



Wind pollination and propagule formation in *Rhizophora mangle* L. (Rhizophoraceae): resource or pollination limitation?

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Manuscript received on April 23, 2012; accepted for publication on April 3, 2013

ABSTRACT

Rhizophora mangle is considered as a self-compatible mangrove, and is pollinated by wind and insects. However, there is no information about fruit production by autogamy and agamospermy and on the foraging behavior of its flower visitors. Hence, the present study analyzed the pollination and reproductive systems of *R. mangle* in a mangrove community in northern Pernambuco, Brazil. Floral morphology, sequence of anthesis, and behavior of flower visitors were described; the proportion of flowers that resulted in mature propagules was also recorded. Autogamy, agamospermy, and wind pollination tests were performed, and a new anemophily index is proposed. The flowers of *R. mangle* are hermaphrodite, protandric, and have high P/O rate. Flies were observed on flowers only during the male phase, probably feeding on mites that consume pollen. *Rhizophora mangle* is not agamospermic and its fruit production rate by spontaneous self-pollination is low (2.56%) compared to wind pollination (19.44%). The anemophily index was high 0.98, and thus it was considered as a good indicator. Only 13.79% of the flowers formed mature propagules. The early stages of fruit development are the most critical and susceptible to predation. *Rhizophora mangle* is, therefore, exclusively anemophilous in the study area and the propagule dispersal seems to be limited by herbivory.

Key words: anemophily index, autogamy, entomophily, mangrove, red mangrove.

INTRODUCTION

Mangrove species occur in tropical coastal regions, occupying intertidal zones and estuarine margins (Tomlinson 1994). True mangroves live exclusively in the ecosystem known as mangal, and they comprise approximately 55 plant species of 20 genera and 16 families (Tomlinson 1994, Hogarth 2007). These species form dense forests, sometimes monospecific, which play an important role in soil

stabilization and primary production, increasing the productivity of nearby communities (Grasso and Tognella 1995, Mantovani 2002, Hogarth 2007).

Mangroves are heavily used by humans for timber, tannin, and bioactive compounds, as well as for silviculture and ecotourism (Grasso and Tognella 1995, Ellison 2000, Hogarth 2007). Hence, this ecosystem has been devastated at a rate higher than 1.5% per year (Ellison 2000). For projects of restoration and sustainable use of mangroves, knowledge about plant-animal

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interactions, population physiology and biology, as well as pollination and reproductive system are needed (Endress 1994, Kearns and Inouye 1997, Kearns et al. 1998, Ellison 2000).

The family Rhizophoraceae, which dominates mangroves all over the world, encompasses 16 genera and approximately 150 species with pantropical distribution, not exclusive to mangroves (Hogarth 2007, Souza and Lorenzi 2008). The tribe Rhizophorae is composed of four genera endemic to mangroves, *Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*, which have as a peculiar characteristic vivipary, i.e., the seedling remains attached to the mother-plant during its development (Tomlinson 1994). *Rhizophora* is the single genus of this tribe that occurs in the western center of mangrove diversity, which comprises the western coast of Africa, the eastern and western coasts of South and Central America, and southern Florida (Tomlinson 1994). In the eastern diversity center, which comprises eastern Africa, southern and southeastern Asia, and northern Oceania, all four genera of the tribe Rhizophorae are found. In Brazil, only three *Rhizophora* species occur, *Rhizophora harrisonii*, *R. mangle*, and *R. racemosa*. *Rhizophora mangle* is broadly distributed, occurring all along the coast, and the other two species have their distribution restricted to northern region (Tomlinson 1994).

There is a wide variety of pollination mechanisms in the family Rhizophoraceae, but *Rhizophora* is considered as mainly anemophilous (Tomlinson et al. 1979). However, there are sporadic records of flower visitors, such as bees, butterflies, and birds, in some species of the genus (Tomlinson et al. 1979). However, the role of these animals in the pollination of *Rhizophora* species has not been determined yet. Although in a *R. mangle* population in northern Brazil the insects observed on flowers were considered as secondary pollinators (Menezes et al. 1997), there is no description of these insects' behavior on flowers that classifies them as pollinators or robbers.

