



## Flowering phenology and reproductive output in two sister species of *Ferocactus* (Cactaceae)

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### Abstract

Flowering phenology is often strongly constrained by phylogenetic history: many closely-related plants have very similar phenologies. On the other hand, divergent flowering phenologies can function as isolating mechanisms, which may be reinforced if related plants occur sympatrically. I investigated flowering phenology and reproductive output of sister species of barrel cacti, *Ferocactus cylindraceus* and *F. wislizeni*, where they occur sympatrically in the Sonoran Desert surrounding Tucson, Arizona. *Ferocactus cylindraceus* began blooming in May, and continued until early or mid-October, with a bimodal pattern of flowering amplitude. Individuals in the study population were moderately well-synchronized phenologically. *Ferocactus wislizeni* began blooming in July, and also continued until early or mid-October, with a single peak of intensity; individuals in the study population were well-synchronized phenologically. In both species, the vast majority of individuals bloom every year. Plant size was positively correlated with flowering amplitude in both species, and with flowering onset in *F. wislizeni*. The study population of *F. cylindraceus* was strongly affected by a flower-eating caterpillar in all years, with the earliest flowers most likely to be destroyed. For *F. wislizeni*, seed number per fruit was highest for flowers open in the middle of the blooming season in 1998. Other components of individual plant phenology, including among-plant synchrony, had little influence on reproductive output.

### Introduction

The timing of flowering can strongly influence the reproductive success of a plant in several ways (Rathcke and Lacey 1985). Such effects may be mediated by factors operating within plants (for instance, plants that flower too young may not have sufficient resources stored to mature fruits), within populations (asynchronously flowering plants may not find mates), between species (plants flowering at the “wrong” time might not be visited by pollinators, or may be disproportionately affected by seed predators), or abiotic factors (plants flowering too late in the season may be killed by frost before they can mature fruits). Thus, flowering phenology can affect the ecology of a plant at multiple levels, including individual plant reproductive success, interactions of the plant with other organisms, plant population dynam-

ics, and ecosystem functioning (e.g., the plant-pollinator landscape; Bronstein (1995)). Examining the relationships between flowering phenology, fruit and seed production, plant size and growth, and the degree of spatial and temporal variability in these relationships can provide insight into the selective forces affecting the evolution of flowering time. Comparing these factors across closely related species can indicate the extent to which the evolution of flowering phenology is constrained by the history of the lineage to which they belong.

I studied the flowering phenology of two species of short-columnar unbranched cacti, *Ferocactus cylindraceus* (Engelm.) Orcutt and *F. wislizeni* (Engelm.) Britt. & Rose during 1996–1998 in the Sonoran Desert near Tucson, Arizona. The genus *Ferocactus* (Cactaceae) contains 25–30 species (Cota and Wallace 1997), most of which occur in México and

the southwestern U.S. The species I studied are largely outcrossing (McIntosh 2001), and are pollinated primarily by large solitary bees that specialize on cactus flowers (Grant and Grant (1979); McIntosh, unpub. data). The seeds are thought to be animal-dispersed; seeds probably germinate in the late summer or early fall (Jordan and Nobel 1981). The flowering periods of populations of *Ferocactus* are generally long (2–3 months), and in those species for which flowering times have been recorded, flowering ranges from spring to late summer and fall (see Discussion). *F. wislizeni* has a more southerly and eastern distribution than *F. cylindraceus* (Turner et al. 1995), but their ranges overlap broadly in Arizona. *Ferocactus wislizeni* and *F. cylindraceus* have recently been found to be sister species, in a phylogenetic analysis of chloroplast DNA (Cota and Wallace 1997). Hence, differences in their phenologies are likely to be the result of recent evolutionary processes in their lineages rather than differing phylogenetic histories.

I quantified and compared the timing and duration of flowering at the level of the plant and the population for these two species. The goals of this study were (1) to compare the flowering phenology of the two species, (2) to determine how flowering time affects the fate of individual flowers, (3) to examine how plant size affects flowering phenology (Schmitt 1983; O’Neil 1997; Bishop and Schemske 1998; Ollerton and Lack 1998), and (4) to determine how flowering phenology affects the reproductive success of individual plants.

## Methods

### *Study organisms and study sites*

Study organisms and study sites are described in detail in McIntosh (2001). In brief, I studied the flowering phenology of a population of *Ferocactus cylindraceus* 45 km NW of Tucson, Arizona in 1997 and 1998 (hereafter: Desert Peak). I marked 128 plants (all the reproducing plants within a 1.5 hectare plot), and studied flowering phenology in detail of a subsample of 22 (1997) or 33 (1998) plants. I also studied a population of *F. wislizeni* at the Santa Rita Experimental Range (hereafter: SRER) 40 km south of Tucson, Arizona in 1996–1998. I marked 55 plants in 1996, and added 50 more plants in 1997 (comprising all reproducing plants in a 3 hectare plot). In 1996, a subsample of 54 plants was studied in detail, and a

subsample of 24 plants was studied in detail in 1997 and 1998. Plants were selected for detailed study using a random stratified sampling method that ensured that all size classes were sampled.

### *Data collection*

To document flowering phenology, I censused selected plants every two weeks (*F. cylindraceus* in 1997, *F. wislizeni* in 1996) or once a week (*F. cylindraceus* in 1998, *F. wislizeni* in 1997–1998) during the flowering period. In October the census interval was usually expanded to two weeks. New flowers were marked at each survey. Fruits were collected when ripe and the seeds were counted. Seed counts were accurate to within  $\pm 1$ –2 seeds for every 100 seeds counted, based on repeated counts. In 1998, seeds from a single fruit were weighed as a group; this was used to calculate mean seed weight per seed per fruit. Three components of female reproductive success were used in data analyses: fruit set, seeds per fruit, and mean seed weight per seed per fruit.

