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TEMPORAL DIOECY IN THREE FINGERS, *THOUINIA DISCOLOR* (SAPINDACEAE), A MEDICINAL SHRUB ENDEMIC TO THE BAHAMAS

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ABSTRACT

Three Fingers, *Thouinia discolor* Griseb. (Sapindaceae), is a shrub or small tree that is endemic to the Bahamas and is used medicinally on San Salvador Island. The breeding system of this species was not previously described. Other Bahamian Sapindaceae are reported to have male (staminate) or female (pistillate) flowers on separate plants (*i.e.* they are dioecious) or with some flowers appearing perfect (bisexual or hermaphroditic). Here we show that *T. discolor* on San Salvador Island is monoecious, having male (staminate) flowers and female (pistillate) flowers on the same plant and inflorescence. However, the sexes are temporally separated within a plant, such that a plant is either male or female at any one time. This temporal separation of the sex phases within monoecious plants has been termed temporal dioecy. All plants (N=9) switched sex once, and five plants switched sex twice. All plants produced fruits. Temporal dioecy may be a common breeding system in the Sapindaceae, but this is the first report from the Bahamas and for the genus. The small white flowers are displayed on spikes and produce nectar. The only flower visitors were wasps; visits were infrequent and fruit set was variable among plants (11-59% of female flowers produced fruit) indicating that plants may be pollination limited.

INTRODUCTION

Three Fingers, *Thouinia discolor* Griseb. (Sapindaceae), is a shrub or small tree that is endemic to the Bahamas. Although about 30 species of *Thouinia* grow in tropical and subtropical America, *T. discolor* is the only species in the Bahamas (Gillis 1976, Correll and Correll 1982). *T. discolor* has many common names, including Three Fingers, Quicksilverbush, Naked-wood and Hard-bark (Correll and Correll 1982, Smith 1993). It grows throughout the Bahama Islands in coppices, scrublands, and pinelands (Figure 1) (Gillis 1976, Correll and Correll 1982) and is a common plant in the blacklands coppice on San Salvador Island (Smith 1993, personal observations). The leaves are used medicinally in the Bahamas as a tea to alleviate weakness (Smith 1993, Randolph 1996).

In searching the literature for information on *Thouinia* species, we found brief species descriptions in floras but nothing on breeding systems or pollination biology. In Correll and Correll (1982) the illustration for *T. discolor* shows male (staminate) and female (pistillate) flowers, but the distribution of the flowers on plants is not described. Their description for the family Sapindaceae notes that species have male (staminate) or female (pistillate) flowers on separate plants [*i.e.* they are dioecious] or with some flowers appearing perfect [*i.e.* they are bisexual or hermaphroditic]. Therefore, some species may exhibit a polygamous breeding system, which is broadly

defined as having male, female or bisexual flowers on the same or different plants (Richards 1997). Within polygamy, species can be variously classified depending upon the sex distribution of flowers. Classifications range from polygamodioecious if plants are mainly dioecious but have some bisexual flowers (Radford 1986) to trioecious (if plants are male, female or bisexual in the same population) (Richards 1997). Here we describe the floral biology, breeding system and sex ratios, fruit set, and flower visitors of *T. discolor* on San Salvador Island.

METHODS

The study site was located near the Gerace Research Center (formerly known as the Bahamian Field Station) on the northeastern coast of San Salvador Island. We studied shrubs in a former slash-and-burn field that had been abandoned and that was along the path (Alfred Pike) to Reckley Hill Pond (see Godfrey *et al.* 1993 for a map). The field now had a dense shrub vegetation, but no tree overstory. Most shrubs were c. 5-6 feet tall in the field, although older plants can reach 10-12 feet tall and are small trees in more developed coppice.

We permanently tagged all the flowering shrubs in the field (nine plants), and we monitored them from December 23, 2000 to January 13, 2001. Individual inflorescences were tagged on each plant, all open flowers were color coded by day with a permanent marker, and the sex of each flower was recorded each day. Most plants had their first flowers at the start of this study. Standing crop nectar was measured in exposed flowers brought back to the laboratory. Nectar was collected in a 1 microliter microcapillary tube and the volume calculated. All flower visitors were recorded.

