PROCEEDINGS
OF THE
NINTH SYMPOSIUM
ON THE
NATURAL HISTORY OF THE
BAHAMAS

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Gerace Research Center
San Salvador, Bahamas
2003

Cover photograph courtesy of David and Sherilyn Smith

Printed in the USA

ISBN 0-935909-73-7

DISPERSAL AND RECRUITMENT OF WHITE MANGROVE ON SAN SALVADOR ISLAND, BAHAMAS AFTER HURRICANE FLOYD

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ABSTRACT

White Mangrove (*Laguncularia racemosa*: Combretaceae) is one of the major mangrove species that grow along the edges of inland hypersaline ponds. Fruits are water-dispersed and mature during the hurricane season (August-October), which suggests that hurricanes may have major influences on fruit dispersal. Here we document the patterns of fruit dispersal and seedling recruitment after Hurricane Floyd at three ponds (Reckley Hill, Osprey, and Oyster Ponds). We also tested whether a hurricane could disperse fruits between inland ponds by sampling litter for fruits and surveying seedling recruitment at inland lakes where White Mangrove populations are absent (Moonrock, Pain, and Crescent Ponds).

Surveys of fruits and seedlings demonstrated that Hurricane Floyd had unique effects on dispersal and recruitment at each pond. At Osprey Pond, most fruits were dispersed into the upland coppice by a storm surge and all seedlings died. At Reckley Hill Pond, fruits were dispersed in the mangrove zone and seedlings had high survivorship. At Oyster Pond, fruits and seedlings occurred far inland in wet limestone crevices. In litter samples, we found a single White Mangrove fruit near the shore of Pain Pond, suggesting that hurricanes can disperse fruits far distances, across land and between isolated ponds. These results indicate that hurricanes can have both negative and positive effects on White Mangrove dispersal and recruitment and that hurricanes can cause long distance fruit dispersal.

INTRODUCTION

Hurricanes can have severe negative effects on woody plants by breaking branches and uprooting trees, as many studies have demonstrated (*e.g.* Brokaw and Grear 1991, Brokaw and Walker 1991, Bellingham *et al.* 1995, Herbert *et al.* 1999). However, hurricanes can also impact seed dispersal and plant recruitment, and these effects can be positive as well as negative (Boucher 1990, Brokaw and Grear 1991, Guzman-Grajales and Walker 1991, Vandermeer *et al.* 1996, Rathcke 2000, Rathcke 2001). Because global warming predictions include increases in both the frequency and the severity of hurricanes (IPCC 2001), it is important to document the effects hurricanes have on dispersal and recruitment. Here we test two hypotheses about hurricane effects on plants: the Hurricane Dispersal Hypothesis and the Hurricane Recruitment Hypothesis.

In the Hurricane Dispersal Hypothesis we propose that hurricanes can affect both local and long-distance seed dispersal patterns. High winds and storm surges can move seeds far from parents and into new microhabitats within local communities. The effect could be either positive or negative, depending on whether or not the local site was suitable. Hurricanes could also carry seeds long distances, where they might establish new populations. High winds and storm surges associated with hurricanes could serve as an infrequent mechanism for gene flow between distant populations, particularly for plants whose seeds mature during the hurricane season. Rare long-distance dispersal is being recognized as a potentially important factor in establishing new populations (Buchan and Padilla 1998) and in gene flow between populations (Cain *et al.* 1998).

In the Hurricane Recruitment Hypothesis researchers propose that hurricanes can cause gaps as a result of breakage or uprooting of mature trees, thereby increasing the recruitment of some plants (Connell 1978, Boucher 1990, Frangi and Lugo 1991, Vandermeer *et al.* 1996). Recruitment could also be reduced if seeds were carried to poor habitat and were unable to germinate or establish themselves. These positive and negative effects could change the relative abundance of species in the community, especially if some species were better seedling competitors than others, if only some species had seeds available for dispersal, or if there were reductions in pollination services (Vandermeer *et al.* 1996, Rathcke 2000, Rathcke 2001).