From flowering data I derived six phenology parameters: **onset** (date first flower opened); **end date** (date last flower opened); **duration** (difference between date of first and last flower); **mean flowering date** (peak of flowering: the mean of the census dates during which that individual was flowering, with each census date weighted by the number of flowers in that period; Bishop and Schemske (1998)); **mean flowering amplitude** (number of flowers produced per unit time, terminology of Newstrom et al. (1994)); and **synchrony** (flowering overlap among individuals). Of these six, all but synchrony were derived for both individual plants and the population as a whole. Although most data were taken from the population subsamples, the onsets were based on all individuals in the plots (both species, each year). The peak flowering date of an individual plant can be difficult to quantify in individual plants whose flowering intensity over time lacks a clear mode. Mean flowering date (Bishop and Schemske 1998) combines the timing of flowering of an individual with the timing of the peak flowering intensity of that plant. Two plants that share the same beginning and end dates may thus have different mean flowering dates. However, this measure is only meaningful for plants with a roughly unimodal flowering pattern.

Because flowering of many *F. cylindraceus* plants was interrupted by a period of days or weeks during which no flowers were produced, in 1998 I also cal-

culated the number of flowering days for each plant, defined as the flowering duration (in weeks) minus the weeks when they skipped flowering. In 1997, censuses occurred at 2-week intervals, and thus the level of resolution was not fine enough to accurately measure number of flowering days.

The flowering synchrony of an individual plant, as defined here, is the degree to which that plant's blooming period overlapped the blooming periods of all the other plants in the population. Synchrony was calculated using the method of Augspurger (1983), modified from Primack (1980). For each individual, the number of weeks that its flowering overlapped with that of other individuals was determined. The index of synchrony ( $X$ ) for an individual plant ( $i$ ) is given by

$$X_i = \left( \frac{1}{n-1} \right) \left( \frac{1}{f_i} \right) \sum_{j \neq i}^n e_{j \neq i}$$

where  $e_j$  is the number of weeks individual  $i$  and  $j$  overlapped in their flowering;  $f_i$  is the total number of weeks individual  $i$  was in flower, and  $n$  is the number of individuals in the sample.  $X$  varies from 1 (plant flowering overlaps with that of all other individuals) to 0 (no overlap with any other individuals).

#### Data analyses

All statistical tests were performed with JMP IN<sup>®</sup> software (SAS Institute Inc. 1989–99a).

I examined three types of relationships: (1) the effect of flowering time on the reproductive success of individual flowers; (2) the effect of plant size on plant phenological parameters; and (3) the effects of plant phenological parameters on plant reproductive success.

To test the hypothesis that time of flowering affects the fate of a flower (i.e. whether or not that flower is aborted), and the seed number and seed mass resulting from that flower, I tested the effect of time of flowering (independent variable) on fruit set, seeds per fruit and mean seed mass per seed per fruit (dependent variables). Time of flowering, a categorical factor, was defined both for the flowering period of the individual plant, and for the flowering duration of the entire population. So, for example, a flower might open during the “middle” period of that individual plant, but during the “early” period of the population. For *F. cylindraceus* plants, whose mean duration was

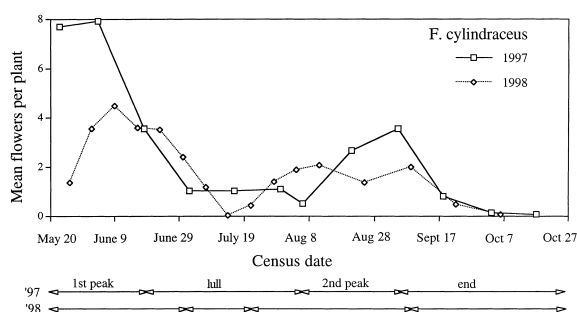


Figure 1. Flowering amplitudes for the *F. cylindraceus* population at Desert Peak, 1997–1998. Census intervals were 2 weeks (1997) or 1 week (1998). Amplitude shown is number of flowers opened during the interval ending on the census date, divided by the number of plants measured that year (to standardize for different sample sizes). In 1997 sampling began after flowering had commenced. Defined “population periods” (first peak, lull, second peak, end) are indicated.

13 weeks, “early” flowers were produced during the first two weeks of that plant’s bloom, “late” flowers during the last two weeks, and “middle” as the intermediate weeks. For *F. wislizeni* plants, whose mean flowering duration was only 6 weeks, I defined the first and last weeks as “early” and “late.” I assigned population periods based on the pattern of flowering amplitude over time for each species in each year (Figures 1 and 2). The flowering duration of the population of *F. cylindraceus* was divided into “first peak,” “lull,” “second peak,” and “late” periods (Figure 1). The flowering duration of the population of *F. wislizeni* was divided into “early,” “middle” and “late” periods (Figure 2). Although plant periods and population periods are not necessarily congruent, they do tend to be correlated, and hence were tested separately. Because flowers from the same plant are likely to not be independent data points, I included individual plant as a factor in all tests. Thus for each dependent variable I performed two tests: one with “plant” and “plant period” as factors, and one with “plant” and “population period” as factors.

