± 4 |
| **Trunks** | | | |
| *Avicennia* | 60 ± 25 | 0.05 ± 0.02 | 25 ± 10 |
| *Laguncularia* | 42 ± 9 | 0.01 ± 0.003 | 7 ± 4 |
| *Rhizophora* | 39 ± 7 | 0.01 ± 0.004 | 10 ± 4 |
| **Roots** | | | |
| *Avicennia* | 26 ± 12 | 0.032 ± 0.15 | 338 ± 156 |
| *Laguncularia* | 18 ± 6 | 0.08 ± 0.03 | 86 ± 30 |
| *Rhizophora* | 12 ± 4 | 0.10 ± 0.03 | 102 ± 34 |

## Prospects for forest recovery

Because mangrove forests are floristically simple compared with other forest types, many biologists assume that complete recovery is almost assured. This feeling has even made it into the scientific literature (Ogden 1992). One reason for this view is that previous hurricanes have struck Florida's mangrove forests (Figure 3), and the forests have appeared to grow back.

There is, however, evidence indicating that mangroves do not always return to their former state following catastrophic disturbance. Craighead (1971) discusses a forest near Flamingo, Florida, that was called the Black Forest because it was dominated by *A. germinans*. It was devastated by the Labor Day

[2]Brian Laponte, 1993, personal communication. Harbor Branch Oceanographic Institute, Fort Pierce, FL.

