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ORIGINAL PAPER

Fruit abortion in the Chihuahuan-Desert endemic cactus *Opuntia microdasys*

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Abstract Resource and pollen limitation, as well as pollen/ovule incompatibility, have been proposed as causes to explain fruit abortion. To assess whether abortion in *Opuntia microdasys* was due to resource and/or pollen limitation and could therefore be reversed fruit set and seed set were studied using controlled pollination experiments on 60 plants that had been randomly assigned a combination of watering and fertilization treatments. On the other hand, to test whether fruit abortion was irreversible, due to pollen/ovule incompatibility, we examined the reproductive biology of the species. This included observations on floral phenology, nectar production, flower visitors, numbers of pollen grains and ovules, and self-pollination experiments. Results showed that *O. microdasys* is a fully self-incompatible species and its floral biology and the activity of the main pollinator allow constant deposition of incompatible pollen onto stigmas, which may contribute to fruit abortion. Reproductive success was limited by nutrients and pollen, but the fruit set increased only by 58%, compared to 47% of the control, after the experimental addition of pollen, nutrients and water. The magnitude of pollen and resource limitation suggests that similar levels of abortion will be present in good as well as in bad years. Selfing as well as incompatibility between ramets from the same clone and between closely related plants seem plausible candidates to explain the large proportion of fruit abortion, and experimental cross pollination between genotypes identified through molecular markers are necessary to fully understand the considerable abortion rate that remains unexplained after pollen and resource addition. Interestingly, the possible reason why the abortion of energetically expensive fruits has not been eliminated by natural selection is that the aborted fruits are propagules able to root and produce new plants with the same genotype of the mother. Abortion would have a dramatic effect on cross-fertilized genotypes because they result in zero fitness, but it would have a positive effect on the fitness of the maternal genotype because a clonal offspring is produced. Evidently, the exact fitness consequences to the maternal plant will depend on the differences in survival and reproduction of these different offspring types.

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Introduction

The limitation of reproductive success in plants is a phenomenon that involves the loss of resources (and of fitness), particularly when it manifests as the abortion of reproductive structures (Stephenson 1981). These limitations have different causes such as resource limitation (Herrera 1991), pollen limitation (Burd 1994), the interaction between resource and pollen limitation (McCall and Primack 1987; Juenger and Bergelson 1997), damage caused by biological agents (Parker 1987), climate conditions (Lee and Bazzaz 1982), and characteristics intrinsic to the reproductive system or genetic makeup of the plant. The latter may result from: discrimination based on pollen quality (Ramsey and Vaughton 2000), self-incompatibility (de Nettancourt 1997), inbreeding or outbreeding depression (Charlesworth and Charlesworth 1987), genetic load (Wiens et al. 1987) or differential genotype selection (Melser and Klinkhamer 2001).

In contrast, adaptive functions have been attributed to the phenomenon of fruit abortion (Stephenson 1981; Guitian 1994). These include: (1) the regulation of seed production; (2) a response to stress; (3) the selective elimination of ovules and seeds, and (4) the male function hypothesis, the production of large quantities of flowers to increase male reproductive success through pollen dispersal (Campbell 1989). A less explored, possible adaptive function of aborted fruits is that they may function as vehicles for clonal propagation (Anthony 1954; Buxbaum 1955). Rooting of aborted fruits would function as an insurance against reproductive failure (Palleiro et al. 2006). This may be particularly important in environments where the establishment of clonal recruits is less uncertain than that of sexually derived seedlings, and guarantees permanence in already colonized habitats (Mandujano et al. 1996).

We hypothesized that if fruit abortion represents an insurance mechanism against reproductive failure due to poor environmental conditions it should be easily reversed experimentally with the addition of resources and pollen. If abortion is not reduced significantly by the addition of resources and pollen, however, an impediment for sexual reproduction which is independent of the provision of pollen and resources must be responsible for its incidence. In this case, an alternative explanation to that of an adaptive insurance against reproductive failure in bad years must be sought because abortion will occur in good as well as in bad years. Thus, this article characterizes the breeding system of *Opuntia microdasys* and assesses experimentally the role that resource and pollen limitation, as well as self-incompatibility, play in the high incidence of fruit abortion.

