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THE NATURAL HISTORY OF WHITE MANGROVE, *LANGUNCULARIA RACEMOSA* (COMBRETACEAE): THE FORGOTTEN MANGROVE

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ABSTRACT

White mangrove (*Laguncularia racemosa* (L.) Gaertn. f. [Combretaceae]) is widely distributed throughout the Neotropics and is a major constituent of mangrove forests in the Bahamas and Florida. Here, we review the literature, including our own studies and unpublished data, to note some interesting characteristics that are typically unknown and to more fully document the natural history of this important, but often forgotten, mangrove species.

White mangrove grows on the landward edge of mangrove communities that show zonation. However, in the Bahamas and Florida, white mangrove often grows intermingled with other mangroves, possibly due to small-scale topographical heterogeneity. White mangrove can produce pneumatophores (breathing roots) under certain conditions, which is often overlooked. The glands at the bases of the leaf blades of white mangrove are extra-floral nectaries that attract wasps and ants, not salt glands, as is commonly assumed. Fruits are semi-viviparous, with the seed germinating on the parent plant but remaining within the fruit until after dispersal. Fruits are water-dispersed, so land is usually an effective barrier to dispersal; however, our studies suggest that hurricanes may disperse fruits overland to hypersaline ponds on San Salvador Island. Our pollination studies have established that the breeding system of white mangrove is variable; while some populations of white mangrove are androdioecious, an extremely rare breeding system characterized by both male and hermaphroditic plants, other populations are strictly hermaphroditic (i.e., they lack male plants). Our studies suggest that pollinators may be a key factor in maintaining androdioecy and, in combination with other factors, may contribute to the current distribution of androdioecious and hermaphroditic populations.

INTRODUCTION

White mangrove (*Laguncularia racemosa* (L.) Gaertn. f. [Combretaceae]) is a major constituent of mangrove communities throughout the Neotropics (Correll & Correll, 1982; Tomlinson, 1994). Despite its wide distribution and abundance, the natural history of white mangrove is not well known and accounts are scattered in the literature. Many people assume that "mangrove" means a species that probes its roots into the ocean (like red mangrove, *Rhizophora mangle* L. [Rhizophoraceae]), or maybe a species that grows in the mudflats, puts up "snorkels" (pneumatophores), and secretes salt from its leaves (like black mangrove, *Avicennia germinans* (L.) Stern [Avicenniaceae]). White mangrove is another major mangrove species, but a species that is often not mentioned, distinguished, or studied. Hence, we entitle this, "the forgotten mangrove." Here, we demonstrate that white mangrove has some unique and poorly understood attributes that make it one of the most interesting mangrove species.

In this paper, we summarize the literature on white mangrove and present information, including unpublished data, which we have gathered

during our research in the Bahamas and Florida. We especially note features that are misunderstood or were previously unrecognized. We first discuss the distribution of white mangrove in mangrove communities. We then summarize information on the vegetative and reproductive characteristics of white mangrove. We have demonstrated that some populations of white mangrove are androdioecious, an extremely rare breeding system with male and hermaphroditic plants, whereas other populations are strictly hermaphroditic (i.e., they lack male plants). We document the distribution of androdioecious white mangrove populations in the Bahamas and Florida, and briefly discuss possible factors that may maintain androdioecy in some populations, but not others.

MANGROVE COMMUNITIES

White mangrove is widely distributed throughout the Neotropics and is also found in northwestern Africa. It is one of three true mangrove species in the Bahamas and Florida, where it is a major constituent of mangrove communities (Correll & Correll, 1982; Tomlinson, 1994). The other true mangroves in this region are red mangrove and black mangrove; mangrove communities usually include buttonwood (*Conocarpus erectus* L. [Combretaceae]) as well, a mangrove associate (*sensu* Tomlinson, 1994). Mangrove communities typically hug saltwater coastlines that do not receive heavy wave action. However, in the Bahamas, mangroves are often found along the shores of inland saline ponds and lakes (Kass & Stephens, 1990; Smith, 1993; Lugo, 1994).

