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Testing hypotheses for excess flower production and low fruit-to-flower ratios in a pollinating seed-consuming mutualism

J. Nathaniel Holland, Judith L. Bronstein and Donald L. DeAngelis

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Pollinator attraction, pollen limitation, resource limitation, pollen donation and selective fruit abortion have all been proposed as processes explaining why hermaphroditic plants commonly produce many more flowers than mature fruit. We conducted a series of experiments in Arizona to investigate low fruit-to-flower ratios in senita cacti, which rely exclusively on pollinating seed-consumers. Selective abortion of fruit based on seed predators is of particular interest in this case because plants relying on pollinating seed-consumers are predicted to have such a mechanism to minimize seed loss. Pollinator attraction and pollen dispersal increased with flower number, but fruit set did not, refuting the hypothesis that excess flowers increase fruit set by attracting more pollinators. Fruit set of natural- and hand-pollinated flowers were not different, supporting the resource, rather than pollen, limitation hypothesis. Senita did abort fruit, but not selectively based on pollen quantity, pollen donors, or seed predators. Collectively, these results are consistent with sex allocation theory in that resource allocation to excess flower production can increase pollen dispersal and the male fitness function of flowers, but consequently results in reduced resources available for fruit set. Inconsistent with sex allocation theory, however, fruit production and the female fitness function of flowers may actually increase with flower production. This is because excess flower production lowers pollinator-to-flower ratios and results in fruit abortion, both of which limit the abundance and hence oviposition rates, of pre-dispersal seed predators.

J. N. Holland, Dept of Ecology and Evolutionary Biology, Rice Univ., MS 170, 6100 South Main St., Houston, Texas 77005-1892, USA (jholland@rice.edu). – J. L. Bronstein, Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, Arizona 85721, USA. – D. L. DeAngelis, U.S. Geological Survey/Biological Resources Division, Dept of Biology, Univ. of Miami, Coral Gables, Florida 33124, USA.

The maximum rate at which plants reproduce is ultimately set by flower production. Yet, hermaphroditic plants commonly produce more flowers than are matured into fruit, resulting in fruit-to-flower ratios less than unity (Stephenson 1981, Sutherland and Delph 1984, Sutherland 1986, 1987). A central question in plant ecology is why hermaphroditic plants produce more flowers than fruit. In other words, what are the fitness consequences of bearing excess flowers?

Fates of flowers include flower abscission, fruit abortion and fruit production. These fates vary with fruit set, i.e. the fraction of flowers making the transition into developing fruit (Stephenson 1981), which is a function of pollination and resource availability. If the number of pollinated flowers is less than the maximum fruit set permitted by available resources, then fruit set is pollen-limited, equaling the number of pollinated flowers. Conversely, if the number of pollinated flowers is greater

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than maximum fruit set permitted by resources, then fruit set is resource-limited. In this case, some pollinated flowers abort so that fruit set matches resources available for fruit maturation (Stephenson 1981, Sutherland 1987).

Many proximate (ecological) and ultimate (evolutionary) hypotheses have been proposed to explain excess flower production and low fruit-to-flower ratios (Stephenson 1981, Sutherland and Delph 1984, Ayre and Whelan 1989). The pollen limitation hypothesis states that low fruit-to-flower ratios result from pollen availability limiting fruit set, whereas the resource limitation hypothesis states that resource availability limits fruit set. The pollinator attraction hypothesis predicts that excess flower production functions to attract pollinators and lessen pollen-limited fruit set (Willson and Rathcke 1974, Willson and Price 1977, Schaffer and Schaffer 1979, Willson and Schemske 1980). The pollen donation hypothesis predicts that excess flower production increases plant fitness through pollen dispersal and the male fitness function of hermaphroditic flowers (Willson and Rathcke 1974, Sutherland and Delph 1984, Sutherland 1987). If resources limit fruit set, then the selective abortion hypothesis predicts that plants can increase their fitness by selectively aborting fruit based on pollen quantity, pollen donor, or pre-dispersal seed predators (Lloyd 1980, Stephenson 1981, Stephenson and Winsor 1986, Winsor et al. 1987, Becerra and Lloyd 1992, Burd 1998). Many of these hypotheses are not mutually exclusive. For example, excess flower production to increase pollen dispersal can lead to resource-limited fruit set and consequently selective fruit abortion. Understanding which one or more of these hypotheses explains excess flower production and low fruit-to-flower ratios can be contingent upon investigating them concurrently.