Methods

Study site

Fieldwork was carried out in the Mapimí Biosphere Reserve (Chihuahuan Desert, Mexico, 26°41′ N, 103°45′ W, 1150 m asl, 264-mm annual precipitation, 20.8°C mean annual temperature, Montaña, 1990). During this study rainfall was 183.8 mm in 2001, 241.7 mm in 2002, and 345.3 mm in 2003.

This study was carried out in an area of approximately 3,500 ha, in a *bajada* (gently sloping terrain, slope: 3–16%, that connects the piedmonts to the bottom of the endorreic basins). The vegetation (Montaña 1990) are scrubs developed on sandy-clayed soils and dominated by *Larrea tridentata* (DC.) Cov. (Zygophyllaceae), *Opuntia rastrera* (Weber) Britton & Rose, *O. microdasys*, *Jatropha dioica* Cerv. (Euphorbiaceae), and *Fouqueria splendens* Engelm. (Fouquieriaceae).

Study plant

Opuntia microdasys (Lehm) Pfeifer is a diploid species with a chromosome number $n = 11$

(Pinkava et al. 1977). Plants have suborbicular articles (cladodes), spine free areoles, with numerous glochids that are easily removed. Plants flower in spring and the fruits mature in summer. Flowers are perfect, 4–6 cm in diameter, the perianth segments are yellow and the stigma lobes are green. Stamens are inserted in a dense circle at the base of the gynoecium where the nectary chambers lie. The fruits are fleshy, spherical, green when immature, reddish when mature, and yellow during the last stage.

Opuntia microdasys is a Chihuahuan-Desert endemic living on igneous soils at 1,100–2,100 m asl (Bravo-Hollis 1978) and little is known about its reproductive biology. As in other cacti and succulents (Franco and Nobel 1989) sexual recruitment (by seed) seems to be rare and sporadic in *O. microdasys* (Mandujano, Montaña, and Golubov unpublished data; Palleiro et al. 2006). In contrast to propagation by cladodes, which is common in the genus but exceptional in *O. microdasys* (Mandujano, Montaña, and Golubov unpublished data), vegetative propagation via the pericarp of aborted fruits is common in this species. Palleiro et al. (2006) found only 3.1% of plantlets derived from cladodes and 2.6% from seeds; the remaining 94.3% were clonal offsprings derived from aborted fruits.

Breeding system

To determine the duration of flowering and quantify flower production, we monitored 60 plants between March 29 and April 29, 2002. To describe floral phenology, the corolla aperture (diameter of the circle formed by the tips of the petals) of 56 flowers on 14 plants was measured hourly with a caliper. Anther dehiscence (visual estimate) and stigmatic receptivity (determined by observing the turgidity of the stigma lobes and pollen adhesion) were observed to assess reproductive synchrony. To estimate the spatial separation between anthers and stigma (herkogamy) we measured the lengths of styles and stamens (five per flower) in 15 flowers**.**

Nectar was extracted hourly using 3 μl microcapillaries both in the presence of floral visitors (20 flowers in 10 plants), and in the absence of visitors (20 flowers covered with fine mesh bags on the same plants).

Pollen grains per anther (two anthers per flower), pollen viability (Kearns and Inouye 1993) and the number of ovules per flower were assessed in 15 flowers from eight plants. The proportion of pollen to ovules (P/O) and the outcrossing index (OCI) were calculated by adding the indices obtained from three aspects of the flower: corolla diameter, spatial separation between the anthers and the stigma, and temporal separation between reproductive functions as proposed by Cruden (1977).

A preliminary study (Piña, H.H. unpublished) showed that automatic self-pollination (flowers bagged before anthesis that remained bagged all day) and apomixis (flowers emasculated and bagged before anthesis that remained bagged all day) did not produce any fruits (n = 20 flowers for each treatment in 20 different plants). Manual self-pollination (deposition of pollen from the flower on its own stigmas with the help of a fine paintbrush) was assessed in 10 flowers of each of 60 plants. The flowers were mesh-bagged the day before their opening, hand pollinated in the morning and immediately covered again with mesh bags. This 60 plants were used in an experiment to assess the effects of pollen and resource limitation on reproductive success; see Section "Effects of resources and pollination on reproductive success" below.

Flower visitors

Flower visitors were observed during the 2001, 2002, and 2003 flowering seasons. Given the predictability of visitor species over the three flowering seasons (see *Flower visitors* in the Results), the quantification of the number of visits throughout the day was done on a single occasion during the peak of flowering in the spring of 2003. Ten plants each with about 20 open flowers were observed, and the behavior of the flower visitors was recorded in each plant for 10 min every 2 h from 9:00 h to 19:00 h by a group or three people.

