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REPRODUCTIVE BIOLOGY OF BUTTONWOOD, *CONOCARPUS ERECTUS* L. (COMBRETACEAE), A POLYGAMOUS POPULATION ON SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

In a previous study of Buttonwood, we noted that plants appeared to have either male (staminate) flowers or female (pistillate) flowers and appeared to be dioecious. We later noticed that some plants we had labeled as male subsequently produced a few mature fruit. To determine if plants having male flowers commonly produce fruits, we surveyed populations of Buttonwood along the roadsides of San Salvador Island. This extensive survey of over 1840 flowering plants showed that 11% of the plants with morphologically male flowers had developed a few fruit. Such morphologically male flowers are cryptically hermaphroditic because they have one functional ovule and produced seeds. Plants having both male flowers and cryptically hermaphroditic flowers on the same individual we term cryptically andromonoecious. Seeds from cryptically andromonoecious plants were viable and had the same low germination success (1.3%) as seeds from female plants. The San Salvador Buttonwood population is polygamous because it includes andromonoecious and dioecious plants.

INTRODUCTION

The breeding system of Buttonwood has been variously described based upon flower morphology. Some authors have reported Buttonwood as being dioecious (plants having either male or female flowers) or bisexual (plants having hermaphroditic flowers). Others have noted that plants may have both bisexual and male flowers, or plants with male flowers occasionally may have functional ovaries and are therefore considered polymorphic. Clearly, the determination of sexual type is difficult or may be variable.

In previous studies, we have noted two morphological types of flowers on separate plants (Rathcke *et al.*, 1996). Some plants have flowers with short pale-yellow stamens with no apparent pollen, and we assumed these plants were female because tagged plants usually produced abundant fruit. Other plants have flowers with long stamens that extend beyond the calyx, and we assumed these plants were male because tagged plants did not produce fruit. However, in 2003 we reexamined a population of 13 permanently tagged plants and found that six plants we had previously identified as male had a few mature fruits.

To determine whether plants having morphologically male flowers typically produce some fruit, we surveyed most populations of Buttonwood along roadsides on San Salvador Island. We also sectioned a subset of developing fruits to determine number and condition of ovules, and we germinated fruits produced from female and from "apparently-male" plants to determine if they were equally viable.

Because past descriptions of the breeding system of Buttonwood have been so varied, we also review the literature and examine how different researchers used floral morphology to make their conclusions about the breeding system. Finally, we present our description of the breeding system of Buttonwood, based upon our findings presented here.

MATERIALS AND METHODS

Study Species

Buttonwood, *Conocarpus erectus* L. (Combretaceae), is a shrub or small tree that commonly grows landward along the mangrove zones in the neotropics (Tomlinson, 1994). Because it shows no obvious biological specializations comparable to root modifications and viviparous tendency of the true mangroves, it is not considered a "true" mangrove (Tomlinson, 1980, 2001). The species grows throughout the Bahamas and southern Florida, Central America and the West Indies to South America, and in tropical West Africa (Correll & Correll, 1982). On San Salvador, Buttonwood grows along many saline ponds (Kass, 2005, pg. 136) and is also common along roadsides.

Flowering occurs throughout the year in the Bahamas (Correll & Correll, 1982), but we observed that our permanently tagged plants exhibited major flowering peaks in December and June. Tiny flowers (2 mm long) are displayed in compact heads, called buttons, and the heads are grouped into loose inflorescences. A flower head may be 5-8 mm in diameter (Figures 1 and 2) and have 25 or more flowers (Tomlinson, 1994). We have observed very few visitors to the flowers and suspect that flowers are mainly wind-pollinated. The flowering head may form a dry cone (button) that shatters to release the winged fruits. Each fruit contains a single seed.

Floral Morphology and Survey

The floral morphology of selected plants was examined closely by LBK and RH using a compound microscope. In January 2003, we examined the presence of pollen in stamens for flowers on male plants and female plants.

