

Flowering Behavior and Pollination Requirements in Climbing Cacti with Fruit Crop Potential

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Abstract. The reproductive biology of the climbing cacti *Hylocereus polyrhizus* (Weber) Britt. & Rose, *H. undatus* (Haworth) Britt. & Rose, *H. costaricensis* (Weber) Britt. & Rose, and *Selenicereus megalanthus* (Schum. ex Vaupel) Moran (syn. *Mediocactus megalanthus*) was studied with the aim of cultivating the cacti in Israel as fruit crops. Flowering in *Hylocereus* spp. occurred in two to three waves during the summer, whereas in *S. megalanthus*, flowering was concentrated at the end of autumn. Flowers of all species opened 1 to 1.5 hours before sunset and closed ≈6 hours after sunrise. In the *Hylocereus* spp., *H. polyrhizus* and *H. costaricensis* were self-unfruitful, and cross-pollination with other species led to high fruit set (100%). *Hylocereus undatus* was self-fruitful, setting fruit with self-pollen. Cross-pollination between the clones of *S. megalanthus* led to a high fruit set and each clone was self-fruitful. In contrast to *H. undatus*, *S. megalanthus* clones could set fruit without pollen vector involvement, although the set was slightly lower than with hand pollination. Pollen source influenced fruit weight. In the self-fruitful species of *Hylocereus*, fruit obtained by hand cross-pollination with other *Hylocereus* spp. were significantly heavier than fruit obtained by hand self-pollination. The largest fruit in each of the *Hylocereus* spp. were obtained by specific cross-combinations within the group. Fruit of *S. megalanthus* had a lower weight than fruit of the *Hylocereus* spp. Flowers of all species were visited by day-active honeybees only. Fruit set and fruit weight with open pollination was lower than with hand pollination in *Hylocereus* spp. Since stigma receptivity and pollen germinability stayed high during anthesis, the low pollination effectivity has to be related to other factors, such as the short bee visits and the absence of specific adaptation by the bees to the flower. In *S. megalanthus*, fruit set and fruit weight with open pollination were similar to values obtained with hand pollination. This similarity is probably related to the fact that pollen transfer in open pollination is achieved by bee visits and direct transfer of pollen to the stigma, which occurs via physical contact between anthers and stigma during flower closing.

Climbing epiphytic cacti, members of the genera *Hylocereus* and *Selenicereus*, are found throughout Central America, the West Indies, and western Mexico (Britton and Rose, 1963). These cacti are branched climbers that attach their slender stems to trees or rocks via adventitious roots, which grow along the stems. These roots also serve to absorb water (Gibson and Nobel, 1986).

Several species of *Hylocereus* and *Selenicereus*, known as strawberry pear (Morton, 1987), produce medium to large fruit, traditionally consumed by the local population (Cacioppo, 1990). In Latin America, the plants and their fruit are known as pitaya or pitahaya (Donají Ortiz Hernandez, 1993). The *Hylocereus* fruit are characterized by a red peel with large scales and a white or red pulp, while those of *Selenicereus* have a knobby yellow peel with spines and a white flesh (Britton and Rose, 1963; Kimmach, 1984;

Seaton, 1991). The juicy, sweet fruit contain numerous edible, tiny black seeds, and the fruit are much appreciated when served chilled (Morton, 1987). Cultivation of selected spe-

cies has begun recently, *H. undatus* in Nicaragua and Vietnam and *S. megalanthus* in Colombia (Barbeau, 1990; Cacioppo, 1990).

Studies are rare on the reproductive biology of the climbing cacti. The flowers are hermaphroditic, nocturnal, and strongly scented. Each flower is large, up to 30 cm long, with a long flower tube that fans out into a funnel-shaped corolla with thin, white petals (Fig. 1). A nectary chamber is located at the bottom of the flower tube (Britton and Rose, 1963). Flowers exhibit characteristics of those pollinated by night-active bats and large hawk-moths (Grant and Grant, 1979; Haber, 1983). Three species, *H. ocamponis*, *H. undatus*, and *S. megalanthus*, are probably autogamous and the visits of pollinators increase fruit set (Cacioppo, 1990; Cullmann et al., 1987; Kimmach, 1967).