Excess flower production and selective abortion are of particular interest in plants relying on pollinating seed-consumers (e.g. yuccas and senita cacti), because selective abortion can minimize seed loss to larvae of the pollinators. Yet, other hypotheses discussed above may also contribute to explaining low fruit-to-flower ratios in these plants. In this study we investigated excess flower production and low fruit-to-flower ratios in senita cacti by concurrently testing the pollen limitation, pollinator attraction, pollen donation, resource limitation and selective abortion hypotheses. We discuss our results in terms of sex allocation theory.

Methods

Study site and study species

We studied senita cacti (*Lophocereus schottii*) at Organ Pipe Cactus National Monument in Arizona (31°57′N, 112°52′W) from April to August 2002. At this site, senita produce 10–40 hermaphroditic, self-incompatible flowers per night. At sunset, anthers dehisce and flowers open. Flowers usually close before sunrise. Senita depend on senita moths (*Upiga virescens*) for reproduction (Holland and Fleming 2002). During flower visitation, moths actively pollinate stigmas, assuring pollination and increasing the likelihood of fruit set and survival of offspring laid in flowers. After actively pollinating, but before departing a flower, moths actively collect pollen. Fruit set (fraction of flowers beginning fruit development) occurs within six days of flower closing. Fruit abortion and flower abscission occur no later than this sixth day, but often occur with 2–3 days (Holland and Fleming 1999a, b). If senita selectively abort fruit, this process should occur for nightly flower crops, because senita allocate resources to fruit set within a few days after flower closing, rather than retaining flowers from many nights and then allocating resources among them.

Pollinator attraction

If plants produce large floral displays to attract pollinators, then moth visits per plant should increase with flowers per plant. Senita moths visit flowers within the first few hours after sunset (Holland and Fleming 1999a). During this time, we counted the number of flowers per plant and the number of moths occupying flowers. In cases when we were unable to census all flowers, we censused as many flowers as possible to determine a proportion of flowers with moths. We extrapolated to total moth number using this proportion and flower number. We analyzed how moth number varied with flowers per plant using a power function, because it explained more variation in data than a linear function. We analyzed the relationship between moths and flowers per plant using least squares regression after natural logarithm transformation. If large floral displays function to attract pollinators, then fruit set should also increase with flower number. We quantified fruit set of open-pollinated flowers for 8–13 plants on each of seven nights throughout the flowering season. Using linear regression, we analyzed how fruit set varied with flower number within plants among nights ($n = 4–6$ nights depending on plant) and within nights among plants ($n = 9–13$ plants depending on night). We do not report the 16 F-tests because none was significant. We performed power analyses for all 16 analyses to determine the probability of committing a type II error of falsely failing to reject the null hypothesis that fruit set does not increase with flower number.

Pollen vs resource limitation

Plants may have low fruit-to-flower ratios because pollination or resources limit fruit set. We tested pollen- and resource-limitation hypotheses by comparing natural-pollinated flowers with (outcross) pollen-supplemented flowers. We quantified fruit set, seed production (seeds per fruit) and seed germinability (proportion of seeds) for 10–17 open- and 10–17 hand-pollinated flowers on each of 11 plants for a total of 177 flowers. Germination was measured for seeds placed in petri dishes with moistened filter paper after 12 days. Fruit set ($n = 11$ plants), seed production ($n = 9$ plants) and germination ($n = 9$ plants) of open- and hand-pollinated flowers were analyzed using paired-sample t-tests. We performed power analyses to determine the probability of committing a type II error of falsely failing to reject the null hypothesis that fruit set, seed production, or germination does not differ between open- and hand-pollinated flowers.

Pollen dispersal

Excess flower production may increase pollen dispersal and the male function of flowers. We tested this hypothesis by estimating pollen dispersal from senita based on moth visits to flowers, because senita moths have unique behavior that almost always includes pollen collection (Holland and Fleming 1999a). We quantified moth visitation as a function of flower number (above). We recognize that not all pollen dispersed will contribute to male fitness, but pollen collection and export should be proportional to pollen donation.

Selective fruit abortion

Plants may increase the quantity and quality of seeds of a flower crop by selectively aborting fruit. We conducted three experiments to assess if senita cacti selectively abort fruit based on pollen quantity, pollen donors, or moth eggs. We tested whether pollen quantity altered fruit set by altering pollen loads deposited on stigmas. Pollen from ~50 anthers is sufficient for a flower to set a fruit (Holland and Fleming 1999b). We established five treatments of pollen quantity: no pollen and pollen from ~25, 50, 75 and 100 anthers. Each treatment was applied to the stigma of one flower on each of 19 plants. We controlled for confounding effects of pollen donor by holding it constant across treatments.