Regarding the reproductive system of *Rhizophora mangle*, self-compatibility has been already recorded, and self-pollination is considered as the main pollination mechanism (Menezes et al. 1997). However, there is no information about the occurrence of agamospermy and the possibility of fruit production by spontaneous self-pollination in *R. mangle*; this information would lead us to a better understanding of the reproductive system of the species. In addition, few studies recorded the proportion of flower buds that become mature propagules and in which phase of their development they are more vulnerable, which are important steps for the process of recruitment and maintenance of mangrove communities (Duke et al. 1984, Coupland et al. 2006). Hence, the present study aimed at answering the following questions: 1) How does the sequence of anthesis occur in *R. mangle*?; 2) Which are the flower visitors of *R. mangle* and what is their role in pollination?; 3) What is the importance of wind for fruit production in *R. mangle*?; and 4) What is the rate of fruit and propagule production in *R. mangle*?

MATERIALS AND METHODS

STUDY SITE AND SPECIES STUDIED

Field observations were carried out in a mangrove area in Goiana, northern coast of Pernambuco, northeastern Brazil (7°40'39.8"S and 34°50'21.8"W). The region exhibits a rainy season from February to August and a dry season from September to January, characterized by monthly rainfall below 100 mm (data provided by Instituto de Tecnologia de Pernambuco – ITEP). The average annual rainfall is 2,053 mm, the average maximum temperature is 29.9°C, and the average minimum temperature is 21.9°C (ITEP).

Rhizophora mangle usually occurs in areas close to the sea or in river margins (Tomlinson 1994, Hogarth 2007). It is a dominant species in the study area, occurring also in the mangrove-‘terra firme’ ecotone, with an average density of

0.6 individuals.m⁻² (T.L. Nadia, unpublished data). Flowering and fruiting occur throughout the year, with both phenophases having their peaks in the rainy season (Nadia et al. 2012).

FLORAL BIOLOGY

Pre-anthesis buds (n = 20) and flowers (n = 20) of ten individuals were collected and fixed in 70% ethanol for the analysis of floral morphology in the laboratory under a stereomicroscope. The length of flower parts (sepals, petals, stamens, and gynoecium) was measured with a millimeter ruler on 18 fixed flowers. The number of pollen grains per flower was estimated for ten young flower buds of ten different individuals in a Neubauer chamber (Maêda 1985). The number of ovules was counted in the same ten flower buds, and the pollen-ovule rate was calculated (Cruden 1977). Pollen viability was observed using the cytoplasmic staining technique with aceto carmine (Radford et al. 1974); approximately 2,000 pollen grains per anther were randomly counted in ten pre-anthesis buds of ten different individuals.

Duration and sequence of anthesis were monitored in 30 previously marked flowers of different individuals. Flower opening was considered as the largest distance between sepals, and was measured with a millimeter ruler at each day of anthesis on the same flowers. Stigma receptivity was tested through cross-pollination in 40 flowers, which were previously covered with semi-impermeable paper bags, at different days of anthesis (n = 10 flowers for day of anthesis). These flowers were collected 4 h after undergoing cross-pollination and fixed in FAA in 70% ethanol for posterior analysis of the germination of the pollen tube and its stigmas (Martin 1959, Dafni et al. 2005).

POLLINATION SYSTEM

Flower visitors were recorded through direct observation in the field on five focal individuals, summing up 192 h of observation. Each visitor's behavior was analyzed in terms of the floral resource sought and

the contact with the reproductive whorls. Animals were collected for identification by specialists and were posteriorly deposited in the entomological collection of the Laboratory of Floral and Reproductive Biology of the Universidade Federal de Pernambuco. To test for the role of wind in the pollination of *R. mangle*, young flower buds (n = 36) of different individuals were used, which were covered with knitted fabric with mesh size of 1.6 mm, allowing the passage of pollen carried by the wind and hindering the access of flower visitors to inflorescences and flowers.

REPRODUCTIVE SYSTEM

Flowers (n = 116) of 23 individuals were marked to observe fruit production under natural conditions (control). The fruits formed in this treatment were followed monthly until the development and dispersal of propagules. The survival rate at each stage of development (anthesis, ovary in development, fruit, and propagule) was calculated as follows:

$$S = \frac{n_i}{N} \times 100, \text{ where:}$$

S = survival rate (%)

N = number of survivors at stage i

n_i = number of survivors at stage i+1

Young buds (n = 36) were emasculated and covered with semi-permeable paper bags to test for fruit production by agamospermy. Other buds (n = 39) were covered to test for fruit production by spontaneous self-pollination. In all treatments 23 individuals were used. To test for differences among reproductive system treatments and fruit production by wind pollination, a chi-square test (χ^2) was performed in the statistical package BioEstat 5.0 (Ayres et al. 2007).