Coastal mangrove communities often exhibit zonation when associated with riverine estuaries; each species grows in a "zone" determined by tidal height, water and soil salinities, and soil aeration (Ellison & Farnsworth, 1993; Ricklefs & Latham, 1993). In Floridian riverine estuaries, white mangrove is typically found on the landward edge of the community in mixed stands with buttonwood. Red mangrove is typically found in shallow water or at the water edge in the intertidal zone, while black mangrove typically occupies the region between the red and white mangrove

"zones". The interface between the white and black mangrove "zones" tends to be somewhat indistinct, with mixed stands common (Ricklefs & Latham, 1993; Sherman *et al.*, 2000; pers. obs.). Several researchers have demonstrated that tidal sorting of propagules produces this zonation pattern, with the long red mangrove propagules stranding in deeper water than white and black mangrove propagules, which disperse inland (Rabinowitz, 1978; Jimeniz & Sauter, 1991).

While many of the mangrove communities in mainland Florida exhibit zonation, we have found white mangrove growing in mixed stands with buttonwood, red mangrove, and black mangrove in non-riverine communities in the Bahamas, in the Florida Keys, and on mainland Florida. Lack of clear zonation has been documented in populations around inland hypersaline ponds on San Salvador Island (Kass & Stephens, 1990) and on the coast of Panama (Rabinowitz, 1978). The lack of zonation in these communities may be caused by small-scale topographical heterogeneity (Lugo, 1994), which can cause small-scale differences in salinity, temperature, and tidal influence on specific localities (Lugo & Snedaker, 1974; Kass *et al.*, 1994). The karst limestone substrate common on Bahamian islands creates a complex topography of jagged rock and depressions or craters around the ponds that provide mangroves with access to underground water resources not discernable from the surface (Godfrey *et al.*, 1994; Edwards, 1996; Godfrey and Page, 2005).

On San Salvador Island, Bahamas, mixed mangrove communities surround many inland hypersaline ponds (Kass & Stephens, 1990; Godfrey & Page, 2005). White mangrove is included in some of these communities (those surrounding Reckley Hill, Osprey, and Oyster Ponds; Godfrey *et al.*, 1994; Rathcke & Landry, 2003) but not others (those surrounding Crescent, Pain, and Moonrock Ponds; Rathcke & Landry, 2003). This restricted distribution could be caused by environmental differences between the ponds or by dispersal limitation. White mangrove fruits are water-dispersed, so land is an effective barrier to dispersal (Tomlinson, 1994; see below for additional discussion). The ponds do not have surface connections to one another or to the ocean (Teeter,

1985), so dispersal between ponds should be limited. However, we found a single intact white mangrove fruit at Pain Pond in November, 1999, two months after Hurricane Floyd (Rathcke & Landry, 2003), suggesting that hurricanes can disperse white mangrove fruits overland to isolated inland ponds. Whether dispersal, rather than environmental factors, limits the distribution of white mangrove to these inland hypersaline ponds remains to be determined.

Topographical heterogeneity can also result from human activities and cause mixed mangrove communities. Mosquito impoundments, designed to reduce mosquito populations, are common in lagoons along the Atlantic coastline of central and south Florida. Impoundments consist of long, narrow, parallel dikes with steep banks made of locally-dredged soils, surrounded by slow moving brackish water. Mangrove communities in these areas are not zoned; white, black, and red mangrove and buttonwood are found in mixed stands on the sides and crests of the dikes, although red mangrove is less often seen on the crests (Landry, pers. obs.). The water-dispersed fruits of all four species probably rapidly colonized the strands of the dikes. In contrast, recruitment of mangroves onto the sides and crests of the dikes probably occurred later, when fruits fell from the reproductively mature trees along the strand. White mangrove matures as early as one year of age under greenhouse conditions (Landry, 2005), so recruitment onto the dikes could have occurred within a few years. Mangroves are usually restricted to saline habitats, but the plants do not require salt for growth; they are probably outcompeted by other plants in most non-saline natural habitats. The high salinity of the dredged soil used to construct the dikes may have limited competition by other plants and, therefore, facilitated recruitment of mangroves onto the sides and crests of the dikes.

