

Phenology of *Pilosocereus leucocephalus* (Cactaceae, tribe Cereeae): a columnar cactus with asynchronous pulsed flowering

Miguel A. Munguía-Rosas · Vinicio J. Sosa

Received: 30 May 2009 / Accepted: 20 April 2010 / Published online: 6 June 2010
© Springer Science+Business Media B.V. 2010

Abstract *Pilosocereus leucocephalus* produces flowers in discrete pulses, suggesting this cactus might exhibit pulsed flowering—a rare flowering pattern among angiosperms. In this study, we (1) describe the phenology of *P. leucocephalus*, (2) explore the influence of temperature, rainfall, and plant size on the flowering pattern, and (3) assess the effect of flowering phenology on the reproductive success of this cactus. Flowering phenology was characterized using the coefficient of variation in addition to traditional descriptors of flowering phenology: flowering onset, flowering duration, number of pulses and flowers, as well as flowering synchrony. The association between temperature, rainfall, plant size, and reproductive success (fruit set) with phenological descriptors was assessed using mixed-effects models. The flowering phenology of *P. leucocephalus* was confirmed as pulsed but was unexpectedly asynchronous. This cactus flowers during the warmest part of the year. We found a significant relationship between temperature and flower production. Plant size has a strong effect on all the flowering phenology descriptors we

studied, except flowering synchrony. Of the phenological descriptors evaluated, only flowering onset has a significant and positive relationship with fruit set. These results strongly suggest that flowering phenology in *P. leucocephalus* (1) is mainly controlled by temperature and plant size and (2) influences its reproductive success.

Keywords Columnar cacti · Flowering phenology · *Pilosocereus leucocephalus* · Plant size · Pulsed flowering · Temperature

Introduction

Several genetic, mechanistic, and ecological factors contribute to shape the reproductive phenology of plants. The study of these factors is fundamental to understanding species interactions and community function (Fenner 1998). Among the abiotic environmental factors, photoperiod, temperature, and moisture are the main variables affecting the flowering phenology of most plant species (Rathcke and Lacey 1985); however, plants can react differently to the same environmental variable (e.g., Petit 2001). Among the biotic factors, plant size, related to the capacity to allocate resources to reproductive functions, is also important as it usually correlates with flowering onset, flowering duration, and number of flowers (e.g.,

M. A. Munguía-Rosas · V. J. Sosa
Red de Ecología Funcional, Instituto de Ecología A. C.,
Apartado Postal 63, Xalapa, Veracruz C.P. 91000, Mexico

M. A. Munguía-Rosas (✉)
Landscape and Biodiversity Research Group, School
of Applied Sciences, University of Northampton,
Park Campus, Northampton NN2 7AL, UK
e-mail: allusion82@hotmail.com

Ollerton and Lack 1998; Bustamante and Búrquez 2008). Other biotic factors, such as pollinator availability and predispersal seed predation, are often mentioned as selective forces shaping flowering phenology (reviewed by Elzinga et al. 2007). In addition, phylogenetic inertia also determines the flowering schedule of some groups of plants (Kochmer and Handel 1986).

Columnar cacti are dominant plants in arid and semi-arid regions in the New World (Fleming and Valiente-Banuet 2002). It has been shown using stable isotopes that columnar cacti are keystone species in arid regions as they provide water and nutrients for a wide variety of animals in the form of nectar and fruit pulp (Nassar et al. 2003; Wolf and Martínez del Río 2003). Therefore, the flowering and fruiting phenology of columnar cacti has an enormous impact on the animals that rely on the flowers and fruits. Columnar cacti comprised at least 170 species (Fleming and Valiente-Banuet 2002). However, we know of only six species for which flowering phenology has been studied in detail. In these few studies, however, we find a wide diversity of flowering phenology patterns in columnar cacti, ranging from unimodal to multimodal (Table 1). Additionally, the individuals of all the species of columnar cacti currently studied produce flowers continuously, and no evidence of pulsed flowering—sensu Michalski and Durka 2007, alternate periods of