A new anemophily index was proposed based on the ratio between the proportion of fruits formed in the treatment of wind pollination (animal exclusion) and the proportion of fruits formed under natural conditions. The value of this new index varies from

0 to 1; 0 (zero) indicates that the wind does not act as a pollinator agent and 1 (one) indicates that the wind acts strongly or exclusively as a pollen vector.

RESULTS

FLORAL BIOLOGY AND FLOWER VISITORS

The flowers of *R. mangle* are pendulous and arranged in axillary dichasial inflorescences, with usually four flowers per inflorescence (Fig. 1A). The calyx consists of four yellow coriaceous sepals and the corolla consists of four white membranaceous petals, alternate with the sepals, exhibiting several trichomes (Fig. 1B and C). Sepals and petals are free. Data on floral morphometry are presented in Table I. The androecium consists of eight sessile stamens with rimose anthers; four opposed to the petals and four opposed to the sepals (Fig. 1B). In the flower bud, two groups of stamens remain enclosed in the petals. The average number of pollen grains per flower was $413,000 \pm 131,593$, with a viability of 97.47%. The gynoecium exhibits inferior ovary with two carpels fused, two loculi and four ovules (two per loculus); pollen-ovule rate was on average $103,250 \pm 32,898$.



Fig. 1 - *Rhizophora mangle* L. (Rhizophoraceae) in Goiana, northern coast of Pernambuco, Brazil. **A.** Cymose inflorescence of the type dichasium; **B.** Flower at male phase on the first day of anthesis; **C.** Flower at the male phase on the second day of anthesis; **D.** Flower at female phase on the third day of anthesis. Bar = 10 mm.

Anthesis lasts approximately four days, starting usually at 5 p.m., but some flowers open at other times of the day. Anther dehiscence occurs already in the pre-anthesis bud; some pollen grains are attached to the trichomes of the petals (Fig. 2), but most pollen grains remain in the anthers (Table I). On the first day of anthesis, the sepals remain close to each other, with an average opening of 13 ± 2.7 mm; the petals become deflexed facing the exterior of the calyx and the stamens become erect (Fig. 1B). On the second day of anthesis (Fig. 1C), the calyx opening increases, measuring on average 18 ± 1.6 mm, the petals follow the opening of the sepals and the anthers fall, releasing a cloud of pollen. On these first two days of anthesis the stigma is not receptive (Fig. 3A and B). On the third day, the calyx reaches its greatest opening, on average 21 ± 1.3 mm; the petals become senescent (Fig. 1D) and the stigma is receptive, remaining so until the fourth day (Fig. 3C and D). On the second and third days of anthesis, there is evidence of nectar production: a shiny liquid was observed on the base of the gynoecium, but the quantity produced was not measurable.

TABLE I

Characteristics of the flowers of *Rhizophora mangle* (Rhizophoraceae) in the northern coast of Pernambuco, Brazil. ¹Anthers removed from young buds; ²anthers removed from pre-anthesis buds; ³height of the stigma.

Floral characters	Number	Length (mm)
Calyx (sepals)	4	12
Corolla (petals)	4	10
Androecium (stamens)	8	6
Pollen per anther:		
Closed Anther ¹	$48,555 \pm 19,414$	-
Opened Anther ²	$32,971 \pm 11,452$	-
Pollen per flower	$413,000 \pm 131,593$	-
Gynoecium (carpel/ovule)	2/4	4.5^3
Pollen/ovule ratio	$103,250 \pm 32,898$	-
Pollen viability	97.47%	-

During the entire male phase of the flower, on the first and second days of anthesis, a high number of mites were recorded, probably feeding on pollen grains. Some fly species of the family

