

Pollination and Predation Limit Fruit Set in a Shrub, *Bouyeria succulenta* (Boraginaceae), after Hurricanes on San Salvador Island, Bahamas¹

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ABSTRACT

Hurricanes have been assumed to reduce the reproduction of plants, either directly by leaf stripping and stress or indirectly by reducing pollinators. I examined the pollination and fruit set of a common shrub, *Bouyeria succulenta*, after hurricanes on San Salvador island, Bahamas. Contrary to the assumption of resource limitation, *B. succulenta* showed unusually prolific flowering after Hurricane Lili stripped leaves from most of the plants in October 1996. I predicted that the abundant flowering would saturate pollinators and that fruit set would be pollination-limited. Fruit set was strongly pollination-limited by 71 percent. Butterflies are probably the major pollinators and were present at the site, but they rarely visited *B. succulenta* flowers even though flowers were brimming with nectar. Nectarivorous birds (Bananaquits and Bahama Woodstars) visit *B. succulenta* flowers, but their populations were decimated by Hurricane Lili and they rarely visited flowers during this time. Fruit set was also severely predation-limited; a moth caterpillar (Gelechiidae) was extremely abundant and ate buds, flowers, and fruits, causing a further 68 percent reduction in fruit set. Together, pollination limitation and predation limitation reduced fruit set to only 7 percent or less. Predation was also intense in 1999 after Hurricane Floyd and resulted in 11 percent fruit set or less. Whether or not hurricanes were the cause of limited pollinators or abundant predators, the resulting low fruit set could have population effects because hurricanes can provide opportunities for the recruitment of new plants. These results emphasize that understanding plant–animal interactions may be necessary for predicting the effects of hurricanes on plant reproductive success, which may affect subsequent recruitment. Species on small islands like San Salvador (150 km²) with relatively few species may be especially vulnerable to environmental disturbances such as hurricanes.

Key words: Bahamas; *Bouyeria*; flower predation; fruit predation; fruit set; hurricane effects; island pollination; plant–animal interactions; pollination limitation; scrublands.

UNDERSTANDING THE EFFECTS OF HURRICANES ON PLANTS is a topic that has received much recent attention. Studies have documented that hurricanes can strip plants of their leaves and provide other stresses, such as high rainfall, high winds, or salt spray, which destroy flower and fruit resources for some time afterwards (Reilly 1991, Walker *et al.* 1992, Boose *et al.* 1994, Zimmerman *et al.* 1994, Bronstein & Hossert-McKey 1995, Grant *et al.* 1997, Pascarella 1998a). These stresses might also be expected to decrease the ability of plants to produce flowers or fruit after the hurricane; however, subsequent flower production after hurricanes was not significantly reduced in an orchid (Ackerman & Moya 1996), a fig species (Bronstein & Hossert-McKey 1995), or *Pavonia bahamensis* on San Salvador, Bahamas (Rathcke 2000a,b), and even increased in a shrub (Pascarella 1998b). In addition, fruit set did not appear to be resource-limited in two of these species, the orchid and fig (Bronstein & Hossert-McKey 1995, Ackerman & Moya

1996), although resource limitation significantly reduced fruit set for *P. bahamensis* (Rathcke 1998, 2000a).

Fruit set also can be limited indirectly by hurricanes if pollinator populations are reduced. Many studies have shown that hurricanes commonly devastate populations of nectarivorous birds, and researchers have assumed that this occurs because these birds are left with few nectar or fruit resources (Askins & Ewert 1991, Lynch 1991, Waide 1991, Will 1991, Wauer & Wunderle 1992, Wunderle *et al.* 1992, Wunderle 1995, Murphy *et al.* 1998). One study has demonstrated that this decline in nectarivorous birds can cause pollination limitation of fruit set (Rathcke 1998, 2000a); however, other pollinators, such as insects, have been found to rebound quickly or perhaps even increase because of hurricane effects. A hawkmoth pollinator of an orchid appeared to become a more common visitor after a hurricane although pollen deposition was lower (Ackerman & Moya 1996). Fig wasps appeared to return to pre-hurricane levels within months after Hurricane Hugo (category 4) in Florida (Bronstein & Hossert-McKey 1995). No

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change in the pollinator community was found in pre- and post-hurricane surveys of a tropical shrub (Pascarella 1998b). Responses by insects to hurricanes are likely to be highly specific and may tend to be positive, whereas responses of nectarivorous birds may be generally negative. Whether insect-pollinated plants typically have a lower risk of pollination limitation than bird-pollinated plants after hurricanes remains to be documented.