synchronous flowering among individuals of a population—has been reported. Although seasonal variation in rainfall is expected to be the primary abiotic factor affecting the flowering schedule in arid lands (Borchert et al. 2004), the influence of temperature and rainfall on phenology is not uniform for the species of columnar cacti studied (Table 1). In contrast, the effect of size on phenology is highly consistent, being positively correlated with flower number and negatively correlated with flowering onset (Table 1). Evidently, more studies are needed to determine whether the response to the prevailing rainfall or temperature conditions before or during the flowering season is species specific. Although three studies have evaluated the influence of temperature, rainfall, and size on the phenology of columnar cacti (Ruiz et al. 2000; Petit 2001; Bustamante and Búrquez 2008), no study has examined the effect of flowering phenology on the reproductive success of columnar cacti.

The flower production of the columnar cactus *Pilosocereus leucocephalus* is not continuous (Munguía-Rosas and Sosa, personal observation). Although it has not been formally described yet, we have observed that individuals in the study area produce flowers in discrete pulses (Munguía-Rosas 2008; Munguía-Rosas et al. 2009b). In light of our field observations, we suspected that flowering phenology was synchronous and pulsed, which is very rare

Table 1 Summary of published studies on the flowering phenology of columnar cacti

Species	Location	Pattern	Influence of rainfall		Influence of temperature		Influence of size		Reference
			Flowers	Onset	Flowers	Onset	Flowers	Onset	
<i>Cereus hexagonus</i>	Tatacoa	Multimodal	0		0		0		Ruiz et al. (2000)
<i>Pilosocereus lanuginosus</i>	Curaçao	Unimodal	+				+	0	Petit (2001)
<i>Pilosocereus</i> sp.	Tatacoa	Multimodal	+		+		0		Ruiz et al. (2000)
<i>Stenocereus griseus</i>	Tatacoa	Bimodal	0		0		+		Ruiz et al. (2000)
<i>Stenocereus griseus</i>	Curaçao	Unimodal	–				+	–	Petit (2001)
<i>Stenocereus thurberi</i>	Sonora	Unimodal	0	0	+	+	+	–	Bustamante and Búrquez (2008)
<i>Subpilosocereus repandus</i>	Curaçao	Unimodal	0				+	–	Petit (2001)
<i>Pilosocereus leucocephalus</i>	Veracruz	Multimodal	0		+		+	–	This study

Pattern in terms of number of flowering peaks (uni-, bi-, or multimodal), the relationship between rainfall, temperature, and plant size with the number of flowers per plant (flowers) and the onset of flowering (onset) are shown. These relationships can be positive (+), negative (–) or absent (0); empty spaces means no available data. The studies were carried out in: La Tatacoa (Tatacoa), Colombia, the Curaçao Island (Curaçao), Netherlands Antilles, The Sonoran Desert (Sonora) and Veracruz (Veracruz), Mexico. References are given in the last column. Notice that two lines report two different studies on the same species with different results

among angiosperms. It has been suggested that this rare phenological pattern evolved as a low-cost strategy to extend the flowering season and thus spread the risk of predation or cope with low availability of pollinators; synchrony of flowering pulses might increase pollination efficiency as well (Michalski and Durka 2007). However, because of the limited number of cases of pulsed flowering phenology, the causes and evolutionary implications of this flowering pattern are still poorly understood. Given the rarity of pulsed flowering phenology, the main goal of our study was to examine whether *P. leucocephalus* exhibits a pulsed flowering schedule. It is more challenging to document pulsed phenology than typical unimodal flowering, because the variables that are traditionally used—such as flowering onset, flowering duration and flowering synchrony—cannot adequately describe pulsed flowering. We followed the approach of Michalski and Durka (2007); these authors used the coefficients of variation for the number of open flowers per individual or population in each observation (CV) as a measure of temporal variability in flowering patterns. The coordinated use of a measure of synchrony and the CV leads to a more accurate description of flowering phenology. In addition to flowering phenology, we addressed the following questions: (1) Do rainfall and temperature affect the flowering phenology of *P. leucocephalus*? (2) Does plant size influence flowering phenology?, and (3) Does variation in flowering phenology affect reproductive success? The descriptors of flowering phenology we used in this study are onset of flowering, flowering duration, number of flowering pulses, number of flowers, and flowering synchrony.