Effects of resources and pollen availability on reproductive success

A total of 60 randomly selected reproductive individuals were assigned to one of four treatments

(15 individuals each): (1) addition of water, (2) addition of fertilizer, (3) addition of water + fertilizer, and (4) no additions. Watering treatments consisted of (1) no water added and (2) addition of 300 l of water. Plants in the latter treatment were watered at two occasions before flowering (September 2001 and March 2002, 150 l each time). The water was poured slowly on a 3 m^2 circular area centered on the base of each plant which was delimited by a 20-cm high border of soil to prevent runoff. Fertilizer treatments consisted of (1) not adding any fertilizer, and (2) addition of 850 g of fertilizer (delivered 425 g at a time, immediately prior to the watering dates). The fertilizer was composed of 350 g of ammonium sulfate, 300 g of simple calcium superphosphate, and 200 g of potassium chloride, and contained sufficient nitrogen to meet the reproductive needs of cultivated *Opuntia* spp. (Pimienta-Barrios 1990). The fertilizer was spread around the base of the plants within a 1 m radius.

Two pollination treatments were randomly assigned to 20 flowers of each experimental plant during the 2002 flowering season, using 10 flowers per treatment. These treatments were: (1) cross pollination by depositing a mix of pollen from the flowers of three individuals located more than 40 m away on previously emasculated flowers of the test plant (Kearns and Inouye 1993), and (2) natural pollination. A third pollination treatment (self-pollination) did not produce any fruit and was eliminated from this analysis (see Section "Breeding system"). In the cross-pollination treatment, the flowers (which in this species only open one day) were bagged with mesh bags the day before their opening, hand pollinated during the morning and covered again with mesh bags after pollination. In natural pollination treatment the flowers were left uncovered, but were bagged at the end of the day of its opening. There were a total of 600 flowers in each treatment (10 flowers per treatment per plant). All flowers were checked to ensure that they were not damaged by larvae of *Olycella* aff. *junctolineella* (Lepidopterae, Pyralidae).

Statistical analyses

The effect of additional water and nutrients on flower production and fruit set (number of fruit/number of flowers) of the open pollinated flowers (i.e., eliminating from the analyses the self- and cross-pollinated flowers) of the 60 experimental plants were analyzed with two separate two-way ANOVAs. The number of cladodes on each plant was used to estimate plant size and was included as a covariate.

The effect of pollination treatments on seed and fruit production (of the 10 cross-pollinated flowers and of the 10 open pollinated flowers used as controls) was analyzed with repeated measures ANOVAs (Potvin et al. 1990; von Ende 2001) and the significance of the main effects and their interactions were calculated for the univariate tests (*F*-tests) as well as for the mutivariate tests (MANOVA procedure, von Ende 2001, *Wilks* λ-tests). The results for the *Wilks* λ-tests closely mirrored the univariate results and only the latter are presented. The main effects were pollination (within subject effects), watering and fertilization (between subject effects). All were treated as fixed effect factors. The response variable (within subject effects) was the number of seeds per fruit produced by the flowers that had received the different pollination treatments. In order to avoid having too many zeros in the data matrix, we used the mean number of seeds produced by the 10 fruits subjected to each level of pollination. A similar analysis was conducted for fruit set (the proportion of the 10 flowers that produced fruits). In all analyses, response variables were Box–Cox transformed to reach normality, and graphical assessment of the standardized residuals did not detect outliers or systematic deviations from fitted values. All ANOVAs were carried out using Statistica software (v 4.3 Statsoft Co. 1993) and the MANOVAs were done with the program JMP (SAS Institute 1995).

Results

Breeding system

Flowering is synchronous and occurs throughout the month of April (Fig. 1). Corolla ($n = 56$ flowers) were closed at 07:30 h. They were 50% open by 10:30 h and fully opened between 11:00 h and 15:00 h. Corolla were 50% closed