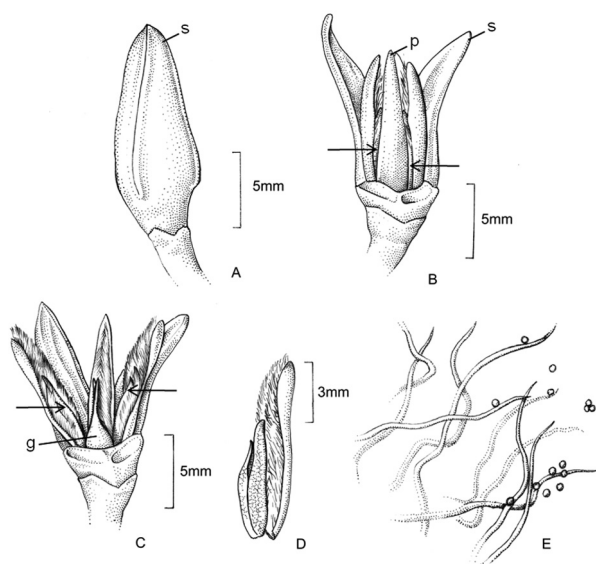


Fig. 2 - Arrangement of floral whorls and deposit of pollen grains on trichomes of the petals of pre-anthesis buds of *Rhizophora mangle* L. (Rhizophoraceae), in Goiana, Pernambuco, Brazil. **A.** Pre-anthesis bud. **B-C.** Arrangement of petals and stamens, evidencing the whorl of stamens (arrows) alternate with the petals (B), and the whorl of stamens (arrows) opposed to the petals, involved by trichomes (C). **D.** Anther dehiscence. **E.** Diagram of pollen grains attached to the trichomes of the petals. s = sepal; p = petal; g = gynoecium.

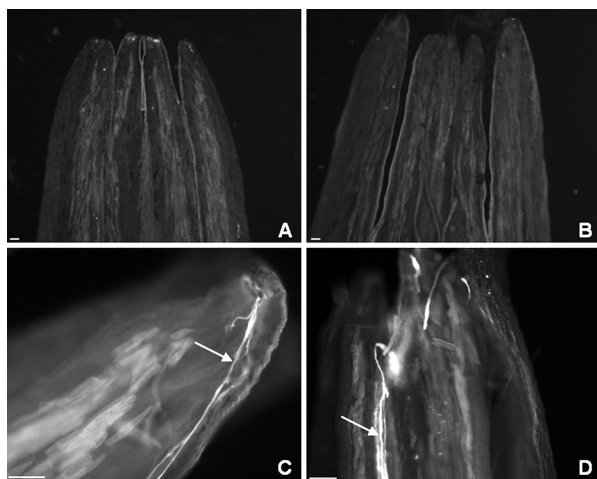


Fig. 3 - Stigma receptivity in flowers of *Rhizophora mangle* L. (Rhizophoraceae) on the first (A), second (B), third (C) and fourth (D) days of anthesis, showing pollen tubes (arrows) germinating only on the third and fourth days. Bar = 0.1 mm.

Sarcophagidae visited the flowers of *R. mangle* also only on the first and second days of anthesis (during the male phase), and no visit was recorded during

the female phase. During their visits, these flies could be feeding on mites present on the flowers or on nectar. A single bee species, *Trigona* sp., was observed collecting pollen on the anthers of the flowers of *R. mangle* on the first day of anthesis. This bee, though, was recorded only once during the whole period of observation.

REPRODUCTIVE SYSTEM

Rhizophora mangle does not form fruits by agamospermy (Table II). The reproductive success by spontaneous self-pollination was lower than under natural conditions (Table II). Natural fruit production resulted in a reproductive success similar to that of wind pollination, around 19% (Table II), reaching a value of 0.98 for the anemophily index. Each fruit develops only one or rarely two seedlings and all fruits observed in the experiment of natural pollination developed only one propagule. Considering the number of flowers and the final number of propagules that were dispersed, the reproductive success was 13.79% (Table II).

TABLE II

Results of wind pollination and reproductive system treatments of *Rhizophora mangle* (Rhizophoraceae), in a mangrove area in Goiana, Pernambuco, Brazil. Superscript letters indicate significant statistic differences ($\chi^2 = 4.52$, d.f. = 1. $p < 0.05$; $\chi^2 = 5.28$, d.f. = 1, $p < 0.05$).

