

**PROCEEDINGS
OF THE
SIXTH SYMPOSIUM
ON THE
NATURAL HISTORY OF THE BAHAMAS**

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**Bahamian Field Station, Ltd.
San Salvador, Bahamas
1996**

Cover Photo: Dr. Lynn Margulis, Symposium Keynote Speaker, describes the structure and ecology of living stromatolites. Some, visible as grayish mounds near her feet, line the shore of Storrs Lake whereas others occur farther out in deep water. (See paper by D. C. Edwards, this volume).

Back Cover Photo: Group photo of the 6th Symposium participants and speakers.

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Printed in USA by Don Heuer

ISBN 0-935909-60-5

**PRELIMINARY OBSERVATIONS ON PLANT REPRODUCTIVE BIOLOGY IN
MANGROVE COMMUNITIES ON SAN SALVADOR ISLAND, BAHAMAS**

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ABSTRACT

From December 19, 1994 through June 16, 1995 we initiated studies on the reproductive biology of mangrove trees and their associates growing near Reckley Hill and Osprey Ponds, San Salvador Island, Bahamas. We studied Red Mangrove (*Rhizophora mangle*), Black Mangrove (*Avicennia germinans*), White Mangrove (*Laguncularia racemosa*), Buttonwood (*Conocarpus erectus*), and Bahama Swamp-bush (*Pavonia bahamensis*) for flowering phenology, flower morphology, sexual system, nectar production, fruit set and visitation by animals. In December-January, Red Mangrove, Buttonwood and Bahama Swamp-bush were in full flower. In June, Black Mangrove was in full flower and White Mangrove was beginning to flower.

Red Mangrove flowers produced little or no nectar but were occasionally visited by flies that were probably ineffective pollinators. Red Mangrove can self-pollinate, but fruit set was low (8-12%). Buttonwood flowers were also occasionally visited by flies, which appeared to be ineffective pollinators for this species as well. Buttonwood appears to be polygamous and therefore, may require cross-pollination. The role of wind pollination in both these species remains to be determined. Black Mangrove flowers produced moderate amounts of nectar (0.28 microliters/flower/day) and were visited mostly by butterflies.

Black Mangrove probably requires visitors for seed set as the flowers are protandrous. White Mangrove flowers also produced moderate amounts of nectar (0.40 microliters/flower/day) and were visited mostly by wasps. White Mangrove probably depends upon visitors for cross-pollination because the flower morphology indicates that this species is androdioecious. The major insect visitors to Red, Black, and White Mangrove were from different orders than those reported for Florida.

We present the first published observations on the reproductive biology and pollination of Bahama Swamp-bush, a Bahama endemic. We determined that the flowers produce copious nectar (74-140 microliters/flower/day), the plant is self-incompatible, and pollination and seed set depend upon two bird species, Bananaquits and Bahama Woodstars. These birds appear to be effective pollinators because fruit set was very high (82%). However, because of its pollination specialization, Bahama Swamp-bush may be especially vulnerable to any environmental changes that affect the population sizes, distributions or behaviors of these two bird species.

We also briefly present two new findings. We found an undescribed species of Ameroseiid mite living within the flowers of Red Mangrove. This record represents a major range extension for this group of mites; related species have previously only been reported for

the Old World tropics. We also saw wasps visiting glands on the leaf petioles of White Mangrove, and we draw the conclusion that these glands are extra-floral nectaries.

INTRODUCTION

Mangroves consist of a diverse, often unrelated, group of woody species that inhabit intertidal areas in tropical and subtropical oceans throughout the world. Mangroves are very important for protecting land from erosion, adding organic matter to land, harboring a rich fauna, and providing a reproductive habitat for many fish and other animals (Bossi and Cintron 1990, Tomlinson 1994). Unfortunately, many species are being threatened by habitat destruction (Bossi and Cintron 1990). Despite their wide distribution and ecological importance, the pollination and reproductive biology of most species are still poorly known (Gill and Tomlinson 1969, Tomlinson et al. 1979, Tomlinson 1994).