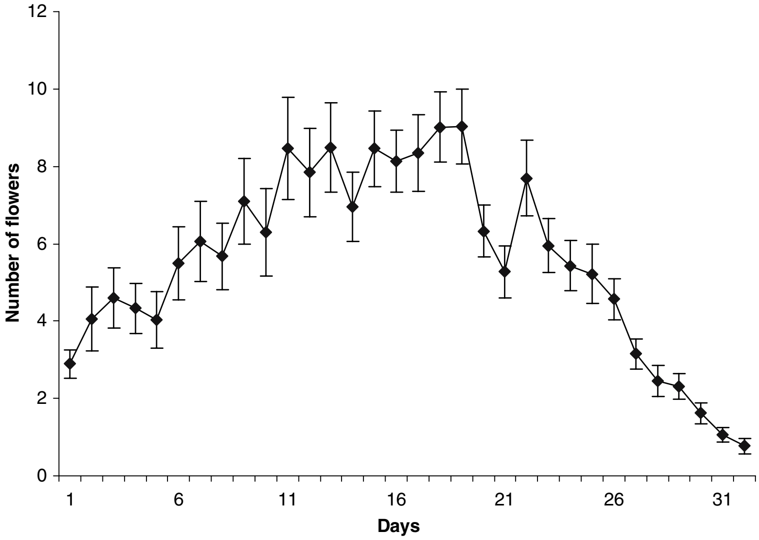

Fig. 1 Daily number of flowers (mean ± SE) produced by *Opuntia microdasys* at the peak of the 2002 blooming period (29 March–29 April, $n = 60$ plants) in the Southern Chihuahuan Desert

by 15:30 h and fully closed by 19:30 h. None of these flowers opened again the following day. The perianth fell off the flowers a few days after it closed. In all the flowers that were monitored, anther dehiscence and stigma receptivity began around 11:00 h and continued until around 17:30 h, indicating a temporal overlap in sexual functions (homogamy). Style length (mean ± SE) was 1.87 ± 0.09 cm and stamen length was 2.13 ± 0.06 cm. Mean separation between these two structures was 0.3 ± 0.08 cm ($n = 15$ flowers). This indicates that, due to their similar lengths, in some flowers anthers may make contact with the stigma lobes when visitor activities trigger thygmotaxis (see Section ‘‘Flower visitors’’ below), but there is not full herkogamy (i.e., in some flowers this contact is possible while in others it is not possible). It was only possible to measure nectar production in bagged flowers (which means that in unbagged flowers nectar was consumed by visitors as it was produced) and we observed that nectar was only produced in the first hour after anthesis (flower opening). Flowers produced 32.03 ± 4.06 µl of nectar per day.

Each anther produced 219.3 ± 12.3 grains of pollen of which only 4.6 ± 1.2 were not viable. The number of pollen grains and ovules per flower was 55,851.13 ± 2911.08 and 158.6 ± 14.55 ($n = 15$), respectively. The pollen to ovule ratio was 396 ± 41 and the OCI was 3 which would correspond to a breeding system of facultative xenogamy (Cruden 1977).

Flowers subjected to manual self-pollination did not produce any fruit ($n = 600$ flowers) indicating strict self-incompatibility (SI).

Flower visitors

During the 3 years of the study the same ensemble of flower visitors was recorded. Only four pollinators (all bees) were observed: the solitary oligoletic bee *Dyadasia* sp. (Anthophoridae), *Perdita* sp. (Andrenidae), *Ashmeadiella* sp. and *Megachile* sp. (Megachilidae both of them). Three reward thieves (all Coleoptera) were also observed: *Acmaeodera* sp. (Acmaeoderidae) and two unknown species of Nitidulidae. Plants received 572 visits in total in a day at the 2002 blooming period. *Diadasia* sp. was the most frequent visitor (92.4% of the recorded visits) and was most active in the morning (58.6% before 1330 h). Its visits to the interior of the plants (geitonogamous) accounted for more than half of all the visits (52.5%). It can be considered as a genuine pollinator because it lands upon the stigma lobes (depositing probably some exogamous pollen), walks down the column of the gynoecium looking for the nectar chambers and triggering thygmotaxis (the curving of the anthers that tighten around the gynoecium due to the mechanical stimuli produced by the contact with the visitor). To leave the flower the insect must open its way out climbing the column of the gynoecium through the stamens tightened to the wall of the gynoecium, thus involuntarily collecting large quantities of pollen in the surface of its body. Finally, it takes off from the stigma lobes depositing autogamous pollen on them. Other visitor bees were *Perdita* sp. (4.8% of the recorded visits) and *Ashmeadiella* sp. (2.6%) which, given their small size and behavior did not triggered thygmotaxis and may be acting as mostly as robber species. *Megachile* sp., a species larger than *Diadasia* sp., was occasionally observed.