Treatments	Flowers	Fruits	Success (%)	Propagule	Success (%)
Wind pollination	36	7	19.44 ^a	-	-
Spontaneous self-pollination	39	1	2.56 ^b	-	-
Agamospermy	36	0	0	-	-
Control	116	23	19.83 ^a	16	13.79 ^a

The gynoecium of *R. mangle* in the month following the beginning of anthesis was still underdeveloped; fruits under development were observed from the second month on. The two first months of fruit development after anthesis exhibited the lowest survival rates, between 40

and 50%, whereas in the following stages until the propagule dispersal the survival rate was over 90% (Fig. 4). The seedling came out of the fruit, characterizing the propagule, in the fifth month of development, and its dispersal occurred from the ninth to the eleventh month (Fig. 4).

DISCUSSION

The floral traits of *R. mangle*, such as tetramerous, diplostemonous flowers and bilocular, inferior ovary with two ovules per locus, are typical of the genus (Tomlinson et al. 1979, Tomlinson 1994). Pendulous flowers, with high pollen/ovule rate (P/O), low quantity of ovules per flower, and development of a single seed per fruit are attributes that characterize the species as anemophilous (Endress 1994, Proctor et al. 1996). The P/O rate of *R. mangle* is much higher than the rates measured by Cruden (2000) for some anemophilous species, though it is the lowest P/O rate recorded so far for species of *Rhizophora* (Tomlinson et al. 1979). A low P/O rate in plants pollinated by the wind, without compromising the reproductive success, can be associated with the low number of flowers

per inflorescence, low stigmatic surface, and short duration of stigma receptivity (Cruden 2000). *R. mangle* seems to follow the same pattern in the present study, but there is no information about other species of the genus to allow comparisons.

Rhizophora mangle exhibited other characteristics that diverge from the pattern of wind-pollinated species, such as non-reduced perianth and bilobate, simple stigma, without many branches and little conspicuity. Some studies suggest that these characteristics are vestiges of an entomophilous ancestral, and that anemophily in *Rhizophora* is a derivative character (Juncosa and Tomlinson 1987, Tomlinson et al. 1979). According to the phylogenetic tree of Rhizophoraceae proposed by Schwarzbach and Ricklefs (2000), the genus *Rhizophora* is at a more terminal position, being a sister-group of the clade composed of *Ceriops* and *Kandelia*, whereas the genus *Bruguiera* is at a more basal position within the tribe Rhizophoreae, which is monophyletic, well-supported, and composed of all the mangrove species of the family. Taking into account that most *Bruguiera* species are pollinated by birds (Tomlinson et al.

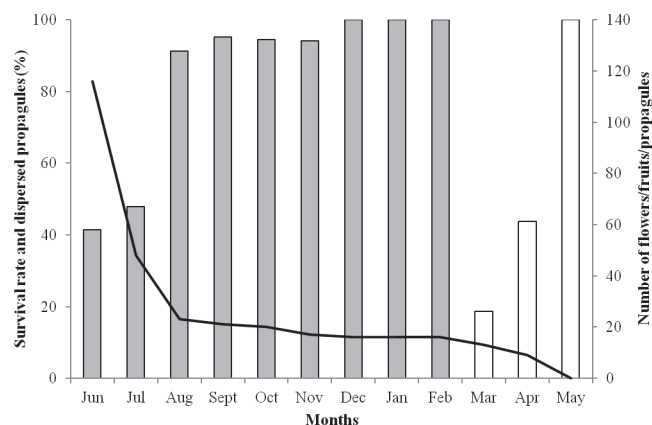


Fig. 4 - Survival rate and percentage of propagules of *Rhizophora mangle* (Rhizophoraceae) in dispersal in a mangrove area of Goiana, Pernambuco, Brazil. The month of June corresponds to the stage of anthesis, July to the stage of the ovary under development, September and October to the stage of the fruit, and from November on to the propagule. — Number of flowers, fruits and propagules; ■ survival rate; □ percentage of dispersed propagules.

1979, Kondo et al. 1987, Noske 1993), except for *B. parviflora*, which is pollinated by insects (Tomlinson et al. 1979), and that there are only records of pollination by insects for species of *Ceriops* and *Kandelia* (Tomlinson et al. 1979, Sun et al. 1998, Coupland et al. 2006), and by wind or wind and insects for *Rhizophora* (Tomlinson et al. 1979, Kondo et al. 1987, Lemus-Jiménez and Ramírez 2003, Coupland et al. 2006), the phylogeny proposed by Schwarzbach and Ricklefs (2000) suggests that pollination by wind is indeed a derivative character. However, information about the pollination biology of mangrove species within Rhizophoraceae and other species of the family, as well as of their external group, is still scarce and inconclusive.