An island-wide survey of the morphological breeding system of Buttonwood plants was conducted by RH (in collaboration with LK and SD) in January-February 2004. Most accessible plants growing along the main highway around the island were examined. Flowering plants were assigned to one of three categories: 1) male (with only male flowers evident and no sign of developing or past fruit), 2) female (with only female flowers and maybe with signs of developing or past fruit), and 3) andromonoecious (plants with only male flowers evident but with developing or past fruit).

Seed Anatomy and Germination

Female Buttonwood plants have female flowers grouped into heads (buttons), which produce a cone-like structure composed of aggregate fruit (drupes). Individual flowers from these buttons are reported to contain two ovules (Tomlinson, 1980; Figure 2). Upon ripening, the cones shatter and release many separate fruits. If each fruit (drupe) produces only one functional ovule, which develops into a viable seed, we can equate one fruit with one seed.

Male plants have flowers that are also grouped into heads, but occasionally have ovaries that commonly include 1 or 2 nonfunctional ovules (Tomlinson, 1994:235). Moreover, some "male flowers may have an apparently well-developed ovary with a single ovule" (Tomlinson, 1980, 2001; Figure 1). Our island-wide survey revealed "apparently male" plants with well-developed ovaries, which produced cone-like structures, and we classified these plants as andromonoecious.

To determine if andromonoecious Buttonwood plants have fruit containing one or two ovules, we (RH and LK) hand-sectioned developing buttons from andromonoecious plants collected at Fresh Lake Causeway in January 2006 and examined them with a dissecting microscope for the number and condition of developing seeds in the ovaries. We compared these with developing buttons from female plants collected from the same locality on the same date.

To learn if andromonoecious Buttonwood plants produce viable seeds, we (RH and LK) collected and germinated mature buttons (aggregate fruits) in January 2006 from plants growing along the Fresh Lake Causeway and compared their germination percentage with mature female buttons collected from the same location in May 2005 (TE). We (RH and LK) also collected mature female Buttonwood fruits from plants along Little Lake in February 2006, and tested seed germination. Seed set could not be tested independently of germination because to do so destroys the fruit and seed. Therefore, Buttonwood fruits used in the germination study may have included aborted and nonviable seeds.

We germinated the 2006 seeds on moist paper towels in a dish that was placed in a large zip loc bag and left at ambient room temperature. Our seeds were collected from plants that had developed for two months without significant rainfall and the germination test was performed within a week of collection. Egan germinated 2005 seeds on wet filter paper in a covered Petri dish over a range of temperatures. Those seeds were germinated up to several months after collection.

Literature Review and Terminology

We reviewed the available literature on the breeding system of Buttonwood. LBK prepared tables in collaboration with Dr. Carol Landry, University of Michigan, showing the floral characteristics that authors used to make their conclusion about the breeding system. Because the terminology for floral morphology and breeding systems are often defined differently, we present a table of definitions that we will use throughout this paper (Table 1). Definitions are modified from Richards (1986).

RESULTS

Floral morphology and survey

Close inspection of flowers using a compound microscope showed that some plants had flowers with short staminodes (stamens with no pollen) and were apparently female flowers (Figure 3). Other plants had male flowers with long exserted stamens with pollen (Figure 4). In addition, we observed that some plants with mostly male flowers also had some flowers that appeared to be setting some fruit (Figure 5) (see also Table 3F). We assumed that fruits on these "apparently male" plants were produced from hermaphroditic flowers (with functional long stamens and a functional ovule), since we observed no female flowers with short staminodes on these plants. Because hermaphroditic flowers look like male flowers, we can only identify hermaphroditic flowers on male plants when they set fruit. By the time we recognized that flowers on "apparently male" plants were developing fruit, the stamens were gone or senesced (Figure 5a). We are calling these flowers cryptically hermaphroditic. Plants with both hermaphroditic flowers and male flowers are termed andromonoecious (Table 1). Plants having cryptically hermaphroditic flowers and male flowers we are calling cryptically andromonoecious.