Because island species often have fewer pollinators than mainland species (Carlquist 1974; Woodell 1979; Feinsinger *et al.* 1982, 1985; Spears 1987; Elmqvist *et al.* 1992; Inoue 1993; Barrett 1996), plants on small islands may be especially vulnerable to disturbances such as hurricanes that disrupt their pollinators or other mutualists (Rathcke 1998, 2000a). In general, environmental changes such as global warming, habitat destruction, or introduced species may have especially strong effects on islands (Loope & Mueller-Dombois 1989; *cf.* Simberloff 1995) because species are so few and little buffering and compensation is possible. Small islands such as San Salvador, which is only 150 km², may be especially vulnerable to environmental disturbances and species changes (Eshbaugh & Wilson 1996).

In this study, I documented the pollination and fruit set of a common shrub, *Bourreria succulenta* (Boraginaceae), or strongback, on San Salvador island, Bahamas, after three hurricanes in 1996. Following these hurricanes in December/January of 1996/1997, flowers of *B. succulenta* were unusually abundant and evident throughout the island (Rathcke *et al.* in press). In two earlier winter visits in 1994/1995 and 1995/1996, the species was flowering, but flowers were not especially abundant or remarkable. As a consequence, I decided to study its pollination and fruit set during this period of unusually heavy flowering. I hypothesized that fruit set may be pollination-limited because flowers were so abundant that they seemed likely to saturate the pollinators. I tested this hypothesis by measuring initial fruit set of naturally pollinated and pollen-augmented flowers. During the study, it became evident that flower/fruit predation was significant, so I quantified predation limitation of fruit set and compared the relative effects of both pollination and predation limitation of fruit. I also report on further observations on pollination and predation in June 1999 and in November/December 1999.

STUDY SPECIES

Bourreria succulenta Jacq. (= *B. ovata* Miers; Boraginaceae), strongback or strongbark, is a shrub or

small tree that grows throughout the Bahamas, Florida, and Cuba in scrublands coppice (Correll & Correll 1982, Al-Shehbaz 1991, Wunderlin 1998). The breeding system, floral biology, and pollination of this species have been described only recently (Rathcke *et al.* in press). Plants are self-incompatible, and flowers require an animal pollinator for fruit set. Flowers last two days; corollas are white on the first day and beige on the second day after anthesis. Flowers have a salverform corolla *ca* 1.5 cm in diameter with a short floral tube (*ca* 1 cm long) and are displayed in cymes (Correll & Correll 1982; Rathcke, pers. obs.). Abundant flowering occurred between mid-December and early January in 1996/1997, and during November/early December in 1999, although the species can flower sporadically throughout the year (Correll & Correll 1982, Scurlock 1987, Wunderlin 1998). A shrub typically displays 5–15 white flowers simultaneously during peak flowering. Fruits are red drupes. The leaves are used medicinally in teas for increasing strength (White 1985) and alleviating back and waist pain (Jordan 1986); the fruits are eaten by people and birds (Scurlock 1987).

STUDY SITE

San Salvador is one of the easternmost islands in the Bahama archipelago (24°05'N, 74°30'W) (Shaklee 1996). The island is *ca* 19 km long and 8 km wide (Smith 1993) and 150 km². The coolest months (January and February) average 22°C, and the warmest months (July and August) average 28°C (Shaklee 1996). Total mean annual rainfall is 1007 mm (Shaklee 1996).

The study site is located near the Bahamian Field Station at the northern end of San Salvador. I studied shrubs growing along the path to Reckley Hill Pond southeast of the Bahamian Field Station. *Bourreria succulenta* grows throughout the scrubland community (Blacklands Coppice), which is the most common vegetation type on San Salvador (Smith 1993). The scrubland coppice is diverse with no dominant species (Smith 1993) and is so dense that paths must be cut in order to walk through the vegetation.