Materials and methods

Study species and sites

Pilosocereus leucocephalus is a slightly branched columnar cactus endemic to Mesoamerica, from north-eastern Mexico to Honduras (Guzmán et al. 2003). In the study area, *P. leucocephalus* occurs from 250 to 1150 m a.s.l. This cactus produces reproductive structures (buds, flowers, and fruits) during the spring and summer. These structures develop in the pseudocephalium at the top of the branches. Flowers are solitary, typically bat-pollinated: bell-shaped, pinkish

to whitish, and release an unpleasant odor (Anderson 2001). Anthesis is nocturnal and flowers only open for one night. The main pollinators are *Glossophaga soricina*, *Choeroniscus godmani* and to a lesser degree *Leptonycteris curasoae* and *Leptonycteris yerbabuena*. The breeding system is mainly xenogamous, and there is no evidence of pollen limitation (Munguía-Rosas et al. 2009b). Fruit is typically ornithochorous (red and fleshy with hundreds to thousands of small seeds), but ants also participate in seed dispersal (Munguía-Rosas and Sosa 2008; Munguía-Rosas et al. 2009a). The fruit sets shortly after blooming and matures in approximately 1 month.

The study area comprised two regions close to two fair-sized towns of the same name: Actopan (19°30'21"N, 96°35'47") and Xalapa (19°35'26"N, 96°58'38"), both located in central Veracruz, eastern Mexico. The two regions are about 25 km apart using the geographical center of each region as points of reference. The vegetation is tropical dry forest growing on shallow soil formed in situ over a rocky substrate (Ortega 1981). Dominant species in the woody stratum are *Lysiloma microphylla*, *Lysiloma acapulcensis*, and *P. leucocephalus*. Other chiropterophilous columnar cacti (*Neobuxbaumia euphorioides*, *Neobuxbaumia scoparia*, and *Stenocereus griseus*) are also abundant, mainly in the Actopan region (the complete floristic list is given in Castillo-Campos 2003).

Field methods

In January and February 2005, 30 and 50 *P. leucocephalus* individuals taller than 2 m were tagged in Xalapa and Actopan, respectively. Based on previous studies (Sosa 1997; Ruiz et al. 2000) and our own observations, columnar cacti ≥ 2 m are very likely to present reproductive structures. However, some of these individuals were not included in the analyses, either because they did not produce any reproductive structures during the 2 years of the study (2005 and 2006) or because the cacti (or their labels) had been removed by people. Therefore, the final numbers of tagged reproductive individuals were 22 in Xalapa and 33 in Actopan. Sometimes the identification of tagged plants or data collection in the field was incomplete. Missing data were deleted from data frames, therefore the degrees of freedom vary among analyses. Every week we counted the number of floral

buds, open flowers, and fruits present at that time by each tagged plant over two reproductive seasons (spring–summer, 2005 and 2006; on one occasion each year there was an interval of 2 weeks between observations). We surveyed the phenology of tagged individuals 16–17 times in the two populations each season. The height of the main branch of all monitored cacti was measured as a surrogate for cactus size. In other species of columnar cacti, plant height is correlated with the number of stems and canopy cover (Bustamante and Búrquez 2008), and the number of stems is correlated with volume in others (Petit 2001). We obtained the daily temperature and rainfall records (from late February to late August) from the Xalapa (8 km away) and Actopan (0.5 km away) meteorological stations. Although the distance from the station to Xalapa is greater than that from the station to Actopan, there is no appreciable difference in the climate of the Xalapa region and that of the Xalapa meteorological station.

Data analysis

Flowering synchrony and coefficient of variation

We calculated Augspurger's (1983) synchrony index per individual (X_i) and population (Z) as follows:

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

where e_i is the number of census dates when plants i and j are both in flower, f_i is the number of census dates when individual i is in flower, and n is the number of individuals in the population. X_i varies from 0 (no overlap) to 1 (plant flowering overlaps completely with that of all other individuals). Z is the average synchrony index across individual plants. In order to quantify the pulsed flowering phenology at the population level, week-to-week variability in flowering was assessed using the population-level coefficient of variation (CV_p) as follows:

$$CV_p = \frac{\sigma}{\mu},$$

where σ is the standard deviation from the mean and μ is the arithmetic mean. CV_p represents the ratio of the standard deviation to the mean and is based on individuals as sampling units and thus reflects the

weekly variance in the number of open flowers per individual. A detailed description of this procedure is given by Michalski and Durka (2007).