In the island-wide survey, plants in twelve geographically-separate populations were examined (Table 2). These populations

Table 1. In our study of the breeding system of Buttonwood, we applied the definitions below as used or modified from Richards (1986).

Floral Terminology
Perfect flower: a flower with both male (staminate) and female (pistillate) morphological structures.

Hermaphrodite flower: a flower with both male (staminate) and female (pistillate) function.

Bisexual: current usage refers to individual plants with both male and female function; former usage referred to either plants with male and female function or to flowers with male and female function (e.g. Graham, 1964).

Definition of Breeding Systems; floral types indicate function (modified from Richards, 1986)
Dioecious: 2 breeding types, male-flowered (staminate) individual and female-flowered (pistillate) individual.

Hermaphroditic: 1 breeding type, hermaphroditic-flowered individual.

Andromonoecious: 1 breeding type, male and hermaphroditic flowers on the same individual.
[Cryptically Andromonoecious breeding systems have male and cryptically hermaphroditic flowers; Cryptically hermaphroditic flowers are identified when the flowers set fruit.]
[Functionally Andromonoecious breeding systems appear at first to have only male flowers, some of which produce fruit; these apparently male flowers are hermaphroditic (cryptically and functionally).]

*Polygamous: 3 or more of the following breeding types: male-flowered individual, female flowered individual, hermaphroditic-flowered individual, andromonoecious individual.
[Functionally polygamous breeding systems include functionally andromonoecious breeding systems.]

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*For our study, these are the only possible breeding types (see Table F); Richards defines the system more broadly.

contained a total of 2156 plants, of which 1843 (85%) were flowering and could be assigned to a breeding system category (Male, Female or Andromonoecious).

All populations had male plants, female plants, and andromonoecious plants, except one population near French Bay, which had no apparent andromonoecious plants (Table 2). The proportion of male plants ranged from 19.2 to 51.1% and the proportion of andromonoecious plants ranged from 0 to 19.2% in different populations. The proportion of plants with male function (male or andromonoecious) ranged from 27.7% to 63.9%. For all flowering plants surveyed, 34.9% were male, 10.9% were andromonoecious, and 45.8% had male function (male or andromonoecious).

Seed Anatomy and Germination

Our preliminary observations on the anatomy of developing buttons from andromonoecious plants showed that one developing green ovule (seed) was centered in the cross-sectional view of the ovary, indicating that there was only one seed in these fruits. Similar observations on developing buttons from female plants showed that one of the two ovules in a developing fruit was green and enlarged and was slightly off-center in a cross-sectional view. The other ovule was brown and shriveled and had aborted, indicating that only one seed was developing in these fruits. Our observations are consistent with floral anatomy of Buttonwood flowers drawn and reported as polymorphic from Florida (Tomlinson, 1980, 2001; Figures 1 and 2).

We observed germination in both andromonoecious and female Buttonwood seeds (Table 5). Seeds collected and germinated in the same year (2006) from andromonoecious and female plants showed the same germination percentage (1.3%), indicating that seeds from andromonoecious plants are as viable as those from female plants on San Salvador. Seeds germinated from female plants collected approximately one-half year earlier (2005) by Egan gave similar results (1.7%).

Literature Review and Terminology

The breeding system of Buttonwood throughout the Caribbean, Florida, and The Bahamas has been described as "essentially dioecious" (Table 3A, Figures 1 and 2), dioecious (Table 3B, Figures 1 and 2), and "polygamous" (Tables 3C and 3E), or were undescribed (Table 3D). While reviewing the literature, we found that the terminology was occasionally inaccurate and/or was inconsistent with current usage. We applied the definitions in Table 1, taken from Richards (1986), to this study (Table 3F). Buttonwood populations on San Salvador are composed of female flowered plants, male flowered plants, and andromonoecious plants with both male and hermaphroditic flowers (Tables 1, 2, 3F, and 4). Therefore, the breeding system of Buttonwood on San Salvador is polygamous (Tables 1, 3F, and 4).

