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Effects of day-length, radiation, flower thinning and growth regulators on flowering of the vine cacti *Hylocereus undatus* and *Selenicereus megalanthus*

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SUMMARY

To obtain out-of-season cropping and flowering of the tropical vine cacti *Selenicereus megalanthus* and *Hylocereus undatus*, the following agricultural manipulations were tested: photoperiodic light applied for 3, 6 or 9 h after sunset; shading (to produce 80%, 60% or 40% of sunlight); flower thinning (when buds were 2–5 cm, 15–25 cm or at anthesis, or by not pollinating the flowers); or separate application of the following growth regulators [N-(2-chloro-4-pyridinyl)-N-phenyleurea (CPPU); gibberelic acid (GA$_3$); a commercial mixture of gibberellins (GA$_3$ and GA$_7$) with benzyladenine (BA) known as Perlan™; paclobutrazol (PBZ); or ethephon (Ethrel™)]. Photoperiod and radiation did not alter the pattern of flowering. Maximum flower yields were obtained under 60% sunlight for *H. undatus* and under 60% or 40% sunlight for *S. megalanthus*. Removal of young flower buds delayed flowering and late cropping in *H. undatus*, but with no loss in total flower yield. In both species, CPPU promoted precocious flowering and, in *H. undatus*, it increased total flower yield, whereas GA$_3$ delayed flowering and decreased total flower yield. Hence, CPPU can be used to obtain early fruit production, and GA$_3$ or flower thinning (in *H. undatus*), to delay cropping.

The fruit-bearing semi-epiphytic vines *Selenicereus megalanthus* and *Hylocereus undatus* (Cactaceae) originate in tropical and sub-tropical South America. These species, known as pitaya, are widely cultivated in Central America, Southern Mexico and Vietnam, and have recently been introduced into Israel (Mizrahi *et al*., 1997). There are, however, few data on the reproductive biology and phenology of these species. In sub-tropical Israel, these species flower for only 3–6 months each year (Weiss *et al*., 1994). To extend the fruiting period, methods to manipulate flowering need to be developed.

Many plants must have reached a certain age or physiological state before they will flower. Environmental cues such as photoperiod, temperature and humidity are also involved. Reports on environmental triggers operating in cacti and succulents refer to photoperiod in *H. undatus* (Yen and Chang, 1997) and in Easter and Christmas cacti (Boyle, 1991); to photoperiod and water status in tropical succulent trees (Philipson, 1990; Borchert *et al*., 2005) and to temperature, flower bud thinning and nutrition in *Opuntia ficus-indica* (Nerd and Mizrahi, 1995; Raveh and Nobel, 1999; Barbera *et al*., 1991; Inglese *et al*., 1999; Nunez-Elisea and Crane, 2000; Nerd and Mizrahi, 1994).

Endogenous growth substances are also involved in the flowering of plants (Meilan, 1997). Exogenous application of cytokinins (CK) can induce flowering in some woody species (Meilan, 1997; Naphrom *et al*., 2001; Werner *et al*., 2001). In contrast, gibberellins (GA) have mixed effects, depending on whether the plants are annuals (positive effect) or woody (negative effect) (Bernier, 1988; Boyle and Marcotrigiano, 1997; Sedgley and Griffin, 1989). Inhibitors of GA biosynthesis, such as paclobutrazol (PBZ) or ethephon (Ethrel™), reduce growth and promote precocious and increased flowering in many species (Klein and Faust, 1978; Edgerton, 1986; Griffin *et al*., 1993; Min and Bartholomew, 1996; Imanishi *et al*., 1997; Davenport, 2000).

This paper reports on studies to develop methods to manipulate the pattern of cropping of *H. undatus* and *S. megalanthus* in Israel. Plants were grown under different day-lengths or radiation levels; flower buds were removed at various times, or flowers were not pollinated; and CPPU, GA$_3$ and other plant hormones were applied.

