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THE FLORAL BIOLOGY AND POLLINATION OF STRONGBACK, *BOURRERIA SUCCULENTA* (BORAGINACEAE), ON SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

Strongback, *Bourreria succulenta* Jacq. (= *B. ovata* Miers) (Boraginaceae), is a common shrub that grows in scrublands coppice in the Bahamas, Cuba, and Florida. The leaves are used medicinally, and its fruits are eaten by birds and people. Here we present the first description of its floral biology, breeding system, pollinators, and fruit set from a population growing on San Salvador Island, the Bahamas. Our pollination studies demonstrate that plants are self-incompatible and require outcross pollen and pollinators for fruit set. Flowers last for two days, changing from white to beige from day 1 to day 2 of floral life. Strongback appears to be mostly butterfly-pollinated, although birds (Bahama Woodstars and Bananaquits) were also observed to visit flowers. The floral traits of Strongback closely match those described for a butterfly-pollination syndrome except for higher nectar production which may reflect the importance of bird pollination for this species on this island.

In 1996 fruit set was strongly pollination-limited, and in both 1996 and 1999 fruit set was further reduced to only 7% and 11% because of fruit predation by a Gelechid moth caterpillar. These results demonstrate that even common plants on small islands, such as San Salvador (150 km^2), can be vulnerable to changes in their interactions with their pollinators or predators. This vulnerability could contribute to the higher extinction rates of species that are assumed to occur on islands.

INTRODUCTION

Islands have been of great interest to ecologists and evolutionists because islands often have fewer species than mainland populations and have different sets of species or different environmental conditions that can drive the evolution of unique traits. Islands typically have fewer, different pollinator species than mainland populations (Carlquist, 1974; Woodell, 1979; Feinsinger, *et al.*, 1982; Spears, 1987; Elmqvist *et al.*, 1992; Inoue, 1993; Barrett, 1996). Changes in the species or abundances of pollinators can promote the evolution of different pollination syndromes (floral traits adapted to a pollinator type) and breeding systems *(e.g.*, Carlquist, 1974; Inoue 1993). About 60% of the plant species on San Salvador are estimated to have come from the Caribbean area and 30-35% from the Florida mainland (Smith 1993), but the floral biology and pollination biology of many Bahamian plants have not been described, so data are not available for island-mainland comparisons (see Rathcke, *et al.* 1996).

Strongback or Strongbark, *Bourreria succulenta* Jacq. (= *B. ovata* Miers) (Boraginaceae), is a shrub or small tree that grows in scrublands on all of the Bahama Islands, Cuba, and Florida (Correll and Correll, 1982; Al-Shehbaz, 1991; Wunderlin, 1998). On San Salvador, Strongback is a common shrub in the Blacklands coppice (Smith, 1993). As the name Strongback implies, people on San Salvador use this plant medicinally. Strongback users mix the leaves with other herbs and make a tea they drink to keep them strong (White, 1985). The leaves are also boiled and used to alleviate back and waist pains (Jordan, 1986). The sweet red fruits are eaten by birds and people (Scurlock, 1987).

Here we provide the first published description of the floral biology, breeding system and pollination of Strongback on San Salvador Island, Bahamas. We describe floral traits, including phenology, morphology, and nectar. We did pollination experiments to determine the breeding system and to test for pollination limitation of fruit set. We report on visitors to flowers (potential pollinators), present a description of the pollination syndrome, and describe a flower/fruit predator and its effect on fruit set.

METHODS

Our study site was located near the Bahamian Field Station on the northeastern coast of San Salvador Island. We studied Strongback shrubs growing along the path to Reckley Hill Pond southeast of the Bahamian Field Station. The coppice is virtually impenetrable and paths have been cut to enable one to walk through the vegetation. Twelve shrubs along the trail to Reckley Hill Pond have been permanently tagged and were followed from December 19, 1996 to January 5, 1997, a period which included the major flowering of this species.