The pollination and reproductive biology of widely-distributed mangrove species are likely to differ for populations between continents and islands and between different islands, but few such comparisons have been made. Species on islands also appear to be especially vulnerable to environmental changes such as habitat destruction, introduced species, and rising sea levels (see Edwards, this volume). Therefore, baseline studies of pollinators and plant reproduction will be valuable for assessments of future changes as well as for comparisons between different islands and mainlands.

Here we summarize our initial observations on the pollination and reproductive biology of all the mangrove species and their close associates on San Salvador Island (Table 1). We studied Red Mangrove (*Rhizophora mangle* L.: Rhizophoraceae), Black Mangrove (*Avicennia germinans* (L.) Stern: Avicenniaceae), White Mangrove (*Laguncularia racemosa* (L.) Gaertn. f.: Combretaceae), Buttonwood (*Conocarpus erectus* L.: Combretaceae) and Bahama Swamp-bush (*Pavonia bahamensis* A.S. Hitchc.: Malvaceae). Buttonwood and Bahama Swamp-bush are not restricted to the typical mangrove habitat (Smith 1993), and, therefore, have been considered to be associates rather

than true mangroves (Tomlinson 1994). On San Salvador, both Buttonwood and Bahama Swamp-bush grow intermingled with the other mangroves along the shores of inland saline lakes and sheltered ocean shores and inlets, and are close associates (Kass and Stephens 1990, Kass 1991, Smith 1993, Kass et al. 1994). All these species, except Bahama Swamp-bush, are found on most islands throughout the Bahamas, the West Indies and on the subtropical and tropical mainland of the Americas (Britton and Millspaugh 1920, Correll and Correll 1982, Howard, 1989). Bahama Swamp-bush is endemic to the Bahama Archipelago (Britton and Millspaugh 1920, Correll and Correll 1982) and its pollination and reproductive biology are previously undescribed.

In this paper we briefly describe various aspects of the pollination and reproductive biology of these plant species, including their flowering phenology, flower morphology, sexual system, nectar production, fruit set and visitation by animals. (More complete accounts will be presented elsewhere.) We compare our results with available data, most of which is from mainland Florida. Using these preliminary results, we also present tentative predictions about the vulnerability of these plant species to potential changes in pollinator populations or pollination services. Mangrove communities are being threatened locally and on other islands in the Bahamas (BBDM 1996; D. Gerace pers. com.). We hope that these results will be valuable for assessing any future changes in the pollinators and reproductive success of these mangroves and their associates on San Salvador and other areas.

METHODS

We studied plants growing along the shores of Reckley Hill Pond and Osprey Pond near the Bahamian Field Station (see map in Godfrey et al. 1994). All species were present in both areas, except for Black Mangrove which does not grow at Reckley Hill Pond (Godfrey et al. 1994). We conducted studies during the following periods: December 23, 1994 to January 2, 1995; April 19, 1995 to May 14, 1995 (L. Kass only); and June 13 to 16, 1995.

TABLE 1. Summary of the reproductive biology of Red Mangrove (*Rhizophora mangle* L.: Rhizophoraceae), Black Mangrove (*Avicennia germinans* (L.) Stem: Avicenniaceae), White Mangrove (*Laguncularia racemosa* (L.) Gaertn. f.: Combretaceae), Buttonwood (*Conocarpus erectus* L.: Combretaceae), Bahama Swamp-bush (*Pavonia bahamensis* A. S. Hitchc.: Malvaceae) on San Salvador Island, Bahamas (see Appendix for definitions). A question mark indicates that description is uncertain and further study is needed.