For all the flowers monitored ($n = 201$), we observed total removal of pollen from the anthers and abundant pollen deposition on the stigmas. This was aided by the contrast in color between the pollen (yellow) and the stigmas (green). The flowers changed color from yellow to pinkish/orange after they were visited by pollinators. This does not happen when the flowers are artificially isolated from flower visitors, thus color change may be associated with pollination, reward consumption, or the end of stigma receptivity (Casper and La Pine 1984).

Diadasia sp. was observed visiting frequently other cacti species (*O. rastrera*, *O. macrocentra*, *Cylindropuntia imbricata*, *C. kleiniae*, *C. leptocaulis* var. *brevispina*, *Echinocereus conglomerates*, and *Coryphanta macromeris*) whose flowering overlap with that of *O. microdasys*.

Effects of resources and pollen availability on reproductive success

Mean plant size was 149.52 ± 6.01 cladodes (range: 71–284) and there was no difference in size among the four treatments combining the addition of water and/or nutrients ($F_{3,56} = 0.504$, $P = 0.68$). The covariate numbers of cladodes (used as an estimator of plant size) was never significant and was eliminated from further analyses. Control plants (no water or nutrients added) produced 129.9 ± 29.9 flowers of which only 36.0% ± 4.0 produced fruit. Mean seed production per fruit was 37.8 ± 5.3, and mean seed production per plant was 1769.0 seeds. Additionally, these plants had 33.7 ± 6.5 aborted flower buds that can be attributed to predation by larvae of *Olycella* aff. *junctolineella* (Lepidopterae, Pyralidae).

The analysis of flower production indicated an effect of nutrient addition (156.6 ± 17.2 vs. 107.9 ± 12.7 flowers, Table 1). The fruit set also increased with the application of fertilizer (45.6% ± 3.9 vs. 35.5% ± 2.7 fruits/flower, Table 1).

The addition of pollen (cross-pollination treatment) increased seed production compared with the naturally pollinated control flowers (44.9 ± 2.9 vs. 37.2 ± 3.3 seeds per fruit, Table 2). Neither watering nor fertilization affected seed production per fruit. However, because fertilization increased the number of flowers and the fruit set (Table 1), the total number of seeds per plant increases with the addition of nutrients.

Table 1 Analyses of the variances of the flower production and of the fruit set (number of fruit/number of flowers) of the open pollinated flowers (i.e., eliminating from the analyses the self- and cross-pollinated flowers) of *Opuntia microdasys* plants as a function of watering and fertilization treatments

Source	df	Flowers			Fruit set		
		MS	*F*	*P*	MS	*F*	*P*
Watering (W)	1	56.07	0.0082	0.93	0.06	0.0002	0.97
Fertilization (F)	1	35624.07	5.1864	0.03	1516.41	4.6126	0.04
W × F	1	345.60	0.0503	0.82	0.18	0.0005	0.98
Error	56	6868.80			343.51		
Total	59						

For each analysis mean squares, *F*-values and their probability under the null hypothesis are shown (degrees of freedom are the same for both analyses)

Fruit set also increased with pollination (58.0% ± 0.02. vs. 47% ± 0.02 fruits/flower, Table 2). Watering and nutrient addition did not affect fruit set in this experiment (in which only 10 flowers per pollination treatment were used, Table 2) and this result contrast with the results obtained when considering all the flowers of the experimental plants regarding the effects of nutrient addition (Table 1).

Discussion

Causes of fruit abortion

The floral characteristics of *O. microdasys* (thigmotaxis, homogamy, and the lack of herkogamy) and some consequences of the foraging activity of its main pollinator (self-pollination, geitonogamy, and pollen exchange with other cacti) encourage the deposition of incompatible pollen on the stigmas. Seed development from self-pollination is prevented by a SI system: none of the experimentally self-pollinated flowers produced fruits. An excess of incompatible pollen could block access to pollen that is compatible with the stigmas, either by blocking the style with pollen tubes, by preemption of certain stigmatic or stylar substances required by the pollen or, if the SI is expressed after fertilization, by preemption of the ovules (Broyles and Wyatt 1993; Ramsey 1995). In addition to this, an important proportion of flower buds (about 25%) abort due to predation by larvae of the lepidopteran *Olycella* aff. *junctolineella*.