In this study, we examined White Mangrove (Combretaceae: *Laguncularia racemosa*) to test these two hypotheses in the aftermath of Hurricane Floyd, which passed over San Salvador Island, Bahamas in September 1999 as a Class-5 hurricane. White Mangrove is an ideal study species for testing these hypotheses on San Salvador Island. Most of the water-dispersed fruits mature during September-October, the peak of the hurricane season (Rathcke *et al.* 1996, Shaklee 1996). Each fruit typically contains only one seed, so fruit counts can be used to quantify seed set. White Mangrove is a common species near oceans in the Neotropics, being found on most islands and along the mainland coasts of the Caribbean region (Correll and Correll 1982). Additionally, on San Salvador Island, the plant has a patchwork distribution, growing around some hypersaline ponds, but not others (Godfrey *et al.* 1994, pers. observations) (Figure 1).Specifically, we tested the Hurricane Dispersal Hypothesis at two scales, for long-distance and for local dispersal. Taking advantage of the patchy distribution on San Salvador, we searched for fruits and seedlings at ponds that do not have White Mangrove populations to test the prediction that hurricanes are can transport seeds over long distances, and in this case, over land. At the local level, we searched for fruits and seedlings at ponds that have White Mangrove populations to test the prediction that hurricanes can carry seeds out of suitable habitat, the mangrove zone, and into the coppice. We defined the mangrove zone as the region where mature mangroves currently exist. These data also allowed us to test the hypothesis that mangrove zonation is the result of dispersal limitation (Rabinowitz 1978). To test the predictions of the Hurricane Recruitment Hypothesis, we established permanent plots at Reckley Hill Pond and Osprey Pond. We noted gaps in the forest in order to test the prediction that gaps created by hurricanes may increase recruitment.

METHODS

To test the long-distance predictions of the Hurricane Dispersal Hypothesis, we surveyed three ponds without White Mangrove (Figure 1: Pain Pond, Crescent Pond, Moonrock Pond), looking for seedlings and collecting litter samples that would later be searched for fruits. All the litter was removed from five randomly selected plots, approximately 0.5 square meters in size, and taken back to the field station for sorting.

To test the Hurricane Dispersal Hypothesis at the local scale, we surveyed three ponds with White Mangrove populations (Figure 1: Reckley Hill Pond, Osprey Pond, Oyster Pond). At each pond we ran three transects, each originating at the edge of the pond and ending high up in the coppice. We searched for seedlings in 0.5 square meter plots every five feet along the transects (every three feet at Reckley Hill Pond), and collected litter samples from every other plot along each transect.

To test the Hurricane Recruitment Hypothesis, we established five permanent plots (one square meter) at Reckley Hill Pond and at Osprey Pond in December 1999 in order to follow the success of seedlings over an indefinite period of time. We surveyed these plots in June 2000, November 2000, and June 2001 to determine the survivorship of seedlings over time.

RESULTS

We found one White Mangrove fruit at Pain Pond, where there are no White Mangrove