MATERIALS AND METHODS

Plant material and growth conditions

The studies were conducted on *H. undatus* (clone 89-024) and *S. megalanthus* (clone 88-028), planted in 1994 and 1995, respectively. *H. undatus* was grown in a trellised house, covered with a 40% shade cloth. Vines were irrigated each week with a nutrient solution containing 70 mg l$^{-1}$ N, 70 mg l$^{-1}$ P and 70 mg l$^{-1}$ K fertiliser with trace elements (Deshanim, Israel) between November and March, and twice a week from April to October (except after rain). *S. megalanthus* was grown in a trellised house with a 60% shade cloth with irrigation, as above, twice a week.

Photoperiod

To test the influence of red light extension on floral initiation, plants were exposed to light from 100 W incandescent bulbs located 30 cm above them every 1.5 m. From March to July 2003, the lighting system was operated for 3, 6 or 9 h after sunset. The natural day-
length in Israel during the time of treatments ranged from a minimum of 11 h 30 min in March to a maximum of 14 h 14 min in June.

**Radiation**

In 2003–05, plants were grown under 20%, 40% or 60% shade cloth or with 60% shading by Aluminet (Polysack Plastic Industries, Nir-Itzhak, Israel), an effective light scattering net. Consequently the shade cloths transmitted 80%, 60% or 40% of sunlight, respectively. Vine cacti cannot be grown under open field conditions (0% shade) in Israel, as they become bleached and die (Raveh et al., 1996).

**Pollination**

Because of problems of self-incompatibility, all flowers of both species were pollinated with *H. polyrhizus* (clone 89-028) to improve fruit-set, as they were grown in actual agricultural plots (Weiss et al., 1994; Dag and Mizrahi, 2005). One exception was made for one treatment in the flower thinning experiment (2003), as described below.

**Flower thinning**

In 2003, in *H. undatus*, 20 – 25 cm flower buds were removed, or flowers at anthesis were enclosed in paper bags to prevent pollination and left on the vines. In 2004, 2 – 5 cm flower buds (small buds), 15 – 20 cm buds (large buds) or flowers at anthesis were removed. Buds were not removed in *S. megalanthus* as flowers produced from new buds would open after 10 November, when temperatures were too low for satisfactory fruit-set (Weiss et al., 1994; Dag and Mizrahi, 2005).

**Plant growth regulators**

*H. undatus* plants were sprayed each month from February to May (2003), before natural flowering, with the following growth regulators: 50 or 200 mg l\(^{-1}\) of the CK forchlorfenuron [N-(2-chloro-4-pyridinyl)-N-phenylurea (CPPU)]; 100 or 500 mg l\(^{-1}\) gibberellic acid (GA\(_3\)); a commercial mixture of gibberellins (GA\(_3\) and GA\(_4\); 100 mg l\(^{-1}\) each) with the CK benzyladenine (BA; 100 mg l\(^{-1}\)) known as Perlan™; 0.2 or 1.0 g l\(^{-1}\) of the anti-gibberellic acid compound paclobutrazol (PBZ); or 0.5 or 1.0 g l\(^{-1}\) Ethrel™.

* S. megalanthus was treated with 100 mg l\(^{-1}\) GA\(_3\), 5 g l\(^{-1}\) PBZ, 1 g l\(^{-1}\) Ethrel or 50 mg l\(^{-1}\) CPPU each month from June to September 2003, after cropping and before natural flowering. To test the cumulative effect of PBZ on *S. megalanthus*, 3 g l\(^{-1}\) PBZ was applied to the same plants in June, July and August. All spray solutions contained 0.7% (v/v) FertiVant, a surfactant adjuvant. Controls received only 0.7% (v/v) FertiVant.

To determine the male and female fertility of flowers induced by hormone treatments, flowers of both species were cross-pollinated with *H. polyrhizus*. Fruits from this cross were compared with those of controls for fruit weight, numbers of viable seeds, total soluble solids (TSS) content and total acid (TA) content (Nerd et al., 1999).