	Red Mangrove	Black Mangrove	White Mangrove	Buttonwood	Bahama Swamp-bush
SEX: PLANTS	hermaphroditic	hermaphroditic	androdioecious or functionally dioecious?	polygamous or functionally dioecious?	hermaphroditic
FLOWERS	perfect; protandrous; autogamous	perfect; protandrous; autogamy unlikely	male or perfect (with functional pollen?); possible autogamy?	male, female or perfect (with functional pollen?); possible autogamy?	perfect; protogynous with herkogamy
COMPATIBILITY	self-compatible	unknown	unknown	unknown	self-incompatible
BREEDING SYSTEM	mostly self-fertilizing	probably outcrossing	mostly outcrossing?	mostly outcrossing?	obligate outcrossing
NECTAR PRODUCTION	little or absent	0.28 microliters/flower/day	0.40 microliters/flower/day	possible nectar or other exudate	74-140 microliters/flower/day
FRUIT SET (fruits/flowers)	low (8-12 %)	under investigation	under investigation	possibly higher for females than hermaphrodites	high (> 80 %)
FLOWER VISITORS	small flies that probably are not effective pollinators; may be wind pollinated	mostly butterflies, some wasps & flies	mostly wasps, occasional butterflies & Bananaquits	flies, mostly <i>Callitriga machelfaria</i> (Calliphoridae); may be wind pollinated?	birds (Bananaquits & Bahama Woodstars)

We permanently tagged plants of all species to follow individuals over time. Flower development was recorded daily for marked flowers. Nectar volume was measured using microcapillary tubes (either one or two microliter) from flowers bagged with bridal-veil netting to exclude visitors. We recorded flower visitors during timed surveys and throughout our studies. Fruit set (the percentage of tagged flowers producing large or mature fruit) was measured for Red Mangrove and Bahama Swamp-bush. Words used to describe different aspects of the reproductive biology are defined in the Appendix.

Insect visitors to flowers were identified with the assistance of Nancy Elliott at Siena College, New York and Mark Deyrup at Archbold Field Station, Florida. Specimens have been placed in the Bahamian Field Station insect collection, and many are mentioned in Elliott's (1993) field guide. More complete species accounts will be published elsewhere.

RESULTS AND COMPARISONS

Red Mangrove (*Rhizophora mangle*)

Red Mangrove is reported to flower throughout the year in the Bahamas (Correll and Correll 1982). On San Salvador Island, we observed many flowers and flower buds in December 1994 and early January 1995 and very few flowers and flower buds from April through June 1995. Flowers open throughout the day or night (Kress 1975, Tomlinson et al. 1979; our observations). Petals and anthers have been reported to fall within 12 hours to a few days after flower opening (Gill and Tomlinson 1971, Kress 1975). We observed that flowers are open for 1.5-2 days, after which the petals and anthers fall. Flowers apparently are protandrous; we observed that anthers release pollen before the flower opens (see also Kress 1975, and Juncosa and Tomlinson 1987) and before the two stigmatic lobes separate. However, the timing of stigma receptivity is unknown (Kress 1975). Nectar was not measurable using microcapillary tubes although we could see small quantities of nectar within some flowers.

Pollination in Red Mangrove is

considered to be via wind or self-pollination. Flowers have many characteristics for wind-pollination such as light, powdery pollen and little or no nectar (Kress 1975, Tomlinson et al. 1979, Tomlinson 1994). Kress (1975) demonstrated that pollen is wind-borne. Flowers can also self-pollinate and self-fertilize (Kress 1975, Teas and Handler 1979). Based on the prevalence of albino seedlings from Red Mangroves on San Salvador, genetic selfing appears to be common (Godfrey and Klekowski 1990, Lowenfeld and Klekowski 1992). Our observations suggest that cross-pollination by insects is rare.

In Florida, many different insect species have been reported to visit Red Mangrove flowers to collect pollen, but Hymenoptera (wasps and bees), especially pollen-collecting honey bees (*Apis mellifera* L.), were the most common visitors (Kress 1975). We saw very few flower visitors at Reckley Hill Pond in December 1994-January 1995. Most of the visits we observed were by a small (*Drosophila*-sized) black fly. These flies are unlikely to be effective pollinators because they remained on the calyx and seldom touched the stigma or anthers. In addition, we commonly saw small mites crawling around within the flowers. In Florida, Kress (1975) observed mites in Red Mangrove flowers but did not identify them.