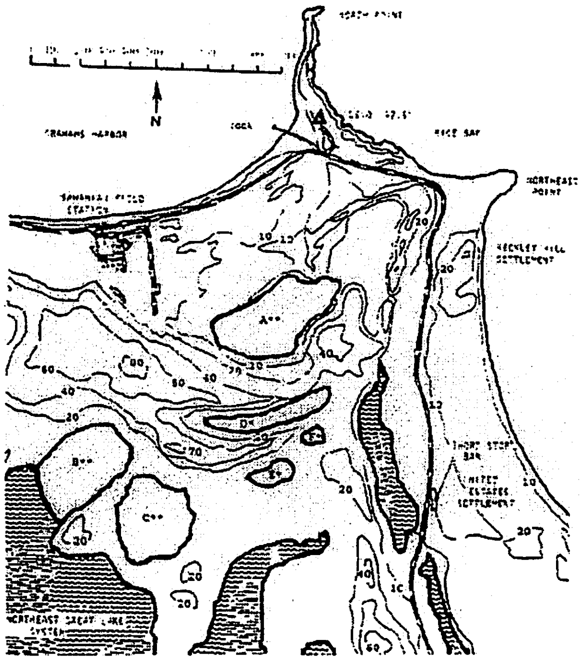

Figure 1. Northeast corner of San Salvador Island, Bahamas. The pond communities included in this study are labeled A-F (A, Reckley Hill Pond; B, Osprey Pond; C, Oyster Pond; D, Crescent Pond; E, Pain Pond; F, Moonrock Pond). Ponds with White Mangrove trees are indicated by two asterisks, while ponds without White Mangrove are indicated by one asterisk. Map revised from Godfrey *et al.* 1994.

trees, indicating that a long-distance dispersal event occurred. We re-sampled at that pond after finding the fruit, but did not find any additional fruits. No fruits were found at either Crescent Pond or Moonrock Pond, the other ponds without White Mangrove populations.

Dispersal patterns varied in local populations. At Reckley Hill Pond, most of the fruits and seedlings were dispersed within the mangrove zone (Figure 2A-B), while at Osprey Pond there were almost no fruits or seedlings within the mangrove zone- nearly all were found in the coppice (Figure 2C-D). All fruits and seedlings found at Oyster Pond were within the mangrove zone (Figure 2E-F), but the zone extends unusually far inland at this pond (see Discussion).

Recruitment patterns differed at the two ponds with permanent plots (Table 1). At Reckley Hill Pond, where most of the fruits were found within the mangrove zone, many seedlings still survived after 18 months. In contrast, there were no survivors at Osprey Pond after six months, where most of the fruits were found outside of the mangrove zone.

DISCUSSION

The unique dispersal patterns of fruits at each pond demonstrate that there is no single "hurricane effect" on local dispersal, even over a relatively small geographic area such as the northern end of San Salvador Island. The different dispersal patterns may be partly explained by the unique topography of the shore surrounding each pond. At Reckley Hill Pond, the land has a small rise through the mangrove zone (5-20 feet wide) but then rises steeply into the coppice. This sharp rise probably restricted the water flow, thus keeping the majority of fruits (and therefore, the seedlings) in the mangrove zone (Figure 2A-B). The fruits could have floated back through the mangrove zone towards the pond's edge if the water receded slowly due to the shallow slope.

In contrast, the shore of Osprey Pond is very different, with a smoother rise over a greater distance through the mangrove zone and into the coppice, thus allowing an ocean surge to carry fruits out of the mangrove zone. Additionally, Osprey Pond is separated from the rest of the Great Lake system only by a very narrow strip of land about one foot above water level (Figure 1). The storm surge could have come across this narrow land bridge from the larger Great Lake system and gained strength as it crossed the pond, thereby carrying fruits out of the mangrove zone and high into the coppice. Mounds of aquatic shells were deposited 50 or more feet from the pond's edge, which indicate that an storm surge event occurred, and it is in this area that we found most of the fruits and seedlings (Figure 2C-D). The ocean surge carried fruits out of the mangrove zone then apparently receded quickly, thus leaving the fruits behind in the coppice.

Table 1. Number of seedlings found in permanent plots established at Reckley Hill Pond and Osprey Pond immediately after Hurricane Floyd (12/99), and in subsequent years. The average number of seedlings (*) is calculated for each visit. Average survivorship (**) is based on the number of seedlings initially found in each plot (12/99).