**Data collection and analyses**

All experiments were performed in large-scale agricultural plots in the northwestern Negev, Israel. Each treatment was replicated independently on at least three different 3 m-trellised units at each location. Flowering was recorded each week as the number of flowers at anthesis 3 m\(^{-1}\) of trellis. Flower yield was defined as the overall number of flowers produced 3 m\(^{-1}\) of trellis during the season.

JMP software was used for statistical analyses of the data. Values are means ± SE for at least three 3 m trellises. For each data set, the F-test was performed (*P* < 0.05), followed by the student’s t-test.

**RESULTS AND DISCUSSION**

Growth and flowering were periodic in the vine cacti species studied here, similar to many tropical and subtropical trees such as mango, lychee and citrus. Vegetative growth flushes can occur throughout the year, whereas reproductive flushes generally occur after extended periods of stem rest, or after cool weather (Menzel, 1984; Davenport, 1990; Nunes-Elisea et al., 1996; Borchert, 2000; Davenport, 2000).

In Israel, *H. undatus* flowers from June to October, and *S. megalanthus* from September to January (Weiss et al., 1994). Various techniques to manipulate flower distribution were tested to extend the flowering period of the two species.

**Photoperiod**

Day-length had no effect on flowering (data not shown). This response is different from that reported by Yen and Chang (1997) in pitaya, or that described by Borchert et al. (2005), who found that minor changes in day-length (30 min) induced flowering in a number of succulents. These contradictory results may be explained by differences in the temperature regimes between the tropical climates of the above-mentioned studies and the sub-tropical climate of Israel.

**Radiation**

In their natural habitat, vine cacti are hemi-epiphytes growing under the shade of trees. In the open field, in Summer, in Israel (with a PAR intensity of approx. 2,200 µmoles m\(^{-2}\) s\(^{-1}\)), plants have to be protected from direct sunlight (Raveh et al., 1996). On the other hand, too much shading can potentially decrease carbohydrate levels in plants and flowering, as was found in apple (Cain, 1971), in peach (Miller and Tworkoski, 2003) and in the tropical trees carambola and mango (Zeng, 2001).

Shading did not affect the pattern of flowering in either species of pitaya (data not shown). *H. undatus* gave the best flower yields with 60% sunlight, and *S. megalanthus* with 40% or 60% sunlight (Table I) (*P* < 0.05). These results agree with those of Raveh et al. (1996).

<table>
<thead>
<tr>
<th>Table I</th>
<th>Flower yield* in <em>H. undatus</em> and <em>S. megalanthus</em> exposed to 80%, 60% or 40% sunlight or 40% sunlight under Aluminet** in 2003/2004</th>
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<tbody>
<tr>
<td>Species</td>
<td>80% Sunlight</td>
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<td>---------------</td>
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<tr>
<td><em>H. undatus</em></td>
<td>50 a</td>
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<tr>
<td><em>S. megalanthus</em></td>
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*Values are mean numbers of flowers (±SE) for four 3 m-trellises. Values followed by different letters in a row denote a significant difference between means at *P* < 0.05.

**Aluminet is an effective (60%) light-scattering net.**

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**Yen and Chang (1997) in pitaya, or that described by Borchert et al. (2005), who found that minor changes in day-length (30 min) induced flowering in a number of succulents.**

**Vegetative growth flushes can occur throughout the year, whereas reproductive flushes generally occur after extended periods of stem rest, or after cool weather (Menzel, 1984; Davenport, 1990; Nunes-Elisea et al., 1996; Borchert, 2000; Davenport, 2000).**
Flower thinning has been used to delay the main flowering period in many fruit trees such as cactus pear, carambola and apple (Inglese et al., 1999; Bayers and Carbaugh, 2002; Crane, 2004). In the pitaya species studied here, removing flower buds at different stages of development extended flowering by 1–2 months (Figure 1). One-third to two-thirds of flower yield was lost when flowers were not pollinated, or were removed at anthesis (Figure 1 B,F); whereas when large buds were removed the loss in flower yield amounted to as little as 5–10% (Figure 1 A,E). No flowers were lost when small buds were removed (Figure 1D).