RESULTS

Floral Biology

During our study, flowering of *T. discolor* started and ended between December 23, 2000 and January 4, 2001, although some plants began producing new inflorescences and probably had a second flowering period starting in late January after a gap in flowering. We have also observed flowering in April-May 2000

and in June 2001 on San Salvador Island. Correll and Correll (1982) note that *T. discolor* flowers throughout the year.

T. discolor has small white flowers that are displayed on 6-13 cm spikes (racemes). Spikes typically had 15-30 open flowers each day. Flowers are either male (staminate) or female (pistillate); we found no bisexual (hermaphroditic) flowers. Male flowers had 8 stamens and an undeveloped pistil. Female flowers had 8 staminodes (nonfunctional stamens) and one pistil with three carpels, each containing one ovule. Four flowers can develop at each bud node on the inflorescence spike and a single node can produce both male and female flowers over time.

Based on marked individual flowers, the phenology of a female flower is as follows: on day 1, the corolla opens, stigmas are exerted and look receptive; on day 2, the corolla is closed but the stigmas remain splayed open and look receptive; on day 3, the stigmas are brown. The phenology of a male flower is as follows: on day 1, the corolla opens, stamens are exerted, and pollen is released; on day 2, the flowers are brown and senescent; on day 3, flowers have fallen.

Each flower had one large nectary gland that produced nectar. Average standing crop nectar per flower was 0.40 microliters (S.D.=0.101, N=10 flowers). Male and female flowers had similar amounts of nectar, but larger sample sizes and bagged flowers are needed to test whether nectar production varies between the floral sexes.

Fruits are three-parted schizocarps that consist of winged samara-like mericarps 8-12 cm long (Correll and Correll 1982, pers. observations). When the fruits mature, the samaras separate and are each wind-dispersed. Each samara contains one seed.

Breeding System and Sex Ratios

On day 1 of the study, we tagged five plants that appeared to have only male (staminate) flowers and four plants with flowers that appeared to be bisexual. The male flowers were unambiguously male; the pistils were undeveloped and stamens were dispersing pollen. The "bisexual" flowers were ambiguous because the corolla was closed around the

stamens and no pollen could be seen. These flowers had well-developed pistils and the three-parted stigma was exerted beyond the corolla and was splayed open and clearly had female function. Closer examination of the flowers with a dissecting microscope revealed that the stamens had no pollen and were staminodes (nonfunctional stamens). Therefore, these four plants with "bisexual" flowers were functionally female. The population appeared to be dioecious, with separate male and female plants (Table 1).

Table 1. Sex phases of *Thouinia discolor* over days. F=female (pistillate) phase; M=male (staminate) phase, -- means no functional flowers; Plant code shown; N = Number of inflorescences tagged and monitored.

Plant	N	Day 1	Day 2-3	Day 4
1	8	M	F	M
5	2	M	F	--
6	4	M	F	M
8	1	M	F	--
9	1	M	F	M
2	5	F	M	F
3	5	F	M	--
4	2	F	M	--
7	2	F	M	F

The same plants were reexamined the next day, and we found that the five formerly "male" plants now had only female flowers and that the four formerly "female" plants now had only male flowers (Table 1). Therefore, each plant had switched sex by producing open flowers of the opposite sex. Subsequently, we examined each plant carefully to determine if opposite sex or bisexual flowers were present. We occasionally found plants with a few (2-3) male and female flowers open at the same time, but this co-occurrence of the sexes was infrequent. However, some small overlap in the sex phases can occur within a plant.

Over the flowering period, four plants made only one switch in sex phase (M-F or F-M), but five plants made two switches (Table 1). Two plants switched from female to male to

female (F-M-F) and three plants switched from male to female to male (M-F-M) (Table 1). After these switches, flowering stopped (Table 1). However, at the end of the study in mid-January, some plants were forming new buds for a second period of flowering.

The ratio of the sex phases (Male or Female) was nearly 50:50 (4:5) on each day (Table 1). The floral sex ratio for plants in this population during this flowering period was female biased; the frequency of female flowers was 0.63 (6 plants, 615 flowers).