The reproductive success of *O. microdasys* was also limited (but to a lesser extent) by both nutrients and pollen. The experiments that evaluated the limitation of resources on the production of reproductive structures of the entire plant reflected the limitation of nutrients on flower production and fruit set. Watering did not have any effect and the lack of statistical interaction between watering and nutrient addition indicate that nutrient addition had a similar (positive) effect both in the plants that received only the water from rains, and in the plants that received water from rains plus additional watering. These results are similar to those reported by Campbell and Halama (1993) for *Ipomopsis agreggata* (Polemoniaceae), i.e., in this species hand-pollination and nutrient addition increased seed production but adding water did not. The experiments that simultaneously evaluated the limiting effect of resources and of pollen revealed that pollen availability limits seed production and fruit set.

How much is maternal fitness affected by fruit abortion?

The inability of *O. microdasys* to form fruit, and therefore seeds, by self-fertilization revealed a strict xenogamous reproductive system (see

Table 2 Repeated measures ANOVAs of the seed set and of the fruit set (of the 10 cross-pollinated flowers and of the 10 open pollinated flowers used as controls) of *Opuntia microdasys* plants as a function of pollination, watering, and fertilization treatments

Source	df	Seed set			Fruit set		
		MS	*F*	*P*	MS	*F*	*P*
Watering (W)	1	1228.69	1.3216	0.26	4.13	2.1039	0.15
Fertilization (F)	1	571.23	0.6144	0.44	0.09	0.0477	0.83
W × F	1	415.93	0.4474	0.50	0.04	0.0228	0.88
Between-subjects error	55	929.70			1.96		
Pollination (P)	1	1773.20	6.6362	0.01	17.63	16.4944	0.01
P × W	1	6.60	0.0247	0.88	3.33	3.118	0.08
P × F	1	507.23	1.8983	0.17	0.03	0.0312	0.86
P × W × F	1	138.06	0.5167	0.48	0.13	0.1247	0.73
Whithin-subjects error	56	267.20			1.07		
Total	118						

For each analysis mean squares, values for the *F*-univariate test and their probability under the null hypothesis are shown (degrees of freedom are the same for both analyses)

Frankel and Galun 1977). It is clear that naturally pollinated flowers received a mix of incompatible and compatible pollen. In the cross-pollination treatment, because plants propagate clonally, we cannot rule out the possibility that some of the selected donors were incompatible, even though they were located a considerable distance from each of the target plants (>40 m). Studies combining the identification of genotypes with a pollen addition experiment (cross pollinations between genetic lineages, Good-Avila and Stephenson 2003) seem to be necessary to address in greater detail the question of incompatibility in *O. microdasys*.

Self-incompatibility occurs in at least 28 of 98 genera of Cactaceae (Boyle 1997). In the genus *Schlumbergera* (Boyle 1997), and in *Cereus peruvianus* (Weiss et al. 1994) and *Hatiora gaertneri* (Boyle et al. 1994) there is evidence of single locus, multiple allelic gametophytic self-incompatibility (GSI). Since this SI system is relatively constant within plant families, it is possible that GSI occurs throughout the Cactaceae (de Nettancourt 1997). Some studies of *Opuntia* point towards this type of incompatibility (e.g., Negrón-Ortiz 1998) and the possibility of it occurring in *O. microdasys* should not be dismissed.

Interestingly, abortion in *O. microdasys* does not result in a zero contribution to fitness because aborted fruits serve as vehicles for propagation. This suggests an innovative function for the phenomenon of fruit abortion: vegetative propagation. Although this phenomenon was described over 50 years ago (Anthony 1954; Buxbaum 1955), its demographic consequences remain to be explored. Abortion generates fruits that are propagules able to produce a new plant from the areoles of the pericarp. Abortion would have a dramatic effect on cross-fertilized genotypes because they would have zero fitness. Abortion, however, would still have a positive effect on the fitness of the maternal genotype because a clonal offspring partially compensates the loss of sexual offspring. The exact fitness consequences to the maternal plant will depend on the differences in survival and reproduction of the different types of offsprings (sexual versus clonal).

We conclude that the reproductive success of *O. microdasys* is simultaneously limited by nutrients, by the availability of compatible pollen, by the effect of florivory, and by genetic incompatibility. However, the incompatibility systems seems to be by far the most important factor, and this suggests that the hypothesis that postulates that fruit abortion functions as an insurance against reproductive failure in bad years is not sufficient to explain the phenomenon because abortion will be present in good as well as in bad years.

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