VEGETATIVE CHARACTERISTICS

White mangrove is a woody shrub or tree with a very open branching architecture. White mangrove trees frequently lose limbs under stressful conditions (Godfrey and Page, 2005). We have

observed that hermaphroditic plants tend to fragment more frequently than male plants, perhaps because the cost of reproduction is higher in hermaphrodites (Willson, 1983), which has implications for the relative fitness of males and male frequency in androdioecious populations.

White mangrove can produce pneumatophores or "breathing roots" (Tomlinson, 1994), which is often not recognized. Pneumatophores are usually associated with black mangrove, perhaps because the production of pneumatophores by white mangrove is sporadic and fairly uncommon in the field. Pneumatophores allow plant respiration to occur despite anaerobic conditions caused by the high water table typically found in mangrove communities. White mangrove does not always produce pneumatophores in dry areas and may not produce them in wet areas either (pers. obs.). However, plants that originated in Coral Gables, Florida, and that were grown under greenhouse conditions at the Matthaei Botanical Gardens (University of Michigan, Ann Arbor, Michigan, U.S.A) commonly produced pneumatophores. These plants were constantly inundated with water, and all plants (N = 87) had at least one root that extended out of the pot and produced pneumatophores every 3-5 cm along its length.

White mangrove is evergreen, but new leaves are produced only during the rainy season (Tomlinson, 1994, 2001). Leaves are opposite, light green and smooth, oblong to obovate in shape, with entire margins. The distal end of the leaf blade is either emarginate (i.e., dimpled) or rounded (Figure 1a). We have observed that trees have a flush of new leaves before flowering begins and appear to produce new leaves so long as the rains continue, as late as November. Trees that were stripped of foliage after Hurricanes Floyd (September 1999, on San Salvador Island, Bahamas) and Jeanne (October 2004, from Sebastian Inlet to Jupiter, central Florida Atlantic coast) were completely leafed out by the end of November in each year.

Leaves possess two large glands near the base of the blade (Figure 1c) (Graham, 1964; Tomlinson, 2001; Kass, 2005) that produce a sweet exudate and function as extra-floral nectaries (Rathcke *et al.*, 1996; Kass, 2005; pers. obs.).

These glands are not salt glands, as is commonly assumed. We have observed ants and wasps visiting the glands on plants in Florida and the Bahamas. Glands on plants grown in the greenhouse at Matthaei Botanical Gardens also produced nectar and attracted ants and wasps (Landry, pers. obs.). Older leaves do not secrete nectar and are not visited by insects; only younger leaves, which are located at the distal ends of branches, have functioning glands. Interestingly, this means that leaves with functioning glands are located where inflorescences form. In addition to attracting mutualistic predators of herbivores, these glands may attract insect pollinators when the plants are not flowering, providing resources and reinforcing their eventual visitation to flowers. Other tiny glands occur on the underside of the leaf blade along the margin (Kass & Stephens, 1990; Tomlinson, 2001), near the junctions of the secondary veins (Figure 1b). While their function is unknown, Kass observed sweet exudate from the tiny glands of young white mangrove leaves (unpubl. data) and has observed ants visiting the glands (pers. obs.), suggesting that they may also function as extrafloral nectaries.

Leaf petioles are usually green, but we have observed red leaf petioles on San Salvador Island (Kass, 2005) and in Florida populations (Landry, pers. obs.). Red petioles may indicate stressful environments, but it remains to be determined whether the red coloration represents environmental or genetic differences. The hypersaline ponds on San Salvador Island have been characterized as an extremely stressful environment due to high salinity, low tidal energy, short or long inundation periods, low soil fertility, and poor growth conditions (Lugo, 1994), and leaf petioles are typically red. We have also observed red petioles on some, but not all, plants in Florida populations, but we have not measured environmental conditions to determine whether or not they are associated with stressful conditions.