Preliminary studies in Israel show that climbing cacti are susceptible to high solar irradiation and become bleached when grown in the open; however, plants develop well and flower when they are shaded (Raveh et al., 1993). In their studies, flowers did not set fruit, suggesting fertilization failure, possibly due to a lack of pollen vector activity, or to compatibility problems. The objective of the present study was to examine flowering behavior and pollination requirements in selected species of *Hylocereus* and in *S. megalanthus*, with the aim of proposing agromanagements that will enable them to be grown commercially.

Materials and Methods

Plant material and study site. Clones of four species were examined (Table 1). For two of them, *H. undatus* and *S. megalanthus*, two genotypes in each one, differing in origin and morphological traits, produced abundant flowers during the study period. The investigation was therefore extended to two clones within these species. Cuttings for propagation were obtained from the Huntington Botanical Garden in California, from a private garden in



Fig. 1. Flower of *Hylocereus polyrhizus*.

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Table 1. Plant material, fruit characteristics, and source for climbing cacti.

Species	Local clone designation	Fruit characteristics	Source
<i>Hylocereus polyrhizus</i> (Weber) Britton & Rose		Fruit oblong; peel dark-red with large scales; pulp violet-red	Huntington Botanical Garden, Calif., collection no. 15885 HBG
<i>H. undatus</i> (Haworth) Britton & Rose	A	Fruit oblong; peel light-red with large scales; pulp white	Private garden, Israel
	B	Fruit oblong; peel light-red with large scales; pulp white	Private garden, Israel
<i>H. costaricensis</i> (Weber) Britton & Rose		Fruit round; peel dark-red with large scales; pulp violet-red	Huntington Botanical Garden, Calif., collection no. 49639 HBG
<i>Selenicereus megalanthus</i> (Schum. ex Vaupel) Moran	A	Fruit oblong; peel yellow with tubercles and spines; pulp white	Plantation, Colombia
Syn. <i>Mediocactus megalanthus</i>	B	Fruit oblong; peel yellow with tubercles and spines; pulp white	Wild, Ecuador

Israel, from commercial plantations in Colombia, and from the wild in Ecuador. The study was carried out in 1992 and 1993 in Beer Sheva, which is situated in the northern Negev Desert of Israel. The experiments were performed on 3- to 4-year-old plants in greenhouses under 50% shade, which were covered with polyethylene during the coldest months (November to March). Six plants of each clone were grown in two greenhouses. The cuttings were planted in sandy soil at a spacing of 1.5 × 1.5 m, and a trellis system 1.5 m in height was installed for supporting the plants. Water containing 20N–20P–20K fertilizer was applied by dripper at a concentration of each 70 ppm N (NH₃NO₃ + KNO₃), P₂O₅ (H₃PO₄), and K₂O (KNO₃) every 2 days at a weekly amount of 5 liters/plant during the hot season (May to October) and 3 liters/plant per week during the cold, wet season. At the beginning of the study, a honeybee hive was placed inside one of the greenhouses. The greenhouse was open on two sides to allow other insects to enter. The average minimum/maximum temperatures in the coldest month (January) were 18/22C and in the hottest month (August) 16/35C in both greenhouses.

Phenology of flowering, flower behavior, and insect visits. During the flowering season, all plants were monitored daily for new flowers. The flowers of three plants for each clone were observed for 5 days to determine the phases of anthesis. The presence of nectar was determined by probing the flowers with pasteur pipettes at half-hour intervals.

Breeding system and pollination type. Three treatments were applied: 1) Hand self-pollination—pollen from the same flower was applied to the stigma after flowers opened in the evening. To prevent open pollination, flowers were kept bagged except during hand pollination. 2) Hand cross-pollination—the stigma was enclosed in a small cloth bag in the afternoon before pollen was shed to prevent self-pollination; pollen gathered from a different concurrently flowering clone was applied the same evening. 3) Covered, undisturbed flowers—flowers were covered with bags throughout anthesis. Fruit set was recorded in all treatments, and fruit weight and seed count were determined. Full skin color change was an indicator for fruit harvest.