The mites we observed within the Red Mangrove flowers are an undescribed species in the family Ameroseiidae (Barry OConnor, University of Michigan, pers. com.). Related species have only been reported previously from the Old World tropics. Ameroseiid mites typically live within flowers and disperse between plants on bees, beetles, or birds. In Australia, *Afrocyphlaelaps africana* Evans lives within the flowers of the River Mangrove, *Aegiceras corniculatum* (Myrsinaceae), feeds on nectar and pollen, and disperses on honey bees (Seeman and Walter 1995). The natural history and dispersal of the mites we observed are unknown.

In Florida, Red Mangrove fruit set ranged from 0-7.2% (Gill and Tomlinson 1971) to 18.6% (Kress 1975). At Reckley Hill Pond, fruit set was similarly low, averaging 8-12% for flowers tagged in winter 1995 (18 plants, 228 flowers).

Black Mangrove (*Avicennia germinans*)

Black Mangrove is reported to flower from January to July in the Bahamas (Correll and Correll 1982). On San Salvador, flowering was heavy in mid-June 1995, with flowering starting at the end of April. We saw developing fruit in early May and June which indicates that plants should have flowered sometime in February-April because fruit development takes four months (Tomlinson 1980). We did not see any flowers, flower buds, or fruit in December 1994 or early January 1995.

Flowers are open for three days and are protandrous (our observations). Anthers dehisce and release pollen on the first and second days. The two stigma lobes begin separating late on the second day and appear to be receptive on the third day (stigmas were sticky and pollen was adhering). To our knowledge the compatibility system is undescribed. However, in Mexico, Rico-Grey (1989) demonstrated that an insect visit is required for fruit set.

In Florida, Black Mangrove flowers have been reported to attract many visitors, especially bees, because of their high nectar production (Craighead 1971). At Osprey Pond during May and June 1995, nectar production averaged 0.28 microliters per flower per day (5 plants, 47 flowers) and did not vary significantly with flower age. Butterflies, especially *Kricogona lyside* Godart (Pieridae), were the most frequent visitors to flowers, and wasps, flies, and ants were occasional visitors. In Mexico, butterflies, bees, wasps and ants were common flower visitors to Black Mangrove (Rico-Gray 1989).

White Mangrove (*Laguncularia racemosa*)

White Mangrove is reported to flower throughout the year in the Bahamas (Correll and Correll 1982). On San Salvador, we observed that White Mangrove was ending flowering in mid-December. We did not see any flowers, flower buds, or fruit in April 1995. In mid-June 1995, plants had many flower buds and were just starting to flower.

White Mangrove is reported to be androdioecious because plants have either only male flowers and are non-fruiting or they have

all perfect flowers and are fruiting (Tomlinson 1980; our observations). However, many species described as androdioecious based upon flower morphology have proven to be functionally dioecious because the pollen of the perfect flowers is sterile (Richards 1986). The perfect flowers of White Mangrove appear to contain functional pollen (Tomlinson 1980; our observations), but this remains to be tested. The male (staminate) flowers have a well-developed style but no ovary so the floral cup is smaller (0.8 mm) compared to that of the perfect flower (1.0 mm) (Tomlinson 1980; our observations). Male flowers are open for only one day, whereas perfect flowers are open for two days (our observations). Nectar production by perfect and male flowers averaged 0.40 microliters during the first day of floral life (32 flowers, 6 plants). On the second day, perfect flowers produced little or no nectar (<0.01 microliters).

In Florida, bees are common visitors to White Mangrove flowers (Tomlinson 1980). On San Salvador, wasps were the most common flower visitors to White Mangrove flowers in both December 1994 and in June 1995. We occasionally saw butterflies and Bananaquits (*Coereba flaveola*), a common bird, visit flowers. We also observed wasps visiting the glands at the apex of the petiole. The glandular exudate tasted sweet (our observations) which suggests that these glands may function as extrafloral nectaries.

Buttonwood (*Conocarpus erectus*)

Buttonwood is reported to flower throughout the year in the Bahamas (Correll and Correll 1982). On San Salvador, we observed many flowers and flower buds in December 1994-January 1995 and no mature fruiting heads. In April, plants had few flowers and many developing fruiting heads. In mid-June 1995, plants again had many flowers and flower buds and either very young fruiting heads or mature fruiting heads that were shattering and dispersing seeds.

