The Relationship between Flower Age and Seed Production in *Hatiora gaertneri* and *Schlumbergera truncata* (Cactaceae)

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Abstract. Flowers of two cacti [*Hatiora gaertneri* (Regel) Barthlott ‘Crimson Giant’ and *Schlumbergera truncata* (Haworth) Moran ‘Eva’] were pollinated at different times between anthesis and senescence to determine the effect of floral age on seed production. Studies were conducted in a growth chamber ($20 \pm 0.5^\circ\text{C}$) to minimize temperature effects. Mean flower longevity (time from anthesis to first signs of senescence) was 4.7 days for *S. truncata* and 10.5 days for *H. gaertneri*. Stigmas of both species were receptive to pollination on the day of anthesis. The maximum number of viable seeds per pollinated flower was obtained when flowers of *S. truncata* and *H. gaertneri* were pollinated (respectively) on the second and fourth days after anthesis. For both species, the relationship between floral age and number of viable seeds per pollinated flower was described by a second-degree polynomial. The rate of pollen tube growth in the style was about $1.7 \text{ mm}\cdot\text{h}^{-1}$ for *S. truncata* and about $0.9 \text{ mm}\cdot\text{h}^{-1}$ for *H. gaertneri*. Some senesced flowers of *H. gaertneri* were capable of setting fruit with viable seed. Flowers of *S. truncata* did not set fruit when pollinated during the late phase of flower opening or after they had senesced. Senesced flowers of *S. truncata* failed to set fruit due to an insufficient number of pollen tubes reaching the ovary.

One of the critical procedures in most crop breeding programs is production of high-quality seed. Due to labor and time constraints, breeders aim to maximize their efficiency at obtaining seed for further breeding efforts or hybrid seed production. One factor that can affect the yield of viable seeds is the timing of pollen arrival on stigmas. Pollen grains arriving on immature or aged pistils may fail to set fruit or, if fruit set does occur, few viable seeds are produced. Floral age at the time of pollination has been shown to affect percent fruit set and/or seed yields in such diverse taxa as *Actinidia deliciosa* (González et al., 1995), *Buchloe dactyloides* (Jones and Newell, 1948), *Cyclamen persicum* (Ewald and Schwenkel, 1999), *Hylocereus* spp. (Weiss et al., 1994a), *Lilium* spp. (Kim and Niimi, 2002), *Malus sylvestris* (Williams, 1965), *Prunus armeniaca* (Burgos et al., 1991), and *Zea mays* (Jones and Newell, 1948). The time of pollination in relation to floral age may influence the extent of pollen germination on the stigma, the rate of pollen tube growth in the style and ovary, and ovule viability. These factors ultimately affect the potential for fruit set and seed production.

Schlumbergera truncata (Christmas cactus) and *Hatiora gaertneri* (Easter cactus) are two

epiphytic or epilithic shrubs grown as flowering potted plants. Individual flowers of Easter cactus last about 7 to 12 d at 20°C whereas flowers of Christmas cactus last for 4 to 6 d (Scott et al., 1994). Flowers of *S. truncata* have a floral tube about 4 cm long, a staminal nectar chamber, exerted stamens and style, and a zygomorphic perianth in shades of red or orange (Anderson, 2001; Boyle, 1996; Buxbaum, 1953). Flowers of *H. gaertneri* are 4 to 7.5 cm in diameter, dark scarlet, and actinomorphic, and they lack a floral tube (Anderson, 2001). Both species produce indehiscent, fleshy berries with numerous seeds (Buxbaum, 1955). The objectives of this investigation were to ascertain the relationships between floral age and seed production in *S. truncata* and *H. gaertneri*.

Materials and Methods

Plants of *H. gaertneri* ‘Crimson Giant’ and *S. truncata* ‘Eva’ were propagated vegetatively and grown in greenhouses. Except for seed germination experiments, all studies were conducted in a growth chamber kept at $20 \pm 0.5^\circ\text{C}$ and $65\% \pm 5\%$ relative humidity with irradiance ($50 \pm 8 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) provided by cool-white fluorescent lamps for 12 h daily. Experiments were performed in a growth chamber to minimize temperature effects on flower longevity, pollen germination, and pollen tube growth (Hartley et al., 1995; Vasilakakis and Porlingis, 1985).

Flower longevity. Flower longevity (number of days from anthesis to senescence) was recorded for 15 flowers per clone. The morphological criteria described by Scott et al. (1994)

were used to determine the commencement of anthesis and senescence.