Pollen germinability and viability. Pollen germinability at anthesis and during the post-anthesis stages was studied by sampling flowers at 12-h intervals, beginning at flower opening and ending 72 h later. Six flowers were sampled for each clone. A sample of 5 mg of pollen was spread on a glass slide in a thin film of 1% agar containing 30% sucrose, 100 ppm H₃BO₃, 100 ppm Ca(NO₃)₂·4H₂O, 100 ppm MgSO₄, and 100 ppm KNO₃. The slide was closed in a petri dish at 25C for 24 h, after which the pollen sample was diluted with 1 ml of 30% sucrose solution; then, germination was examined under a microscope. Grains were scored as germinated when tube length exceeded the diameter of the grain itself. Pollen viability was assessed by a fluorochromatic assay (Heslop-Harrison et al., 1984).

Effective pollination period. The time interval following anthesis during which pollination will result in a commercial crop is

defined as the effective pollination period, and it is a function of ovule longevity and the rate of pollen tube growth (Dennis, 1986). The effective pollination period was studied in two species, *H. costaricensis* and *H. polyrhizus*. Stigmas of flowers were bagged before anthesis and then cross-pollinated by hand with pollen of *H. undatus* (clone A) at flower opening (evening) and again in the morning and evening of the following days. [Previous unpublished studies have shown that *H. undatus* (clone A) was highly compatible with the two other species]. Fresh pollen gathered during the morning or evening, at which times in vitro pollen germinability was high, was used for pollination. Seven to 11 flowers were pollinated in each species at a time and fruit set and fruit weight were determined.

Effect of open pollination on fruit set and fruit weight. Two treatments were applied in 1993 to flowers on plants growing in the

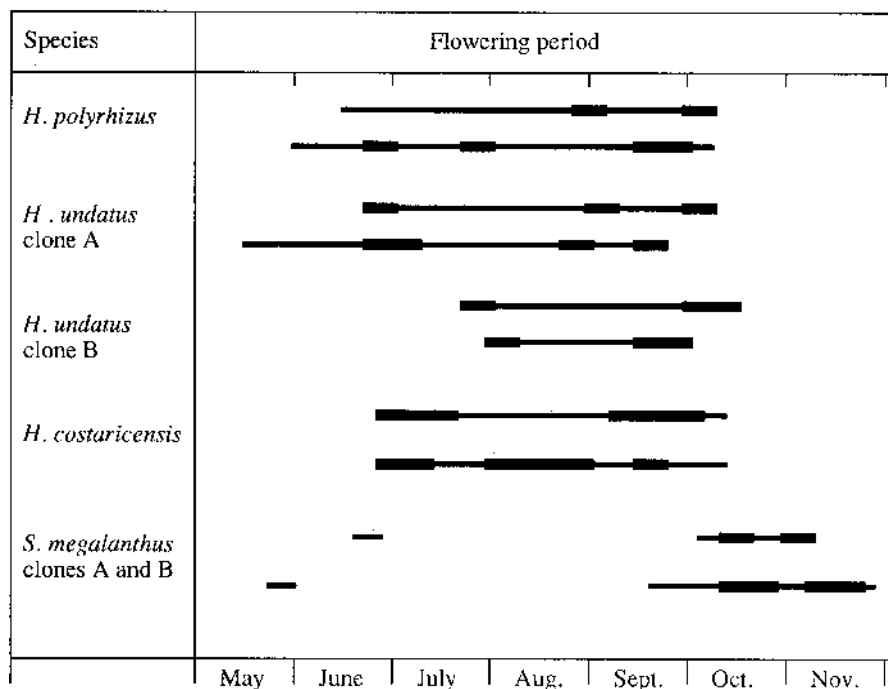


Fig. 2. Flowering periods for various species of *Hylocereus* and *Selenicereus* during the 1992–93 flowering seasons (upper line—1992, lower line—1993). The thickened sections of the lines indicate periods of concentrated flowering; at least four flowers per species were monitored each day.

greenhouse in which the bee hive had been placed: 1) hand cross-pollination and 2) open pollination, in which flowers were exposed to insects. In all treatments, fruit set was evaluated and fruit were picked at full color change for fruit weight determination. *Hylocereus* spp. were studied for two consecutive years, whereas *S. megalanthus* clones were studied only in the second year due to an inadequate flower set in the first year.