The phenology and development of individual flowers are difficult to follow because these flowers are tiny and are grouped into compact heads. A head may be 5-8 mm in diameter at flowering time (Correll and Correll 1982) and have 25 or more flowers

(Tomlinson 1994; our observations). Groups of these heads are on branchlets in racemes, forming an inflorescence. The compact flowering and fruiting heads are referred to as "buttons."

The sexual system of Buttonwood has been variously described based upon flower morphology; actual sexual function remains to be established. Bornstein (1989) reports that flowers are perfect, or that both perfect and staminate flowers can occur in the same inflorescence. Fawcett illustrates female flowers, and male flowers with a single ovule (Tomlinson 1980: Figs. 46 and 47; Correll and Correll 1982: Figs. 437A and 437B). Tomlinson (1994) describes plants of Buttonwood as being dioecious with male flowers commonly having one or two non functional ovules (but see Tomlinson 1980). Graham (1964) reports that plants may have only perfect flowers or both perfect and male flowers on the same inflorescence. By examining flower morphology, we have identified plants that have only male flowers, others that appear to have only perfect flowers, and one plant that appears to have only female flowers, so we are tentatively describing the species as being polygamous. To date, plants identified as males have produced no fruiting heads on the entire plant, plants with perfect flowers had low fruit set (0-6% of 307 flowering heads set fruit), and the one female had high fruit set (56% of 75 flowering heads set fruit). To our knowledge, it is unknown whether perfect flowers are functionally both male and female or whether they can self-pollinate and self-fertilize.

We have not found any published reports on flower visitors to Buttonwood. At Reckley Hill Pond in December 1994-January 1995, we observed infrequent visits by insects (mostly flies). The most common visitor was a housefly-sized, black fly, *Callitrega macellaria* (Calliphoridae). Other species included a small, *Drosophila*-sized fly (also seen visiting Red Mangrove flowers), other flies (especially Syrphidae), and an occasional butterfly. Visitors appeared to be eating some exudate on the floral heads. In June, we did not see any flower visitors during a few rapid surveys. Based on these limited observations, insect visitors to Buttonwood do not appear to be reliable or effective pollinators. It is

possible that flowers are mostly wind-pollinated although this remains to be tested.

Bahama Swamp-bush (*Pavonia bahamensis*)

Flowering of Bahama Swamp-bush is reported to occur all year in the Bahamas (Correll and Correll 1982). On San Salvador, Bahama Swamp-bush was in full flower in December 1994-January 1995. In April, very few, scattered flowers and many mature fruit were seen. In mid-June 1995, plants were at the end of flowering.

Throughout the flowering period, individual plants have only a few flowers (1-6) opening each day. Flowers are open for three days and are protogynous. On the first day, the stigma is exerted beyond the corolla while the corolla remains closed and pollen is often deposited at this time. Later in the day, the corolla opens and some stamens start to release pollen. On the second day, the remaining stamens release pollen. On the third day, the style retracts and the corolla closes. Self-pollination within a flower is unlikely because the anthers and stigma are spatially separated (herkogamy). Our studies indicate that plants are self-incompatible and cannot self-fertilize. Bagged flowers produced no fruit, whether or not self-pollen was placed on the stigma (5 plants, 18 flowers). Nectar production averaged 74 microliters per flower per day (23 flowers, 6 plants). Nectar production was greatest during the second day (140 microliters).

Nectar production by Bahama Swamp-bush flowers was high (70-140 microliters/flower/day), and two species of birds, Bananaquits (*Coereba flaveola*: Coerebidae) and Bahama Woodstars (*Caliphlox evelynae*: Trochilidae) were the only flower visitors that we observed. Bananaquits were more frequent visitors than Bahama Woodstars. These birds apparently were effective pollinators because fruit set was very high (82 %) (6 plants, 22 flowers).

