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CHANGES IN THE POLLINATION ECOLOGY OF WHITE MANGROVE FOLLOWING HURRICANE WILMA (2005)

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ABSTRACT

Hurricanes are infrequent disturbance events that can directly and indirectly affect the reproductive ecology of species in mangrove communities; all mangrove species are long-lived, so individuals are likely to experience a hurricane during their lifetimes. Hurricanes could indirectly affect reproduction in white mangrove (*Laguncularia racemosa*), an insect-pollinated species, by altering the composition of the insect pollinator community. Some populations of white mangrove are androdioecious, with plants that produce male flowers and other plants that produce hermaphroditic flowers. Theoretically, males require a fitness advantage in order to be maintained in populations with hermaphrodites; changes in the pattern of pollinator foraging behaviors could increase relative male fitness. In this study, I compared the insect pollinator community composition, floral visitation rates and foraging bout lengths to male and hermaphroditic plants in one Hollywood, Florida population of white mangrove, before and after Hurricane Wilma (2005).

Most insect species commonly observed before the hurricane were present after the hurricane, but the relative proportions of some species changed dramatically. There was a 433% increase in the number of honeybees (*Apis mellifera*), and a 36% decrease in the total number of individuals of all other insect species observed visiting white mangrove flowers. Overall, the floral visitation rate to male plants was significantly greater than the visitation rate to hermaphrodite plants. Prior to the hurricane, both males and hermaphrodites received more visitors making short foraging bouts versus long foraging bouts, a pattern of foraging behavior that promotes outcrossing. After Hurricane Wilma, males received more visitors making long foraging bouts than short foraging bouts, which increases pollen wastage, and hermaphrodites had equal numbers of visitors making long and short foraging bouts, which increases the probability of selfing. Honey bees were responsible for a significant fraction of visits made to male and hermaphroditic plants after the hurricane. The effect of honey bees on floral visitation rate was significantly greater after the hurricane; honey bees were also primarily responsible for changes in foraging bout distributions. Male plants in this population did not incur a fitness advantage due to changes in the pattern of pollinator foraging behaviors following Hurricane Wilma.

INTRODUCTION

Hurricanes are major disturbance events in mangrove communities; high winds and storm surge can strip foliage, flowers, and fruits from the branches, and can cause significant structural damage to the woody portions of the plants (Imbert *et al.* 1996, Sherman *et al.* 2001, Smith *et al.* 2009). All mangrove species are long-lived woody plants (Tomlinson 1986), so individuals are likely to experience multiple hurricane events during their lifetimes. Hurricanes can have direct effects on the reproductive success of mangroves. The effect can be negative if flowering or fruiting is reduced following a hurricane (Rathcke 2000). However, hurricanes can also have positive effects on recruitment if structural damage to the forest results in an increase in habitat suitable for mangrove recruitment (Pascarella 1998, Rathcke and Landry 2003).

In addition to direct effects, hurricanes can have indirect effects on the reproductive success of animal-pollinated plants, if the number of pollinators is reduced (Rathcke 2000, Rathcke 2001) or the relative abundances of pollinators with different foraging behaviors is altered (Roubik and Villanueva-Gutierrez 2009). White mangrove (*Laguncularia racemosa* (L.) Gaertn. f. [Combretaceae]) is insect-pollinated (Rathcke *et al.* 1996), but hermaphroditic flowers are capable of autogamous self-pollination when they are not visited by insects (Landry *et al.* 2005). Some populations of white mangrove are androdioecious, a rare breeding system with two breeding types: plants that produce male flowers; and other plants that produce hermaphroditic flowers, with both male and female function (Landry and Rathcke 2007, Landry *et al.* 2009). Other populations lack male plants, i.e. they are hermaphrodite-only populations. In order to persist, male plants theoretically require at least a two-fold increase in fitness relative to the male fitness component of hermaphroditic plants (Lloyd 1975, Charlesworth 1984). Changes in the pattern of pollinator foraging behaviors following hurricane events could alter the fitness relationship between the two breeding types.