We established four outcross-pollen donor treatments: pollen of one donor (~150 anthers), two donors (~75 anthers from each), three donors (~50 anthers from each) and four donors (~25 anthers from each, plus ~25 anthers from each of two of them). This protocol controlled for pollen quantity among treatments, isolating the effect of number of outcross pollen donors. Treatments were applied to one flower on each of 12 plants. Pollen donors per treatment were held constant across plants.

We examined if egg quantity altered fruit set by establishing five treatments of eggs per flower (0, 1, 2, 3, or 4 eggs). Because senita moths lay their eggs on open flowers, we were able to collect and add eggs to treatment flowers. Handling eggs does not alter hatching success (Holland 2003). Each treatment was applied to one flower on each of nine plants. All treatment flowers were hand-pollinated with ~50 anthers. Flowers typically receive zero or one egg (Holland and Fleming 1999a). Thus, treatments included natural egg numbers, as well as 2- to 4-fold increases.

For all three experiments, flowers were treated shortly after sunset and then covered with bridal-veil netting. For each flower of each experiment, we scored fruit set, that is, whether the flower began fruit development or whether it aborted as an immature fruit within six days after flower closing. Each experiment was analyzed using Cochran's Q-test for repeated measures designs (Zar 1999).

Results

Pollinator attraction

The number of senita moths attracted to a plant increased with flowers per plant, but the increase in moths diminished as flower number increased (Fig. 1; $F_{1,347} = 258.6$, $p < 0.0001$). However, fruit set did not vary with flower number for an individual plant throughout the flowering season (Fig. 2A; 9 plants analyzed, slopes ranged from -0.008 to 0.005 and r^2 ranged from 0 to 0.18) or for different plants within particular nights of study (Fig. 2B; seven nights,

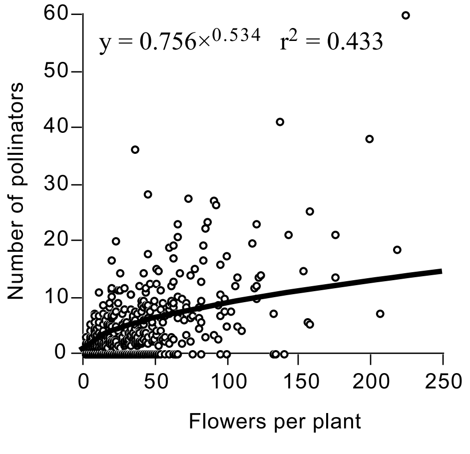

Fig. 1. Number of pollinators, senita moths (*Upiga virescens*), visiting senita cacti (*Lophocereus schottii*) as a function of flower number per plant.

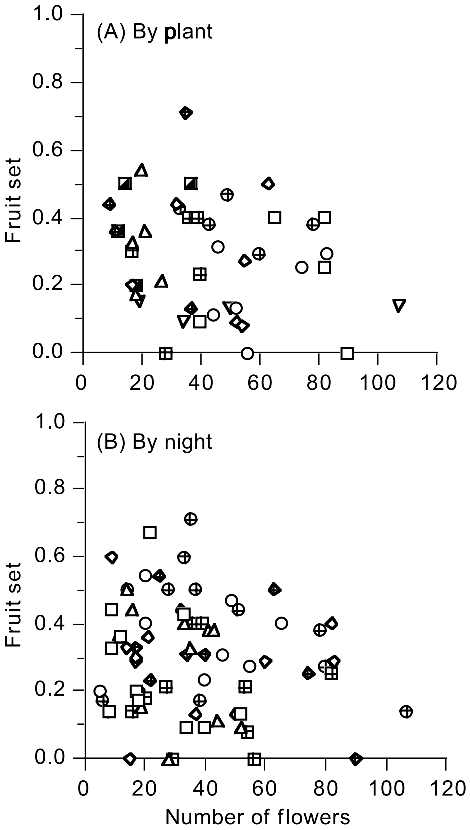

Fig. 2. Fruit set (fraction of flowers) as a function of the number of flowers produced per senita cactus. (A) Symbols are fruit set for the same plant at different time periods of study during the flowering season. (B) Symbols are fruit set for the same time period among plants.

n = 8–13 plants per night; slopes ranged from −0.004 to 0 and r^2 ranged from 0 to 0.24). Power analyses of the nine statistical tests for individual plants throughout the flowering season ranged from 0.773 to 0.973, with a mean (±SD) of 0.888 (±0.085), indicating a low likelihood of falsely failing to reject the null hypothesis of fruit set not varying with flower number. Power analyses of the seven statistical tests for different plants within a particular night of study ranged from 0.885 to 0.967, with a mean (±SD) of 0.938 (±0.029), again indicating a low likelihood of falsely failing to reject the null hypothesis of fruit set not varying with flower number. These results suggest that senita cacti likely do not produce excess flowers to attract pollinators and increase fruit set.