DISCUSSION AND CONCLUSIONS

Island and mainland comparisons of flower visitors to the same mangrove species indicate that they differ greatly between

Florida and San Salvador Island. In Florida, Hymenoptera (wasps and bees), especially honey bees, were major visitors to Red, Black and White Mangroves whereas the major visitors we observed on San Salvador were flies (order Diptera) to Red Mangrove, butterflies (order Lepidoptera) to Black Mangrove, and wasps (order Hymenoptera) to White Mangrove (Table 1). In contrast to Florida, honey bees and bumble bees (*Bombus* species) are absent from the island of San Salvador, although San Salvador has a number of other bee and wasp species (Elliott 1993). Based on general descriptions, the number of visitor species and frequency of visitation appear to be lower on San Salvador than on mainland Florida, but quantitative data for mainland populations are lacking. Also, visitors and frequency of visits are likely to vary between locations and years on San Salvador, and more local data are needed before reliable comparisons can be made.

Comparisons of the flowering periods of these plant species reveal that flowering is more limited and seasonal for our populations than the flowering periods described by Correll and Correll (1982) for these species throughout the Bahama Archipelago. Instead of continuous flowering throughout the year, we found that Red Mangrove, White Mangrove, and Buttonwood had seasonal flowering with major flowering in December and in June. Bahama Swamp-bush also flowered seasonally, in December-January, rather than continuously as reported by Correll and Correll (1982). These differences are not unexpected given that taxonomic descriptions include data from herbarium specimens collected over many years throughout the Bahamas. However, our results indicate that such general descriptions have limited usefulness for understanding the pollination ecology of different plant species (see Rathcke 1988a, 1988b). More detailed descriptions of flowering phenologies from populations on different islands and mainland areas and over longer time periods are needed.

Our results on the pollination ecology of these species can offer some insights into the potential vulnerability of plant reproduction to environmental changes on this island and other areas. Plant species that are specialized to be pollinated by only one or a

few pollinator species are more likely to have lower seed set due to limited pollination than more generalized species with many pollinators (Rathcke and Jules 1993). Therefore, we suggest that the pollination of Bahama Swamp-bush may be especially vulnerable because it exclusively depends upon two bird species, Bananaquits and Bahama Woodstars, for pollination and seed set. Reductions in these bird populations or changes in their distributions and behaviors could affect the reproductive success of this endemic plant species. Black Mangrove and White Mangrove probably also depend upon animal pollinators for seed set. These two mangrove species have many species of flower visitors, which may make them less vulnerable to the decline of any one visitor species (see Rathcke 1988a, Rathcke and Jules 1993). However, each mangrove showed some specialization for different pollinator types and shared few flower visitors when they were flowering together (Table 1). Also, the pollination effectiveness of the different visitors may vary greatly. Therefore, it is possible that the decline or loss of a few key pollinator species could reduce the reproductive success of these two mangrove species.

Our literature review and research have pointed out several aspects of reproductive biology that need further study before any comparisons can be made. The sexual systems of Black Mangrove, White Mangrove and Buttonwood especially need further study. More data collected from more areas and over longer time periods are needed on the pollination ecology of all these species. The dispersal and the role of the mites in the flowers of Red Mangrove needs to be examined. The function of the glands on the leaf petioles of White Mangrove needs further investigation. We plan to address these problems in future studies.

ACKNOWLEDGMENTS

We are indebted to the Bahamian Field Station and the staff on San Salvador Island, Bahamas for logistical and financial support for this study, Project # B-176. We thank the Bahamas Ministry of Agriculture for permits to conduct this research project and to collect flowers, insect and mites. Lee Kass

acknowledges receipt of an Elmira College Faculty Travel Grant and a Faculty Development Committee Grant for partial support of this project. We thank Alverno College students Therese Ann Burdey and Mary Lee Blodgett for help in collecting data on Red Mangrove flower development. We are grateful to Elmira College students Erica Berglund, Sarah Boyle, Janine Iszkewicz, Debbie Lenda, Jen Metrafalio, and Russell Sage College student, Deborah Tomak, for helping collect data on fruit set of Red Mangrove. We thank Freeke and Jerry Kohl and Bill Thomas for help with observations of flower visitors. We gratefully acknowledge all creatures great and small for making this study possible. We thank Mark Deyrup, Nancy Elliott, and Barry OConnor for insect and mite identifications, and John Kress for providing us with a copy of his unpublished Honor's Thesis.