Aborted flowers were extremely rare for plants of *F. wislizeni* in all years (range: 0%–4%; McIntosh (2001)), hence I did not test for effects of phenology on fruit set for this species. For *F. cylindraceus*, flower abortions were classified as “bud abortions” (flower bud aborted before anthesis), or “flower abortions” (flower aborted after anthesis, before forming a fruit). I used nominal logistic tests to test the effects of both individual plant and flowering period (either plant period or population period; independent variables) on abortion (yes or no; dependent variable),

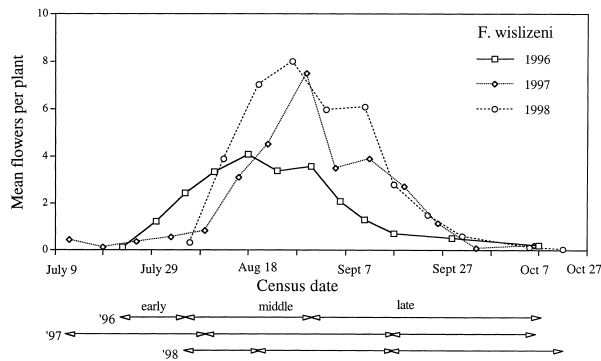


Figure 2. Flowering amplitudes for the *F. wislizeni* population at the Santa Rita Experimental Range, 1996–1998. Amplitude shown is number of flowers opened during the interval ending on the census date, divided by the number of plants measured that year (to standardize for different sample sizes). Defined “population periods” (early, middle, late) are indicated.

with the experimental unit being the individual flower.

I used two-way ANOVAs to test the effect of individual plant and of flowering period (either plant period or population period; independent variables) on seeds per fruit, and on mean seed mass per seed per fruit (dependent variables), with the individual flower as the experimental unit. In some analyses, a significant “lack of fit” (SAS Institute, Inc. 1989–99b) was found, indicating the presence of an untested interaction between factors. However, because of unbalanced data I was not able to test for interactions (lost degrees of freedom). When a significant lack of fit was reported, I record it in the results. In some analyses, the residuals from the model were found to have a non-normal distribution, and I also report this. However, ANOVA is generally robust to this violation of assumptions (Zar 1996).

To test the hypothesis that plant size affects plant phenological parameters, I used linear regressions of the natural log of plant volume (independent variable) against each of 5 plant phenological parameters: onset, duration, mean date, and mean flowering amplitude (dependent variables). To calculate plant volume, I measured the size of all *F. cylindraceus* plants within the plot at Desert Peak in April 1998, and all *F. wislizeni* plants within the plot at the SRER in July of 1997 and 1998. A detailed description of measuring technique is given in McIntosh (2001). In brief, I measured the height and width of each plant, and used these to calculate plant volume. Volume is a good surrogate for plant biomass, because the vast majority of biomass occurs above-ground in these cacti.

To test whether individual plants showed between-year consistency in their flowering phenology, I calculated Spearman rank correlations of those parameters (onset, end date, mean date, duration) for individual plants across years.

To test the hypothesis that plant phenological parameters affect the reproductive output of individual plants, I tested 3 phenological parameters: onset, mean date, and synchrony (independent variables), against mean fruit set (*F. cylindraceus* only), mean seeds per fruit, and mean seed mass per seed per fruit (dependent variables). Individual plant was the experimental unit. Linear regressions were used to test for correlations between phenology and reproductive output. Because flowering onset, mean date, and synchrony are inter-related, each parameter was tested separately.

## Results

### Flowering phenology

The *F. cylindraceus* population had a bimodal amplitude of flowering in both years (Figure 1). The rate of flower production rose quickly to the first peak in 1998 (in 1997, censuses did not begin until about two weeks after flowering onset). A lull followed the first peak in May-June, then the second smaller peak occurred in August to early September. Flowering continued sporadically into October. Flowering amplitude was greater in 1998 (following a wet winter) than in 1997 (following a dry winter; Table 1). Greater amplitude can also be the result of plant growth (McIntosh 2001). The total flowering duration of the population was 23 weeks in 1997 and 20 weeks in 1998 (Table 1). Because flowering is bimodal in this population, the phenological parameter “mean date” does not apply.

The pattern of flowering amplitude was quite different for *F. wislizeni* (Figure 2). In all three years there was a single peak of flower production. Time between onset and peak varied from 3 weeks (1998) to 7 weeks (1997). As in *F. cylindraceus*, flowering continued into October. Amplitude increased each year (Table 1). Population duration was much less than for *F. cylindraceus*: 13 to 15 weeks, as opposed to 20 to 23 weeks. Although flowering onset varied from early July to early August, mean flowering date was remarkably similar across years, ranging only from August 29 to August 31 (Table 1).

Table 1. Phenology data at the plant and population levels. For plant data, values shown are the mean of all plant values  $\pm 1$  standard deviation, and range of values.  $n$  = number of plants. For population data, values shown are for the whole population (i.e., the onset is the date of the first flower on the first plant in the population). Dates are given in Julian date format first, followed by the calendar date.

	F. cylind.97	F. cylind.98	F. wis.96	F. wis.97	F. wis.98
onset: (mean of plant values)	145 $\pm$ 15 (May 25) 128–261 $n$ = 131	162 $\pm$ 15 (June 11) 139–223 $n$ = 140	213 $\pm$ 9 (August 1) 202–246 $n$ = 54	225 $\pm$ 15 (August 13) 188–269 $n$ = 99	225 $\pm$ 7 (August 13) 205–243 $n$ = 103
onset: (population)	~ 128 (May 8)	139 (May 19)	202 (July 21)	188 (July 7)	205 (July 24)
duration: plants	107 $\pm$ 22 d 57–153 $n$ = 23	81 $\pm$ 32 d 1–129 $n$ = 33	42 $\pm$ 16 d 3–78 $n$ = 54	41 $\pm$ 17 d 5–93 $n$ = 98	41 $\pm$ 10 d 28–70 $n$ = 24
duration: population	162 d (23 wk)	140 d (20 wk)	87 d (13 wk)	105 d (15 wk)	90 d (13 wk)
# days blooming	not available	55 $\pm$ 22d 7–98 $n$ = 33			
mean date: plants	186 $\pm$ 18 (July 5) 147–227 $n$ = 23	200 $\pm$ 22 (July 19) 168–273 $n$ = 32	235 $\pm$ 9 (August 23) 221–266 $n$ = 54	244 $\pm$ 9 (Sept. 1) 228–260 $n$ = 24	243 $\pm$ 5 (August 31) 237–253 $n$ = 24
mean date: population	181 (June 30)	194 (June 13)	241 (Aug 29)	243 (Aug 31)	243 (Aug 31)
synchrony: plants	not available	0.50 $\pm$ 0.10 0.125–0.664 $n$ = 33	0.77 $\pm$ 0.086 0.57–0.91 $n$ = 53	0.755 $\pm$ 0.12 0.536–0.913 $n$ = 24	0.84 $\pm$ 0.07 0.63–0.92 $n$ = 24
amplitude (fls/plant/day): plants	0.28 $\pm$ 0.15 0.08–0.74 $n$ = 23	0.41 $\pm$ 0.23 0.08–1.00 $n$ = 33	0.54 $\pm$ 0.22 0.03–1.40 $n$ = 54	0.625 $\pm$ 0.29 0.29–1.48 $n$ = 24	0.88 $\pm$ 0.37 0.39–2.00 $n$ = 24
amplitude: population	0.1871 fls/plant/day	0.2271 fls/plant/day	0.2629 fls/plant/day	0.2743 fls/plant/day	0.4029 fls/plant/day