HURRICANES ON SAN SALVADOR—In the Bahamas archipelago, hurricanes occur on average every three years; but in an unusually quiet period, no hurricanes affected San Salvador between 1981 and 1994 (Shaklee 1996). In 1995, one mild hurricane (Erin) passed west of San Salvador with winds up to 75 miles per hour, causing little damage. In

1996, three hurricanes struck San Salvador. Hurricane Bertha in July and Hurricane Fran in September caused little damage (Bahamas Department of Meteorology n.d.); but on October 19, the eye of Hurricane Lili passed directly over the island with winds up to 105 miles per hour and heavy rainfall (711 mm on San Salvador over four days starting 17 October; Bahamas Department of Meteorology n.d.). Lili was a category 2 storm and caused extensive damage to buildings. It stripped many trees of their leaves (Murphy *et al.* 1998) and was an unusually severe hurricane for the island. On 14 September 1999, Hurricane Floyd, an intense category 4 hurricane, passed directly over San Salvador with winds up to 150 miles per hour and dropped 196 mm of rain in one day on San Salvador (Bahamian Field Station records).

METHODS

Twelve *B. succulenta* trees at the study site were permanently tagged and followed from 19 December 1996 to 5 January 1997, which included the major flowering period. Abundant flowering also occurred in November/early December 1999 (N. Elliott, pers. comm.). I recorded fruit set for these and other trees in mid-December 1999. *Bourreria succulenta* flowers sporadically throughout the year (Correll & Correll 1982; Scurlock 1987; Wunderlin 1998; Rathcke, pers. obs.). For example, in June 1999, four individuals were seen flowering in extensive general surveys of the coppice at three sites (Reckley Hill Pond, Osprey Pond, and Hard Bargain Trail) in which hundreds of *B. succulenta* trees were surveyed.

Flower visitors were noted and recorded throughout the study in 1996/1997 and in June 1999. N. Elliott noted visitors in November 1999. In 1996/1997, spot surveys lasting about one minute per tree were made periodically throughout the day for all trees along the path. In addition, timed ten-minute watches of a known number of flowers were made on several occasions.

Standing crop of nectar was measured as an indicator of pollinator visitation. Standing crop of nectar was measured in exposed, unbagged flowers on the same plants at the same time as nectar production in bagged flowers was measured. Nectar in flowers was measured using 5-microliter capillary tubes. A Bellingham refractometer was used to measure sugar concentrations. Brix values were converted to sucrose equivalents according to Bolton *et al.* (1979).

To test for pollination limitation of fruit set, two

budded inflorescences (cymes) on each of 15 shrubs were tagged and assigned to one of two pollination treatments. (1) In the augmented cross-pollen treatment, cross-pollen from an individual at least 4 m distant was added to stigmas each day the stigma was glistening (usually two days). (2) In the natural pollination treatment, flowers were marked but were unmanipulated and exposed to natural pollination. Flower predators were removed; any inflorescences with predator damage were excluded.

Fruit set was calculated as: percent 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. Ten days after flower opening, it was apparent whether or not the ovary would develop or would fall. Many ovaries were 5–7 mm in diameter at the termination of this study. Mature fruit was 10–12 mm in diameter (Correll & Correll 1982). For the final assessment of fruit set, all buds that did not have sufficient time to potentially develop fruit or were ambiguous as to ovary development or loss, were excluded from the calculations of fruit set. These excluded buds consisted of unopened buds, recent flowers, and damaged or eaten buds, flowers, or developing fruit. Fruit set from control inflorescences was also calculated, taking into account both potential pollination limitation and predation. Fruit set from an additional random sample of 10 to 12 inflorescences/tree was also recorded to further quantify the fruit set of flowers exposed to natural pollination and predation.

A relative measure of pollination limitation (PL) of fruit set (Rathcke 2000a) was calculated by comparing the percent fruit sets (%FS) of pollen augmented (P+) flowers and naturally pollinated flowers (NP): $\%PL = 100(\%FS \text{ of } P+) - (\%FS \text{ of } NP)/(\%FS \text{ of } P+)$. If fruit set of naturally pollinated flowers and augmented flowers are equal, then PL = 0 percent. If fruit set is zero for naturally pollinated flowers and >0 for pollen-augmented flowers, then %PL equals 100 percent.