Fruit and seed set in relation to timing of pollination. Plants with mature flower buds (about 1 to 2 d before opening) were transferred from a greenhouse to the growth chamber. Plants were examined twice daily and each flower was tagged on the day of opening (= day 0). Newly opened flowers were tagged on six consecutive days for *S. truncata* and 12 consecutive days for *H. gaertneri*. Flowers of *S. truncata* and *H. gaertneri* were pollinated on the sixth and twelfth day, respectively.

Nonsenesced as well as senesced flowers were pollinated using fresh pollen collected from several cross-compatible genotypes (Boyle, 2001). Each flower was pollinated once. Emasculation was not necessary due to presence of self-incompatibility (Boyle, 1996; Boyle et al., 1994). The experimental procedure yielded flowers ranging from anthesis to senescence in 1-d intervals. Eight or more flowers were pollinated per time interval. Plants were returned to the greenhouse 48 h after pollination. Fruit were harvested 3 months after pollination for *H. gaertneri* (Boyle et al., 1994) and 8 months after pollination for *S. truncata* (Boyle et al., 1995). Seeds were cleaned as described previously (Boyle, 1994) and sown in 10-cm-diameter petri dishes containing one layer of blue blotter paper (Anchor Paper Co., St. Paul, Minn.) moistened with deionized water. Each dish contained seeds from one fruit. Dishes were sealed with parafilm and placed in an incubator kept at $25 \pm 1^\circ\text{C}$ day/ $22 \pm 1^\circ\text{C}$ night with irradiance ($50 \pm 8 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) supplied for 12 h daily by cool-white fluorescent lamps. The numbers of germinated seeds (radicle $\geq 1 \text{ mm}$) were recorded 30 d after sowing. Percent fruit set, number of viable seeds per fruit, and number of viable seeds per pollinated flower [(fraction of fruit set) $\times$ (no. viable seeds per fruit)] were calculated for each treatment.

Kinetics of pollen tube growth, fruit set, and seed set. Plants of *H. gaertneri* and *S. truncata* with mature flower buds (about 1 to 2 d before opening) were transferred from the greenhouse to the growth chamber. Flowers were pollinated 1 or 2 d after opening using compatible pollen collected from two or more flowers. Each flower was pollinated once. Styles were excised at the point of attachment to the ovaries at various intervals after pollination. Styles remained intact on control plants. Plants were returned to the greenhouse upon completion of the last stylar excision treatment. Ten or more flowers were used for each treatment and treatments were randomized over 4 or more plants.

Style length. Ten flowers of each cultivar were harvested and median longitudinal sections were prepared by removing the ovary walls on both sides of the pistil with the stigmas and style remaining attached to the ovary. Styles were measured from the distal end of the stigma lobes to the ovary.

Effect of flower age on pollen tube growth. Senescent and nonsenescent flowers of *S. truncata* were pollinated using fresh compatible pollen. Pistils were harvested at 40, 64, and 93 h after pollination and fixed in 95%

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ethanol and glacial acetic acid (3:1, by volume) for ≥ 24 h. Styles were softened for 1 h at 100 °C in 10% (w/v) Na_2SO_3 , stained overnight in 0.1% (w/v) decolorized aniline blue in 0.1 M K_3PO_4 (Martin, 1959), and viewed with an epifluorescence microscope using a filter set for UV-violet waveband excitation (exciter filter BP 395-425, dichromatic beam splitter FT 425 and barrier filter LP 450). Ten styles were examined per time interval.

Data analysis. Percentage data were analyzed by the χ^2 test with Yates correction (Yates, 1934). Numbers of viable seeds per fruit were analyzed using the SAS General Linear Model (GLM) procedure (SAS Institute, Inc., Cary, N.C.). Single degree-of-freedom contrasts were used to test for treatment differences in the stylar excision experiment.

Results

Mean flower longevity was 4.7 ± 0.3 d (mean $\pm$ SD) for *S. truncata* 'Eva' and 10.5 ± 0.8 d (mean $\pm$ SD) for *H. gaertneri* 'Crimson Giant'. In both species, senescence was characterized by loss of perianth turgor, fading of petal color, and changes in stigma lobe orientation. During the early phase of flower opening, stigmatic lobes of *H. gaertneri* were oriented at a 30 to 45° angle to the style and became increasingly reflexed ($\geq 90^\circ$) as flowers aged. Stigmatic lobes in *S. truncata* were appressed in the early phase of flower opening and oriented at about a 15° angle to the style at senescence, but remained erect during the entire period of flower opening.