Leaves often show severe damage by the time they senesce, and much of this damage appears to be due to insect herbivores. Kass and Rathcke observed mangrove skipper larvae (*Phocides pigmalion*), unidentified tent caterpillar species, and unidentified beetle species feeding on

the leaves on San Salvador Island (pers. obs.). Unidentified tent caterpillar species have also been observed on white mangrove in Florida populations (Landry, pers. obs.).

REPRODUCTIVE CHARACTERISTICS

Breeding and mating systems

Although white mangrove was previously described as "functionally dioecious" (Tomlinson, 1994), we have demonstrated through pollination experiments that some populations of white mangrove are androdioecious (Rathcke *et al.*, 2001b; Landry, 2005), whereas other populations are strictly hermaphroditic (Landry, 2005; Landry & Rathcke, unpubl. data). Androdioecy is a rare breeding system in which male plants and hermaphroditic plants occur together in a population (Darwin, 1888). In white mangrove, hermaphroditic flowers are capable of self-pollination and self-fertilization (Rathcke *et al.*, 2001b; Landry, 2005).

Flowers

Flowers are small, white to greenish-white, and have no obvious fragrance. The size of hermaphroditic flowers from greenhouse plants grown at the Matthaei Botanical Gardens from seeds collected in Florida varied between 3.5-5.0 mm long and 2.5-3.5 mm wide (N = 13 plants) (Landry, 2005). Nearly all of the hermaphroditic flowers are urn-shaped, narrower at the base than at the terminus, and flattened along the axis (except see "feather anther" morph below). Hermaphroditic flowers are sessile and are firmly held on the inflorescence. They have an inferior ovary containing two ovules, a single style and stigma, and ten stamens arranged in two whorls of five (Tomlinson, 2001; Kass, 2005). Hermaphroditic flowers are open for two days: the anthers dehisce in the morning on the first day, and the stigma becomes receptive by morning of the second day (Rathcke *et al.*, 1996; Landry, 2005). If they are not pollinated, the flowers senesce and drop off on the third day.
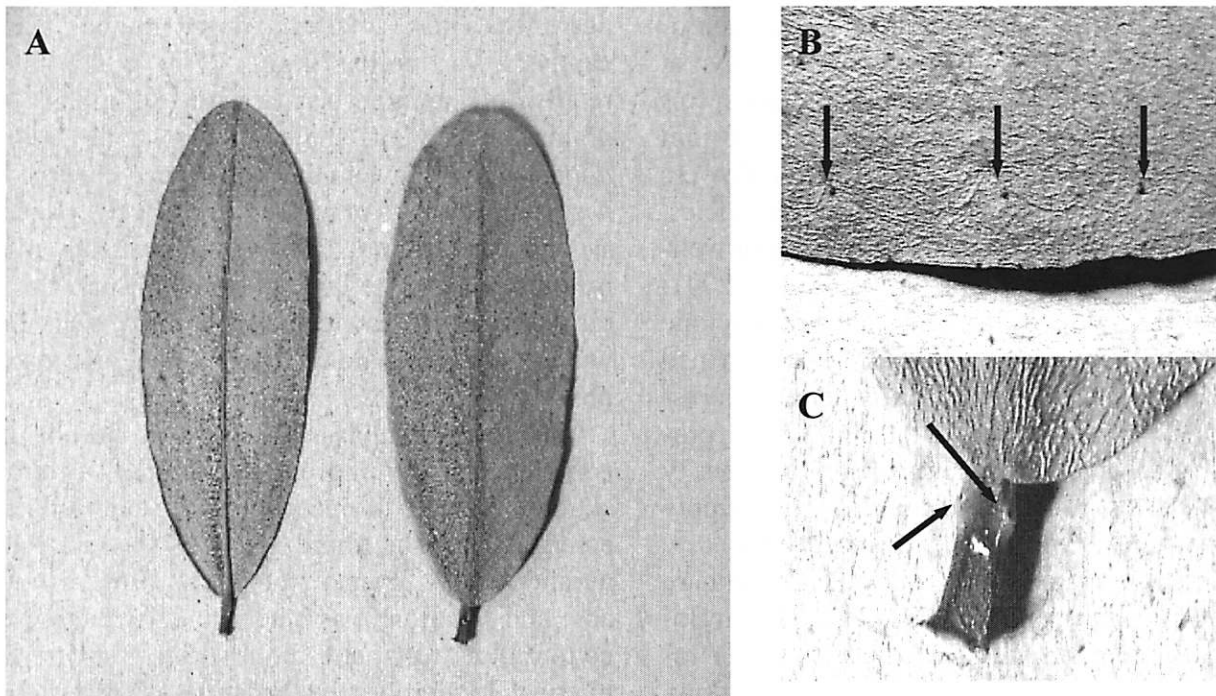
Figure 1. White Mangrove leaves, A) abaxial (bottom, on left) and adaxial (top, on right) views, B) close-up of abaxial leaf margin, with glands (arrows). C) close-up of extra-floral nectaries (arrows) located on the petiole near the base of the blade. Photos by C. L. Landry.