Effect of temperature and rainfall on flowering phenology

Using linear mixed-effects models (LMEs), we evaluated the effect of mean temperature and total rainfall 1, 3, and 6 weeks before each observation day (predictor variables) on the total number of open flowers observed weekly, as well as on the proportion of cacti exhibiting floral structures (flower buds or open flowers; i.e., the response variables). We used the log-transformed number of flowers and the arcsine square root of the proportion of cacti with floral structures to normalize the data. We selected LMEs because we have fixed and random factors that can be assessed simultaneously with these models. Factors in the fixed part are of interest in the magnitude and significance of their parameters (coefficients) while factors in the random part of the model account for variance components due to the grouping structure (Pinheiro and Bates 2000; Zuur et al. 2009). In this specific model, we included only the main effect of temperature (1, 3, and 6 weeks before observations) and rainfall (1, 3, and 6 weeks before observations)—six predictors in total—as numeric co-variables in the fixed part of the model. No interaction was included to avoid running out of degrees of freedom and because some variables cannot interact in nature; i.e., there can be no interaction between temperature 1 and 3 weeks before data collection. Region (two levels: Xalapa and Actopan) and year (two levels: 2005 and 2006) were included in the random part of the model to account for spatial and temporal correlations. Two models were fitted, one per response variable. Although these models allow us to include the same predictor in the fixed as well as in the random part of the same model, we did not do this because our random factors only have two levels each and they are nested (year in region). Therefore, the year in each region is not replicated and this precludes any test of significance. The grouping structure also affects calculation of denominator degrees of freedom used for the F tests; in this particular case, random structure uses three degrees of freedom in addition to those needed to estimate coefficients (see

Pinheiro and Bates 2000, for algorithm to calculate degrees of freedom). There is no strong correlation among predictor variables (of the 15 possible pairs of the six predictors, only three show a weak correlation after Bonferroni correction: $r = 0.3\text{--}0.6$, see Appendix). Sample size for this analysis was 17 observations for each region in 2005 and 16 observations for each region in 2006).

Effect of plant size on flowering phenology

In order to test whether phenological variables are explained by plant size, we fitted LMEs to the following response variables: onset of flowering of each cactus (the first day of the year we observed open flowers), flowering duration per cactus (estimated as the number of observation days we detected flowers), number of pulses, total number of flowers produced per cactus (see “[Relationship between flowering phenology and fruit set](#)” section), and flowering synchrony (see “[Flowering synchrony and coefficient of variation](#)” section). By flowering pulse we mean the discrete period of time that one plant bears floral buds and/or open flowers, preceded and followed by the lack of any floral structure on the plant. The only reproductive structures on the plant during the interpulse period were developing or mature fruits. In all cases, the predictor variable in the fixed part of the models was plant size (five models in total, one per response variable). As in the previous sections, year and region were included as random factors. After filtering missing data from the data frame, sample size was 18 and 19 cacti in 2005 and 2006, respectively, in Xalapa, 26 and 29 cacti in 2005 and 2006, respectively, in Actopan.

Relationship between flowering phenology and fruit set

Fruit set was calculated following the approach of Fleming (2007). Flowers open for only one night and we counted flowers every week, so the total number of flowers produced per individual was estimated by calculating the area under the curve. Since the fruit remain on the plant for about 1 month, the number of fruit produced per individual in each year and region was estimated by adding the maximum number of fruits in each fruiting peak. Although this method

underestimates fruit set, it is useful as a relative measure of fruiting success and it is suitable for comparisons and correlations (Fleming 2007). In a LME, we defined fruit set as the response variable and flowering onset, flowering duration, number of flowering pulses, number of flowers, and synchrony as predictor variables. We included the year and region in the random part of the model as explained previously. Sample size for this analysis was 19 records of cacti for Xalapa in 2005 and 2006, and 26 and 29 cacti in Actopan in 2005 and 2006, respectively. All statistical analyses were run in R 2.5.1 (R Development Core Team 2007). The R code used is available upon request.