LITERATURE CITED

- Bahamas Biodiversity Data Management (BBDM) Committee. 1996. Bahamas Biodiversity Data Management Workshop Workbook, April 15 to 19, 1996. The Bahamas Environment, Science and Technology Commission (BEST), Office of the Prime Minister: Nassau, Bahamas.
- Bornstein, A. J. 1989. Combretaceae. PP. 451-457 in R. A. Howard. Flora of the Lesser Antilles, Leeward and Windward Islands. Vol. 5, Dicotyledoneae-Part 2. Arnold Arboretum, Harvard University: Jamaica Plain, MA.
- Bossi, R. and G. Cintron. 1990. Mangroves of the Wider Caribbean. Caribbean Conservation Association, Panos Institute and UNEP: Washington, DC.
- Britton, N. L. and C. F. Millspaugh. 1920. The Bahama Flora. Published by the Authors: New York.
- Correll, D. S. and H. B. Correll. 1982. Flora of the Bahama Archipelago. Vaduz: Cramer.
- Craighead, F. C. 1971. The Trees of South Florida. University of Miami Press: Coral Gables, FL.
- Edwards, D. C. 1996. The inland saline waters of the Bahamas as distinctive scientific resources. (This volume).
- Elliott, N. 1993. Guide to the Insects of San Salvador Island, Bahamas. Second edition. Bahamian Field Station: San Salvador, Bahamas.
- Gill, A.M. and P. B. Tomlinson. 1969. Studies on the growth of red mangrove (*Rhizophora mangle* L.). 1. Habit and general morphology. Biotropica 1: 1-9.
- Gill, A.M. and P. B. Tomlinson. 1971. Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. Biotropica 3: 109-124.
- Godfrey, P. J., D. C. Edwards, R. L. Davis, and R. R. Smith. 1994. Natural History of Northeastern San Salvador Island, a "New World" where the New World began. Bahamian Field Station: San Salvador Island, Bahamas.
- Godfrey, P. J. and E. Klekowski, Jr. 1990. Mutations for chlorophyll-deficiency ("albinism") in the Red Mangroves of San Salvador Island: Mendel's law in Bahamian swamps. PP. 25-39 in R. R. Smith (Ed.) Proceedings of the Third Symposium on the Botany of the Bahamas. Bahamian Field Station: San Salvador, Bahamas.
- Graham, S. A. 1964. The genera of Rhizophoraceae and Combretaceae in the southeastern United States. Journal of the Arnold Arboretum 45: 285-301.
- Howard, R. A. 1989. Flora of the Lesser Antilles, Leeward and Windward Islands. Volumes 5, Dicotyledoneae-Part 2. In collaboration with Allan J. Bornstein. Arnold Arboretum, Harvard