Figure 2. White Mangrove inflorescences (male at left, hermaphrodite in center) and infructescence (right) collected on San Salvador Island, Bahamas. Photo by Lee B. Kass.

Male flowers are smaller than hermaphroditic flowers; the flowers of male plants grown at the Matthaei Botanical Gardens from seeds collected in Florida were 3.5 mm long and 3.0 mm wide (N = 3 plants) (Landry, 2005). Male flowers are cup-shaped and borne on small peduncles. They have two whorls of five stamens and a well-developed style, but no ovary (Tomlinson, 2001; Kass, 2005). Male flowers are open for only one day, and are so weakly held that freshly opened flowers can be easily shaken from the inflorescence (pers. obs.). As the flowering season progresses, it becomes increasingly easy to identify male plants as "male" because of the empty flower stalks of the inflorescences (pers. obs.).

Both hermaphroditic and male flowers are displayed in loose panicles (Figure 2). The inflorescence is indeterminate; the floral stalk (or rachis) continues to extend and branch as the flowering season progresses. Individual branches of an inflorescence are not uniform in size and do not bear equal numbers of flowers, although there is symmetry in branch length and flower number for each pair of branches along the axis of each rachis (Figure 2). Flowers first open at the base of the inflorescence; new flowers develop at the distal ends of the inflorescence throughout the season. Inflorescence branch extension and flower development do not terminate simultaneously for all inflorescences on a tree.

Flowers produce small amounts of nectar, ranging from 0.20-0.40 µl per day (Rathcke *et al.*, 2001a; Rathcke & Landry, unpubl. data). Male and hermaphroditic flowers produce similar amounts of nectar (Rathcke & Landry, unpubl. data). Bees and wasps mostly visit the flowers, but flies and butterflies are also common visitors (Rathcke *et al.*, 2001a; Landry, 2005; Landry *et al.*, 2005). While most insects appear to visit flowers for nectar, bees may also collect pollen.

Pollen production per flower was not significantly different between flowers from male plants (7420 grains/flower) and hermaphroditic plants (5531 grains/flower) plants (Landry, 2005). However, some hemaphroditic plants produce unusually small hermaphroditic flowers that are tubular in shape and the anthers are flattened along the long axis, giving the anthers a featherlike ap-

pearance. These smaller flowers produce significantly fewer pollen grains (769 grains/anther) relative to the large hermaphrodite flowers (7648 grains/flower) and male flowers. The *feather-anther morph* flowers have only been observed on hermaphroditic plants; they are tightly clustered around the terminal ends of the branches of the inflorescences. The larger hermaphroditic flowers (as well as the male flowers) are much more widely separated along the rachis (Landry, pers. obs.).