Pollen vs resource limitation

Fruit set, seed production and seed germination did not differ between open- and pollen-supplemented flowers (Table 1). Power of the statistical analyses for differences between open- and hand-pollination flowers for fruit set, seed production and seed germination were 0.929, 0.916 and 0.907, respectively, indicating a low likelihood of falsely failing to reject null hypotheses. This lack of differences between open- and hand-pollination flowers commonly occurs for senita cacti among years and throughout their geographic range (Holland and Fleming 1999a, b, 2002, Holland 2002). These results, coupled with the fact that senita cacti do not differentially allocate resources between open- and hand-pollinated flowers (Holland and Fleming 2002), support the hypothesis that fruit set and fruit-to-flower ratios are limited by resources (Zimmerman and Pyke 1988), rather than moth pollination.

Table 1. Mean (±SE) fruit set (percent of flowers), seed production (seeds/fruit) and seed germination (percent of seeds) for open-pollinated and pollen-supplemented flowers of senita cactus, *Lophocereus schottii*.

	Open pollination	Hand pollination	t	df	p
Fruit set	38.0±6.5%	33.5±4.4%	0.673	10	>0.50
Seed production	129.1±15.1	138.0±19.1	0.735	8	>0.20
Germination	87.0±3.5%	84.3±4.1%	0.565	8	>0.50

t equals calculated t-value, df equals degrees of freedom and p equals p-value.

Pollen dispersal

Assuming that rates of flower visitation approximated rates of pollen dispersal, then pollen dispersal increased, but at a diminishing rate, as flowers per plant increased (Fig. 1). While the number of pollinators visiting flowers was best described as a power function, in nature this function likely saturates, as pollinator abundance cannot increase indefinitely. This result provides support for pollen donation increasing with flower production.

Selective fruit abortion

Because fruit set was resource-limited (Table 1), senita cacti aborted some fruit. Fruit set did not differ among flowers receiving different pollen quantities (Table 2), except when flowers received no pollen, in which case fruit set was zero. Increasing outcross pollen donors from one to four did not alter fruit set, nor did increasing the quantity of eggs per flower (Table 2). All flowers had an equal chance of fruit set regardless of pollen quantity, pollen donors, or egg number. These results suggest that selective fruit abortion cannot explain excess flower production and low fruit-to-flower ratios in senita cacti.

Table 2. Percent of flowers setting fruit within treatments among plants. Treatments 0, 1, 2, 3 and 4 correspond to progressively greater pollen quantity, pollen genotype diversity and egg number (see Methods for precise quantities of pollen, genetic diversity and egg abundance).

	0	1	2	3	4	Q	df	p
Pollen quantity		68.4	36.8	57.9	42.1	4.63	3	> 0.20
Pollen genotype		66.7	66.7	88.9	66.7	1.38	3	> 0.50
Egg quantity	66.7	44.4	22.2	55.6	66.7	5.60	4	> 0.20

Q is Cochran's Q-test for repeated measures experiments and p is the p-value for that test.

Discussion

An emergent pattern among hermaphroditic plants is excess flower production and low fruit-to-flower ratios. We tested hypotheses for this pattern in senita cacti, which rely on a pollinator whose eggs, laid in flowers, hatch to produce larval seed predators. Results suggest that senita cacti do not produce excess flowers to attract pollinators and increase fruit set. This and other studies indicate that low fruit-to-flower ratios routinely occur in senita because resources, rather than pollen, limit fruit set (Holland and Fleming 1999a, b, 2002, Holland 2002).

Trade-offs in resource allocation between flower and fruit production are fundamental to sex allocation theory in hermaphroditic plants (Charlesworth and Charlesworth 1981, Charlesworth and Morgan 1991, Campbell 2000). Increasing resource allocation to flower production has the consequence of reducing resources available for fruit production. If low fruit-to-flower ratios result solely from the supply of resources available to plants, then, to decrease the disparity between flower and fruit production, fruit set but not flower production should increase with resource availability. However, both fruit set and flower production increased in a water augmentation experiment of senita (Holland 2002). Hence, low fruit-to-flower ratios and resource-limited fruit set in senita cacti are a consequence of excess flower production and resource partitioning between flower and fruit production.