*Table 2. Breeding system survey of Buttonwood (*Conocarpus erectus *L.) populations on San Salvador Island, Bahamas. TN = total number of plants examined; TFlw = total number of flowering plants; %Male = % of plants with only male flowers and no fruit; %And (andromonoecious) = % of plants with male flowers and fruit; %M+A = % of plants with male function; the remaining flowering plants have all-female flowers.*

Location	**TN**	**TFlw**	**%Male**	**%And**	**%M+A**
~9 miles south of GRC gate	87	71	31.0	15.5	46.6
South of Cockburn Town, just south of smaller cemetery	123	88	51.1	4.5	55.6
Bay just north of Club Med	60	36	50.0	13.9	63.9
Fresh Lake causeway	52	44	27.3	15.9	43.2
Fresh Lake shore	86	72	47.2	12.5	59.7
Storrs Lake	857	723	30.0	7.1	37.1
Salt Pond	34	26	26.9	19.2	46.1
Pigeon Creek	416	391	31.5	11.5	43.0
Pigeon Cay	172	157	26.8	12.1	38.9
French Bay	158	130	19.2	8.5	27.7
Depression just north of French Bay	32	32	43.8	0	43.8
Reckley Hill Pond	79	73	34.2	9.6	43.8
TOTALS	**2156**	**1843**	**34.9**	**10.9**	**45.8**

Tables 3. A, B, C, D. Buttonwood breeding systems reported in the literature: two breeding types.

Table 3A. "ESSENTIALLY" DIOECIOUS POPULATION (Tomlinson, 1980:148, 2001:115).

	Male Plant	Female Plant
Inflorescence:	smaller than females	larger than males
Floral Morphology:	perfect	perfect
Stamens (male):	5-10 functional	5 staminodes [non-functional stamens]
Ovary/ovule: (female)	some male flowers with an apparently well-developed ovary with a single ovule	well-developed ovary, 2 ovules
Fruit:	[not mentioned]	cone-like, shatters when ripe
Illustrations:	Fig. 1	Fig. 2

Table 3B. DIOECIOUS POPULATION (Tomlinson, 1994:233, 235).

	Male Plant	Female Plant
Floral Morphology:	perfect	perfect
Stamens:	5-10 functional stamens, prominent	5 staminodes, inconspicuous
Ovary/ovule:	ovaries narrow, commonly including 1-2 non-functional ovules	well developed ovary
Fruit:	[not mentioned]	head composed of 5 mm long nutlets, fruit released by shattering of head
Illustrations:	Fig. 1	Fig. 2

Table 3C. "POLYGAMOUS" POPULATION (Bornstein, 1989:451).

	[Plant type 1]	[Plant type 2]
Floral Morphology:	perfect and staminate in the same inflorescence	perfect
Stamens:	5-10 stamens, exserted; or 5 by abortion	[not distinguished from plant type 1]
Ovary:	flattened with 2 ovules	[not distinguished from plant type 1]
Fruit:	in heads to 17 mm	[not distinguished from plant type 1]
Illustrations:	[see Bornstein pg. 455]	[not distinguished from plant type 1]

Table 3D. BREEDING SYSTEM UNDEFINED (Graham, 1964:299).

	[Plant type 1]	[Plant Type 2]
Floral Morphology:	male and bisexual in the same inflorescence	bisexual
Stamens:	5-10 stamens, well-exserted	[not distinguished from plant type 1]
Ovary:	not described	[not distinguished from plant type 1]
Fruit:	globose conelike heads	[not distinguished from plant type 1]
Illustrations:	[not illustrated]	[not illustrated]

Tables 3E and 3F. Buttonwood breeding systems on San Salvador reported in the literature (TABLE 3E) and presented in this study (TABLE 3F): three breeding types.