Plant growth regulators

Our results for pitaya support the idea that many factors control flowering (Faust, 1989; Melian, 1997; Davenport, 2000), with the role of one specific factor being dependent on the state of the whole plant and on environmental factors. In our experiments with plant growth regulators, only CPPU and GA₃ altered the pattern of flowering under certain conditions.

All H. undatus plants treated with CPPU in May flowered 1.5 – 2.5 months before the controls (Figure 2). Although flowering was brought forward by 50 and 200 mg l⁻¹ CPPU, the higher concentration resulted in variations in flower yield (76 ± 28% of controls). The lower concentration not only brought forward flowering, but also increased the total number of flowers (128 ± 5% of controls). CPPU also reduced apical dominance, compared with controls (Figure 3). The majority of areoles (meristematic regions) in H. undatus treated with CPPU in May or June produced flower buds (Figure 3B). In contrast, the majority of areoles in plants treated in mid-April produced vegetative shoots (Figure 3A). The mid-March application of CPPU was similar to the

**Fig. 1** Effects of flower thinning on flowering of H. undatus. In 2003, all floral buds of the first flush were removed (Panel A) or the flowers were not pollinated (Panel B) and compared with controls (Panel C). In 2004, small (Panel D) or large (Panel E) buds, or flowers at anthesis (Panel F) were removed and compared with controls (Panel G). Values are means (±SE) of total flower yield for three 3 m-trellises, tested by F-test, \( P < 0.05 \).

**Fig. 2** Effects of 200 mg l⁻¹ (Panel A) or 50 mg l⁻¹ (Panel B) CPPU applied in May 2003 on flowering of H. undatus compared with unsprayed controls (Panel C).
Fig. 3
Effects of CPPU (50 mg l\(^{-1}\)) on phenology of *H. undatus* in 2003. Vegetative buds 1 month after CPPU-treatment in mid-April (Panel A); flower buds 2 weeks after treatment in mid-May (Panel B). Controls in July (Panel C). Bars = 30 cm.

Fig. 4
Effects of 50 mg l\(^{-1}\) CPPU applied in June (Panel A) or July (Panel B) 2003 on flowering of *S. megalanthus* compared with unsprayed controls (Panel C).

Fig. 5
Effects of 100 mg l\(^{-1}\) (Panel A) or 500 mg l\(^{-1}\) (Panel B) GA\(_3\), on flowering of *H. undatus* compared to unsprayed controls (Panel C).
control. Thus, cytokinins are effective only under certain conduce conditions.

The effects of CPPU on flowering in *S. megalanthus* were similar to those in *H. undatus* (Figure 4). Flower buds with reduced apical dominance emerged 2 weeks after CPPU applications in June and July, earlier than in the controls. Later applications gave flowering patterns similar to those of controls. The total number of flowers was not affected by CPPU (data not shown).

GA₃ inhibited flower emergence. In *H. undatus*, flowering was delayed by 1–2 months by 100 or 500 mg l⁻¹ GA₃ compared with controls. The treated plants flowered later, from July to October (Figure 5). The effects of GA₃ were much more pronounced at the higher concentration. Flower yield was reduced by 58 ± 7% with 500 mg l⁻¹ GA₃ in both species of cactus, and by 19 ± 4% with 100 mg l⁻¹ GA₃ in *H. undatus*. On the contrary, application of PBZ to *S. megalanthus* did not alter flowering times, but increased flower yield by 41 ± 23%.

Fruit-set and fruit quality were not affected by growth regulators (data not shown). Flowering in the season following the treatments was similar to that in the controls.

Our results thus indicate that the time of cropping can be manipulated in vine cacti. Flowering can be accelerated by CPPU, and delayed by GA₃ or flowering thinning.

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REFERENCES


Flowering in vine cacti