Results

Flowering phenology, flower behavior, and insect visits. The number of flowers per plant averaged 9 ± 7 in *Hylocereus* spp. and 4 ± 1 in *S. megalanthus* and ranged between 5 and 25 flowers in the *Hylocereus* group and between 3 and 8 in *S. megalanthus* in the second year of the study. Flowering in the *Hylocereus* spp. occurred in two to three waves, mainly during summer and early autumn (May to October), whereas flowering in *S. megalanthus* was concentrated in autumn (October to November) (Fig. 2).

In all the species, the phases of anthesis followed a very similar pattern so that a single representative scheme is presented (Fig. 3). Flowers stayed open for one night. They began to open 1 to 1.5 h before sunset, were fully open by sunset, began to close ≈ 1.5 h after sunrise, and were fully closed by midday. Anthers dehiscence 0.5 to 1 h before flower opening. The upper part of the anthers in the *Hylocereus* spp. were at least 2 cm below the stigma, whereas in *S. megalanthus*, they were at the same height as the stigma, touching it when the flowers closed. The first nectar secretion was evident when the flowers were fully open. The flowers were visited by the honeybee, *Apis mellifera* L. The bees foraged for pollen and contacted the stigma frequently during their visits, which were confined to the morning, and they did not appear to reach the nectar at the base of the flower tube.

Breeding system and pollination type. Synchronization of flowering determined the type of crossing combinations (Table 2). The *Hylocereus* clones were crossed with each other, as were the *S. megalanthus* clones. Among the *Hylocereus* spp., *H. polyrhizus* and *H. costaricensis* were self-unfruitful, and cross-pollination with other species led to high fruit set (100%). *Hylocereus undatus* was self-fruitful, setting fruit with self-pollen, but self-fruitfulness was partial since a higher fruit set was obtained by cross-pollination with the other species (50% to 80% vs. 100%).

Cross-pollination between the *S. megalanthus* clones led to a high fruit set and each clone was self-fruitful. In contrast to *H. undatus*, they also set fruit without the involvement of a pollen vector (automatic self-pollination).

Pollen source influenced fruit weight (Table 3). In the self-fruitful species of *Hylocereus*, fruit obtained by hand cross-pollination with other *Hylocereus* spp. were significantly heavier than fruit obtained by hand self-pollination. The largest fruit in each of the *Hylocereus* spp. were obtained by specific

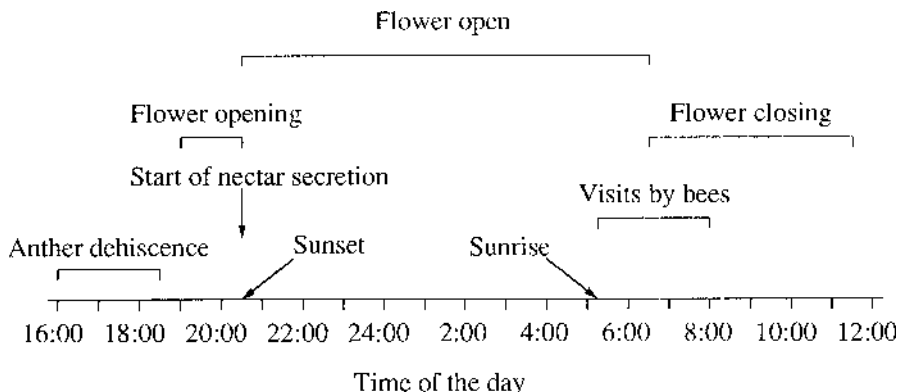


Fig 3. Anthesis phases and timing of insect visits to flowers in various species of *Hylocereus* and *Selenicereus*.

Table 2. Percentage of fruit set for climbing cacti in relation to the breeding system used.

Species	Fruit set (%)		
	Hand cross-pollination	Hand self-pollination	Covered, undisturbed flowers
<i>Hylocereus polyrhizus</i>	100 ^z	0	---
<i>H. costaricensis</i>	100 ^z	0	---
<i>H. undatus</i> clone A	100 ^z	50.0	0
<i>H. undatus</i> clone B	100 ^z	79.6	0
<i>Selenicereus megalanthus</i> clone A	100 ^y	100	73.0
<i>S. megalanthus</i> clone B	100 ^y	100	60.0

^zCrossings with pollen from a different, concurrently flowering *Hylocereus* clone.

^yCrossing with pollen from the other clone of *S. megalanthus*.