To describe the flowering display of Strongback, the number of new (white, first-day) flowers per day was counted for each shrub on most days during the study. The development of individually-marked flowers was followed throughout the day on several plants. The viability of pollen from flowers of different ages was tested using Alexander's stain (Kearns and Inouye, 1993).

To describe the breeding system, at least four budded inflorescences (cymes) per shrub were tagged and assigned to one of four pollination treatments. 1) To determine if flowers can self-pollinate and self-fertilize, buds were bagged with bridal-veil netting and left unmanipulated (Bagged, No Hand-pollination Treatment). 2) To determine if plants are self-compatible, buds were bagged and flowers were hand-pollinated with self-pollen from within the same flower (Bagged, Self-pollen Added Treatment). 3) To determine a maximum fruit set with cross-pollen, open flowers were augmented with cross-pollen collected from at least one individual at least four meters distant (Open, Cross-pollen Added Treatment, P+). Flowers were selfed or outcrossed during the morning of the first day of flower opening when stigmas looked glistening and were sticky. 4) To determine fruit set under natural pollination, flowers were left exposed (Open, Natural Pollination or Control Treatment, NP). Each of the twelve shrubs had one full set of the four pollination treatments.

Subsequent fruit set was monitored for all pollination treatments. Fruit set was calculated as % Fruit set = 100 (fruits/flowers). Fruit set was based on the development and expansion of the ovary because the study had to be terminated before any fruits had matured. Any flowers that were ambiguous as to ovary development or loss were excluded from the calculation of fruit set.

We tested for pollination limitation by comparing fruit set of naturally-pollinated (NP; control) flowers with flowers that had been augmented with cross-pollen (P+) so that pollen was not limiting (see Rathcke, 2000).

Nectar in flowers of known ages was measured using 5 microliter capillary tubes. A Bellingham Refractometer was used to measure sugar concentrations. Brix values were converted to sucrose-equivalents (Bolten *et al.*, 1979). Nectar production was measured in flowers bagged with bridal-veil netting.

All visitors to flowers of Strongback were recorded during ten days of study in December 1996. In June 1999, visitors were recorded to an individual shrub that was flowering on the Bahamian Field Station grounds. In November 1999, Nancy Elliott recorded insect visitors to flowers. Nomenclature for insect visitors is based on Riley, 1975; Elliott, 1993; and Smith *et al.*, 1994.

Statistics were done using Systat version 5.01. Significant differences were tested using Student's t-tests. Percentage data were arcsine transformed to normalize their distributions for statistical tests.

RESULTS

Flowering Phenology

Strongback shrubs showed major flowering in December 1996 and November 1999. On December 19, 1996 some shrubs were ending flowering and others were beginning flowering. By January 5, 1997, most shrubs had ceased flowering. In 1999, shrubs were flowering abundantly in mid-November (N. Elliott, pers. obs.) and had ceased flowering by December 6 or were in decline (B. Rathcke, pers. obs.). Minor flowering can occur at other times on San Salvador. For example, in June 1999 we saw four individuals in flower during general surveys along paths in three different sites (Reckley Hill Pond, Osprey Pond, and Hard Bargain Trail), but no individuals were flowering along the Reckley Hill Pond trail (>20 individuals); none of the permanently tagged shrubs were flowering. The species is described as flowering throughout the year (Correll and Correll, 1982; Scurlock, 1987; Wunderlin, 1998). Our observations on San Salvador indicate that Strongback has a major peak of flowering in winter (November-December). However, the abundant flowering we observed in winters 1996 and 1999 may be in response to earlier hurricanes in these two years.

In December 1996, Strongback showed unusually intense flowering throughout the island (Rathcke, in press). In the study site, most shrubs observed were in flower, and individual shrubs had an average of 10.6 white, first-day flowers per day (SD = 8.60, range = 2-30, N = 12 plants; 7 census days). This intense flowering was subsequent to three hurricanes on San Salvador. Hurricane Bertha in July and Hurricane Fran in September caused little damage (Bahamas Department of Meteorology, undated), but on October 19, 1996 the eye of Hurricane Lili (a Category 2 storm) passed directly over the island with winds up to 105 miles per hour (Bahamas Department of Meteorology, undated). It stripped many trees of their leaves (Murphy *et al.*, 1998) including Strongback. In December, 1996 almost all the older leaves of Strongback marked previously for a leaf demography study were gone and most leaves were new (pers. obs.). In November 1999 flowering was also unusually abundant (N. Elliott, pers. comm.), and this was subsequent to Hurricane Floyd, an intense Category 4 hurricane, that passed over San Salvador on September 14, 1999.

