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## WHITE MANGROVE: ARE MALES NECESSARY?

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### ABSTRACT

Based on flower morphology, White Mangrove (*Laguncularia racemosa*: Combretaceae) has been described as being androdioecious, *i.e.* having plants with male flowers only and other plants with hermaphroditic (perfect) flowers only. However, most morphologically-described androdioecious species have been found to be functionally dioecious when pollination tests have been done because the morphologically hermaphroditic plants are shown to have no male function and to function only as females. To test whether White Mangrove is functionally androdioecious, we did experimental pollinations on plants on San Salvador Island, Bahamas.

Our pollination results establish that White Mangrove is functionally androdioecious. Hermaphroditic plants have both male and female function. Also, we found that hermaphroditic flowers can self-pollinate and self-fertilize. These results indicate that not only are male plants nonessential for fruit set, but that outcrossing is not required and insect visitors are unnecessary for fruit set. However, most local populations, but not all, had some males. The proportions of males in different local populations varied from 0 to 0.25. We discuss how males may be maintained in these populations.

### INTRODUCTION

Androdioecy is a very rare mating system comprised of plants with hermaphroditic (perfect) flowers and plants with male flowers in the same breeding population (Darwin, 1877). Most plant species that have been described as androdioecious based on floral morphology have been found to be cryptically dioecious when experimental pollinations are done; the apparently hermaphroditic plants cannot act as males because anthers or pollen are not functional (Charlesworth, 1984). In species that are functionally androdioecious, males contribute genetically to the next generation only through male function (pollen) whereas hermaphrodites can contribute through both male (pollen) and female (ovules) functions. Mathematical models based on Evolutionary Stable Strategies (ESS) show that the maintenance of males in androdioecious species requires males to have at least a two-fold greater fitness than the male function of hermaphrodites in the population (Lloyd, 1975; Charlesworth and Charlesworth 1978; Charlesworth, 1984). This stringent condition required for the invasion of males into a hermaphroditic population has led authors to conclude that androdioecy should be rare or nonexistent (Lloyd, 1975; Charlesworth, 1984).

Androdioecy is a very rare mating system. To date, only six plant species have been experimentally demonstrated to be functionally androdioecious (Table 1). When androdioecy does occur, ESS models predict that the proportion of males in populations will be lower than the 0.50 that is predicted for

Table 1. Plant species experimentally determined to be functionally androdioecious (*i.e.* populations have plants with only male flowers and plants with only hermaphroditic flowers that have both male and female function).

Family	Species	Citation
Sapindaceae	<i>Xerospermum intermedium</i> Radlk	Appanah (1982)
Datisceae	<i>Datisca glomerata</i> (Presl.) Baill.	Liston <i>et al.</i> (1990)
Oleaceae	<i>Phillyrea angustifolia</i> L.	Lepart and Dommee (1992)
Saxifragaceae	<i>Saxifraga cernua</i> L.	Molau and Prentice (1992)
Oleaceae	<i>Fraxinus lanuginosa</i> Koidz.	Ishida and Hiura (1998)
Cucurbitaceae	<i>Schizopepon bryoniaefolius</i> Maxim.	Akimito <i>et al.</i> (1999)

dioecious species (Fisher, 1929; Charlesworth, 1984). The proportion of males in androdioecious species should vary depending upon selfing rates, inbreeding depression, and the relative fitness of males in the populations (Lloyd, 1975; Charlesworth, 1984).

White Mangrove, *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae) is considered to be androdioecious based on floral morphology (Tomlinson, 1980; Rathcke *et al.*, 1996). The sexual type of plants appears to be constant for individual trees from year to year (Tomlinson, 1980), but whether White Mangrove is functionally androdioecious or cryptically dioecious has not been established. The proportion of males has not been reported for any population of White Mangrove.

In this study we test whether White Mangrove on San Salvador Island is functionally androdioecious. We specifically ask if males are necessary for fruit set, *i.e.* do hermaphrodites function only as females, and therefore require male plants, or do hermaphrodites function as both females and males? We did pollination experiments to test whether the pollen from morphologically hermaphroditic plants is functional and can produce fruits. We also tested whether White Mangrove is self-compatible and whether hermaphrodites can self-pollinate and self-fertilize. We counted the number of males

and hermaphrodites and calculated the proportion of males in several local populations.