Because predation on buds, flowers, and developing fruit was common, I also calculated a relative predation limitation index (PRL) by comparing fruit sets of naturally pollinated flowers that had no predation in treatments (PR-) with naturally pollinated flowers that were exposed to predation: (PR+): $\%PRL = 100(\%FS \text{ of } PR-) - (\%FS \text{ of } PR+)/(\%FS \text{ of } PR-)$. If predation does not reduce fruit set, then %FS of PR+ = the %FS of PR- and the %PRL is zero. If predation kills all the

TABLE 1. Standing crop of nectar and nectar production is not significantly different, indicating low nectar removal from flowers of *Bourreria succulenta* (based on per-day measurements). Means, standard deviations, and numbers of plants and flowers are shown in parentheses. Means are not significantly different for any index; Student's *t*-tests, $P > 0.30$, $N = 7$ plants.

	Nectar/flower (μ l)	Sucrose equivalents	
		mg/ml	mg/flower
Standing crop (7, 21)	8 ± 5.4	0.29 ± 0.068	2.5 ± 1.64
Nectar production/day (7, 36)	10 ± 5.7	0.29 ± 0.070	3.0 ± 1.76

fruits (%FS of PR+ = 0), then %PRL = 100 percent.

Statistics were done using Systat version 5.01. Significant differences were tested with Student's *t*-tests. Data sets with percent fruit set were tested using arcsine-transformed values to normalize distributions. Sample sizes (*N*) are plants, each plant having many experimental flowers unless otherwise noted.

RESULTS

Fruit set was strongly pollination-limited (Table 2). Naturally pollinated flowers (with no predation) had 22 percent fruit set ($SD = 23.7$), whereas flowers with cross-pollen added had 77 percent fruit set ($SD = 20.6$; $P < 0.0001$; Student's *t*-test on arcsine-transformed data; $N = 12$ plants). Plants are self-incompatible and require pollinators for outcrossing and fruit set (Rathcke *et al.* in press).

This pollination limitation was caused by lack of flower visitors. Visitors to flowers were seldom observed in winter 1996/1997. During five days of one to four spot surveys of 30 plants and two ten-minute watches, no flower visitors were seen. While making other observations during the ten days of study, the following visitors were seen on flowers: one pierid butterfly (possibly *Kricogonia lyside* Godart), two wasps, one large black bee (possibly a carpenter bee, *Xylocopa* [*Neoxylocopa*] *cubaecola* Lucas; Elliott 1993), two warblers (including one Yellow Warbler, *Dendroica petechia*; Parulidae), and

one Bananaquit (*Coereba flaveola*; Emberizidae, Coerebinae). All of these individual visitors stayed only briefly on a plant, visiting one or a few flowers before leaving, except the Bananaquit, which visited four flowers and then visited a nearby red annelia (*Calliandra haematomma*). During this study, many butterflies (especially Pieridae and Lycaenidae) and wasps were seen flying close to the shrubs. These species almost never visited flowers of *B. succulenta*, although they visited flowers of other species. In November 1999, Nancy Elliott observed four butterfly species visiting flowers, although visits were infrequent (Rathcke *et al.* in press). Migratory warblers (especially Yellow Warblers) occasionally visited flowers of many species, but visits were infrequent and they seemed unlikely to be major pollinators of *B. succulenta* even during the winter season.

The lack of flower visitors during winter 1996/1997 is supported by lack of nectar removal from flowers. The standing crop of nectar (microliters) in open flowers measured at the end of the day was not significantly different than nectar production in bagged flowers over the same time period (Table 1). The sugar concentration of nectar (sucrose equivalents) was equivalent between open and bagged flowers; so total milligrams of sugar (measured as sucrose equivalents) was also not significantly different between open and bagged flowers (Table 1).

In 1996/1997, fruit set was strongly predation-limited by a moth caterpillar (Gelichiidae) (Table 2). Fruit set of flowers exposed to predation was 7

TABLE 2. Relative pollination limitation and predation limitation of fruit set in *Bourreria succulenta* on San Salvador island, Bahamas. Percent fruit set = % (fruit/flowers). Limitation shows the percent reduction of maximum fruit by pollination, predation, and both. See text for equations and discussion.