Stigmas of *H. gaertneri* and *S. truncata* were receptive on the day of anthesis (= day 0) (Tables 1 and 2). Fruit set for *S. truncata* was 100% on days 0 to 2 but declined to 30% on day 4 and finally to 0% on day 5. Nonsenesced flowers of *S. truncata* pollinated between day 0 and day 4 produced similar numbers of viable seeds per fruit while those flowers pollinated on day 2 yielded the greatest number of viable seeds per pollinated flower. Flowers of *S. truncata* that were pollinated after senescence failed to set fruit (Table 1). Fruit set was $\geq 84\%$ for nonsenesced flowers of *H. gaertneri* that were pollinated between days 0 and 11. Flowers of *H. gaertneri* pollinated between day 0 and day 7 yielded similar numbers of viable seeds per fruit (Table 2). Although seed yields in *H. gaertneri* decreased after day 7, nearly all of the nonsenesced flowers pollinated between day 8 and day 11 produced viable seeds and 35% of the senesced flowers formed seed-bearing fruit.

The relationship between flower age and seed yields is shown in Fig. 1. Numbers of viable seeds per pollinated flower were converted to percentage values by setting the maximum seed yields (= day 2 for *S. truncata* and day 4 for *H. gaertneri*) to 100%. For both species, the functional relationship between floral age and number of viable seeds per pollinated flower was described by a second-degree polynomial. The regression equation for *S. truncata* is $Y_s = 71.50 + 28.81D_A - 8.89D_A^2$ ($r^2 = 0.92$), where Y_s is the number of viable seeds per pollinated flower and D_A is the number

of days after anthesis. For *H. gaertneri*, the regression equation is $Y_s = 74.18 + 10.87D_A - 1.43D_A^2$ ($r^2 = 0.93$).

Styles of *S. truncata* averaged 73.7 ± 2.0 mm (mean $\pm$ SD) in length while those of *H. gaertneri* were 24.0 ± 1.6 mm (mean $\pm$ SD) long, and this difference was highly significant ($P < 0.001$).

For *S. truncata*, stylar excision at 48 h after pollination or later resulted in $\geq 92\%$ fruit set and seed yields similar to intact styles (Table 3). When *H. gaertneri* styles were excised 30 h after pollination, fruit set was 100% and seed yields did not differ significantly from intact styles (Table 4). Graphical analysis of the data in Tables 3 and 4 (Fig. 2) indicated that the number of viable seeds per pollinated flower was about 50% of maximum yields when styles of *S. truncata* and *H. gaertneri* were excised at 44 and 26 h (respectively) after pollination.

Relatively few pollen tubes traversed to the base of the styles when senesced flowers of *S. truncata* were pollinated (Fig. 3). At 64 h after pollination, flowers pollinated before senescence had 124.4 ± 8.4 (mean $\pm$ SD) pollen tubes at the base of the style, whereas flowers pollinated after senescence had only $11.6 \pm$

18.5 (mean $\pm$ SD) pollen tubes at the base of the style (Fig. 3).

Discussion

Schlumbergera truncata and *H. gaertneri* exhibited quadratic relationships between seed yields and floral age at the time of pollination. These results demonstrate that the probability of viable seed production in these two species is dependent on the timing of pollen arrival on the stigma. Although stigmas of *S. truncata* and *H. gaertneri* were receptive to pollination on the day of anthesis (day 0), seed yields per pollinated flower were greatest on day 2 for *S. truncata* and day 4 for *H. gaertneri* (Tables 1 and 2; Fig. 1). The latter two dates coincide with the stage in which the perianths of these species reach their maximum expansion and turgor (Scott et al., 1994). Some cultivars of *Malus sylvestris* (Williams et al., 1984), *Prunus armeniaca* (Burgos et al., 1991), and *Pyrus communis* (Herrero, 1983) exhibit this same trend, with flowers pollinated a few days after anthesis setting more fruit than those pollinated on the day of anthesis. In her study of 'Agua de Aranjuez' pear, Herrero (1983) found that

Table 1. Influence of floral age at the time of pollination on fruit and seed set of *Schlumbergera truncata* 'Eva'.