### The Plant Species

White Mangrove, *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae), is a shrub or tree that grows on the landward edge of the mangrove community. It is widely distributed along coastal areas in the Caribbean, the east and west coasts of Florida and Central America, the eastern coast of South America, and the coast of West Africa (Correll and Correll, 1982). On San Salvador Island White Mangrove grows along the shores of many inland saline lakes (Kass and Stephens, 1990; Smith, 1993). Flowers are small and white and are displayed in branched inflorescences. The male (staminate) flowers have a well-developed style but no ovary so the floral cup is small (0.8 mm in diameter) compared to that of the perfect flower (1.0 mm in diameter) (Tomlinson, 1980, pers. obs.). Flowers of male plants last only one day whereas flowers of hermaphrodites last two days (Rathcke *et al.*, 1996). Sex determination in this species is unknown. On San Salvador Island the major pollinators of White Mangrove are insects, especially wasps, but Bananaquits (*Coereba flaveola*; Emberizidae), a resident nectarivorous bird species, were also seen visiting flowers (Rathcke *et al.*, this volume).

On San Salvador, major flowering of White Mangrove occurs in June-July (Rathcke *et al.*, 1996, pers. obs.), and fruit is mature and ready for dispersal in September-October. White Mangrove is semi-viviparous (cryptoviviparous) because the embryo generally only pierces the seed coat and does not burst through the fruit wall (pericarp) while on the tree (Graham, 1964). The fruits with the germinated seedlings can float and are water dispersed. The seedling emerges rapidly after the fruit becomes stranded (Tomlinson, 1980). Mature fruits are c. 1 cm x 1.5 cm in size (Landry, unpub. data). We have observed seedlings in November-December on San Salvador.

## METHODS

We studied White Mangrove plants growing along the shores of Reckley Hill Pond, Osprey Pond, and Oyster Pond near the Bahamian Field Station on San Salvador Island (see map in Godfrey *et al.* 1994). We (B. Rathcke and L. Kass) conducted studies of White Mangrove during the following research periods: December 23, 1994 to January 2, 1995, April-May 1995 (L. Kass only), June 13-16, 1995, June 9-21, 1997, November 1997 (L. Kass only) and June 15-23, 1999 (with C. Landry).

To determine whether the pollen of hermaphroditic plants is functional, we hand-pollinated flowers in a White Mangrove population at Osprey Pond in June 1997. Inflorescences in bud were bagged with bridal-veil netting and assigned to one of the following four pollination treatments: 1) flowers were hand-pollinated each day with self-pollen (Self-pollen added), 2) flowers were hand-pollinated each day with pollen from two or three other hermaphrodites (Hermaphroditic cross-pollen added), 3) flowers were unmanipulated (i.e. not hand-pollinated) to determine if flowers could self-pollinate and self-fertilize (No hand-pollination) or 4) inflorescences were left exposed for natural pollination (Open-pollinated controls). The peduncle of each hand-pollinated flower was color-coded with a Magic Marker, so fruit set could be followed. Not all buds in the

bagged inflorescences were hand-pollinated as not all had opened before the study was terminated.

Each shrub had all four pollination treatments. However, some inflorescences were eaten (4/31) and other treatments (bags or tags) were destroyed and not recovered, so sample sizes vary. Because flowering was just beginning, nearly all inflorescences having open flowers in the populations were used in the treatments, but sample sizes were small. Pollen from males was very limited and was not used in a pollination treatment.

Initial fruit set of marked flowers was measured at the end of the study on June 20; only flowers with enlarging ovaries were included; however, some abortion may have occurred after this count. Percent initial fruit set was calculated as  $100 \text{ (number of fruit) / (number of flowers pollinated)}$ . Each fruit had only one seed, so fruit set and seed set are equivalent; we have found no developed fruit without a developed seed.

After this fruit census, we enclosed the inflorescences in muslin bags to ensure that the bags with fruit would remain until the mature fruit were counted and collected in November 1997 by L. Kass. At this time the individually color-coded fruit could not be distinguished from other fruit. However, most bagged inflorescences had large numbers of fruit, largely due to self-pollination of flowers that were not manipulated. Therefore, the mature fruit set was analyzed to determine if self-pollinated inflorescences had significantly different fruit set than open-pollinated inflorescences. Percent mature fruit set was calculated as  $100 \times \text{(total fruit set per inflorescence) / (initial bud count per inflorescence)}$ .