- University: Jamaica Plain, Massachusetts.
- pollination among coflowering shrubs. *Ecology* 69: 446-457.
- Howard, R. A. 1989. Flora of the Lesser Antilles, Leeward and Windward Islands. Volume 6, Dicotyledoneae-Part 3. Arnold Arboretum, Harvard University: Jamaica Plain, Massachusetts.
- Juncosa, A.M. and P. B. Tomlinson. 1987. Floral development in mangrove Rhizophoraceae. *American Journal of Botany* 74: 1263-1279.
- Kass, L. B. 1991. An Illustrated Guide to the Common Plants of San Salvador Island, Bahamas. A. J. Kowalski, illustrator. Bahamian Field Station: San Salvador, Bahamas.
- Kass, L. and L. Stephens. 1990. The trees of the mangrove swamp community of San Salvador Island, The Bahamas and their "succession" patterns. PP. 53-65 in R. R. Smith (Ed.) Proceedings of the Third Symposium on the Botany of the Bahamas. Bahamian Field Station: San Salvador, Bahamas.
- Kass, L. B., L. J. Stephens, M. Kozacko, and J. C. Carter. 1994. Continued studies of mangrove ecosystems on San Salvador Island, Bahamas. PP. 50-56 in L. B. Kass (Ed.) Proceedings of the Fifth Symposium on the Natural History of the Bahamas. Bahamian Field Station: San Salvador, Bahamas.
- Kress, W. J. 1975. The floral biology of *Rhizophora mangle* in South Florida. Undergraduate Honors Thesis. Biology Department, Harvard University: Cambridge, MA.
- Lowenfeld, R. and E. J. Klekowski, Jr. 1992. Mangrove genetics. I. mating systems and mutation rates of *Rhizophora mangle* in Florida and San Salvador Island, Bahamas. *International Journal of Plant Science* 15: 394-399.
- Rathcke, B. 1988a. Interactions for
- Rathcke, B. 1988b. Flowering phenologies in a shrub community: competition and constraints. *Journal of Ecology* 76: 975-994.
- Rathcke, B. and E. Jules. 1993. Habitat fragmentation and plant-pollinator interactions. *Current Science* 65: 275-277.
- Rico-Gray, V. 1989. The importance of floral and circum-floral nectar to ants inhabiting dry tropical lowlands. *Biological Journal of the Linnean Society* 38 (2): 173-182.
- Richards, A. J. 1986. Plant Breeding Systems. George Allen & Unwin: Boston, MA.
- Seeman, O. D. and D. E. Walter. 1995. Life history of *Aefrocyptholaelaps africana* (Evans) (Acari: Ameroseiidae), a mite inhabiting mangrove flowers and phoretic on honey bees. *Journal of the Australian Entomological Society* 34: 45-50.
- Smith, R. R. 1993. Field Guide to the Vegetation of San Salvador Island, The Bahamas. 2nd Edition. Bahamian Field Station: San Salvador, Bahamas.
- Teas, H. J. and S. H. Handler. 1979. Notes on the pollination biology of *Rhizophora mangle* L. Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere. Auckland, New Zealand. Volume 1: 357-361.
- Tomlinson, P. B. 1980. The Biology of Trees Native to Tropical Florida. Petersham, MA: published privately. Printed by Harvard University Printing Office: Allston, MA.
- Tomlinson, P. B. 1994. The Botany of Mangroves. Second edition. Cambridge University Press: Cambridge, UK.

Tomlinson, P. B., R. B. Primack, and J. S. Bunt. 1979. Preliminary observations on floral biology of mangrove Rhizophoraceae. *American Journal of Botany* 11: 256-277.

Willson, M. F. 1983. *Plant Reproductive Ecology*. John Wiley: NY.

APPENDIX

DEFINITIONS OF TERMS USED FOR PLANT REPRODUCTIVE BIOLOGY (after Tomlinson 1980, Willson 1983, and Richards 1986)

ANDRODIOECIOUS: plants can function either as males or as hermaphrodites (as both male and female)

AUTOGAMY: within-flower pollination (pollen transfer); not necessarily self-fertilization

DIOECIOUS: plants function either as males or as females

FUNCTIONALLY DIOECIOUS: plants function either as males or as females although they may have perfect flowers

HERKOGAMY: anthers and stigmas are spatially separated enough that self-pollination is unlikely

***HERMAPHRODITE:** each plant can function as both male and female

***PERFECT FLOWERS:** a flower morphologically has both male (stamens) and female (pistils) organs

POLYGAMOUS: plants are either male, female or hermaphroditic

PROTANDRY (PROTANDROUS): within a flower, anthers release pollen before stigmas are receptive

PROTOGYNY (PROTOGYNOUS): within a flower, stigmas are receptive before anthers release pollen

***These terms are often used interchangeably in the literature. We use the term "hermaphrodite" if the plant can function as both male and female. We use the term "perfect" if a flower has both male and female organs whether or not it has been demonstrated to function as both male and female.**