Days from anthesis to pollination	Flowers pollinated (no.)	Fruit set (%)	Viable seeds/fruit (no.)	Viable seeds/pollinated flower (no.) ²
Nonsenesced flowers				
0	23	100	84.0	84.0
1	22	100	93.0	93.0
2	29	100	113.0	113.0
3	34	91	111.4	101.6
4	43	30 ^y	98.0	29.6
5	8	0 ^y	---	0
Senesced flowers				
4 and 5	20	0 ^y	---	0
F test ^x			NS	

^x(Fraction of fruit set) $\times$ (number of viable seeds/fruit).

^yTreatment significantly different from day 1 (100% fruit set) by chi-square test, $P = 0.05$; $\chi^2 = 3.84$ for 1 df.

^xF test performed on data from days 0, 1, 2, 3, and 4.

^{NS}Nonsignificant at $P > 0.05$.

Table 2. Influence of floral age at the time of pollination on fruit and seed set of *Hatiora gaertneri* 'Crimson Giant'.

Days from anthesis to pollination	Flowers pollinated (no.)	Fruit set (%)	Viable seeds/fruit (no.)	Viable seeds/pollinated flower (no.) ²
Nonsenesced flowers				
0	31	84 ^y	132.2 ab ^x	111.0
1	27	100	145.8 a	145.8
2	19	95	140.8 a	133.8
3	28	93	142.4 a	132.4
4	28	100	155.0 a	155.0
5	23	96	142.6 a	136.9
6	18	94	137.2 a	129.0
7	18	100	140.8 a	140.8
8	16	100	110.4 bc	110.4
9	23	93	92.4 c	85.9
10	8	100	64.6 d	64.6
11	9	89	28.8 e	25.6
Senesced flowers				
8 to 11	17	35 ^y	20.2 e	7.1
F test			***	

^x(Fraction of fruit set) $\times$ (number of seeds/fruit).

^yTreatment significantly different from day 1 (100% fruit set) by chi-square test, $P = 0.05$; $\chi^2 = 3.84$ for 1 df.

^xMean separation by Duncan's multiple range test at $P = 0.05$.

***Significant F test at $\alpha \leq 0.001$.

Fig. 1. Influence of flower age on the number of viable seeds per pollinated flower in *Schlumbergera truncata* 'Eva' (●, solid line) and *Hattoria gaertneri* 'Crimson Giant' (○, dashed line).

Table 3. Effect of timing of styler excision after pollination on fruit set and number of viable seeds per fruit for *Schlumbergera truncata* 'Eva'.

Time of styler excision (hours after pollination)	Flowers pollinated (no.)	Fruit set (%)	Viable seeds/fruit (no.)	Viable seeds/pollinated flower (no.) ^z
24	11	0 ^y	---	---
30	20	0 ^y	---	---
36	20	0 ^y	---	---
42	20	50 ^y	46.4	23.2
48	20	95	106.8	101.5
54	22	95	103.8	98.6
60	26	92	88.8	81.7
Intact style	20	100	95.8	95.8
F test ^a			*	
Contrasts				
42 h vs. intact style			**	
48 h vs. intact style			NS	
54 h vs. intact style			NS	
60 h vs. intact style			NS	

^z(Fraction of fruit set) × (number of seeds/fruit).

^yTreatment significantly different from intact style (control) by chi-square test, $P = 0.05$; $\chi^2 = 3.84$ for 1 df.

^aF test performed on data from 42, 48, 54, 60, and intact style (control) treatments.

NS, **Nonsignificant or significant F test of contrast between treatments at $0.05 \geq \alpha > 0.01$, or $0.01 \geq \alpha > 0.001$.

Table 4. Effect of timing of styler excision after pollination on fruit set and number of viable seeds per fruit for *Hattoria gaertneri* 'Crimson Giant'.

Time of styler excision (hours after pollination)	Flowers pollinated (no.)	Fruit set (%)	Viable seeds/fruit (no.)	Viable seeds/pollinated flower (no.) ^z
16	11	0 ^y	---	---
20	10	10 ^y	16.0	1.6
24	11	45 ^y	62.0	27.9
30	15	100	108.5	108.5
Intact style	10	100	94.5	94.5
F test ^a			*	
Contrasts				
24 h vs. intact style			*	
30 h vs. intact style			NS	

^z(Fraction of fruit set) × (number of seeds/fruit).