These feather-anther flowers do not open completely; the receptive stigma protrudes slightly beyond the petals but the anthers never emerge from the floral cup. While reduced in number, pollen grains from these flowers are viable and functional, as determined by lactophenol cotton blue tests and pollination tests, respectively. The reproductive function of these flowers is not understood. The flowers may be functionally female, capable of receiving pollen from outside sources because the stigma protrudes from the floral cup, but incapable of donating pollen due to the severe reduction in pollen grain number and the partially-closed condition of the flowers. Alternatively, the flowers may be functional selfers, providing hermaphrodites with some degree of reproductive assurance as the flowering season ends because hermaphroditic flowers are capable of self-pollination and self-fertilization (Rathcke *et al.*, 2001b; Landry, 2005). The morphology of these flowers suggests that they would be good selfers, if selfing occurs via the mechanism proposed by Kass (unpubl. data). Unopened petals would push the anthers closer to the center of the flower, and as the filaments lengthened, the dehiscent anthers would be forced against the sides of the stigma with greater frequency than they do in the larger, more open, hermaphroditic flowers. The low pollen production also suggests selfing. Cruden (1977) found that pollen production is lower in species that self than in species that are outcrossing.

Flowering phenology

The flowering phenology of white mangrove is seasonal and varies between geographical

areas and years. In the Bahamas, Correll and Correll (1982) reported that white mangrove flowers "throughout the year." Our observations of plants on San Salvador Island support this statement. Kass has seen white mangrove flowering on San Salvador Island during April and has also observed well-developed fruits on plants at Fresh Lake in June, which indicates that the plants in this population flowered in the previous 2-4 months. We have also observed flowering in other populations during November, December, January, April, and June on San Salvador Island (Rathcke *et al.*, 1996, pers. obs.). Flowering was observed on the other Bahamian Islands included in our studies (Great and Little Abaco, Eleuthera, New Providence, North Andros, Cat Island, and Great and Little Exuma) in either June or July (Rathcke & Kass, pers. obs.), but no published data are available on the variation in flowering phenologies on other islands.

In Florida, Tomlinson (2001) reported that flowering begins in April and continues throughout the early summer. Landry has observed that peak flowering in Florida occurs during June and July, although male plants in south Florida have been observed flowering in late August and early September. In general, male plants appear to flower earlier in the season than hermaphroditic plants. However, the difference in the flowering phenologies of male and hermaphroditic plants has not been quantified.

Rain appears to be necessary for flowering in white mangrove and may explain the different flowering patterns that have been observed. This is exemplified by the following phenology from Florida during an unusually severe drought that occurred at the beginning of the 1998 rainy season (Landry, pers. obs.). According to the United States National Oceanic and Atmospheric Administration's archives (1998), much of the state received <60% of the average rainfall that year, and most of the rain came after July 1. At Coral Gables, in mid-June, only a few plants with small inflorescences were flowering (Landry, pers. obs.). However, when we returned in early September, most hermaphroditic plants produced large fruit crops and most male plants still had a few flowers born on long, otherwise empty flower

stalks, which suggests that all the plants had flowered profusely during the interim, after the rains began (Landry, pers. obs.).

Fruit characteristics

White mangrove is semi-viviparous, which means that the seed germinates and seedling development begins within the fruit while it is still attached to the maternal plant, but the seedling does not emerge from the fruit until it has been dispersed. Precisely when seed germination occurs is not known; we have found seedlings in all the intact fruits we have dissected, regardless of the size of the fruit (Landry, pers. obs.). Fruits are almond-shaped drupes lined with aerenchymatous tissues ("airy cells", dead at functional maturity) that provide buoyancy for the water-dispersed fruits (Ridley, 1930; Correll & Correll, 1982; Tomlinson, 2001; Kass, 2005). Each fruit contains a single seedling, located in the central axis of the fruit; pre-emergent seedling size is positively correlated with fruit size. Kass and Rathcke bagged inflorescences in mid-June 1997 and returned to collect fruits (N = 279) in early November of that year. Kass found that these fruits varied in size, from 5.5-23 mm in length and 3-10 mm in width (unpubl. data).