Floral Biology and Breeding System

Strongback flowers are white and fragrant. Flowers have a salverform corolla (Correll and Correll, 1982); the petals are fused at the bottom to form a slender tube and expand into a flat, 5-lobed top (Kass, 1991). The floral tube is 0.9 cm long (SD = 0.05, N = 10 flowers) and the corolla is 1.5 cm wide (SD = 0.8, N = 16 flowers). Flowers have five stamens on the corolla tube and a 4-celled ovary (Correll and Correll, 1982). Fruits are red drupes, 10-15 mm. in diameter (Correll and Correll, 1982).

Flowers are displayed in cymes and have an average of 12 total flowers per cyme (SD = 4.7, range = 3-21, N = 12; 12 plants, 44 inflorescences). Flowers last two days (are in anthesis) and are creamy white the first day, changing to beige the second day. Each cyme typically had only two first-day (white) flowers open on the same day. The phenology of an individual Strongback flower is as follows: a flower remains open (in anthesis) for 1.5-2 days. During the first day the corolla is creamy white.

Anthers initially appear white due to exposure of the white pollen as the anthers dehisce. Later in the day, the anthers begin to turn brown as the pollen is dispersed. The stigma is covered with a green, gelatinous mass during the first day. During the second day, the corolla turns beige, the anthers are usually brown, and the stigma is unchanged or occasionally becomes dry. The corolla sometimes falls on the second day, although in some cases the corolla turns brown and persists as the fruit develops.

Nectar volume and milligrams sugar (sucrose-equivalents) per day per flower were greater for first-day flowers than second-day flowers, but sucrose-concentration (mg/ml) was similar (Table 1).

Pollen from both first-day (white) and second-day (beige) Strongback flowers was viable based on Alexander's stain (Kearns and Inouye, 1993). Viability (the percent of pollen grains that turned pink with the stain) was estimated to be 95% for first-day flowers (N=75 pollen grains) and 84% for second-day flowers (N=38 pollen grains).

Flowers are hermaphroditic (i.e. perfect), having both male and female parts. Although flowers can self-pollinate, plants are self-incompatible and require outcross pollen for fruit set (Table 2). Bagged flowers with self-pollen added to stigmas did not produce fruit whereas most of the flowers with added cross-pollen developed fruit (Table 2). Flowers that were bagged and unmanipulated also did not produce fruit.

Fruit set was significantly pollination-limited: fruit set of flowers with augmented pollen was significantly greater than the fruit set of flowers that were naturally pollinated (Table 2).

Flower Visitors

During December 1996 and January 1997, flower visitors to Strongback were rarely seen but over the ten days of study, the following visitor species were recorded: one Pierid butterfly (possibly *Kricogonia lyside*), two wasps, one large black bee (possibly a carpenter bee, *Xylocopa (Neoxylocopa) cubaecola* Lucas) (Elliott, 1993), two warblers (including one Yellow Warbler, *Dendroica petechia* (Emberizidae, Parulinae) and one Bananaquit, also called the Bahama Honeycreeper, (*Coereba flaveola*: Emberizidae, Coerebinae).

In June 1999 during the 8th Symposium on the Natural History of the Bahamas, Bahama Woodstars (*Calliphlox evelynae*: Trochilidae) were observed regularly visiting flowers of one Strongback shrub growing on the grounds of the Bahamian Field Station. No other flower visitors were observed, but cymes had an average of 14 fruits which was high (SD = 7.3, N = 16). The nearest other known flowering Strongback was several hundred meters away suggesting that pollen dispersal had to be over a relatively long distance because plants are self-incompatible.