^yTreatment significantly different from intact style (control) by chi-square test, $P = 0.05$; $\chi^2 = 3.84$ for 1 df.

^aF test performed on data from 24, 30, and intact style (control) treatments.

NS, **Nonsignificant or significant F test of contrast between treatments at $0.05 \geq \alpha > 0.01$.

flowers pollinated on the day of anthesis set fewer fruit compared with those pollinated two days later, and the difference in fruit set

was attributed to lack of stigma maturity on the day of anthesis.

In *S. truncata* and *H. gaertneri*, pollen

grains germinate within about 0.4 h after landing on stigmas and pollen tubes penetrate the stigma by about 0.6 h after pollination (Boyle et al., 1995; T.H. Boyle, unpublished data). Mean pollen tube growth rate in the style was estimated as mean style length ÷ [time required for half-maximum seed yields - 0.6 h]. The estimates are about 1.7 mm·h⁻¹ for *S. truncata* and about 0.9 mm·h⁻¹ for *H. gaertneri*. The rates of pollen tube growth rate in styles of *S. truncata* and *H. gaertneri* are positively correlated with style length but negatively correlated with flower longevity.

Schlumbergera truncata and *H. gaertneri* exhibited dissimilar responses to late pollinations. Between days 3 and 4, percent fruit set in *S. truncata* declined 61% while the numbers of viable seeds per fruit decreased just 12% (Table 1). In *H. gaertneri*, percent fruit set declined only 4% between days 9 and 11 while numbers of viable seeds per fruit fell 69% during this period (Table 2). *Hylocereus polyrhizus* and *H. costaricensis* are two cacti cultivated as fruit crops (Mizrahi et al., 1997), and fruit weight is positively correlated with number of seeds per fruit ($r^2 = 0.75$ to 0.81) in these two species (Weiss et al., 1994a). When flowers of *H. polyrhizus* and *H. costaricensis* were pollinated 12 or 24 h after anthesis, percent fruit set remained at 100% while fruit weight dropped significantly when pollination was delayed 12 h (Weiss et al., 1994a). Hence, a delay in pollination had little or no effect on fruit set but markedly decreased seed yields in *H. gaertneri*, *H. polyrhizus*, and *H. costaricensis*.

Some senescent flowers of *H. gaertneri* yielded fruit with viable seeds (Table 2). Under natural conditions, pollinators are unlikely to visit senescent flowers of *H. gaertneri* because access to pollen and/or nectar is thwarted by a flaccid perianth (Scott et al., 1994). However, the fact that senescent flowers of *H. gaertneri* are capable of producing viable seed indicates that the pistil retains its essential functions (stigma receptivity and ovule viability) after perianth senescence. Likewise, flowers of *H. polyrhizus* and *H. costaricensis* are capable of producing seed-bearing fruit when pollinated up to 20 h after senescence (Weiss et al., 1994a). Senescent flowers of *S. truncata* flowers failed to set fruit (Table 1) due to few pollen tubes reaching the ovary (Fig. 3). Whether this was caused by a reduction in the percentage of pollen grains germinating on the stigma and/or slow pollen tube growth in the style remains to be determined.

Cactus flowers have a reputation of being short-lived. Many arborescent and climbing species of cacti produce large, funnelform, white (or pale) flowers that remain open for <24 h (Fleming et al., 1996; Nassar et al., 1997; Weiss et al., 1994a, 1994b). Primack (1985) examined six Cactaceae species growing under greenhouse conditions and found that the average flower longevity was 2.9 ± 1.8 d (mean $\pm$ SD), with all of the species having flowers that lasting <6 d. By comparison, flowers of *H. gaertneri* lasted for 10.5 days, which is an exceptionally long flowering period for a cactus flower. Long-lived flowers are a

Fig. 2. Time required from pollination to 50% yield of viable seeds per pollinated flower in *Schlumbergera truncata* 'Eva' (●, solid line) and *Hattiora gaertneri* 'Crimson Giant' (○, dashed line).

Fig. 3. Number of pollen tubes at the base of the style at different times after pollinating nonsenesced (●, solid line) and senesced (○, dashed line) flowers of *Schlumbergera truncata* 'Eva'.

major investment in terms of water, essential elements and photosynthates (Primack, 1985) and therefore likely serve some purpose for the plant's survival. The long-lived flowers of *H. gaertneri* may enhance the plant's floral display and increase the likelihood of flower visitation by potential pollinators.

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