Results

Flowering synchrony and coefficient of variation

During the 2 years of the study, the cacti bloomed in spring and summer, between day 90 and 240 in both regions (Fig. 1a, b). Fruiting started about 2 weeks later (Fig. 1c, d). The beginning of the flowering season in this species coincided with the warmest part of the year (days 90–212, April–July; Fig. 1e, f). The cacti in both regions and years produced flowers and set fruit during the dry as well as rainy seasons (Fig. 1a–d, g, h). The flowering period of each plant in Xalapa (Fig. 2a, b) and in Actopan (Fig. 2c, d) was not continuous but pulsed, with brief periods ($\approx 4\text{--}12$ days) of flowering followed by 1–3 weeks with no identifiable floral structures (buds or flowers). Some individuals, e.g., individuals 1 and 13 in Xalapa; and individuals 5 and 15 in Actopan, had only one pulse (4–7 days; Fig. 2).

The synchrony index for Xalapa (0.36) was slightly greater than that of Actopan (0.35), and the difference was greater in 2006 (Xalapa: 0.41; Actopan: 0.25). Similarly, the coefficient of variation of the number of open flowers was higher in Xalapa (1.71) than in Actopan (1.31) in 2005 and 2006 (Xalapa: 1.58; Actopan: 0.95).

Effect of temperature and rainfall on flowering phenology

Only the temperature 1 week before the collection of phenological data explained positively the variation in