Fruit dispersal and recruitment

Fruits are water-dispersed, floating in the ocean or estuary until they land on a suitable substrate (Ridley, 1930; Tomlinson, 1994). Because they are semi-viviparous, the seedlings quickly emerge from the fruits after grounding (Tomlinson, 1994; Tomlinson, 2001; Kass, 2005). Fruits are mature 2-3 months after pollination, so flowers produced in June and July develop into mature fruits by September or October, when the probability of hurricanes is highest. Because fruits are water dispersed, hurricanes may be important in long-distance dispersal and could even disperse fruits overland to hypersaline ponds (Rathcke & Landry, 2003). Fruiting is often abundant, and seedlings often form dense mats if suitable open substrate is available. Fruits appear to be dispersed all at once, regardless of when the flowers

were pollinated (Landry, pers. obs.). In 2004, large numbers of fruits were observed on the trees in south Florida at the end of November; a few fruits were observed on the ground and floating in the water at that time, but no seedlings were observed (Landry, pers. obs.).

Because fruits continue to grow as long as they are attached to the maternal plant, fruits derived from flowers pollinated in June are larger than those derived from flowers pollinated in July or August. This difference in fruit size has implications for the maintenance of male plants in androdioecious populations. If seedling size is positively correlated with successful recruitment, then early flowers may contribute disproportionately to the seedling cohort. Male plants appear to flower earlier than hermaphroditic plants, so they have proportionally more flowers early in the season. This means that male plants could incur a fitness advantage because the pollen from male plants could fertilize proportionally more ovules early in the season, resulting in larger fruits (and seedlings) that can significantly increase seedling recruitment. In addition, if hurricanes occur early in the season, fruits (and seedlings) developing from early flowers would be more mature than those developing from later flowers, which would promote a higher frequency of male plants in cohorts during hurricane years.

DISTRIBUTION OF ANDRODIOECY

In extensive population surveys of white mangrove, we have found that some populations of white mangrove are androdioecious, whereas other populations are strictly hermaphroditic. In the Bahamas, we have found androdioecy only on San Salvador Island after surveys of nine islands (Great and Little Abaco, Eleuthera, New Providence, North Andros, Cat Island, San Salvador Island, and Great and Little Exuma). In Florida, all the east coast populations north of 26° 30' N latitude are hermaphroditic, whereas the southern populations are mostly androdioecious. On the west coast, androdioecious populations extend to 28° 00' N latitude, but male frequencies decrease rapidly from 34% to 1% with increasing latitude (unpubl. data). Rathcke has also determined

through pollination studies that androdioecious populations of white mangrove exist on the Pacific coast of Mexico (unpubl. data).

A number of factors in combination may explain the distribution of androdioecy in white mangrove. A mathematical model constructed by Landry (2005) demonstrates that pollinator behavior could affect the maintenance of males and male frequencies. In androdioecious populations in southern Florida, the most abundant pollinators are small bees and wasps that move between plants frequently and promote outcrossing, which increases the mating opportunities for male plants. In contrast, most pollinators in the strictly hermaphroditic populations in northern Florida are large bees and wasps that tend to move within a plant and promote selfing (Landry, 2005). The combination of pollinator foraging patterns and relative visitation rates, interacting with other factors that may increase male fitness such as inbreeding depression, pollen production, or longevity, may be important in maintaining androdioecious populations. Dispersal could also affect the distribution of androdioecy. Future phylogeographic studies of white mangrove throughout its geographical distribution will be essential for understanding the evolution and distribution of this rare breeding system in white mangrove.

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