*F. cylindraceus* individual plants had longer flowering durations and more evenly distributed amplitudes than *F. wislizeni* individuals (Figure 3). *F. cylindraceus* plants also usually had at least one gap in flowering, whereas *F. wislizeni* plants did not (Figure 3). As a result, for *F. cylindraceus* individuals, mean flowering duration (first flower to last flower) was 81 days, but number of days actually flowering was only 55 (1998; Table 1). Because of these gaps in blooming, mean synchrony of plants was much lower for *F. cylindraceus* (0.50) than for *F. wislizeni* (0.75 to 0.84; Table 1).

The vast majority of plants of both species flowered every year. In each population, only once (one plant, one year) did a plant that had flowered previously fail to flower in a subsequent year.

#### Flowering time of individual flowers

For *F. cylindraceus*, individual plant was a significant factor in bud abortions in 1998, but not in 1997 (Table 2). Plant period (whether the individual flower

opened in the early, middle, or late portion of the flowering duration of the individual plant) was a significant factor in both years: bud abortions increased over time within a plant's bloom period. Population period (whether the flower opened during the first peak, lull, second peak, or late period of the population flowering duration) was also significant in both years: in 1997, bud abortions increased over time, whereas in 1998, although they were still lowest in the early population period, they were highest in the lull and second peak periods (Table 2). Patterns in abortions can be incongruent between plant periods and population periods, because plant periods and population periods are not exactly correlated (e.g., a flower can occur late in a plant's flowering duration, but early in the population period).

Individual plant was not a significant factor in flower abortions (Table 2), and plant period was also not significant. In other words, it is not the case that *F. cylindraceus* plants routinely abort flowers early, or late, in their flowering duration, as do many other plants (Stephenson 1981). In 1997, population period

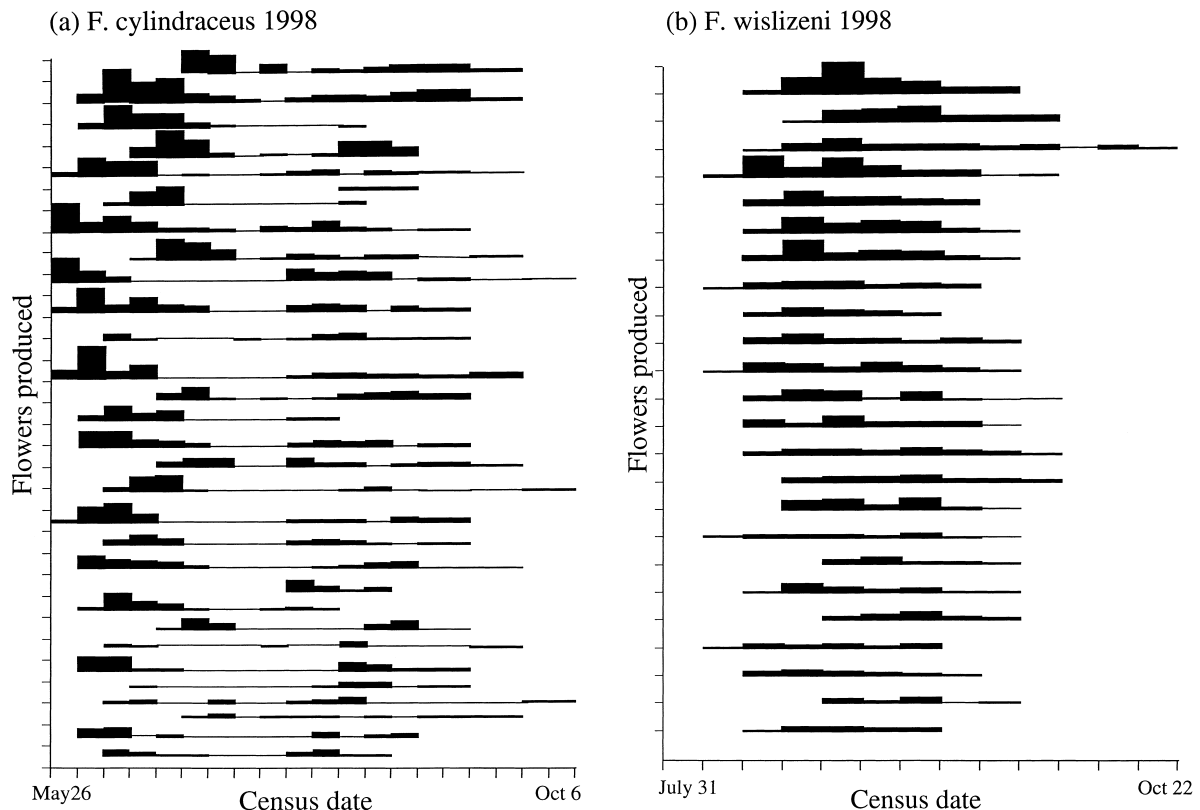


Figure 3. Flowering amplitudes of individual plants, 1998. Each row of lines and rectangles represents one plant. The height of the rectangles indicates the number of flowers opened on the plant during that census interval. Plants are arranged along the y-axis in ascending order of plant size (based on plant volume). Dashed lines indicate periods when a plant did not bloom. (a) *F. cylindraceus* (b) *F. wislizeni*. Each tick-mark on the x-axis delimits one week. Each tick-mark on the y-axis represents (a) 15 flowers, or (b) 23 flowers.