Population	Plot	Number of Seedlings			
		12/99	6/00	11/00	6/01
Reckley Hill	A	9	5	5	5
	B	11	5	4	2
	C	5	3	3	0
	D	112	33	25	7
	E	25	12	6	3
Mean*		32.4	11.6	8.6	3.4
Survivorship**		100%	47.9%	39.9%	18.6%
Osprey	A	71	0	0	0
	B	72	0	0	0
	C	80	0	0	0
	D	52	0	0	0
Mean*		68.8	0	0	0
Survivorship**		100%	0.0%	0.0%	0.0%

Oyster Pond is different in having a very unusual topographic setting, in that it is surrounded by a "moonrock" terrace- a large, flat expanse of rock that supports very little vegetation. The rock is pocked with holes that are sometimes connected via conduits to the pond and that fill up with detritus, providing the only habitat available to most plants, including mangroves, on the terrace. Consequently, mature mangrove trees can be found 60 or more feet from the edge of the pond in small pockets, separated from one another by 10-15 feet of bare rock in any direction. We have defined the mangrove zone as the area supporting mature mangrove trees, so all the fruits and seedlings were technically found within the mangrove zone (Figure 2E-F). However, the vast majority of this "zone" is unsuitable habitat for most plants, including mangroves.

Hurricane Floyd apparently effected long-distance dispersal as evidenced by the one fruit dispersed to Pain Pond, which does not have a White Mangrove population. The topography of the surrounding region is hilly and the pond is isolated from all other ponds, so we are convinced that the fruit was dispersed over land via high winds, not water. We do not know the origin of the fruit we found, so we do not have any evidence concerning the distance it traveled. The fact that only one fruit was found may indicate that such dispersal events are relatively rare over land, but similar long distance dispersal events could occur more easily over water or along shorelines. White Mangrove fruits float, and if they were picked up by high winds and carried over water, or picked up by an ocean surge, they might eventually make it to distant suitable habitats. This long-distance dispersal could be a mechanism for gene flow between otherwise isolated populations or for founding new populations of White Mangrove.

The effect of Hurricane Floyd on recruitment also varied between ponds. Seedling recruitment at Reckley Hill Pond was high, with many seedlings surviving over one year, while recruitment at Osprey Pond was zero after six months (Table 1). The recruitment at Reckley Hill represents the largest number of seedlings surviving that we have encountered on San Salvador Island over five years (Rathcke, personal observation), and may indicate that major climatic events like hurricanes are necessary for White Mangrove recruitment on San Salvador. Many, if not all, of the leaves were stripped from the trees in this population, and while there was little visible damage to the branches of these trees, the complete removal of leaves would have allowed more light to the penetrate the forest than normally occurs, because all the trees are evergreen. Therefore, while new gaps were not formed along Reckley Hill Pond, the increased light availability caused by leaf removal appeared to favor seedling recruitment, as was also observed by Brokaw and Grear (1991).

At Osprey Pond, very few fruits were found in the mangrove zone. While several trees were uprooted in one region of the mangrove zone, forming a fairly large gap, no fruits or seedlings were found in this area. Therefore, the opportunity for White Mangrove to recruit into the newly formed gap was lost because most of the fruits were carried into the coppice. The resulting seedlings all died within six months of the hurricane, probably due to desiccation, as White Mangrove does not require salt to grow (Landry, unpublished data). These results demonstrate that dispersal does not limit the distribution of mangroves, as suggested by Rabinowitz (1978).

Overall, these results demonstrate that hurricanes can have either positive or negative effects on local dispersal and recruitment, and the effects are not easily predictable, even for local sites after the same hurricane. In addition, the general importance of rare long-distance dispersal events has recently been recognized (Cain *et al.* 1998), and these results indicate that hurricanes may be an important mechanism for long-distance dispersal of mangroves.