Limitation factor	Equation (%)	Limitation (%)
Pollination	$PL = (77 - 22)/77$	71
Predation	$PRL = (22 - 7)/22$	68
Pollination and Predation	$PPL = (77 - 7)/77$	91

percent (SD = 6.1, $N = 12$ plants), whereas fruit set of protected flowers with natural pollination was 22 percent (SD = 23.7, $N = 15$ plants; means were significantly different, $P = 0.03$, Student's t -test on arcsine-transformed data). The caterpillars bored into the buds or entered the flowers and ate the filaments and style and ovaries or bored directly into the developing ovary. Caterpillars moved between flowers and often damaged most of the flowers in a cyme. The gelichid caterpillar was probably an undescribed species (D. Davis & D. Adamski, pers. comm.).

Because of both pollination and predation limitation in 1996/1997, fruit set was very low (7%). Pollination limitation is estimated to have reduced fruit set by 71 percent, and predation is estimated to have further reduced fruit set by another 68 percent (Table 2). It is possible that predators would have limited fruit set to the same low level without pollination limitation occurring. Regardless of their interaction, pollination and predation limitation together are estimated to have reduced fruit set from its potential maximum by 91 percent (Table 2). In a larger survey of nonexperimental inflorescences on shrubs, fruit set with both pollination and predation limitation was estimated to be 7.3 percent (SD = 6.14, $N = 12$; 12 plants, 127 inflorescences, 1154 flowers). The 7 percent fruit set is probably a conservative value because predation continued after the study had to be terminated and may have caused a complete failure of fruit set.

In December 1999 after Hurricane Floyd, the gelechid caterpillar was abundant and again damaged or killed many buds and developing fruits. Fruit set was estimated to be 9 percent based on the average fruit per inflorescence on 10 December 1999 (1.11 ± 1.245 , $N = 14$; 14 plants, 270 inflorescences) and average inflorescence size in 1998 (12 ± 4.7 flowers, $N = 12$; 12 plants, 44 inflorescences). Further fruit mortality probably occurred after this assessment. Pollination studies were not done in 1999; thus pollination limitation cannot be assessed, although fruit production (before predation) appeared to be low. In June 1999 when flowering was very sparse, this gelechid caterpillar was also found in flowers or fruits on two of the four shrubs that were observed flowering.

DISCUSSION

Fruit set of *B. succulenta* was strongly limited by both pollination and predation in winter 1996/1997 after major hurricanes. The extremely low fruit set (7%) of *B. succulenta* was caused by both

pollination and predation limitation, although predation alone may have been able to cause the 91 percent reduction in fruit set observed. Predation by a moth caterpillar (Gelechiidae) probably continued after the study was terminated and may well have caused a total failure of fruit set. Predation by this caterpillar also caused low fruit set (11% or less) in 1999 after Hurricane Floyd. Why did pollinators and predators limit fruit set so strongly in this common shrub after the hurricanes?

Although I had hypothesized that fruit set would be pollination-limited after the hurricanes because the unusually abundant flowering would saturate the pollinators, this was true only in a trivial sense. More accurately, virtually no pollinators were observed visiting the flowers; and seemingly potential pollinators such as butterflies and wasps ignored the *B. succulenta* flowers while occasionally visiting flowers of other nearby species. Nectar was available but seldom removed although it appeared to be accessible to many insects and birds (because it accumulated at the top of the corolla). The reason for this lack of flower visitation is puzzling.