was significant, with very low flower abortion rates during the lull, and flower abortions in the remaining three periods approximately equal, ranging from 10%–14% (Table 2).

Abortions resulting from damage caused by a florivorous lepidopteran larvae (McIntosh 2001) were highest in the early population period, and declined over time, in both years (McIntosh, unpublished data).

Individual plant was always a significant factor in seeds per fruit and in mean seed mass per seed per fruit for both species (Table 3). For *F. cylindraceus*, the only other significant factor affecting seed number per fruit was population period, with seed number highest in the first peak and declining over time (Table 3a). Population period was also the only factor besides individual plant affecting seed mass, with seeds from flowers in the second blooming peak and late periods having the greatest mass (Table 3a).

For *F. wislizeni* in 1997, seed number increased over time, in terms of both plant period and popula-

tion period (Table 3b). In 1998, seed number was highest in the middle periods at both the plant and the population levels. When seed number is plotted against time a clear temporal pattern is evident in 1998 (Figure 4), with the most seeds being produced by flowers that bloomed in the middle of the population bloom period. In both years, seed number per fruit peaked at nearly the same date (1997: August 29, 1998: Sept. 2; Figure 4) and these dates correspond closely to the mean population dates (1997: Sept. 1; 1998: August 31; Table 1). Seed mass per seed per fruit was not affected by flowering time (Table 3b).

#### *Plant size and other plant effects*

Large *F. wislizeni* plants began flowering earlier in the season (Figure 3, Table 4), and flowered for a longer duration (Table 4) than small plants, in both years. However, plant size had no effect on flowering onset or duration for *F. cylindraceus*. Plant size was not correlated with mean flowering date (*F. wislizeni*),

Table 2. Effects of time of flowering on bud abortions and flower abortions (fruit set), *F. cylindraceus*. Experimental unit is the flower. Results from nominal logistic tests, with response (dependent variable) being abort, Y or N, weighted by counts. "Plant period" is the period within the flowering duration of the individual plant. "Population period" is the period within the flowering duration of the entire population. Plant period and population period are correlated to some extent, and hence were tested separately. If the flowering period was significant, I report the abortion percentages for the time periods. (a) bud abortions. (b) flower abortions

(a) Bud abortions	1997			1998		
	Independent variable	df	$\chi^2$	$P$	df	$\chi^2$
Plant	22	32.76	0.0653	30	82.07	0.0000
Plant period	2	37.32	0.0000	2	16.70	0.0002
early	0% (217)			5% (405)		
middle	5% (443)			10% (607)		
late	29% (85)			17% (184)		
Plant	22	31.14	0.0933	30	65.13	0.0002
Population period	3	44.92	0.0000	3	31.88	0.0000
1st peak	2% (452)			3% (668)		
lull	4% (92)			16% (77)		
2nd peak	13% (165)			17% (430)		
late	31% (36)			10% (21)		
(b) Flower abortions						
Plant	22	18.99	0.6458	30	20.86	0.8921
Plant period	2	0.685	0.7099	2	1.52	0.4673
Plant	22	24.11	0.3413	30	19.36	0.9321
Population period	3	10.95	0.0120	3	2.15	0.5411
1st peak	10% (408)					
lull	13% (77)					
2nd peak	1% (142)					
late	14% (22)					

and large *F. wislizeni* plants were less synchronized with other plants in the population than small plants (1998 only), probably because of their longer flowering duration. In both species, plant size was positively correlated with mean flowering amplitude (Table 4).

The flowering onsets of individual plants were significantly correlated across years for both species (*F. cylindraceus* 1997–1998, Spearman  $r = 0.4705$ ,  $P < 0.0001$ ,  $n = 125$  plants; *F. wislizeni* 1996–1997, Spearman  $r = 0.6195$ ,  $P < 0.0001$ ,  $n = 53$  plants; *F. wislizeni* 1997–1998, Spearman  $r = 0.5927$ ,  $P < 0.0001$ ,  $n = 97$  plants). For *F. cylindraceus* in 1997–1998, duration and end date were not correlated across years ( $P = 0.0555$  and  $0.6198$  respectively). For *F. wislizeni*, mean date, duration, and end date were all significantly correlated for both year comparisons (mean date: 1996–1997, Spearman  $r = 0.7556$ ,  $P = 0.0003$ ; 1997–1998, Spearman  $r = 0.5402$ ,  $P = 0.0078$ ; duration: 1996–1997, Spearman  $r = 0.6009$ ,  $P < 0.0001$ ; 1997–1998, Spearman  $r = 0.5601$ ,  $P = 0.0054$ ; end date: 1996–1997, Spearman  $r = 0.4455$ ,  $P = 0.0009$ ; 1997–1998, Spearman  $r = 0.4445$ ,  $P = 0.0336$ ).