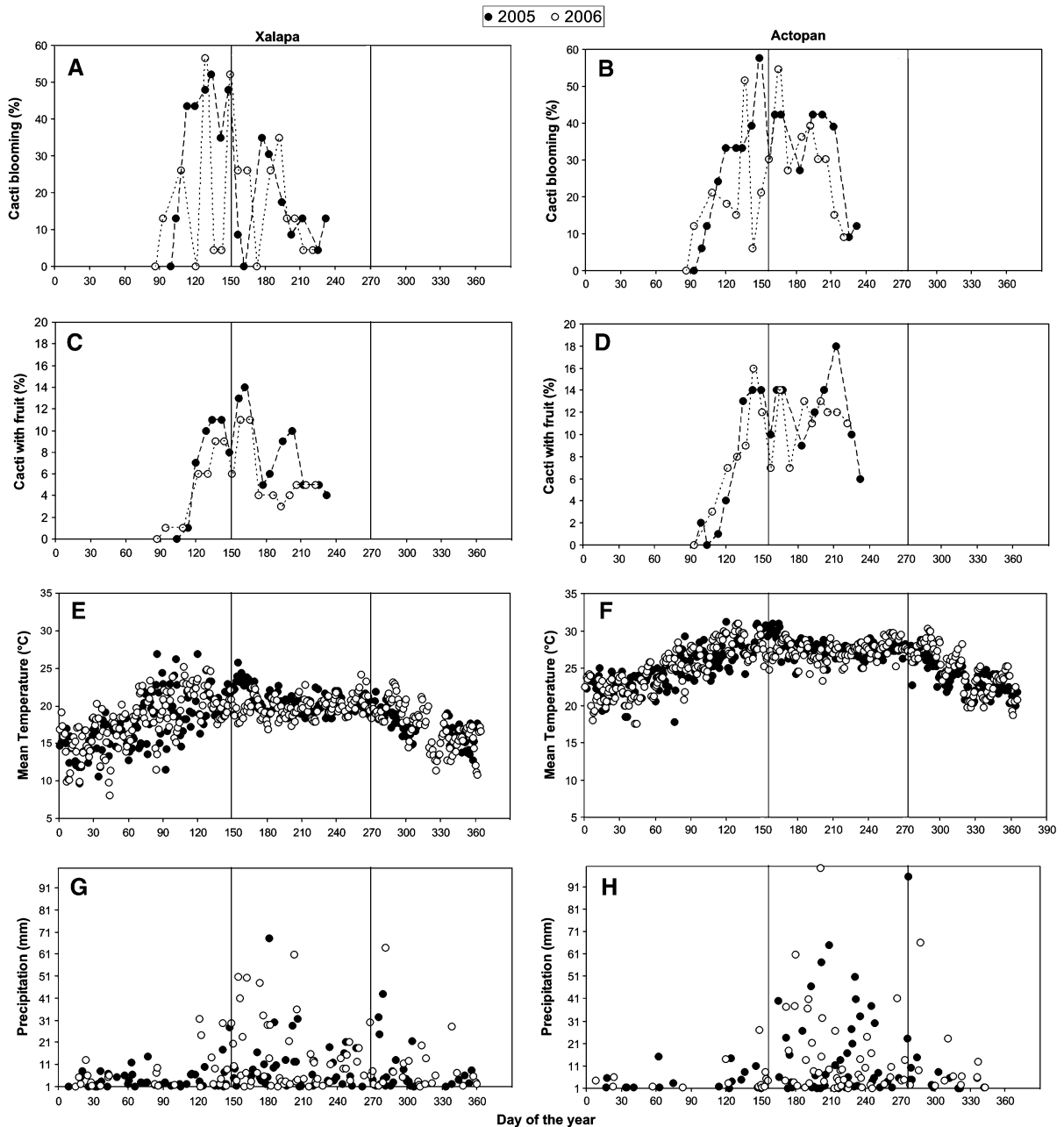


Fig. 1 Proportion of monitored cacti exhibiting reproductive structures (flowers: **a, b** and fruits: **c, d**) over 2 years (2005, filled circles and 2006, open circles) in two different regions (Xalapa on the left and Actopan on the right). Mean daily

temperature (**e, f**) and rainfall (**g, h**) are also shown. Figures on the X-axis indicate the day of the year (January 1 = 1, December 31 = 365). The area delimited with vertical lines (from \approx day 150 to \approx day 280) is the rainy season

both the number of open flowers and in the proportion of cacti exhibiting reproductive structures ($F_{1,56} = 12.3$, $F_{1,56} = 8.7$, respectively; $P < 0.01$). In contrast,

there was no significant relationship between rainfall and the number of open flowers or the proportion of cacti with reproductive structures (Table 2).