One explanation for the lack of pollinators is that *B. succulenta* is specialized for a insect pollinator that was rare or absent during this flowering season, perhaps because of the hurricane. Campbell (1978) has described *B. succulenta* as one of the "butterfly trees" of the scrublands coppice on New Providence island, and has documented how the white fragrant flowers attract hundreds of ringlet butterflies (*Calisto herophile*). A subspecies, *Calisto herophile apollinis* Bates (Satyridae), occurs on San Salvador, but is not common (Riley 1975, Elliott *et al.* 1980, Elliott 1993) and has never been observed visiting *B. succulenta* flowers; however, we observed four other butterfly species visiting *B. succulenta* flowers, although visits were infrequent (Rathcke *et al.* in press). Miller *et al.* (1992) recorded ten butterfly species visiting flowers in the southern Bahamas. J. Ackerman (pers. comm.) observed butterflies visiting a *Bourreria* species (possibly *B. succulenta*) on Mona island. Butterflies are frequent flower visitors to *B. succulenta* in Florida (Scurlock 1987). Other insects occasionally visited *B. succulenta* flowers on San Salvador, including wasps and bees (*Xylocopa*). J. Pasarella (pers. comm.) caught a carpenter bee, *Xylocopa micans*, visiting flowers in Florida. These observations suggest that *B. succulenta* is not specialized for one or a few pollinator species; instead, many butterfly species, as well as other insect species, visit flowers and may be pollinators.

Resident nectarivorous birds, Bahama Woodstars

and Bananaquits, also visit *B. succulenta* flowers, but these were rare after being decimated by Hurricane Lili in October 1996 (Murphy *et al.* 1998; Rathcke 1998, 2000a). Severe population reductions after hurricanes also have been observed for nectarivorous birds in other studies (Askins & Ewert 1991, Lynch 1991, Waide 1991, Will 1991, Wauer & Wunderle 1992, Wunderle *et al.* 1992, Wunderle 1995). The scarcity of these two bird species caused severe pollination limitation of fruit set in another shrub species, *P. bahamensis* (Malvaceae) on San Salvador island (Rathcke 1998, 2000a) and may have contributed to the pollination limitation of fruit set in *B. succulenta*. Bahama Woodstars were the only species seen visiting flowers in June 1999 when fruit set was high, and thus appear to be effective pollinators (Rathcke *et al.* in press).

Although several types of insects and birds visited flowers of *B. succulenta*, the pollination syndrome (floral traits adapted to a pollinator type) most closely matches that of a butterfly-pollinated species (Rathcke *et al.* in press). Flowers are white, fragrant, and small; *i.e.*, the corolla is 1.5 cm wide and the floral tube is 0.9 cm long, and the stamens and styles are short, extending only a few millimeters above the corolla. These traits do not match those described for a bird-pollination syndrome in which flowers are expected to be red and odorless with long corolla tubes and exerted anthers and stigmas. In addition, nectar was more concentrated (29%) and volume was lower (*ca* 10 microliters/flower/day) than that reported for most bird-pollinated flowers, although nectar production was higher than reported for most butterfly-pollinated flowers (Rathcke *et al.* in press). It is possible that both butterflies and birds are major pollinators of *B. succulenta* on San Salvador. The lack of a match between pollinators and a pollination syndrome is not unusual and recently has caused pollination syndromes to be viewed skeptically and cautiously (Schemske 1983, Herrera 1996, Ollerton 1996, Waser *et al.* 1996). Often, flowers categorized in one pollination syndrome are pollinated effectively by other types of pollinators, and specialization for a single pollinator type seems to be relatively rare (Baker *et al.* 1971, Schemske 1983, Schemske & Horvitz 1984, Feinsinger 1987). Specialization for a few pollinator species can increase the risk of pollination limitation (Rathcke & Jules 1993; Rathcke 1998, 2000a,b), whereas generalization for many pollinators may reduce this risk (Rathcke 1988, Waser *et al.* 1996).

Bourreria succulenta appears to be quite gener-

alized for pollinators, but fruit set was still pollination-limited. Butterflies, wasps, bees, and birds, which are generalists on many flowering species, all visited *B. succulenta* flowers but were rare visitors. The lack of visits by birds can be explained by the devastation from Hurricane Lili (Murphy *et al.* 1998; Rathcke 1998, 2000a), but why insects did not provide adequate, compensatory pollination is not clear. In contrast to other studies in which insect pollinators rebounded quickly after hurricanes and were abundant flower visitors (Bronstein & Hossert-McKey 1995, Ackerman & Moya 1996), insect pollinators were rare for *B. succulenta*. Whether this insect rarity on San Salvador was caused by the hurricanes is not known. The lack of compensatory pollination could reflect the low species richness and low population sizes on small islands like San Salvador (150 km²). San Salvador has 43 butterfly species (Elliott *et al.* 1980, pers. comm.); however, we observed only 4 species visiting *B. succulenta* and they were infrequent. Honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.) were absent and other native bees were relatively rare (Elliott 1993; Rathcke *et al.* in press); so bees typically may be infrequent visitors. Whatever the cause of the scarcity of pollinators, these results have demonstrated that a common plant species with a generalized pollination system can be pollination-limited on a small island.