We surveyed all the White Mangrove plants in local populations, recorded the number of male and hermaphroditic plants, and calculated the proportion of males in each population. We surveyed populations around three inland ponds (Reckley Hill Pond, Osprey Pond and Oyster Pond), near North Point, along the East Beach Causeway, and at two sites on Pigeon Creek (see map in Godfrey *et al.* 1994, p.

Table 2. Pollination treatments and initial fruit set of White Mangrove, *Laguncularia racemosa*, on San Salvador Island, Bahamas. Flws. = flowers. Herm.=hermaphroditic. Number of plants (buds), Means and Standard Deviations of % Fruit set (fruit/flowers) and the range of % Fruit set (FS) values per inflorescence for each treatment is shown. Pollination treatment is not significant; ANOVA test on arcsine-transformed values, P = 0.30, N = number of plants.

Treatment	N plants (flws.)	% Fruit set
No hand-pollination	3 (30)	30 ± 04.2
Self-pollen added	3 (21)	60 ± 29.1
Herm. cross-pollen added	4 (25)	35 ± 32.0
Open pollinated control	4 (69)	58 ± 29.7

Table 3. Sex ratios in populations of White Mangrove, *Laguncularia racemosa*, on San Salvador Island, Bahamas. Hermaphroditic (herm.) and male plants are shown for different sites. Herm.=hermaphroditic plant. Prop.= proportion in total population (herm. + males). Mean ± SD shown for all sites.

Site	N herms.	N males	Prop. of males
Reckley Hill Pond	67	9	0.12
northwestern shore	20	0	0
southern shore	36	2	0.05
eastern path to Reckley	11	7	0.39
Osprey Pond	6	2	0.25
Oyster Pond	42	12	0.22
North Point	13	0	0
East Beach Causeway	5	0	0
Pigeon Creek Lucayan Site	30	0	0
Pigeon Creek Jetty	21	4	0.16
<b>ALL SITES</b>	<b>251</b>	<b>36</b>	<b>0.12 ± 0.128</b>

15). We found no White Mangrove plants at Crescent, Dilly, Moonrock, or Pain Ponds.

Statistical analysis of fruit set was done using ANOVA in SYSTAT, version 5.01. Percent fruit set data were arcsine transformed to normalize their distributions for statistical testing.

## RESULTS

Initial fruit set was abundant in all pollination treatments, including the no hand-pollination treatment, and pollination treatments were not significantly different (Table 2). Sample sizes were small due to the limited number of flowers available, so the lack of significant differences in fruit between treatments may not hold with larger samples. Mature fruit set was also abundant and was not significantly different for bagged pollination-treatments (pollinators excluded throughout) and control

treatments (exposed to pollinators initially and bagged later for final fruit set measurements) (t-tests on arcsine transformation fruit set data:  $P = 0.79$ ; mean  $\pm$  SD shown; bagged treatments =  $42\% \pm 50$ , range = 0 - 100%,  $N = 10$  plants; open controls =  $47\% \pm 29$ , range = 33-100%,  $N = 5$  plants). Problems caused by low flower availability, small sample size, and destruction of treatment replicates preclude any conclusions about how pollen source affects fruit set, whether inbreeding depression occurs, or whether fruit set is pollination limited (*i.e.* fruit set of naturally-pollinated flowers is lower than that of flowers augmented with outcross pollen). We also discovered that new buds could have formed subsequent to the initial bud counts that we used as the basis for calculating percentage of mature fruit set. Therefore, fruit set values may be high estimates. However, the fruit set values do clearly demonstrate that flowers can self-pollinate and self-fertilize. Experimental pollinations are being done to determine if pollen source affects fruit set (Landry, unpub. data).

In our surveys of different White Mangrove populations, the proportion of males varied from none to 0.25 for different local populations (Table 2). Along the shores of Reckley Hill Pond and Pigeon Creek, males were clumped in local areas (Table 3).