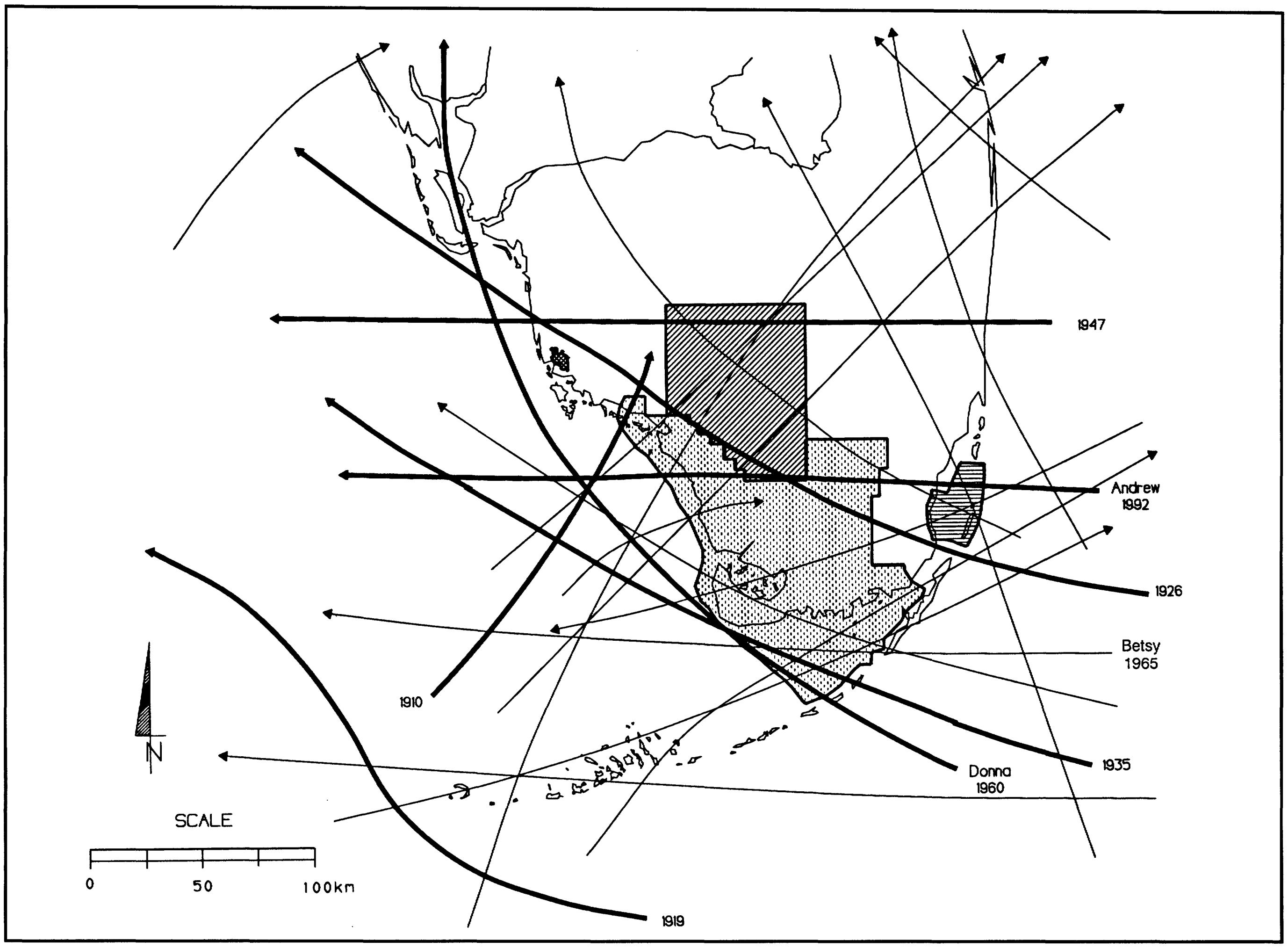


**Figure 3.** Tracks of hurricanes across the south Florida peninsula. Major storms (classes 4 and 5) are shown as bold lines, minor storms (classes 1–3) as narrow lines. Data are from DOC (1979) for the period 1899–1977. Federal protected areas are shown: Rookery Bay National Estuarine Reserve Reserve (crosshatched), Big Cypress National Preserve (diagonal lines), Everglades National Park (stippled), and Biscayne National Park (horizontal lines).

storm of 1935 (Figure 3). Before that storm, the average age of the trees was an estimated 250 yr, and the DBH of the trees was approximately 1 m. *Avicennia* of this size are exceedingly rare in southwest Florida mangrove forests today. After the 1935 storm, *Rhizophora* invaded the site, and it increased further in abundance after the passage of Hurricane Donna in 1960. The *Avicennia* that was replaced by *Rhizophora* has not recolonized.

Hurricane Donna in 1960 destroyed the mangrove forests along the northwest coast of Cape Sable. Spackman et al. (1964) describe this area as actively eroding. In many of the areas they discuss, *Rhizophora* trunks that have yet to decompose can still be found. Although the area is within the intertidal zone, mangroves have not recolonized large expanses of barren mudflat. It is not known why these areas of seemingly suitable habitat have not been recolonized.

A key to understanding mangrove forest recovery may lie in comparing the processes influenced by the two scales of disturbance. When lightning opens a small gap in the forest canopy, it alters several physical parameters within the gap compared with those under the surrounding canopy (Table 2): humidity in the gap is less, soil salinity is less because of a lessened evapotranspiration stream, soil temperature is higher, light levels are dramatically higher, and the soil nutrient status may also be different (Smith 1987). Additionally, gap formation may lead to changes in species composition of the burrowing macrofauna, which may alter biological processes in the gap such as predation on mangrove seeds and seedlings (Osborne and Smith 1990). Certain of these changes are beneficial to mangrove seedling establishment and growth (e.g., increased light and nutrients), whereas others are detrimental (e.g., lessened humidity and increased soil temperature).

Large-scale loss of the canopy mimics in many ways the creation of a gap. There are other important considerations, however. Two closely related factors are soil redox potential and soil pore-water sulfide concentrations. Both *Rhizophora* and *Avicennia* have the ability to aerate reduced soils (Mckee et al. 1988). Around a small light gap, the large numbers of living man-

Table 2. Changes in the physical environment that influence seedling establishment and growth of mangroves due to two scales of disturbance. Comparisons are made to the undisturbed forest canopy. Question marks indicate uncertainty in our understanding and represent testable hypotheses.

| Parameter | Light gap | Total loss of canopy |
|---|---|---|
| Light | Increased | Increased |
| Salinity | Decreased | Decreased |
| Humidity | Decreased | Decreased |
| Soil temperature | Increased | Increased |
| Redox potential | Unchanged? | Decreased? |
| Sulfide concentration | Unchanged? | Increased? |

grove roots can still aerate the soil. But when all the trees in a large area are dead, no living roots remain. Redox decreases and sulfide increases, possibly to levels lethal to mangroves and other vascular plants.

Preliminary measurements indicate both increased sulfide and more highly reducing conditions in those areas most heavily damaged by Hurricane Andrew,[3] which could effectively preclude recolonization by mangrove propagules. In addition, levels of anaerobic decomposition could increase and actually reduce the surface level of peat soils. This effect could have profound consequences for mangrove forests when considered in conjunction with the recently reported rate of sea level rise for south Florida (2.3 mm/yr; Maul and Martin 1993).

Knowledge of mangrove ecosystems is still incomplete. Based on our studies, it is too early to predict the system's response to Hurricane Andrew. However, our data suggest that the recovery of Florida's mangrove forests is by no means assured.

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[3]William Wiebe, 1993, personal communication. Department of Microbiology, University of Georgia, Athens.

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