Theoretically, male plants incur a fitness advantage if they receive more visits from insect pollinators than hermaphroditic plants receive; this advantage is maximized when two conditions are met. First, an insect must visit enough flowers on a male plant such that most of the pollen grains on that insect are from that plant. Insects simultaneously lose pollen and pick up new pollen as they forage on the flowers of a plant, so the relative fraction of pollen grains on an insect from a single plant increases as the number of flowers visited on that plant increases, i.e. as the length of the foraging bout within the plant increases (Harder and Barrett 1996, Snow *et al.* 1996). Throughout this paper, *foraging bout* refers to the number of flowers that are visited by an insect on an individual plant before that insect moves to a different plant. Secondly, the insect must move from the male plant to the flowers of a hermaphroditic plant. It is unlikely that an insect will always alternate between plant breeding types. In order to maximize the number of times an insect leaves a male plant and travels to a hermaphroditic plant, male plants must be visited more frequently than hermaphroditic plants. Therefore, the male fitness advantage is maximized when insects move frequently between plants, visit few flowers during foraging bouts within plants, and visit male plants more frequently than hermaphroditic plants.

Foraging bout lengths within hermaphroditic plants can affect the mating system of white mangrove, which can also alter the fitness relationship between males and hermaphrodites (Lloyd 1975, Charlesworth 1984). Long foraging bouts within hermaphroditic plants increase the frequency of self-pollination, while short foraging bouts increase the frequency of outcrossing (Snow *et al.* 1996). If the progeny from selfed flowers are less fit than the progeny from outcrossed flowers due to inbreeding depression, then as the frequency of selfing increases, the fitness of hermaphroditic plants declines relative to male fitness.

In order to estimate the indirect effects of hurricanes on the reproductive ecology of white mangrove, I compared pollinator species composition, pollinator visitation rates, and pollinator foraging bout lengths to male and hermaphroditic plants in one androdioecious population before and after Hurricane Wilma. This Category 2 hurricane passed over the white mangrove population at Hollywood, Florida on October 24, 2005.

Study species

White mangrove is an insect-pollinated shrub or tree found in mangrove forests throughout the Neotropics and northwestern Africa (Correll and Correll 1982, Tomlinson 1986). The species was first described as morphologically androdioecious on San Salvador Island, Bahamas (Rathcke *et al.* 1996). The small white flowers are displayed on racemes and typically bloom in June-August in Florida (Landry *et al.* 2007), although flowering is reported to occur as early as April in Florida (Tomlinson 2001) and throughout the year in the Bahamas (Correll and Correll 1982, Kass 2005, Landry *et al.* 2007). Hermaphroditic plants bear only hermaphroditic flowers, which are urn-shaped and either sessile on the rachis of the raceme (Landry *et al.* 2007) or firmly held on the rachis by a short pedicel (Kass 2005). In contrast, the flowers on male plants are smaller and cup-shaped, and are always weakly held on the rachis by a short pedicel; male flowers typically dehisce after 1-2 days, leaving the rachis bare. Pollination studies conducted in Florida (Landry and Rathcke 2007) and in the Bahamas (San Salvador Island; Rathcke *et al.* 2001a) determined that morphological hermaphrodites have both male and female function; therefore, populations with both hermaphroditic and male plants are functionally androdioecious. White mangrove flowers are visited by many insect species, including bees, wasps, flies and butterflies (Rathcke *et al.* 2001b, Landry 2005, Landry *et al.* 2005), although hermaphroditic flowers can also self-pollinate and self-fertilize (Rathcke *et al.* 2001a, Landry 2005, Landry and Rathcke 2007). White mangrove is semi-viviparous; the seed germinates inside the fruit while attached to the maternal plant, but the seedling does not emerge from the fruit until after dispersal. The fruits are water-dispersed (Tomlinson 2001, Kass 2005, Landry personal observations).

METHODS

Insect visitors were observed in the white mangrove population at West Lake Park, Broward County Parks and Recreation, Hollywood, Florida during June and July of 2001, 2002, and 2008. Insect voucher specimens are stored at the University of Michigan Museum Of Natural History-Insect Division. Insects were observed during 10-minute watches, conducted between 9:00 am and 5:00 pm. Equal time was spent observing insects at hermaphroditic and male plants in 2008 (40 watches at each breeding type), but the number of timed watches performed before Hurricane Wilma varied (47 watches at hermaphroditic plants, 44 watches at male plants). In order to make direct comparisons between plants with different floral densities, the number of open flowers in a watch zone was estimated every day for each tree included in the study. In most cases, multiple inflorescences were included in each watch zone. Floral visitation rates (FVR) were calculated for each watch using the following formula:

FVR = (# Flowers visited / # Flowers / 10 minutes). Average floral visitation rates were calculated for each breeding type before and after Hurricane Wilma. A three-way ANOVA test was performed using Systat 12 to test for differences in floral visitation rates between breeding types (male plants versus hermaphroditic plants) before and after Hurricane Wilma, and to determine the effect of *Apis mellifera.*

A median test was used to compare the foraging bout length distributions of visitors to male plants and hermaphroditic plants before and after Hurricane Wilma. A Chi-square test was performed to determine whether the foraging bout length distributions diverged from expected values. The proportional contributions of short and long foraging bouts to the divergence were compared to determine their relative importance.

RESULTS

The number of pollinator species observed visiting white mangrove declined following Hurricane Wilma; 22 insect species were observed visiting white mangrove flowers before the hurricane, but 16 insect species were observed after the hurricane, including four species not observed before the hurricane (Appendix). Most of the species not seen following the hurricane were rare (representing ≤ 5 % of visitors), but two species that were common before the hurricane were either seen very rarely (unknown species in the Calliphoridae; Diptera) or not at all (*Scolia nobilitata*; Hymenoptera) following the hurricane. *Apis mellifera* (Hymenoptera) was common before the hurricane but was the dominant species after the hurricane. Unidentified dipterans (flies) and hymenopterans (wasps and bees) represented approximately 20 % of insect visitors observed before and after the hurricane.

Overall, floral visitation rates to male plants were significantly greater than visitation rates to hermaphrodite plants (Figure 1; df = 1, F-ratio = 4.907, p = 0.027). The effect of honey bees on visitation rate was estimated *a posteriori* because the relative number of honey bees increased dramatically following the hurricane (Appendix). Honey bees significantly increased floral visitation rates to male and hermaphroditic plants (df = 1, F-ratio = 8.380, $p = 0.004$), and the effect was significantly stronger following the hurricane (df = 1, F-ratio = 4.560, $p = 0.034$).

The median foraging bout length was three flowers. The distribution of foraging bouts to male and hermaphroditic plants differed significantly from expected (df = 3, $\chi^2 = 10.2366$, $p < 0.025$). Before the hurricane, there were more short foraging bouts (1-3 flowers per bout) and fewer long foraging bouts (4-38 flowers per bout) than expected to male and hermaphroditic plants. The distribution of foraging bouts to male plants was responsible for 41.8% of the divergence from expected, while the distribution of foraging bouts to hermaphroditic plants was responsible for 28.0% of the divergence. After the hurricane, there were fewer short foraging bouts and more long foraging bouts to male plants than expected (30.1% of the divergence), and the number of short and long foraging bouts to hermaphrodite plants did not differ from expected (0.1% of the divergence).

DISCUSSION

Overall, changes in the pattern of insect foraging behaviors at male plants after Hurricane Wilma were more dramatic than changes in the pattern of foraging behaviors at hermaphroditic plants. Prior to the hurricane, the floral visitation rate to male plants was slightly higher than to hermaphroditic plants, but the difference was not significant (Landry 2005). The floral visitation rate to male plants increased significantly following the hurricane (Figure 1), but the increase was due to a proportional increase in long foraging bouts (Figure 2), mainly by honeybees. Long foraging bouts within male plants increase pollen wastage, which theoretically reduces male fitness (Lloyd 1975, Charlesworth 1984), so males did not incur a fitness advantage due to increased visitation rate. There was no difference in the floral visitation rate to hermaphroditic plants before and after the hurricane, but honey bee visitors made most of the visits after the hurricane (Figure 1), and there was in increase in the proportion of long foraging bouts (Figure 2), which increases the frequency of selfed flowers. Increased selfing may reduce hermaphrodite fitness due to inbreeding depression, but it also reduces the number of ovules available for outcrossing events, thereby increasing competition for pollen from male plants. Since hurricanes may open up new sites for recruitment (Pascarella 1998), reduced reproductive opportunities for male plants immediately following a hurricane could have an overall negative effect on male fitness.