The pollen donation and selective fruit abortion hypotheses suggest that excess flower production and resource partitioning between flower and fruit production can increase plant fitness. Hermaphroditic plants may produce excess flowers to increase pollen dispersal and their male fitness function. Because senita moths have unique behavior that almost always includes active pollen collection, flower visitation can be proportional to pollen dispersal. Thus, pollen dispersal does increase, but at a diminishing rate, with flower production in senita cacti (Fig. 1). Not all pollen dispersed will contribute to seed production, but the male fitness function should be proportional to pollen export. Hence, excess flower production and resource-limited fruit set in senita cacti may have evolved at least in part for increased fitness via pollen dispersal.

If fruit set of a flower crop is resource-limited, then plants may selectively abort fruit based on pollen quantity, pollen donors, or pre-dispersal seed-predators to increase the quantity and quality of seeds of that flower crop. Among pollinating seed-consuming mutualisms, selective abortion has been reported in some *Yucca* species (Pellmyr and Huth 1994, Wilson and Addicott 1998, Addicott and Bao 1999) and in *Lithophragma* (Thompson and Cunningham 2002), but not in fig trees (Bronstein 1988) or globeflowers (Jaeger et al. 2000). Even though senita cacti had resource-limited fruit set and did abort fruit, they did not selectively abort fruit on the basis of pollen quantity, pollen donors, or seed predators (Table 2). One caveat about the interpretation of the pollen quantity experiment needs to be mentioned, however: all treatments may have exceeded a pollen threshold on which selective abortion is based. If such a threshold occurs, the common lack of difference in fruit set and seed production between natural- and hand-pollinated flowers suggests that it is not often encountered (Table 1; Holland and Fleming 1999a, b, 2002, Holland 2002).

It is not surprising that senita do not selectively abort fruit. Excess flower production and resource-limited fruit set for the sole function of selective abortion provide only marginal fitness gains (Burd 1998). In addition, selective abortion may not be favored if low variance occurs among flowers in the quantity and quality of pollen deposited on stigmas, or in the number of seed predators (Burd 1998). Senita moths oviposit uniformly among senita cactus flowers, such that flowers typically have either zero or one egg (Holland and Fleming 1999a). Although receiving zero versus one egg per flower can have important fitness consequences, this variation does not represent a continuous range of variation on which plants can employ a selective fruit abortion strategy. If senita did selectively abort fruit with an egg, it could lead to the demise of both cactus and moth populations by severely limiting moth recruitment and future pollination. This is in contrast to selectively aborting species of *Yucca*, in which individual flowers often receive many ovipositions (Addicott and Bao 1999, Huth and Pellmyr 1999). In addition, yucca moths often repeatedly pollinate a single stigma, at times with pollen from the same flower, providing variation in pollen quantity and quality among flowers (Pellmyr and Huth 1994, Huth and Pellmyr 1999, 2000, Marr et al. 2000). Flowers of senita are rarely pollinated more than once, as suggested by the uniform egg distribution (Holland and Fleming 1999a). Furthermore, unlike *Yucca*, senita are entirely self-incompatible; moths must deposit outcross pollen for their offspring survival.

In addition to pollen dispersal and resource-limited fruit set, there is another hypothesis that may contribute to explaining why plants with specialized pre-dispersal seed-predators produce excess flowers and have low fruit-to-flower ratios. Stephenson (1981) speculated that fruit abortion resulting from excess flower production and resource-limited fruit set may "limit the population size of some insect seed predators." Holland and DeAngelis (2001, 2002, Holland et al. 2002) demonstrated that fruit abortion, whether selective or random, can impose density-dependent mortality on pre-dispersal seed predators and limit their abundance. They further showed that such population regulation can in turn reduce seed predation and increase seed production. Fundamental to analyses of Holland and DeAngelis are functional responses of pollination, seed predation and seed production based on the ratio of pollinators (seed predators) to flowers (Fig. 3). At high pollinator-to-flower ratios, both pollination and seed predation are large, such that seed production is low. At low to intermediate ratios, seed production is greatest. Hence, different resource allocation strategies between flower and fruit production (i.e. variation in flower production among plants) may result in different pollinator-to-flower ratios. The empirical relationship between pollinator-to-flower ratio and flower production can be evaluated by re-analyzing the data in Fig. 1, plotting pollinator-to-flower ratio on the abscissa, instead of pollinator number. Pollinator-to-flower ratios decline rapidly with increases in flowers, but the rate at which pollinator-to-flower ratios decline diminishes with increases in flowers (Fig. 4; least squares regression after natural logarithm transformation, $F_{1,347} = 216.2$, $p < 0.0001$). Given this relationship and functional responses of pollination, seed predation and seed production (Fig. 3), individual plants with few flowers have disproportionately high pollinator-to-flower ratios and consequently low seed production and maternal fitness. On the other hand, individual plants with many flowers have lower pollinator-to-flower ratios and consequently higher seed production and maternal fitness. Holland et al. (unpubl.) have shown with optimality and evolutionary stable strategy models that it is feasible for selection on flower production to operate at the level of individual plants, but yet regulate moths at the population level via fruit abortion. Thus, excess flower production may not only increase pollen dispersal and the male fitness function of flowers, but fruit production and the female fitness function as well.