Table 3. Effect of pollen source on fruit weight (grams) in *Hylocereus* spp.

Male	Female			
	<i>H. polyrhizus</i>	<i>H. undatus</i> clone A	<i>H. undatus</i> clone B	<i>H. costaricensis</i>
<i>H. polyrhizus</i>	---	580	567	384
<i>H. undatus</i> clone A	476	182	337	298
<i>H. undatus</i> clone B	410	287	301	329
<i>H. costaricensis</i>	539	633	495	---
Tukey's LSD _{0.05} , n = 8	155	90	102	46

Table 4. Effect of pollination method on fruit weight (grams) in *Selenicereus megalanthus*.

Pollination method	<i>S. megalanthus</i> clone A	<i>S. megalanthus</i> clone B
Self	77	86
Cross	98	108
Covered, undisturbed flowers	38	51
Tukey's LSD _{0.05} , n = 8	44	50

cross-combinations within the group.

Fruit of *S. megalanthus* weighed less than fruit of the *Hylocereus* spp. (Table 4). Hand cross-pollination and hand self-pollination in *S. megalanthus* produced fruit with similar fruit weights, which were about twice that with automatic self-pollination.

Regression analysis showed that the seed count per fruit explained 75% to 91% of the variability in fruit weight (Fig. 4). Seed count was much higher in fruit of the *Hylocereus* group than in those of *S. megalanthus*: maximum values ranged between 3918 and 6505 in the *Hylocereus* vs. 26 and 446 in *S. megalanthus*. Ovules were counted in two species: *H. undatus* (clone A) with many seeds and *S. megalanthus* (clone A) with relatively few. The average number of ovules was 7184 ± 613 and 1969 ± 176 , respectively.

Pollen germinability and viability. Pollen germinability in all species was highest when flowers started to open (Fig. 5). In *H.*

polyrhizus, a sharp decline was recorded the next morning when flowers began to close, while in *H. undatus* (clone A) and *H. costaricensis*, pollen germinability declined only the following evening, by which time the flowers had already closed. Pollen of *S. megalanthus* sampled when flowers started to open or 12 h later had very low germinability ($<4\%$). Changing the concentration of the medium components or using other germination methods, such as hanging-drop, standing-drop, and mass culture techniques (Calzoni et al., 1979), did not affect the germination of *S. megalanthus* pollen, which remained low (data not shown). Viability of fresh pollen was high, 90% to 94%, in the *Hylocereus* spp. and about one-third of it in *S. megalanthus* (Fig. 6).

Effective pollination period. Pollination of *H. polyrhizus* and *H. costaricensis* with fresh pollen of *H. undatus* (clone A) led to high fruit set and heavy fruit (Table 5). Pollination was conducted during the period between the time