In November 1999, N. Elliott observed a few butterflies visiting Strongback flowers, and she recorded the following butterfly species (see Table 3 for complete nomenclature): *Kricogonia lyside*, *Ascia monuste*, *Battus polydamus lucayus*, and *Agraulis vanillae insularis*. She also observed the butterfly, *Lucinia sida albomaculata* Rindge (Nymphalidae), on old flowers or young fruits. She observed one wasp species, *Campsomeris trifasciata nassauensis* Bradley (Scoliidae), visiting flowers.

Pollination Syndrome

Butterflies are the most commonly recorded visitors to Strongback flowers. The floral traits of Strongback closely match the traits characteristic of a butterfly-pollination syndrome (Howe and Westley, 1988), except for nectar (Table 4). Nectar volume/flower/day is much higher than the 0.1-2.3 microliters per flower reported by Opler (1983), sugar production per day is much higher than the 0.024-0.73 mg sugar/flower reported by Cruden *et al.* (1983), and sugar concentration (in sucrose-equivalents) is at the high end of values (range 14% - 29%) reported by Baker and Baker

Table 1. Nectar production per flower of Strongback, *Bourreria succulenta*, on San Salvador, Bahamas. Volume, concentration and mg of sucrose (sucrose-equivalents) are shown for flowers after the first day and after the second day of floral life. Means ± Standard Deviations are shown. Probability levels and significant differences are based on Student's t-tests. NS = not statistically significant; * $P \leq 0.10$.

	FLOWER AGE		
NECTAR	DAY 1	DAY 2	P-levels
Volume (microliters/flower/day)	10.2 ± 5.48	6.6 ± 4.89	0.04 *
Concentration (mg/ml)	28% ± 6.3	31% ± 8.6	0.32 NS
Mg sucrose-equivalents/flower/day	2.87 ± 1.70	2.00 ± 1.47	0.10 *
Number of flowers	46	12	

Table 2. Breeding system and pollination limitation of Strongback, *Bourreria succulenta*, on San Salvador, Bahamas. % Fruit set = 100 (fruit/flowers). Means and Standard Deviations are shown. *N* = number of. Fruit sets of treatments with Cross-pollen added and Natural pollination are significantly different (Student's t-test on arcsine transformed data, *N* = 12 plants, *** $P < 0.0001$).

TREATMENT	N plants	N flowers	% Fruit set
Bagged, Self-pollen added	12	49	0
Bagged, No hand-pollination	12	97	0
Open, Cross-pollen added	12	74	77 ± 20.6***
Open, Natural pollination	12	43	22 ± 23.7***

(1983) for butterfly-pollinated plants. Birds were also occasional visitors to Strongback flowers, but the floral traits of Strongback do not closely match those predicted for a bird-pollination syndrome (Table 4). Nectar volume per flower per day of Strongback is much lower that the 100 microliters or greater reported for most bird-pollinated flowers (Baker, 1975; Feinsinger, 1983; Opler, 1983; Rathcke, in press), and the sugar concentration is much higher than the 20% reported for bird-pollinated plants (Baker, 1975; Bolten and Feinsinger, 1978; Feinsinger, 1983; Opler, 1983).

Flower/Fruit Predator

A small moth caterpillar was abundant in the flowers and developing fruit in December 1996, June 1999, and December 1999. Larvae bored into the buds or entered the flowers and ate the filaments and style and ovaries or bored directly into the developing ovary. Specimens of the caterpillars were deposited in the insect collection at the Bahamian Field Station and at the Smithsonian Institution. David Adamski at the Smithsonian Institution identified the larvae to the family level as Gelechiidae and believes it is likely to be an undescribed species. No adult Gelechid moths are in the insect collection at the Bahamian Field Station, and an adult male will be necessary for a positive identification.

DISCUSSION

Strongback requires outcross pollen for fruit set and depends upon animal pollinators.