Although insect pollinators were rare for *B. succulenta*, an insect predator (a moth caterpillar: Gelechiidae) was extremely abundant and caused severe predation limitation of fruit set in winter 1996/1997 and winter 1999. Whether the high abundance of this moth was caused by the hurricanes cannot be ascertained because hurricanes occurred in both years, and no pre-hurricane information exists. Possibly, hurricanes reduced its predators, although insectivorous birds were not reduced after Hurricane Lili (Murphy *et al.* 1998). Or perhaps this moth responded to the unusually abundant floral resources of *B. succulenta*. Larvae, however, were common in buds, flowers, and fruit on three of the four shrubs seen flowering in June 1999 when flowering was extremely sparse; only four shrubs had some flowers in a general survey of hundreds of shrubs on the island. Therefore, the high predation may not be unusual and may be unrelated to the hurricanes. In any event, the moth predator was not saturated by the unusually abundant flowering in winter 1996/1997, and the high predation, coupled with pollination limitation, caused extremely low fruit set in *B. succulenta*. In contrast, Pascarella (1998b) found that high levels

of flowering satiated a moth predator and predation levels were low the year immediately following a hurricane.

Whether resource limitation would have reduced fruit set from a maximum as was seen for another species, *P. bahamensis*, at this site is not known (Rathcke 2000a); however, flowers given unlimited cross-pollen had high fruit set (77%) and may not have been resource-limited as has been found in other species (Ackerman & Montalvo 1990, Bronstein & Hossert-McKey 1995). Also, the unusually prolific flowering of *B. succulenta* suggests that resources were more available after the hurricane or that this species had a positive reproductive response to leaf stripping and disturbance. With Hurricane Lili, the tops of taller trees were broken and the leaves of most plants were stripped. This may have increased the availability of sunlight and other resources to *B. succulenta*. On the other hand, the leaves of *B. succulenta* were new, indicating that its leaves were also stripped by the hurricane and plants would have had to incur the cost of new leaf production. *Bourreria succulenta* was the only shrub species at the site exhibiting unusually high flower production after the hurricane. Other species that had their leaves stripped by Hurricane Lili showed normal flower production (e.g., *P. bahamensis*; Rathcke 2000a) or reduced flower production (e.g., *C. haematomma*) (Rathcke, pers. obs.).

The low fruit set of *B. succulenta* appears to be unusual for this species, although quantitative data are unavailable to test this. Fruits are commonly collected and eaten by local people (Kass, pers. comm.), suggesting that fruit set can be substantial at times. Examination of past photographs show that single cymes, which typically have 10–20 flowers, had 10–20 fruit, indicating that most of the flowers set fruit. There were no hurricanes on San Salvador between 1981 and 1994 (Shaklee 1996) when these photographs were taken. Whether or not the strong pollination and predation limitation

of fruit set seen in this study was caused by hurricane effects or was coincidental, the low fruit set after hurricanes could put this species at a disadvantage for recruitment. Hurricanes can promote the recruitment of new plants by opening gaps in the canopy and can be important in maintaining high diversity in plant communities (Connell 1978, Boucher 1990, Vandermeer *et al.* 1996). Low fruit set after a hurricane could limit the chances of seedling recruitment. Two years after Hurricane Lili, no *B. succulenta* seedlings were observed, although seedlings of some other shrub species were relatively abundant (Rathcke, pers. obs.).

These results emphasize that a consideration of plant–animal interactions, including pollinators and predators and their unique responses, may be necessary for predicting how disturbances, such as hurricanes, will affect plant recruitment and the maintenance of plant diversity in plant communities. Plant species on small islands like San Salvador (150 m²) or in habitat fragments with few species may be especially vulnerable to disturbances that affect their mutualists or antagonists (Rathcke & Jules 1993).

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