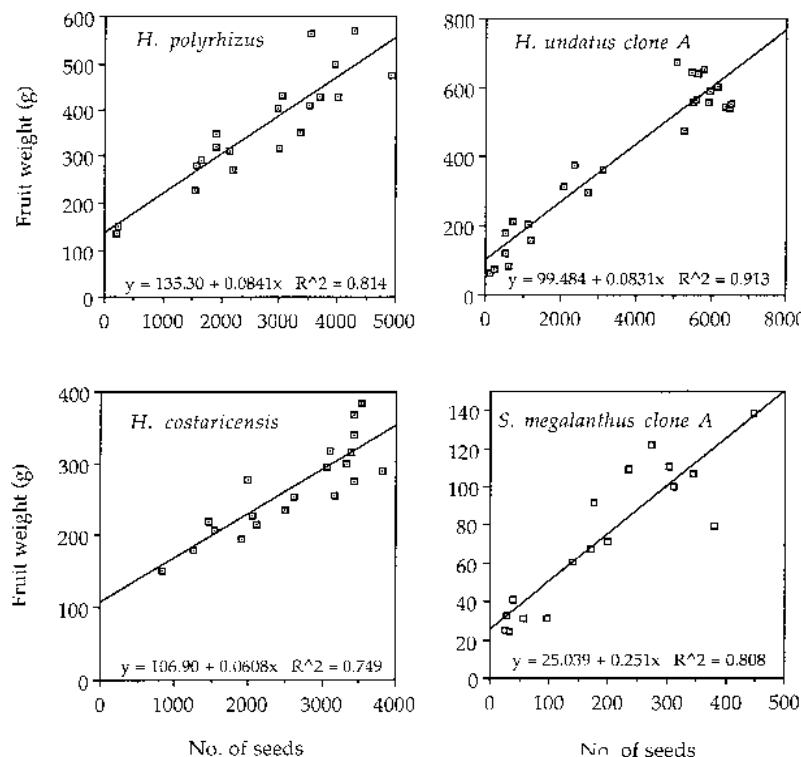


Fig. 4. Relationship between fruit weight and seed count in *Hylocereus* spp. and in *Selenicereus megalanthus*. Fruit included in the analysis were from open- and hand-pollination treatments. Calculations are based on measurements of 17 to 25 fruit for the various species ($P = 0.01$).

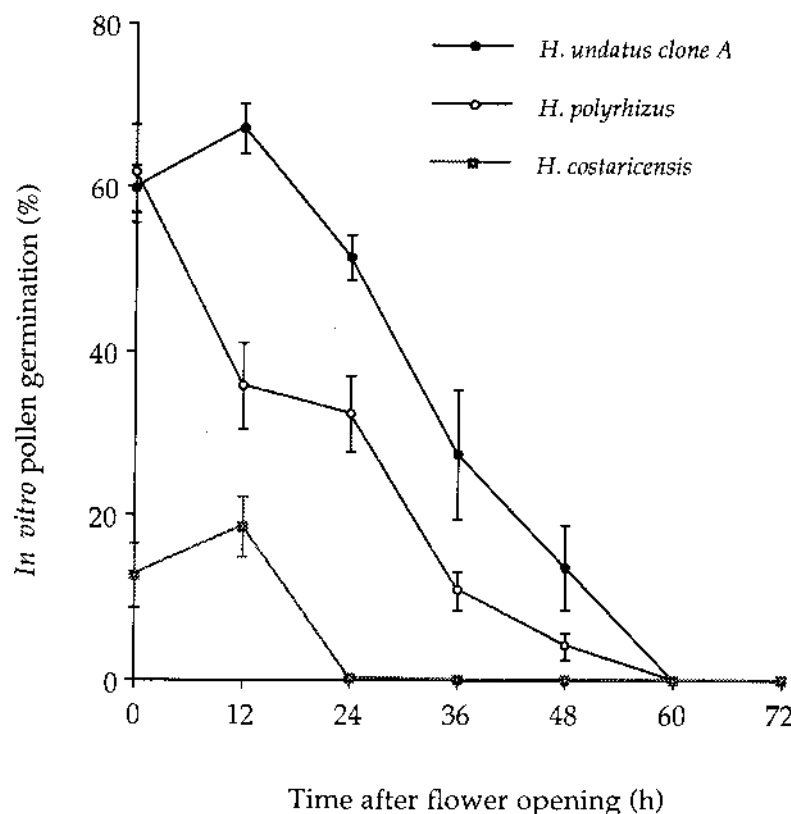


Fig. 5. In vitro germination of pollen of *Hylocereus undatus* clone A, *H. polyrhizus*, and *H. costaricensis* sampled from flower opening over 60 h. Values are the average of counts of 100 pollen grains from six randomly selected flowers.

of flower opening in the evening and the evening of the following day. Later pollination produced significantly lower fruit weights, and no fruit set when pollination was conducted 2 days after flower opening.

Effect of open pollination on fruit set and fruit weight. Fruit set with open pollination was higher in *S. megalanthus* (80%) than in *Hylocereus* spp. (12.5% to 50%) (Table 6). Hand cross-pollination resulted in higher fruit set and heavier fruit than were achieved by open pollination in the *Hylocereus* spp. In *S. megalanthus*, fruit weight in open pollination was similar to fruit weight after hand pollination. Open-pollinated flowers were visited only by honeybees, indicating that pollen transfer was related to honeybee activity.

Discussion

Studies on the pollination requirements of orchard crops usually examine the compatibility between cultivars within species. In the case of the climbing cacti under discussion, some are not cultivated at all, and for the commercially cultivated species, no defined cultivars are available (Barbeau, 1990). Since preliminary studies had shown us that cross-pollination between the investigated species was successful, the study set out to examine the possibility of using particular species as pollinators for other species. For the commercial species, *H. undatus* and *S. megalanthus*, the availability of clones differing in origin and in some morphological traits allowed us to extend the study within these species.