Fruit Set

On average, 34% of the female flowers set fruit (S.D. = 17.8, range 11-59% for different plants) (7 plants, 22 inflorescences, 389 female flowers). Flowers that produced fruit had an average of 2.24 samaras (seeds) per flower, so the percent of ovules producing seeds was 75% (8 plants, 140 flowers).

Flower Visitors

During this study, we observed only two flower visits, and these were by wasps that appeared to be collecting nectar. The wasps were tentatively identified as a *Polistes* species and as *Campsomeris trifasciata nassauensis* Bradley (Scoliidae) by comparison with specimens in the insect collection at the Gerace Research Center and descriptions by Elliott (1993). The *Polistes* wasp moved systematically from flower to flower over one inflorescence. Unidentified caterpillars ate flowers and developing fruits of several inflorescences on two tagged plants.

DISCUSSION

These results demonstrate that Three Fingers, *Thouinia discolor*, exhibits a monoecious breeding system, *i.e.* male and female flowers occur on the same plant. We found no functionally bisexual flowers; female flowers had staminodes (nonfunctional stamens) and male flowers had undeveloped pistils. However, we found that the sexes are temporally separated, such that the plants appear to be dioecious (either male or female) at any one time. This sexual system has been termed "temporal dioecy," which is defined as a

temporal alteration of male (pollen presentation) and female (stigma receptivity) function within an individual plant through a single flowering season (Cruden and Hermann-Parker 1977, Cruden 1988).

Although temporal dioecy is very descriptive of sex phase switching by plants, the term does not reflect the biological sexual system, which is monoecy, *i.e.* each plant can function as both male and female. Other terms used for temporal dioecy are based on the word, dichogamy, which originally was used to refer to the temporal separation of sex function *within a flower*. These terms include second-order dichogamy, interfloral dichogamy or holodichogamy, all of which describe the temporal separation of flowers with different sexes *within a plant* (Cruden 1988). We have chosen to use "temporal dioecy" because this more clearly denotes the dramatic change in sexual phases and is a more broadly understandable term.

Temporal dioecy is fairly unusual in angiosperms in general but is relatively common in the Sapindaceae (Cruden 1988, Ajuri *et al.* 1998). The other species of Sapindaceae in the Bahamas are described as being hermaphroditic, polygamodioecious or dioecious (Correll and Correll 1982). Further studies might show that some of these species are monoecious and exhibit temporal dioecy.

The duration of the sex phases has been found to vary greatly between different species. Durations can vary from long (5-11 day) phases in each sexual stage, to long male (staminate) phases and short female (pistillate) phases, to short phases (one day or less) in each sexual stage (Cruden 1988). *T. discolor* fits the latter category with plants staying only one day in the male phase and two days in the female stage. The number of switches between sex phases can also vary. Species can exhibit heterodichogamy (switch only once in mid-season) or duodichogamy with two switches (Cruden 1988). In this *T. discolor* population, plants exhibited duodichogamy. Most *T. discolor* shrubs (5/9 individuals) exhibited at least two switches, either male-female-male or female-male-female, during one flowering period. Duodichogamy appears to be common in the Sapindaceae (Bawa 1977, Cruden 1988). In this

population, some plants started producing new buds for a second flowering period after a gap in flowering, and these plants will exhibit more switches. Whether plants "reset" sex phase flowering after gaps in flowering has not been documented.

The sex phase ratio plants for *T. discolor* was nearly 50:50 (male:female). This 50:50 ratio fits Fisher's prediction of equal distribution of sexes (Fisher 1930) and is typically found for plants of temporally dioecious species (Cruden 1988). However, the floral sex ratio was somewhat female biased (the frequency of female flowers on a plant was 0.63). In monoecious species, larger plants or plants with high resources typically show more female-biased floral sex ratios because seed production requires higher resources than pollen production (Lloyd and Bawa 1984, Richards 1997, Rathcke and Kass, this volume). In this study, the population of *T. discolor* may have been in a relatively high resource environment because the field had recently been abandoned from agriculture and shrubs were growing in full sunlight. Whether flower production becomes more male-biased in shaded or lower resource environments remains to be determined.