## DISCUSSION

Are males of White Mangrove necessary for reproduction? The answer is "No". Our pollination studies show that hermaphroditic plants have male function as well as female function. These results confirm that White Mangrove is functionally androdioecious. In addition, flowers can self-pollinate and self-fertilize. Self-pollination (autogamy) can occur when the anthers move within a flower and brush the stigmas (L. Kass, pers. obs.). Therefore, pollen from males is not necessary for fruit set in these populations. Pollination studies done on White Mangrove in Florida show the same results; hermaphroditic plants have functional pollen and can self-pollinate and self-fertilize (Landry, *et al.* 1999; Landry, unpub. data). Alternatively, the high fruit set we observed in all

the pollination treatments could reflect apomixis, *i.e.* fruits develop without fertilization. However, mature fruit set ranged from 0-100% between inflorescences, which is not expected for an apomictic system where most flowers produce seed (Harper, 1977).

The proportion of males in different local populations varied from 0 to 0.25. These values are lower than the 0.50 proportion of males predicted for dioecious species (Fisher, 1929; Charlesworth, 1984) and further supports our conclusion that White Mangrove is functionally androdioecious.

The proportion of males in androdioecious species is expected to depend upon selfing rates, inbreeding depression, and other factors affecting the relative fitness of males (Lloyd, 1975; Charlesworth, 1984). High selfing rates will reduce mating opportunities for males and select against males, whereas strong inbreeding depression will reduce the fitness of selfed progeny and favor the maintenance of males (Lloyd, 1975; Charlesworth, 1984; Fritsch and Rieseberg, 1992; Akimoto *et al.*, 1999). Therefore, androdioecious species are expected to have low selfing rates and/or strong inbreeding depression. Contrary to these expectations, our initial results for White Mangrove suggest that selfing rates may be high because flowers can self-pollinate and self-fertilize and because pollinators can be infrequent on San Salvador (Rathcke *et al.*, this volume). In addition, inbreeding depression appears to be weak or absent because fruit set in bagged, self-pollinated treatments was often abundant (Table 2). However, the pollination results from this study do not allow us to determine the degrees of selfing or inbreeding depression, and these need to be determined in further studies. Also, the role of pollinators in determining selfing rates and the relative fertility of males needs to be examined.

Males in androdioecious species may be maintained by other factors that increase the fertility of males relative to the male fertility of hermaphrodites (Lloyd, 1975; Charlesworth, 1984). The relative fertility of males could be increased if resources formerly used for female function are reallocated to male function (Bawa, 1980; Charlesworth, 1984). Males could have

more flowers and pollen and increase their proportionate contribution to the pollen pool (Willson, 1979), or they could have traits that increase pollinator attraction and pollen transfer (Beach and Bawa, 1980). Having more flowers, more pollen, or more nectar may attract relatively more pollinators or increase their effectiveness in transporting pollen to stigmas (Real and Rathcke, 1991; Rathcke, 1992). We are comparing floral traits and pollinator interactions of males and hermaphrodites in White Mangrove (unpub. data). Interactions with pollinators could be an important factor determining the relative fertility of males and the variation in the proportion of males between different populations.

This variation in the proportion of males seen here for different populations on San Salvador Island appears to exhibit the type of pattern predicted by the geographic mosaic of coevolution (Thompson, 1994, 1999). Thompson (1999) predicts that traits will vary between populations of a species because interactions with other species vary in type and intensity and cause different local selection on traits. However, gene flow between these populations can maintain traits (even maladaptive traits) that would not be predicted from studies of local populations. Because the populations of White Mangrove on San Salvador Island are geographically isolated around inland saline ponds, populations could experience different selection regimes due to different pollinator interactions. Even in populations where the maintenance of males is not favored by selection, males could be maintained by gene flow from other populations with males. It is not known whether White Mangrove populations around different inland saline ponds are genetically isolated or not. The ponds do differ in their degree of isolation from each other, which could affect gene flow caused by pollinators or fruit dispersal. Although the fruits are water-dispersed, severe hurricanes could disperse fruits across land (pers. obs.), especially since fruits mature and remain on the trees in September-October, which is the prime hurricane season in this region (Shaklee, 1996). Further studies on San Salvador Island and in Florida will examine how these factors determine the

proportion of males in different populations of this androdioecious species.

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