Two species, *H. undatus* and *S. megalanthus*, were self-fruitful. For both species, the involvement of pollen vectors was important for fruit production: *H. undatus* set fruit only when hand self-pollinated, and *S. megalanthus*, which set fruit by self-pollination without a pollen vector, produced heavier fruit when hand self-pollinated. The ability of flowers to set fruit without the involvement of a pollen vector was associated with flower morphology: upper anthers touched the stigma lobes in *S. megalanthus* during flower closing, but anthers were separated spatially from the stigma in the *Hylocereus* spp.

Studies of the breeding system lead to some practical conclusions with regard to the desired orchard design: a) *S. megalanthus* can be planted alone (one or two clones) because of the high fruit set obtained by self- and cross-pollination between the clones. b) Fruit production in *H. undatus* would benefit from planting this species with pollinizers of two other *Hylocereus* spp., *H. polyrhizus*, and *H. costaricensis*, which induced both high fruit set and heavy fruit in *H. undatus*. The flowering period of the two proposed pollinizers was parallel to that of *H. undatus*. c) In the self-unfruitful species, *H. polyrhizus* and *H. costaricensis*, any of the *Hylocereus* spp. may be planted as pollinizers in relation to their influence on fruit set and fruit weight and synchronous flowering.

As is the case for other fruit crops producing abundant seeds, such as kiwifruit [*Actinidia deliciosa* (A. Chev.) C.F. Liang et R. Ferguson

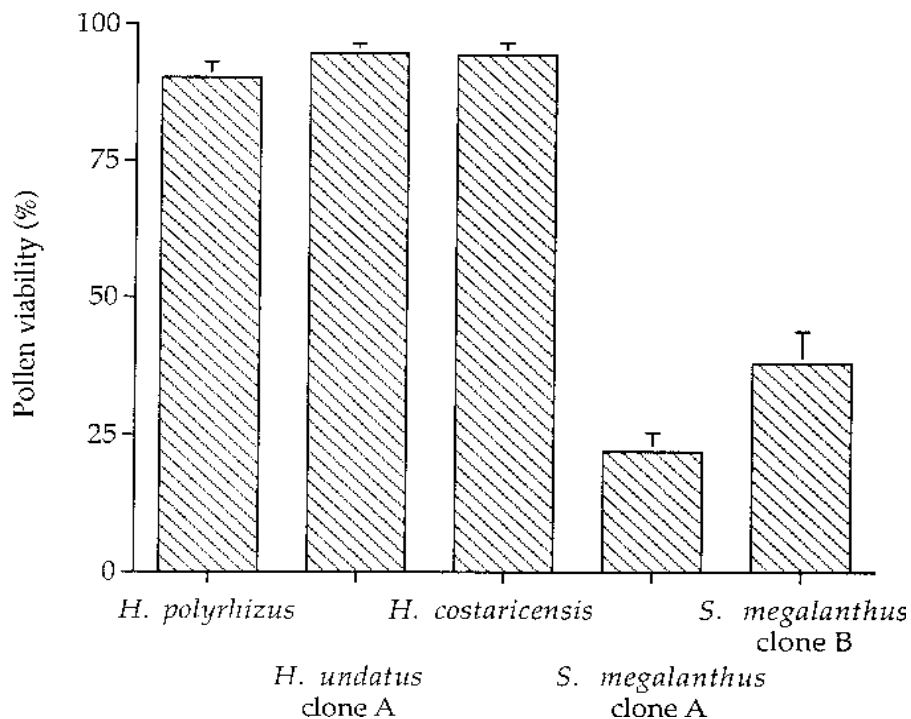


Fig 6. Pollen viability of *Hylocereus* spp. and *Selenicereus megalanthus* clones. Pollen viability was determined by a fluorochromatic assay. Pollen samples were taken shortly after flower opening. Values are the average of counts of 100 pollen grains from six randomly selected flowers.

var. *deliciosa*] (Hopping and Jerram, 1979) or feijoa (*Feijoa sellowiana* Berg.) (Patterson, 1990), fruit weight in the cacti was highly correlated with seed count. Thus, attention must be paid to obtain efficient pollination in the plantation. The maximum percentage of ovules that developed into seeds was 23% in *S. megalanthus* (clone A), whereas a maximum of 90% of the ovules set seed in *H. undatus* (clone A). The low seed set in *S. megalanthus* (clone A) can be related to the low viability and germinability of its pollen. Higher seed set and, therefore, higher fruit weight could probably be obtained by pollinating with highly viable pollen of other clones of *S. megalanthus* or other *Selenicereus* spp.