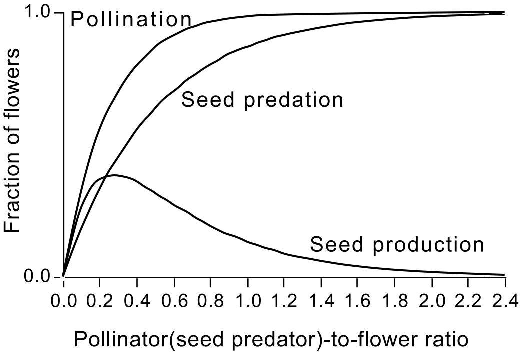

Fig. 3. Functional responses for pollination, seed predation and seed/fruit production. Pollination, seed predation and seed production are represented as a fraction of flowers and as a function of the pollinator-to-flower ratio. Seed production is the difference between the pollination and seed predation functional responses. (Adapted from Holland and DeAngelis 2001).

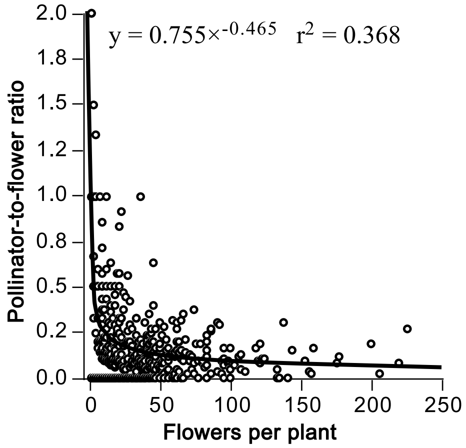

Fig. 4. Pollinator-to-flower ratio as a function of flower number per plant for senita moths (*Upiga virescens*) and senita cacti (*Lophocereus schottii*). This data-set is the same as that in Fig. 1, but the abscissa is pollinator-to-flower ratio rather than absolute number of pollinators.

In conclusion, excess flower production, pollinator (seed predator) to flower ratios and fruit abortion may be particularly important for plants routinely attacked by pre-dispersal seed predators, including not only plants involved in pollinating seed-consumer interactions like senita and yucca, but also in masting and other species (Kelly and Sork 2002). Aside from selective abortion, the reproductive biology of senita and yucca is remarkably similar, including dependence on obligate pollinating seed-consumers, excess flower production, low fruit-to-flower ratios, routinely resource-limited fruit set and fruit abortion. Although numerous hypotheses have been proposed to explain excess flower production and low fruit-to-flower ratios in yuccas (Schaffer and Schaffer 1979, Udovic and Aker 1981, Aker 1982a, b, Pellmyr and Huth 1994), pollen dispersal and resource limitation are the most likely explanations, as has been shown here for senita. The partitioning of resources between flower and fruit production, coupled with routinely resource-limited fruit set, are consistent with sex allocation theory in plants in which excess flowers increase pollen dispersal and the male fitness function. However, excess flower production, resource-limited fruit set and fruit abortion can also function to lower pollinator-to-flower ratios, reduce pre-dispersal seed predation and increase fruit production and the female fitness function. That more than one hypothesis (pollen donation, resource limitation, limitation of seed predators) may explain excess flower production in senita cacti and that excess flower production may actually increase female fitness function, are consistent with other studies (Ehrlén 1991, 1993). Whether excess flower production by senita has evolved solely for increasing the male fitness function, or possibly in combination with reducing seed predation, remains a difficult question to address empirically.

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