Table 3. Lepidopteran species (butterflies and skippers) observed visiting flowers of Strongback, *Bourreria succulenta*, in the Bahamas. All species occur on San Salvador Island although subspecies may differ (Elliott 1993).

Family	Species	Common Name
Hesperiidae	*Ephyriades brunnea brunnea* (Herrich-Schaeffer)[1]	Dusky Wing Skipper
	Wallengrenia sp.[1]	skipper
Lycaenidae	*Strymon acis armouri* Clench[1]	Drury's Hairstreak
	Hemiargus thomasi bahamensis Clench[1]	Thomas's Blue
Pieridae	*Phoebis agarithe antillia* F.M. Brown[1]	Large Orange Sulphur
	Ascia monuste L.[3]	Great Southern White
	Kricogonia lyside (Godart)[1,3]	Guayacan Sulphur
Papilionidae	*Battus polydamus lucayus* Rothschild and Jordan[3]	Polydamas Swallowtail
	Heraclides andraemon bonhotei (E. Sharpe)[1] (formerly in *Papilio*)	Bahamian Swallowtail
Satyridae	*Calisto herophile* Huebner[2]	Common Ringlet
Nymphalidae	*Euptoieta hegesia hegesia* Cramer[3]	Mexican Fritillary
Heliconiidae	*Agraulis vanillae insularis* Maynard[1,3] (formerly in *Dione*)	Gulf Fritillary
Heliconiidae	*Dryas iulia carteri* (Riley)[1]	Flambeau, Orange Julia

[1] recorded by Miller *et al.* (1992) on Crooked, Acklins or Mayaguana Islands
[2] reported by Campbell (1978) on New Providence
[3] observed by N.B. Elliott on San Salvador in November 1999

Most evidence suggests that Strongback is mainly butterfly-pollinated, although we observed a few bees and birds visiting flowers. We recorded four butterfly species visiting Strongback flowers on San Salvador (Table 3), although they were rare visitors, especially in 1996. Miller, *et al.* (1992) recorded ten butterfly species visiting Strongback flowers on Crooked, Acklins, and Mayaguana Islands (Table 3). In Florida, butterflies are frequent visitors (Scurlock, 1987). On New Providence, Campbell (1978) considered Strongback to be one of the "butterfly trees" of the scrublands coppice on New Providence Island. In his book, The Ephemeral Islands, Campbell (1978) describes how the white fragrant flowers attract hundreds of ringlet butterflies (*Calisto herophile*) and writes that "sometimes towards the end of a long, hot summer afternoon, the flowering Strongback seems covered with a storm of brown flowers, for it is one of the "butterfly trees" of the coppice and its fragrant white flowers attract hundreds of fast flying ringlet butterflies (*Calisto herophile*)". San Salvador has a subspecies of the Common Ringlet, *Callisto herophile apollinis* Bates (Satyridae) (Elliott, 1993), but it is not common (Riley, 1975; Elliott *et al.*, 1980). However, forty-three butterfly species have been collected on San Salvador (Elliott *et al.*, 1980, pers. comm., and cited in Deyrup 1998). Many butterfly species are abundant and could be common pollinators. A carpenter bee (*Xylocopa*) was seen visiting flowers. In Florida, a carpenter bee, *Xylocopa micens*, was caught visiting Strongback flowers (Pascarella, pers. comm.). Honeybees (*Apis mellifera*) and Bumblebees (*Bombus* species) are absent on San Salvador (Elliott 1993), and other bees are infrequent visitors to shrubs in the coppice

Table 4. The pollination syndrome of Strongback, *Bourreria succulenta*, on San Salvador, Bahamas compared to the floral traits characteristic of a butterfly-pollination syndrome and a bird-pollination syndrome (based on Howe and Westley 1988; see also text for discussion). *indicates a match between Strongback and the butterfly-pollination syndrome. Conc. (nectar concentration) = mg/ml sucrose-equivalents of nectar. Vol. (nectar volume) = microliters/flower/day. Anthesis = flower opening.