Although the flowers of both genera displayed the characteristics of those pollinated by night-active pollinators (Grant and Grant, 1979; Haber, 1983), the only pollen visitor to *Hylocereus* and *Selenicereus* was a day-active honeybee. The honeybee is a polytropic pollinator and forages on many nocturnal cactus flowers, including the saguaro [*Carnegiea gigantea* (Engelm.) Britt. & Rose], the organ pipe cactus [*Stenocereus thurberi* (Engelm.) Britt. & Rose] (Alcorn et al., 1962; McGregor et al., 1962; Schmidt and Buchmann, 1986), and the apple cactus [*Cereus peruvianus* (L.) Miller] (Weiss et al., 1993). The low rate of fruit set and the low fruit weight recorded for open pollination in the *Hylocereus* spp. indicates that the bees were not effective pollinators for these species under the conditions of our study. The bees visited the flowers only in the morning before flower closing. Since pollen germinability and female receptivity were high at this time, the low pollination effectiveness has to be related to other factors, possibly

the brevity of the visits and the lack of specific adaptation to the flower; for example, bees did not reach the nectar accumulated at the base of the flower tube. In *S. megalanthus*, fruit set and fruit weight with open pollination were similar to those obtained in hand pollination. This feature may be related to the fact that

pollen transfer in open pollination is achieved by bee visits and by direct transfer of pollen to the stigma, which occurs via physical contact between anthers and stigma during flower closing.

Further studies will have to be made on improving the efficiency of the bees as pollinizers for the *Hylocereus* spp. with regard to the interaction between the flowers of the climbing cacti and bee behavior in the plantation. The problems associated with pollination by bees do not occur when pollination is carried out artificially. Hand pollination ensured high fruit set and heavy fruit when conducted during the entire period of anthesis. Hand pollination can thus be carried out conveniently during the morning hours, if economically feasible. Other potential pollinators of the climbing cacti exist in Israel; for example, the large carpenter bee (*Xylocopa pubescens* L.) potentially could be introduced successfully inside the shaded greenhouse.

The results of this study clarify various aspects of the reproductive biology of promising climbing cacti, including the flower phenology, the compatibility system, and the pollination type, which will enable the grower to define the agromanagement required for productive plantations. More studies concerned with clones are needed to determine if solid species plantations, consisting only of different clones of one species, may be established.

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Table 5. Effect of timing of pollination on percentage of fruit set and fruit weight in two *Hylocereus* spp. *Hylocereus undatus* clone A was the pollen source.

Species ²	Time after flower opening (h)	Fruit set (%)	Fruit wt (g)
<i>H. polyrhizus</i>	0	100	392 ab ^y
	12	100	396 a
	24	100	304 bc
	36	38	228 c
	48	0	---
<i>H. costaricensis</i>	0	100	316 a
	12	100	369 a
	24	100	241 b
	36	20	154 bc
	48	0	---

²In each species 7 to 11 flowers were pollinated at a time.

^yMean separation by Fisher's PLSD test, $P \leq 0.05$.

Table 6. Effect of pollination type on fruit set and fruit weight in climbing cacti. For the *Hylocereus* spp., fruit set and fruit weight are the mean of 2 years of observation.

Species	Pollination type	No. flowers	Fruit set (% of total)	Fruit wt (g)
<i>H. polyrhizus</i>	Hand cross	37	100	599 ± 25
	Open	24	20.8	108 ± 11
<i>H. undatus</i> clone A	Hand cross	30	100	588 ± 15
	Open	44	43.2	120 ± 13
<i>H. costaricensis</i>	Hand cross	30	100	291 ± 19
	Open	16	12.5	113 ± 12
<i>Selenicereus megalanthus</i> clones A and B	Hand cross	15	100	116 ± 4
	Open	10	80	121 ± 5

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