The sequence of anthesis exhibited by *R. mangle* characterizes protandry, and it is considered as an adaptive character that favors cross-pollination (Lloyd and Webb 1986). The opening of anthers during the bud phase and the deposit of pollen grains on the trichomes of petals is common to all mangrove species of the family Rhizophoraceae (tribo Rhizophorae), and is considered as a synapomorphy of the family (Judd et al. 2008). The smaller calyx opening during the male phase and the trichomes on the petals provide the pollen grains better protection, hindering dispersal under unfavorable conditions (with little wind). The larger calyx opening during the female phase and the senescence of petals and stamens increase stigma exposition to receive pollen. Hence, temporal separation of the sexual phases in *R. mangle* seems to be total on a same flower, but fruit production by spontaneous self-pollination may indicate that possibly there is an overlap between the two phases at some time, characterizing partial protandry (*sensu* Lloyd and Webb 1986).

The set of floral traits of *R. mangle*, both morphological and functional, raises some questions. How did the evolution of wind pollination occur in *Rhizophora*? It is likely that

wind pollination has evolved in lineages with small, inconspicuous and unisexual flowers (Friedman and Barrett 2008), and was also favored by protogyny (Sargent and Otto 2004). Since *R. mangle* exhibits different characteristics (medium to large flowers, showy, hermaphrodite and protandric) these hypothesis may be rejected. Pollen limitation by competition may also lead to the development of wind pollination from a lineage pollinated by animals (Friedman and Barret 2008). However, not only western mangrove communities consist of few species (Tomlinson 1994), but also the flowering peak of the community studied differs from the flowering peak of other local mangrove species (Nadia et al. 2012), minimizing the competition for pollinators. It is possible that the high density of individuals of *R. mangle*, as occurs in the study area, may have favored wind pollination. The genus *Rhizophora* is usually very abundant in the mangroves where it occurs (Tomlinson et al. 1979), and, in general, low richness and high quantity of individuals of a dominant species, as occurs in mangrove communities, favor the development of anemophilous species (Endress 1994, Proctor et al. 1996). However, to answer these questions, information as presented in this study for other species of *Rhizophora*, as well as for other genera of the family, is needed, in order to be used in future evolutionary analyses.

Despite constant visits of Sarcophagidae flies, their behavior does not allow classifying them as pollinators, since they were on the flowers only during the male phase. *Trigona* sp. (Apidae) can be considered as a pollen robber, because it collected grains from anthers without pollinating the flowers. Flies cannot be considered as robbers because apparently they did not collect any floral resource, but only fed on the mites that robbed pollen on flowers. Hence, we can consider flies' visits as beneficial for *R. mangle*, since these insects removed pollen grains predators. Bees and flies on flowers of *R. mangle* have already been

recorded in other localities and were classified as pollinators (Tomlinson et al. 1979, Menezes et al. 1997, Lemus-Jiménez and Ramírez 2003), though no study described the behavior of flower visitors associated with the process of anthesis. Probably, also in these localities, these insects are indeed not acting as pollinators.

The fruit production rate of *R. mangle* under natural conditions in the northern coast of Pernambuco was significantly higher than that observed by Menezes et al. (1997) in the state of Pará, also in Brazil, in which the reproductive success was 0.64% ($\chi^2 = 67.17$; d.f. = 1; $p < 0.001$). In Pará, mangroves are dominated by *Avicennia*, and *Rhizophora mangle* is less common (Schaeffer-Novelli et al. 2000). Wind pollination efficiency is related to the large number of individuals close to each other, making the species dominant in the community as already mentioned (Endress 1994, Proctor et al. 1996). This is probably the explanation for the difference in reproductive success of *R. mangle* between the northern and northeastern regions of Brazil.

The early stages of fruit development in *R. mangle* may be considered as the most critical and vulnerable, as they have the lowest survival rates. The low survival rate in the first month after anthesis may be related to pollination limitation, whereas in the second month it may be related to resource limitation for the mother-plant, since propagule development has high costs (Coupland et al. 2006). Similar results were found in other species of Rhizophoraceae, such as *Ceriops australis* and *Rhizophora stylosa*, in a community in Australia (Coupland et al. 2006). In addition to resource limitation, the low survival rate may be also related to predation of propagules observed in some species of Rhizophoraceae (including *R. mangle*), reducing their viability (Robertson 1991), in which the early development stages are the most vulnerable.