#### *Flowering phenology and the reproductive success of individual plants*

For *F. cylindraceus* plants, neither their flowering onset nor their synchrony affected their overall flower abortion rates (onset: 1997,  $R^2 = 0.0177$ ,  $P = 0.5454$ ,  $n = 23$ ; 1998,  $R^2 = 0.0001$ ,  $P = 0.9166$ ,  $n = 27$ ; synchrony: 1998,  $R^2 = 0.0260$ ,  $P = 0.4204$ ,  $n = 27$ ). For individuals of both species, neither seeds per fruit nor mean seed mass per seed per fruit was affected by phenological parameters (Table 5).

## Discussion

### *Individual flowers*

The number of aborted flower buds increased over time in *F. cylindraceus*, both in the overall population bloom season, and within the blooming periods of individual plants. This suggests that bud abortions may be affected by climatic factors, and/or by plant fac-

Table 3. Effects of phenology on seed number and seed mass. The experimental unit is the individual fruit.

Dependent variables	Independent variables	df	F-ratio	P
(a) <i>F. cylindraceus</i> , 1998				
seeds per fruit	Plant	27	7.9692	<.0001
	Plant period	2	1.8764	0.1579
seeds per fruit (significant lack of fit)	Plant	28	8.4259	<.0001
1st peak 629 ± 285 (66)	Pop. period	3	4.3871	0.0059
lull 532 ± 369 (16)				
2nd peak 536 ± 312 (51)				
late 410 ± 276 (11)				
mean seed mass per seed per fruit	Plant	26	4.2736	<.0001
	Plant period	2	2.7933	0.0665
mean seed mass per seed per fruit	Plant	27	5.1016	<.0001
	Pop period	3	7.6043	0.0001
1st peak 1.6 ± 0.380 (54)				
lull 1.5 ± 0.351 (15)				
2nd peak 1.8 ± 0.443 (45)				
late 1.8 ± 0.328 (7)				
(b) <i>F. wislizeni</i> , 1997				
seeds per fruit	Plant	21	10.4437	<.0001
early 429 ± 310 (15)	Plant period	2	13.5052	<.0001
middle 779 ± 530 (51)				
late 848 ± 447 (6)				
seeds per fruit	Plant	21	6.5882	<.0001
early 355 ± 339 (21)	Pop period	2	6.8936	0.0023
middle 826 ± 501 (43)				
late 1033 ± 377 (8)				
(c) <i>F. wislizeni</i> , 1998				
seeds per fruit	Plant	23	10.7113	<.0001
(residuals non-normal)	Plant period	2	8.3018	0.0004
early 653 ± 325 (24)				
middle 820 ± 389 (107)				
late 624 ± 370 (22)				
seeds per fruit	Plant	23	11.0230	<.0001
early 640 ± 321 (24)	Pop period	2	9.9197	<.0001
middle 822 ± 386 (107)				
late 629 ± 386 (22)				
mean seed mass per seed per fruit	Plant	23	15.1321	<.0001
	Plant period	2	1.7918	0.1711
(significant lack of fit; residuals non-normal)				
mean seed mass per seed per fruit	Plant	23	14.5691	<.0001
	Pop period	2	0.6764	0.5104
(significant lack of fit; residuals non-normal)				

tors (e.g., levels of stored resources) that change as the season progresses. Rates of flower abortion were unrelated to the timing within the flowering periods of individual *F. cylindraceus* plants, and individual plant was not a significant factor in flower abortions (Table 2). Thus these plants do not routinely abort

early or late flowers preferentially (Stephenson 1981). It seems more likely that flowers are aborted when they fail to receive enough pollen to set seed (McIntosh 2001). The lack of a temporal pattern in flower abortions suggests that the levels of pollination are not substantially different in different periods of the

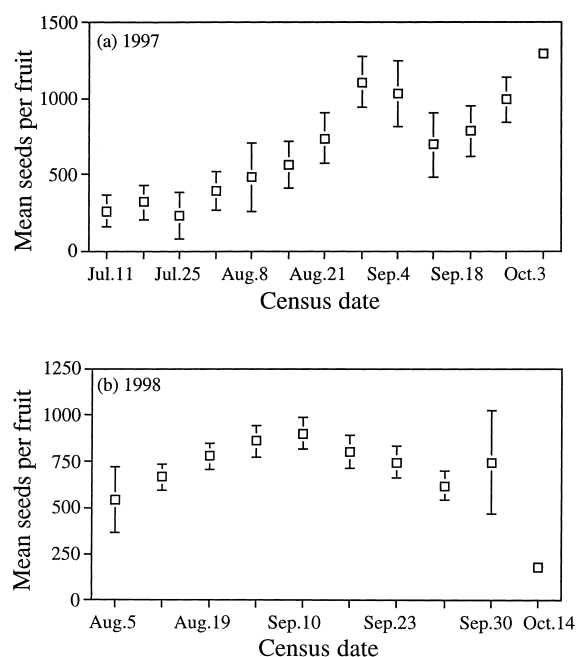


Figure 4. Mean seeds per fruit over time, *F. wislizeni*. Error bars denote one standard error of the mean. Point with no error bars represents one fruit. (a) 1997;  $n = 72$  fruits from 22 plants. (b) 1998;  $n = 153$  fruits from 24 plants.

flowering duration of *F. cylindraceus*. The low levels of flower abortion in *F. wislizeni* suggest that these plants receive adequate pollination services throughout their flowering duration.

Seed production was affected by timing of flowering for both species. Seed production in *F. cylindraceus* was highest in the first peak of flowering, and decreased over time (Table 3). For *F. wislizeni*, in 1997 seed production was lowest early in the flowering period (in both plant periods and population period) and increased over time (Table 3). In 1998 seed production was highest in the middle of flowering (both plant periods and population period; Table 3). Peak seed production (Figure 4) coincided with peak flowering (Figure 2) in both 1997 and 1998.