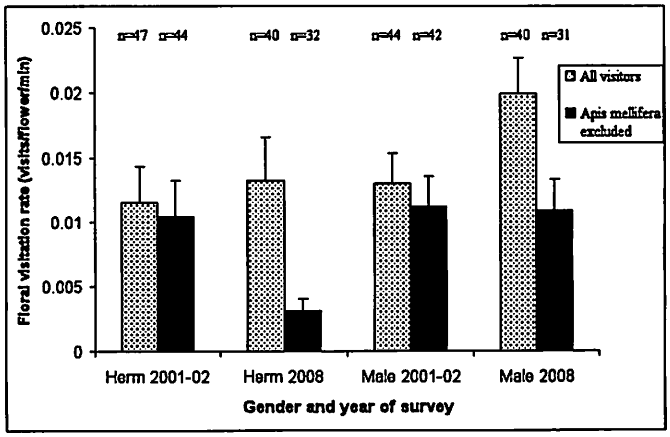

*Figure 1. Floral visitation rates to male and hermaphrodite plants, before (2001-02) and after (2008) Hurricane Wilma, calculated for all visitors and with honey bees (*Apis mellifera*) excluded. n = number of 10-minute watches.*

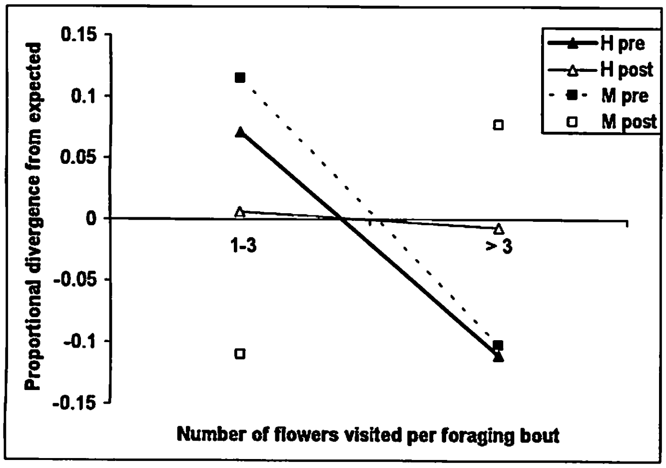

Figure 2. Proportional divergence from the expected number of foraging bouts less than or equal to the median length bout (1-3 flowers) and above the median length bout (> 3 flowers) for hermaphrodite (H) and male (M) plants, before (pre) and after (post) Hurricane Wilma.

The large increase in honey bee visitors to white mangrove following the hurricane was not expected (Appendix), and the reason for the increased number of honey bees is not known. Before the hurricane, honey bees were common visitors to white mangrove (15-20% of visitors); the bees made 0.5-3 times more short foraging bouts to white mangrove plants than long bouts (Table 1). After the hurricane, honey bees were the dominant visitors to white mangrove (56%-63% of all visitors), and made twice as many long foraging bouts as short foraging bouts (Table 1), which theoretically increases the frequency of selfing. However, when the honey bee visits are excluded from the analysis, the pollinator visitation rate to hermaphrodites declined significantly (Figure 1; $p = 0.004$), which means outcrossing opportunities would have declined as well. White mangrove is capable of autogamous pollination (self-pollination without insect visitation), so a decrease in the frequency of insect visitation could result in an increase in selfed flowers. After Hurricane Wilma, many flowers were untouched by insects at the end of each day (Landry personal observations), but the proportion of untouched flowers that self-pollinated is not known. Further, it is not possible to determine whether the frequency of autogamous pollination increased following Hurricane Wilma because the frequency of untouched flowers before the hurricane is not known.

A sustained increase in the number of honey bees could impede the recovery of populations of other insect pollinators following the hurricane (Roubik and Villanueva-Gutierrez 2009). Honey bees efficiently gather floral resources from many different plant species; large quantities of nectar and pollen are necessary to support a honey bee colony, which can weigh five or more kilograms (Buchmann 1996). The honey bees were also observed visiting the flowers of two additional mangrove species at the Hollywood site, black mangrove (*Avicennia germinans* L. [Avicenniaceae]) and buttonwood (*Conocarpus erectus* L. [Combretaceae]). If honey bees outcompete native insect species for the floral resources provided by all three mangrove species, then populations of native insect species may be slow to recover following the hurricane disturbance or may disappear from this mangrove community (Kato and Kawakita 2004, Thomson 2004, Cairns *et al.* 2005). Other plant species in adjacent plant communities may also be affected by short and long term changes in the pollinator community, since many pollinator species are active year-round residents. Continued monitoring of the pollinator community at this site is necessary to determine the long-term effects of Hurricane Wilma on pollinator community composition.