Table 3E. POLYGAMOUS (tentatively) POPULATIONS (Rathcke* et al., *1996:89, 92).

	Perfect-flowered Plant	Male Plant	Female Plant
Floral Morphology:	perfect	perfect	perfect
Stamens:	assumed functional	functional	non-functional
Ovary:	assumed functional	non functional	functional
Fruit:	low fruit set	no fruit	high fruit set
Illustrations:	[not illustrated]	[not illustrated]	[not illustrated]

Table 3F. POLYGAMOUS POPULATIONS (This study).

	Andromonoecious Plant	Male Plant	Female Plant
Floral Morphology:	perfect, both male and hermaphroditic flowers	perfect	perfect
Stamens:	long, 5 observed, male flowers have pollen; hermaphroditic flowers, pollen not examined	long, 5 exserted, pollen present	short, 5 staminodes, no pollen
Ovary:	non-functional in male flowers; enlarged ovary in hermaphroditic flowers, one functional ovule	non-functional	functional, style, exserted; only one of two ovules is functional
Fruit:	low fruit set in hermaphroditic flowers; no fruit produced by male flowers	no fruit	high fruit set
Illustrations:	Fig. 5	Fig. 4	Fig. 3

DISCUSSION AND CONCLUSIONS

The results of our survey of Buttonwood plants on San Salvador (>1840 flowering individuals in 12 populations) indicated that approximately 11% of plants are cryptically andromonoecious (Table 2). We consider the breeding system to be best defined as cryptically andromonoecious (Table 1) because flowers that appear morphologically male sometimes produce fruit and are functionally hermaphroditic. Because populations have functionally male and female plants as well as cryptically andromonoecious plants, the breeding system can be considered to be polygamous on San Salvador (Tables 1 and 2).

Fruit set was low on these andromonoecious individuals relative to the abundant fruit set of females, indicating that they function more as males then as hermaphrodites. In our tagged population, and also on roadside plants, andromonoecious plants were typically larger than functionally male plants, suggesting that males may have the ability to produce hermaphroditic flowers but do not allocate resources to female function until they are either larger or older. This appears to be the reason for the recent occurrence of andromonoecious plants in our tagged plants after 12 years growth (1994-2006).

Table 4. A summary table for Buttonwood breeding system. The breeding system of Buttonwood appears to be polygamous based on morphology. There are plants with female flowers, plants with male flowers, and plants with both male and hermaphroditic flowers.

Plant type	Flower Morphology	Flower Function	Stamens/ pollen	Ovary
Male Plants	morphologically perfect	male	stamens/ pollen	non-functional
Female Plants	morphologically perfect	female no pollen	staminodes/	functional
Andromonoecious Plants				
- Male Flowers	morphologically perfect	male pollen	stamens/	non-functional
- Hermaphroditic Flowers	morphologically perfect	hermaphrodite pollen not-examined	stamens/	functional

Table 5. Percent germination of Buttonwood seeds (fruits) from female and andromonoecious plants collected at the Fresh Lake Causeway[a] and Little Lake[b] on San Salvador Island in 2005 and 2006.

Seed (fruit) collection dates	Number germinated	Plant gender	Germination (%)
May 1, 2005[a.]	1250	Female	1.7
Jan. 26, 2006[a.]	300	Andromonoecious	1.3
Feb. 4, 2006[b]	2008	Female	1.3

Andromonoecious plants have fruit with one ovule that is functional, although germination is low (see below). These results are consistent with those described by Tomlinson (1980, 2001), who found that male Buttonwood flowers "may have an apparently well-developed ovary with a single ovule" (Figure 1). In dioecious populations of Buttonwood, Tomlinson (1994) reported that male flowers may commonly include 1 or 2 non-functional ovules. We have not examined the ovules of male flowers on male plants in our population. If, however, male plants have the potential to produce hermaphroditic flowers as they age, we would expect such flowers to include 1 or 2 ovules that may have the capacity to be functional.