Traits	Strongback	Butterfly	Bird
Color	*white, turning beige	*variable; often pink	Vivid; often red
Odor	*very sweetly fragrant	*sweet	None
Shape	*tubular corolla, .9 cm	*deep corolla tube or spur	*tubular corolla
	*radial symmetry	*radial symmetry	*radial or bilateral
Anthesis	*day	*day/night	*day
Nectar			
Concentration	*29 %	14-*29 %	c. 20 %
Volume	10 microliters/flower/day	0.1-2.3	>100

(pers. obs.) and are unlikely to be major pollinators of Strongback.

Birds may also be pollinators of Strongback. In June 1999 we observed Bahama Woodstars regularly visiting the flowers of a single Strongback shrub. We saw no other visitors and fruit set was abundant suggesting that these birds were effective pollinators. The nearest other known flowering Strongback was several hundred meters away, so pollen had to be dispersed over a long distance, which is quite possible for these birds. We also observed a Bananaquit visit flowers in December 1996. Whether Bahama Woodstars or Bananaquits typically act as effective pollinators remains to be determined.

Pollination by very different pollinator types, such as butterflies and birds, is not particularly surprising. Evidence is accruing that plants often have many more pollinator species than indicated by a syndrome analysis and that floral traits do not always fit the predictions from classic syndromes (Herrera, 1996; Ollerton, 1996; Waser *et al.*, 1996). The question that arises is whether these different pollinators select for compromise traits, *i.e.*, traits that do not fit either pollinator type well. For Strongback, most floral traits fit those predicted by a classic butterfly-pollination syndrome, except for nectar (Table 4). Nectar volume is higher than that predicted for butterfly-pollinated species and is lower than that predicted for bird-pollinated species, perhaps indicating some selective compromise in Strongback for attracting bird pollinators in addition to butterfly pollinators.

Despite unusually abundant Strongback flowering in winter 1996-7, flowers were seldom visited, and fruit set was strongly pollination-limited. Such pollination limitation more typically occurs in plants that are specialized and dependent upon a few pollinator species (Rathcke and Jules, 1993; Rathcke, 1998). In contrast, Strongback appears to have many potential pollinators (many butterfly species, bees, and two bird species) that are generalists on many flowering plant species. These results demonstrate that pollination limitation can occur for plant species that has many potential pollinator species and different types of pollinators.

Fruit set of Strongback was also predation-limited. A moth caterpillar destroyed many flowers and ovaries causing very low fruit set in 1996 (7%) and 1999 (9%) (Rathcke, in press). The strong pollination-limitation of fruit set in 1996 and predation-limitation of fruit set in

1996 and 1999 demonstrate that a common shrub can experience nearly total failure of fruit set.

Whether Strongback experiences similar risks of pollination- or predation-limitation of fruit set on other, larger islands or mainland areas would be interesting to investigate and remains to be determined. Islands typically have fewer pollinator species than mainlands (Carlquist, 1974; Woodell, 1979; Feinsinger *et al.*, 1982; Spears, 1987; Elmqvist *et al.*, 1992; Inoue, 1993; Barrett, 1996), and small islands, like San Salvador (150 km^2) may be especially depauperate. Pollinators have been found to be less reliable for plants on islands than on mainlands (Spears 1987) although other studies have found no significant differences (Feinsinger *et al.*, 1982). If pollination limitation of fruit set is more common for plant populations on islands than on mainlands, this could help account for the higher extinction rates postulated to occur on smaller islands (MacArthur and Wilson, 1967). If the failures of fruit set documented for Strongback commonly occur, such failures could significantly reduce the probability of the recruitment of new individuals into the population. Fruit failure could be especially detrimental to recruitment when it occurs after hurricanes that open up forest canopies and provide opportunities for plant recruitment (Rathcke, 1998; Rathcke, 2000). The results of this study emphasize that species on small islands may be especially vulnerable to habitat and species changes (Eshbaugh and Wilson, 1996). These results also demonstrate that a consideration of plant-animal interactions, including both pollinators and predators, may be necessary to predict the future persistence and success of plant species, especially on oceanic islands and in fragmented terrestrial "island" habitats.

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