Further, a honey bee-dominated pollinator community could cause a long-term change in the mating system of this white mangrove population. In Florida, honey bees are the dominant floral visitors in most white mangrove populations that lack male plants (i.e. hermaphrodite-only populations. Previous studies in these hermaphrodite-only populations have demonstrated that when large honey bee populations are present, the number of long foraging bouts is increased relative to the number of short foraging bouts (Landry 2005). It is not clear why this occurs; it is possible that the range of foraging bout lengths made by honey bees is only recognized when a large number of honey bees are observed, or it may be that honey bees make longer foraging bouts when they do not encounter other insect species visiting flowers on the same plant. What is clear is that the foraging bout distribution patterns in these hermaphrodite-only populations are more similar to the distribution of foraging bouts to hermaphroditic plants observed at the Hollywood population following Hurricane Wilma than they are to foraging bout distribution patterns at Hollywood prior to Hurricane Wilma. Additional studies are planned to further investigate the effect of honey bees on the mating system of white mangrove.

*Table 1. Number of honey bees (*Apis mellifera*) making short and long foraging bouts (1-3 flowers and >3 flowers, respectively) to male and hermaphrodite white mangrove plants, before (2001-02) and after (2008) Hurricane Wilma.*

Plant Gender	Bout length	# honey bee visitors in 2001-02	# honey bee visitors in 2008
Hermaphrodite	Short	9	16
	Long	3	29
Male	Short	9	24
	Long	6	48

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Appendix. Proportion of visitors of each insect species to hermaphroditic (Herm) and male white mangrove flowers, before (2001-02) and after (2008) Hurricane Wilma. n = number of insect visitors observed.

Insect Family	Insect Species	Herm 2001-02 (n = 59)	Herm 2008 (n = 71)	Male 2001-02 (n = 103)	Male 2008 (n = 129)
Coleoptera	*Euphoria sepulchralis*	---	---	0.04	---
Coleoptera	Unknwn. Coleopteran	---	---	---	0.01
Diptera	*Eristalis albifrons*	---	---	---	0.01
Diptera	*Eristalis sp.*	---	0.01	0.01	0.03
Diptera	*Toxomerus sp.*	---	---	0.02	---
Diptera	*Volucella sp.*	---	---	0.01	---
Diptera	Unknwn. Calliphoridae	0.22	---	0.29	0.02
Diptera	Unknwn. Syrphidae	---	---	0.01	---
Diptera	Unknwn. Dipteran	0.10	0.11	0.06	0.12
Hymenoptera	*Agapostemon sp.*	0.05	0.03	0.02	---
Hymenoptera	*Apis mellifera*	0.20	0.63	0.15	0.56
Hymenoptera	*Augochlora sp.*	0.02	0.04	0.01	---
Hymenoptera	*Euodynerus sp.*	0.03	0.03	0.02	---
Hymenoptera	*Myzinum sp. #1*	0.02	---	0.02	---
Hymenoptera	*Myzinum sp. #2*	---	---	---	0.04
Hymenoptera	*Myzinum sp. #3*	0.03	---	0.03	---
Hymenoptera	*Polistes annularis*	---	---	0.01	---
Hymenoptera	*Polistes exclamans*	0.02	---	---	---
Hymenoptera	*Scolia nobilitata*	0.09	---	0.08	---
Hymenoptera	*Sphex jamaicensis*	0.03	0.03	0.06	0.05
Hymenoptera	*Xylocopa virginica*	---	0.01	---	---
Hymenoptera	Unknwn. Hymenopteran	0.12	0.07	0.13	0.11
Lepidoptera	*Junonia evarete*	0.02	---	---	0.01
Lepidoptera	*Phocides pigmalion*	0.05	0.01	0.03	0.02
Lepidoptera	Unknwn. Pyralidae	---	---	0.01	---
Lepidoptera	Unknwn. Lepidopteran	---	0.01	0.01	0.03