Our preliminary examination of Buttonwood seed germination demonstrated that seeds from both female and andromonoecious plants are equally viable, although germination was low (1.3%-1.7%) for all seeds tested (Table 5). Germination here reflects both seed set (viable seeds produced per ovule) and germination of viable seeds, because we did not examine seed set independently. Previous studies have found low seed set in Buttonwood. Guppy (1917) estimated 4% seed set in Jamaican Buttonwood and reported 3-4% from populations in

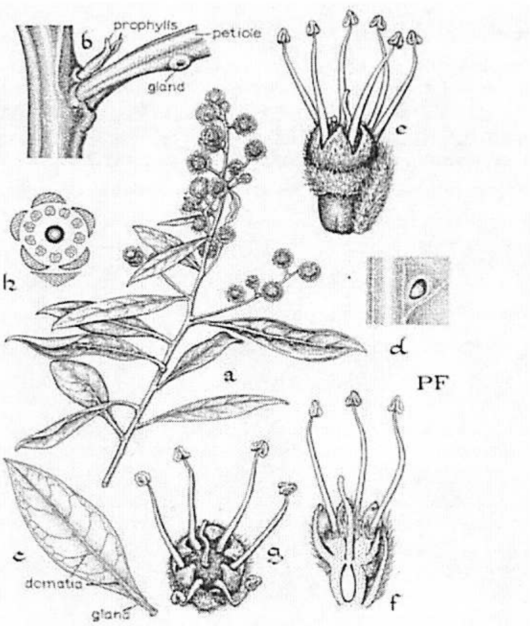


Figure 1 *Conocarpus erectus*, male. a. Habit with male flowers (x 2/3); b. detail of leaf axil with dormant axillary bud enclosed by prophylls, and one of a pair of petiolar glands (x 4); c. leaf from below, with domatia (x 2/3); d. detail of single domatium (x 6); e-h. male flower (x 13), (e) from side, (f) in longitudinal section, (g) from above (x 13). (h) floral diagram.