#### Plant effects

In work reported elsewhere (McIntosh 2001), plant size was found to be positively correlated with the number of flowers produced by a plant in a season for both species. Size was not found to impact fruit set rates or seed mass in that study, however. The overall effect of size on fecundity was strong (McIntosh 2001), as is the case with many other plants (references summarized in Schmitt (1983); O'Neil

(1997); Bishop and Schemske (1998); Ollerton and Lack (1998)). In this study, I found that size had a strong positive correlation with flowering amplitude in both species. Because amplitude is defined as number of flowers divided by flowering duration, this relationship could result from a positive correlation between flowers and size (as found in McIntosh (2001)), from a negative relationship between duration and size, or from both. However, the relationship between duration and size was positive for *F. wislizeni* (Table 4), as it is for many other plants (Schmitt 1983; Ollerton and Lack 1998). Thus at least for this species, large plants make so many more flowers than small plants, that even though they also flower for a longer period, their mean flowering amplitude is still higher than that of small plants.

Larger *F. wislizeni* plants also begin blooming earlier than smaller ones (Table 4, Figure 3b), but this was not the case for *F. cylindraceus* (Table 4, Figure 3a). In other studies, correlation between plant size and flowering onset, when it occurs, was positive for some plants (large plants begin flowering earlier) and negative for others (summarized in Ollerton and Lack (1998)), and these effects were often variable in time and space. Plant effects other than those related to plant size were also found here: for *F. wislizeni*, mean date was correlated for individual plants across years, although mean date was not related to plant size (Table 4).

The peak flowering date of an individual plant has been linked to the relative reproductive success of that plant in other studies (Bishop and Schemske 1998; Ollerton and Diaz 1999), but that relationship was not found here: there was no correlation between mean date and seed production or seed mass for *F. wislizeni* (Table 5). In fact, none of the phenological parameters examined in this study (flowering onset, mean flowering date and synchrony) affected female reproductive success of individual plants. Because plants were surveyed only once a week, however, the level at which I calculated synchrony may be too coarse to detect actual correlations with reproductive output or success.

Producing large numbers of seeds may be one way for desert perennials to survive the difficult recruitment (germination and establishment; Clark et al. (1999)) phase of their life history (Bowers 1994; Pier-son and Turner 1998). With annual per-plant fecundities of 14,000 to 25,000 seeds (*F. cylindraceus* and *F. wislizeni*, respectively; McIntosh (2001)), these cacti may be able to beat the recruitment lottery by sheer

Table 4. Effect of plant size on phenological parameters. Correlations were tested using linear regressions. Independent variable is the natural log (ln) of plant volume. The sign of the trend, if significant, is in parentheses.  $n$  = number of plants.

Dependent variable	<i>F. wislizeni</i> 1997	<i>F. wislizeni</i> 1998	<i>F. cylindraceus</i> 1998
onset	$R^2 = 0.124$ , $P = 0.0005$ , $n = 94$ (negative)	$R^2 = 0.040$ , $P = 0.0427$ , $n = 103$ (negative)	$R^2 = 0.005$ , $P = 0.4311$ , $n = 133$
duration	$R^2 = 0.268$ , $P < 0.0001$ , $n = 93$ (positive)	$R^2 = 0.321$ , $P = 0.0039$ , $n = 24$ (positive)	$R^2 = 0.004$ , $P = 0.7247$ , $n = 33$
mean date	$R^2 = 0.013$ , $P = 0.5990$ , $n = 24$	$R^2 = 0.046$ , $P = 0.3136$ , $n = 24$	$R^2 = 0.015$ , $P = 0.5117$ , $n = 32$
synchrony	$R^2 = 0.124$ , $P = 0.0919$ , $n = 24$	$R^2 = 0.209$ , $P = 0.0248$ , $n = 24$ (negative)	$R^2 = 0.067$ , $P = 0.1445$ , $n = 33$
amplitude	$R^2 = 0.562$ , $P < 0.0001$ , $n = 24$ (positive)	$R^2 = 0.584$ , $P < 0.0001$ , $n = 24$ (positive)	$R^2 = 0.400$ , $P < 0.0001$ , $n = 33$ positive

Table 5. Effects of phenological parameters on (a) mean seeds per fruit and on (b) mean seed mass per seed per fruit. Shown are results of linear regressions. Because phenological parameters are inter-related, each was tested separately.

(a) Effects on mean seeds per fruit per plant

	<i>F. cyl</i> 98 ( $n = 28$ )		<i>F. wis</i> 97 ( $n = 21$ )		<i>F. wis</i> 98 ( $n = 24$ )	
	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$
onset	0.002	0.8043	0.007	0.7189	0.060	0.2862
mean date			0.017	0.5700	0.001	0.8916
synchrony	0.095	0.1115	0.000	0.9659	0.029	0.4596

(b) Effects on mean seed mass per seed per fruit per plant

	<i>F. cyl</i> 98 ( $n = 27$ )		<i>F. wis</i> 98 ( $n = 24$ )	
	$R^2$	$P$	$R^2$	$P$
onset	0.112	0.0884	0.152	0.0595
mean date			0.031	0.4094
synchrony	0.132	0.0626	0.004	0.7670

number of entries. The magnitude of lifetime seed production, which is probably most strongly influenced by numbers of flowers produced (McIntosh 2001) may thus affect lifetime reproductive success much more than, for example, the exact timing of individual flowers. In this study, although the timing of individual flowers did affect their reproductive success (whether or not the flower set a fruit, seeds per fruit, and mean seed mass per seed per fruit), the flowering phenology of individual plants had no effect on their overall fruit set or seed production. It may indeed be the case that in these species, flowering phenology is a trait not under strong selection (Ollerton and Lack 1992).