Temporal dioecy may be an adaptation to avoid self-pollination and inbreeding because the temporal separation of the sexual phases requires that plants are cross-pollinated (Cruden 1988). Whether, *T. discolor* is self-compatible is not known and not easily testable. However, temporal dioecism occurs most commonly among groups of plants that are self-compatible (Cruden 1988). *T. discolor* produces nectar and is insect-pollinated. Although flower visitors were rare and only two wasps were seen visiting flowers, fruit set was moderately high (33%) but it was also highly variable among plants (11-59% of flowers on different plants produced fruit). If a flower set fruit, it had a 75% probability that all three ovules would develop seeds suggesting that pollinator visits were effective. Other Sapindaceae species have been found to be pollinated by wasps and bees (Cruden 1988, Aluri *et al.* 1998). More studies are needed to determine if this species is specialized for wasp pollination and whether the high variability in fruit set represents pollination-limitation of some flowers.

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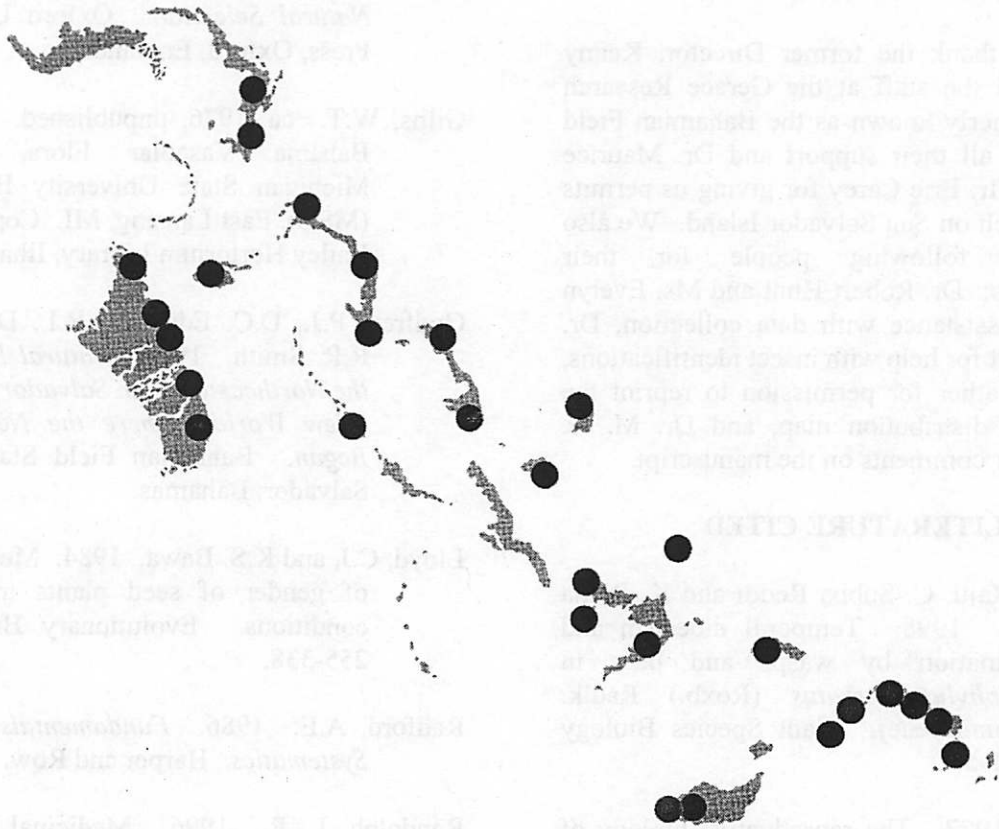


Figure 1. Distribution map for Three Fingers, *Thouinia discolor* Griseb. (Sapindaceae), in the Bahama Archipelago (from Gillis 1976). Dots denote where specimens have been collected. Reprinted here with permission of Dr. Alan Prather, Michigan State University Herbarium (MSC), East Lansing, MI.