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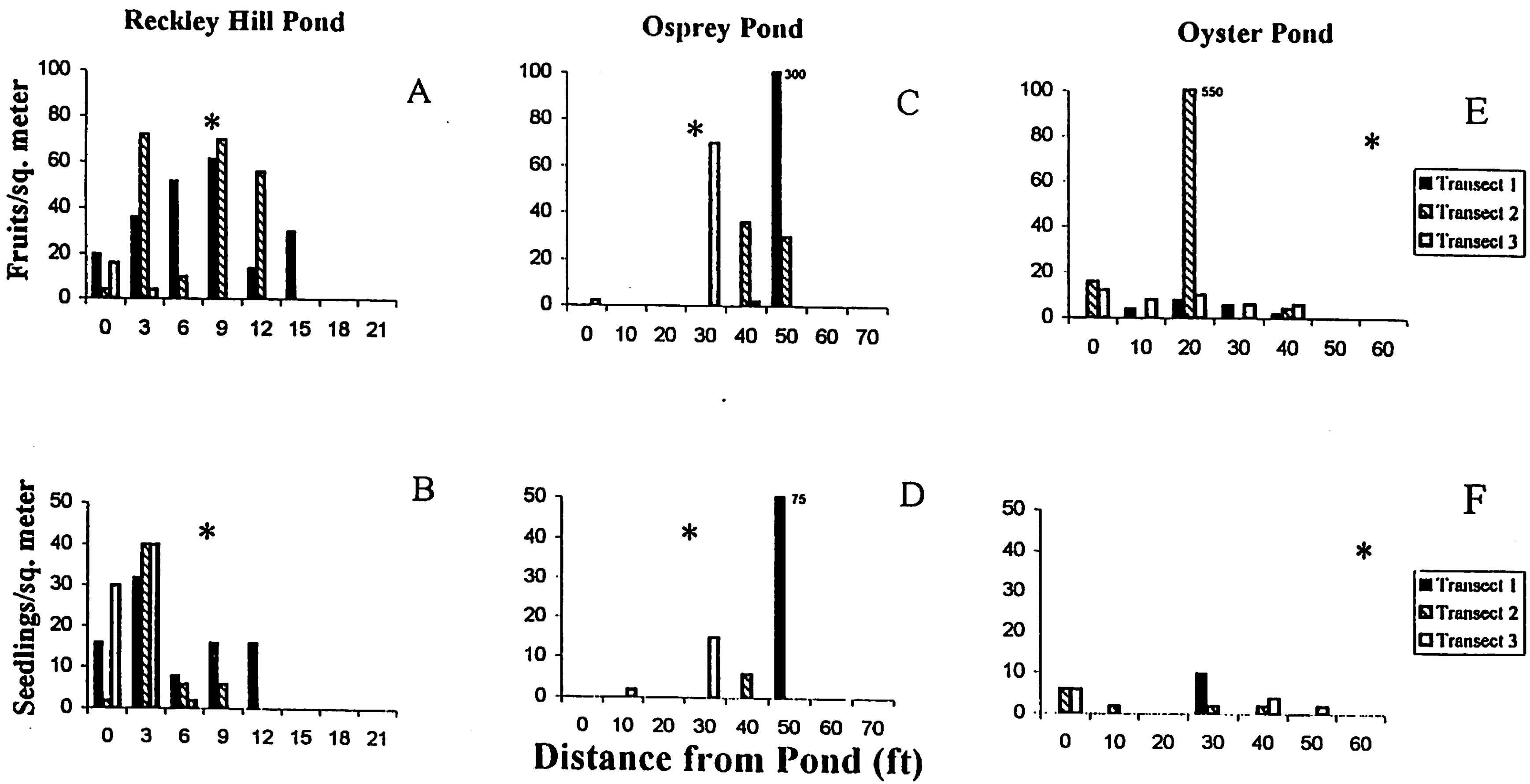

Figure 2: Distributions of fruits and seedlings at Reckley Hill Pond (A and B), Osprey Pond (C and D), and Oyster Pond (E and F). Bars represent three transects at each pond. The asterisks note the landward edge of the mangrove zone. Actual numbers of fruits or seedlings are shown on graphs C, D, and E because they were off the scale. Note that the distances on the x-axes differ between ponds.