The relatively slow development of propagules of *R. mangle*, which remain attached to the mother-

plant for at least nine months, may favor both flowering and fruiting of this species. Although *Rhizophora* species flower all year round (Tyagi 2004), they usually present positive correlation with rainfall; the flowering peak of *R. mangle*, in the study area, occurred in the middle of the rainy season (Nadia et al. 2012). In addition, propagule dispersal of *R. mangle* is hydrochorous and should also occur in the rainy season. As dispersal occurs nine months after anthesis, it coincides with the beginning of the rainy season, as recorded for *R. mangle* in the study area (Nadia et al. 2012). A long period of propagule development is common in the genus *Rhizophora*, and it may vary from eight to 35 months, depending on the species (Duke et al. 1984).

The number of fruits formed by spontaneous self-pollination was very low in relation to natural pollination, suggesting that *R. mangle* is pollinated mainly by vectors. The similarity in reproductive success between natural fruit production and experimental wind pollination, resulting in a high anemophily index, together with the behavior of flower visitors, indicate that in the study area, apart from this low rate of spontaneous self-pollination, *R. mangle* is exclusively pollinated by wind. These results show also that the anemophily index is a good indicator of wind pollination rate.

Fruit production rate in *R. mangle* was higher than in other already studied species of *Rhizophora*, whose fruit production rate varied from 3.8 a 12.1%, similar to *Bruguiera gymnorhiza*, which exhibited 19.9% of fruit production and 16.8% of propagule production (Duke et al. 1984). The observation that *R. mangle* had higher reproductive success than other species of the genus suggests that resource limitation should be higher than pollination limitation in the study area.

In short, several morphological and structural characteristics of *Rhizophora mangle* classify the species as anemophilous. The permanence of protective verticils, calyx and corolla may be not

only remains of an entomophilous ancestral, but also an adaptation to protect and disperse pollen grains by wind under more favorable conditions. Associating the sequence of anthesis with the behavior of flower visitors and the anemophily index, it is possible to conclude that *R. mangle* is exclusively pollinated by wind in the study area. Because it is an anemophilous species, a high density of individuals is important for the effectiveness of wind pollination and, hence, for the maintenance of the species in the community.

ACKNOWLEDGMENTS

Dr. Ana Virgínia Leite (UFRPE) and Dr. Elisângela Lucia Bezerra helped us in the field, Dr. Marcelo Guerra (UFPE) authorized the use of the fluorescence microscope of the Laboratory of Plant Cytogenetics, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) granted the first author a PhD scholarship and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) granted the second author a research productivity fellowship.

RESUMO

Rhizophora mangle é uma espécie de mangue considerada como autocompatível e polinizada por vento e insetos. No entanto, não há informações sobre produção de frutos por autogamia ou agamospermia e sobre o comportamento de forrageio de seus visitantes florais. Dessa forma, o presente estudo analisou os sistemas de polinização e reprodução de *R. mangle* em uma comunidade de mangue no norte de Pernambuco, Brasil. A morfologia floral, sequência de antese, e comportamento dos visitantes florais foram descritos; a proporção de flores que resultou em propágulos maduros também foi registrada. Foram feitos testes de autogamia, agamospermia e polinização pelo vento, sendo proposto um novo índice de anemofilia. As flores de *R. mangle* são hermafroditas, protândricas, com elevada razão P/O. Foram observadas moscas visitando as flores apenas durante a fase masculina, provavelmente

para se alimentar de ácaros que estavam consumindo pólen. *Rhizophora mangle* não é agamospérmica e a formação de frutos por autopolinização espontânea é baixa (2,56%) em relação à polinização pelo vento (19,44%). O índice de anemofilia foi alto 0,98, sendo considerado um bom indicador. Apenas 13,79% das flores produziram propágulos maduros. Os estágios iniciais do desenvolvimento do fruto são os mais críticos e suscetíveis à predação. *Rhizophora mangle* é, portanto, exclusivamente anemófila na área de estudo e a dispersão de propágulos parece estar sendo limitada pela herbivoria.

Palavras-chave: índice de anemofilia, autogamia, entomofilia, manguezal, mangue vermelho.

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