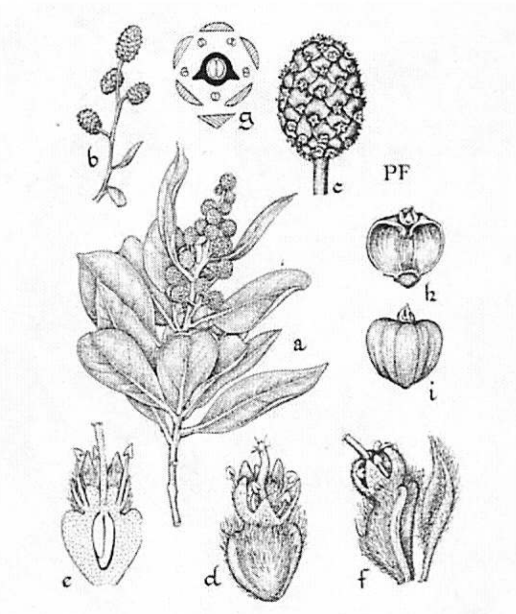
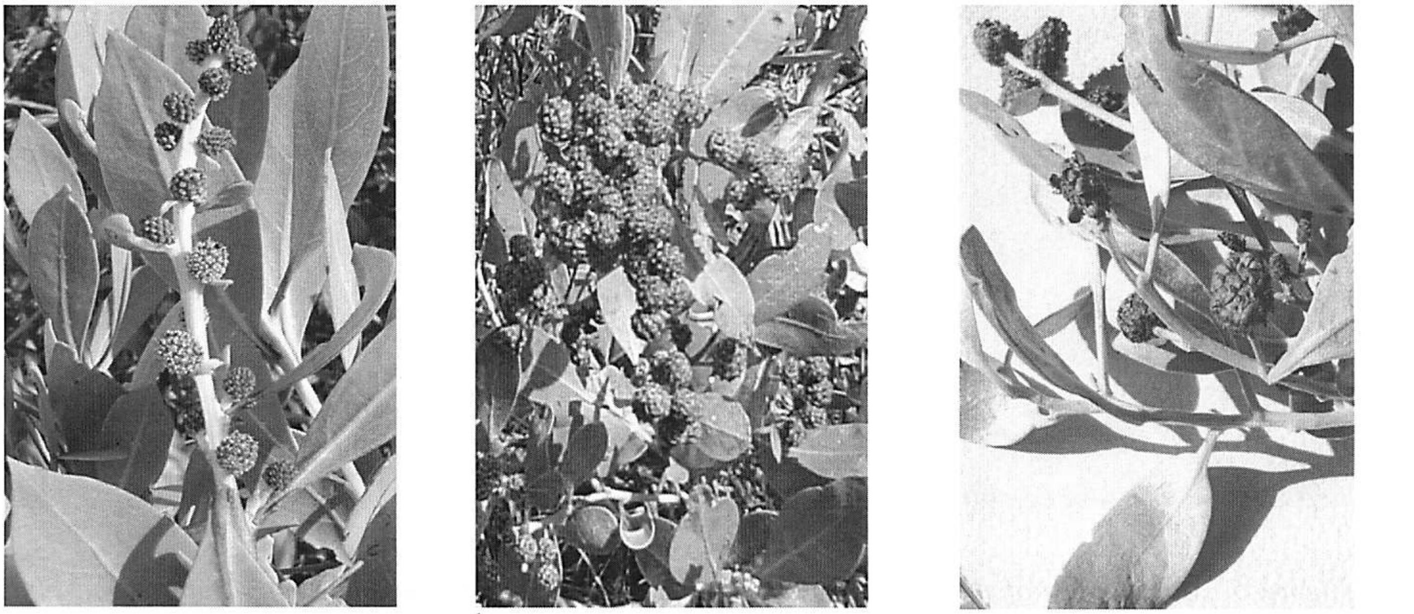


Figure 2 *Conocarpus erectus*, female. a. Habit with female flowers (x 2/3); b. branch with fruiting heads (x 2/3); c. single fruiting head (x 3); d-g. female flower (x 13), (d) from side, (e) in longitudinal section, (f) with bract from the side, (g) floral diagram with 5 staminodes; h and i. fruit from two aspects (x 7).

Figures 1-2. Conocarpus erectus L. *male and female (reprinted with permission from Tomlinson, 1980: 146,147); note that these illustrations of Florida specimens were also reproduced in Correll and Correll (1982:1031, 1032); see Kass (2005:136).*



a b c

Figure 3. Typical morphology of female buttons (Photos by R.E. Hunt). a) Female flowers; swollen buttons have extended stigmas. b) Developing fruit showing typical abundance of cone-like clusters of fruits on female trees. c) Mature buttons with fruit; note that the button on left is beginning to shatter and disperse its fruit.

a b

Figure 4. Male buttons exhibiting typical morphology (Photos by R.E. Hunt). a) Developing male flowers with a few extended stamens. b) Fully developed male flowers with extended stamens and a few buttons that have senesced stamens.

a b c

Figure 5. Morphology of male and hermaphroditic buttons on andromonoecious Buttonwood plant (Photos by R.E. Hunt). a) Developing fruit from hermaphroditic flowers; west end of Fresh Lake Causeway. b) Male flowers and developing fruit on same inflorescence; BW 6 in Reckley Hill Pond. c) Developing fruit on an andromonoecious plant; roadside just north of Club Med.

the Turks Islands. Francis and Rodriguez (1993) observed 12% germination of "seeds" from Buttonwood in Puerto Rico (we found no other records of Buttonwood germination in the literature). To compare these results directly with our own, we multiplied 4% seed set (estimated by Guppy, 1917), with 12% germination (determined by Francis & Rodriguez, 1993), which results in 0.48% germination—a percentage that is even lower than our results (1.3%) from San Salvador Island. Tomlinson (1994) hypothesized that either many Buttonwood seeds are aborted or germination is difficult. We have never observed dense seedling populations of Buttonwood and have only occasionally seen a few scattered seedlings near Buttonwood adults. This suggests that recruitment of new plants may be limited.