#### Comparison of the two species

Although phylogeny plays a dominant role in the flowering phenologies of many plants (Kochmer and Handel 1986; Wright and Calderon 1995; Ollerton and Diaz 1999), in some cases members of the same genus or family can differ significantly in their phenologies (Haddock and Chaplin 1982; Proença and Gibbs 1994; Pickering 1995; Madeira and Fernandes 1999; Soliva and Widmer 1999), and these differences can function as isolating mechanisms for related plants occurring in sympatry. Despite the fact that *F. cylindraceus* and *F. wislizeni* are sister species, they exhibit strikingly different flowering phenologies. They begin blooming at different times (May for *F.*

*cylindraceus*, July or August for *F. wislizeni*), and flowering exhibited two peaks in *F. cylindraceus* but only one in *F. wislizeni*. *F. cylindraceus* individuals flower for more than twice the time that *F. wislizeni* individuals do (12–15 weeks for *F. cylindraceus*, 6 weeks for *F. wislizeni*). The *F. cylindraceus* population was also in bloom much longer than the *F. wislizeni* population (20–23 weeks for *F. cylindraceus*, 12–15 weeks for *F. wislizeni*). Patterns at the individual level are different also: *F. cylindraceus* individuals usually have a lull in the middle of their blooming period.

The bimodal flowering pattern of *F. cylindraceus* was one of the more surprising findings of this study. However, because only one population of this species was studied, it is unknown whether this pattern is characteristic of the species as a whole, or just this population. This population is near the edge of the range for this species (Turner et al. 1995) and many plants are known to reproduce differently at the edge of their range than they do in the center. It could also be that introgression from *F. wislizeni*, if such is occurring, is responsible for the second period of bloom (McIntosh 2001).

Conceivably, the extended bloom period could also be a response to the loss of early flowers and fruits to caterpillars. Resources that would have been invested in early fruits may be redeployed to later fruits if early fruits are destroyed. In the first peak of flowering, 43–44% of all fruits were lost to caterpillar damage, whereas only 11–13% were lost in the second peak of flowering (unpublished data). Hence, plants may achieve higher fecundity during the second blooming peak, even though their flowering amplitude is lower than in the first peak. Thus the bimodal flowering pattern may be currently adaptive in this population, whatever its original causes or underlying mechanisms. However, the most likely explanation is that it is an adaptive response to the abundant summer rains that occur in southeastern Arizona. *F. cylindraceus* has been reported to bloom sporadically following summer rains where these occur (Benson 1982). Phenological data from other populations are needed to resolve this question.

The difference in the timing of flowering onset (as opposed to peak flowering) may also be related to the differing rainfall patterns that occur in different parts of the Desert Southwest. In California, the center of distribution for *F. cylindraceus*, most of the annual rain falls in winter, whereas in New Mexico and Texas (the center of the range of *F. wislizeni*) most

rain falls in the summer. *F. wislizeni* has been described as occurring only in areas where summer rains occur, and where the summer rains are greater than the winter rains if there are two rainy periods (Benson 1982; Turner et al. 1995). Summer and winter rains are about equal at the Santa Rita Experimental Range. It seems plausible that the two species have evolved to flower partly in response to different rainfall periods, with *F. cylindraceus* responding to winter rains and *F. wislizeni* to summer rains. The timing of flowering onset may be indirectly tied to resource allocation. Flower production is meristem limited (each areole flowers only once, hence flower production is limited by production of new areoles; McIntosh (2001)), and if meristem production is water-limited, this might account for the link between flowering onset and local rainfall patterns. However, these plants do not respond facultatively to significant rain regardless of the timing within the year, as does (e.g.) *Larrea tridentata* (Bowers and Dimmitt 1994).

The flowering periods of other species of *Ferocactus* span the range from March to September (Kearney and Peebles 1951; Shreve and Wiggins 1964; Benson 1982), and many cannot be simply categorized as spring-bloomers or summer-bloomers. In fact, a purported subspecies, *F. wislizeni tiburonensis*, is recorded as blooming in April and May on Tiburon Island in the Gulf of California (Shreve and Wiggins 1964). Further work is needed to determine the exact nature of the climatic triggers for flowering onset.

Flowering phenology can also be indirectly constrained if selection acts upon the timing of seed dispersal and germination (Primack 1987), rather than on the timing of flowering. The fruits of *F. cylindraceus* mature about 6 weeks after pollination, remain fleshy for a few weeks thereafter, and then become desiccated. *F. wislizeni* fruits mature about 80d (11–12 weeks) after pollination, and although they can remain fleshy for at least a year thereafter, the fruits do not normally remain on the plant that long. Seed dispersal has not been studied in *Ferocactus*, but it would appear that they are primarily animal-dispersed. Seed germination requirements, which are related to timing of seed dispersal, suggest that *Ferocactus* seeds germinate best at 29–30 °C, and require light but not cold treatment (Jordan and Nobel 1981; Romero-Schmidt et al. 1992). Periods when *Ferocactus* seed germination near Tucson would seem likely are mid-April to late May, and from late Sept. to late October (both are periods when daily highs in Tucson average 27 °C to 33 °C). Late summer or early fall

has in fact been proposed at the most likely germination time for *F. cylindraceus* (Jordan and Nobel 1981). If *Ferocactus* seeds remain viable for extended periods, however, it may be that timing of seed dispersal is not critical. Again, more work would be needed to determine if selection acting upon the timing of seed dispersal and germination is affecting flowering phenology.

### Conclusions

This study has shown that these two cacti possess markedly different flowering phenologies, despite their shared evolutionary history. These differing phenologies may in turn be related to climatic factors rather than to selection acting directly on the timing of flowering. However, their flowering periods do overlap considerably, and hence cannot function as isolating mechanisms, at least at Desert Peak, where both species occur. Although flowering time did affect the reproductive output of individual flowers, differences among individual plants in reproductive output are probably more closely linked to flower production (strongly correlated with plant size) and with pollinator-mediated seed production, than to the differing flowering phenologies of those plants.

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