In our review of the literature on the breeding system of Buttonwood, we found that most terms are used inconsistently (Tables 3A to 3D). We now consider the breeding system to be best defined as cryptically andromonoecious. To our knowledge, this is the first documented case of cryptic hermaphroditism in a flower and the first case of cryptic andromonoecy in a species.

FUTURE RESEARCH

We plan to determine whether plants with hermaphroditic flowers can self-pollinate, and if plants from other islands and on mainland Florida exhibit similarly low germination. Our finding of low seed germination may be due to dry climate conditions on San Salvador. Egan plans to continue seed germination trials from different localities on San Salvador. Future studies will measure seed set and test whether seed set is pollination limited.

Many more questions concerning the breeding system of Buttonwood remain unanswered. Do all the flowers on andromonoecious plants produce ovules? What is the number of ovules in flowers on male plants? Will all apparently male plants eventually produce fruits and seeds? What is the relative proportion of male vs. hermaphroditic flowers, and does it vary with the size or age of the plant? And with respect to female plants, do flowers ever produce pollen?

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REFERENCES

Bornstein, A. J. 1989. Combretaceae. Pp. 451-457 *in* Howard, R. A. *Flora of the Lesser Antilles, Leeward and Windward Islands.* Vol. 5. Dicotyledoneae-Part 2. Arnold Arboretum, Harvard University Press, Jamaica Plain, Massachusetts, U.S.A.

Correll, D. S., and H. B. Correll. 1982. *Flora of the Bahama Archipelago.* J. Cramer, Vaduz, Liechtenstein [Printed in Germany].

Francis, J. K., and A. Rodriguez. 1993. Seeds of Puerto Rican trees and shrubs: second installment. Research Note USDA Forest Service, Southern Forest Experiment Station, Research Note SO-374 (http://www.srs.fs.usda.gov/pubs/rn/uncaptured/rn_so374.pdf).

Guppy, H. B. 1917. *Plants, Seeds, and Currents in the West Indies and Azores.* Williams and Norgate, Covent Garden, England.

Graham, S. A. 1964. The genera of Rhizophoraceae and Combretaceae in the southeastern United States. Journal of the Arnold Arboretum 45:285-301.

Kass, L. B. 2005. *An Illustrated Guide to the Common Plants of San Salvador Island, Bahamas*, 2nd ed. A. J. Kowalski, illustrator. Gerace Research Center, San Salvador, Bahamas.

Richards, A. J. 1986. *Plant Breeding Systems.* George Allen and Unwin, Boston, Massachusetts, U.S.A.

Rathcke, B., L. B. Kass, and R. E. Hunt. 1996. Preliminary observations on plant reproductive biology in mangrove communities on San Salvador Island Bahamas. Pp. 87-96 *in* Elliott, N. B., D. C. Edwards, and P. J. Godfrey, eds., *Proceedings of the 6th Symposium on the Natural History of the Bahamas*. Bahamian Field Station, San Salvador, Bahamas.

Tomlinson, P. B. 1980. *The Biology of Trees Native to Tropical Florida.* P. Fawcett, illustrator. Harvard University Printing Office, Allston, Massachusetts U.S.A.

Tomlinson, P. B. 1994. *The Botany of Mangroves* [rev. ed.]. Cambridge University Press, Cambridge, UK.

Tomlinson, P. B. 2001. *The Biology of Trees Native to Tropical Florida*, 2nd ed. P. Fawcett, illustrator. Harvard Printing and Publications Services, Allston, Massachusetts, U.S.A.