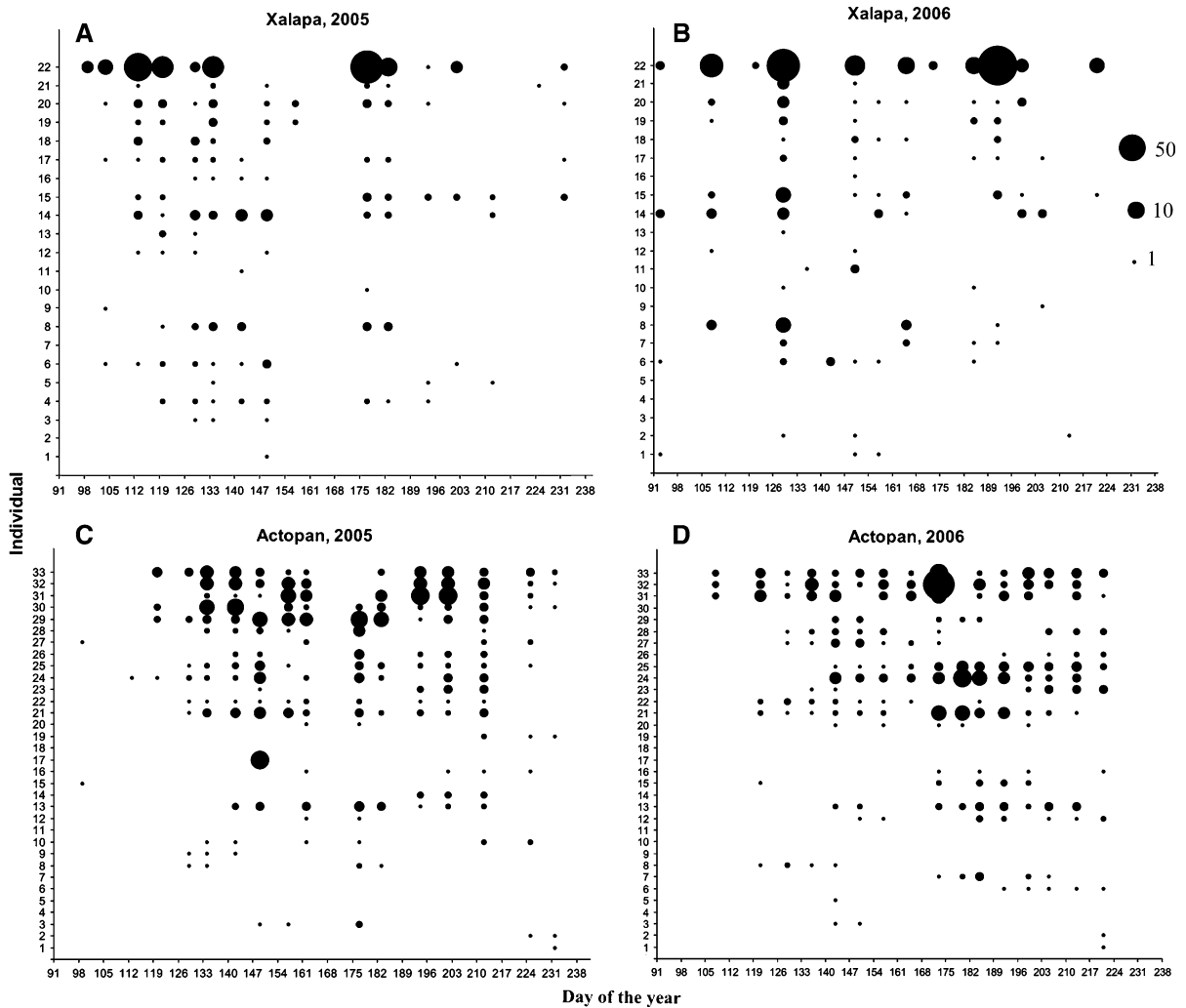


Fig. 2 Flowering schedule of 22 *Pilosocereus leucocephalus* cacti from the region around Xalapa (**a**, **b**) and 33 from Actopan (**c**, **d**) over two reproductive seasons: spring–summer 2005 (**a**, **c**) and spring–summer 2006 (**b**, **d**). The *bubbles* indicate that on that day of the year (January 1st = 1) at least

one floral structure (bud or flower) was observed. Bubble size is proportional to the number of flowers + floral buds per sampling date. Individuals in each region were ranked by size (the smallest = 1)

Effect of plant size on flowering phenology

Only flowering synchrony was not explained by plant size (Table 3). The remaining variables—the onset of flowering, flowering duration, number of flowering pulses, and the number of flowers produced per cactus—were strongly related to plant size. The relationship between size and the onset of flowering is negative, but size is positively correlated with the other variables: duration of flowering, number of flowers per cactus, and number of pulses (Table 3). In

other words, taller plants started flowering earlier, produced more flowers, and their flowering period was longer (Fig. 2a–d).

Relationship between flowering phenology and fruit set

Flowering onset had a significant and positive effect on fruit set ($F_{1,83} = 4.12$, $P < 0.05$), meaning that the fruit set of late flowering plants is larger. No other descriptor of flowering phenology included in the

Table 2 Statistics of the linear mixed-effects models to assess the relationship between temperature and rainfall with flowering phenology represented by the number of open flowers on the focal individuals (open flowers) and the proportion of focal plants exhibiting reproductive structures (proportion)

Source of variation	Response variables			
	Open flowers	Coefficient	Proportion	Coefficient
Temperature 1w	$F_{1,56} = 12.29^{**}$	0.55	$F_{1,56} = 8.66^{**}$	0.32
Temperature 3w	$F_{1,56} = 1.88$ n.s.	0.05	$F_{1,56} = 2.08$ n.s.	-0.03
Temperature 6w	$F_{1,56} = 2.39$ n.s.	-0.26	$F_{1,56} = 0.48$ n.s.	-0.10
Rainfall 1w	$F_{1,56} = 0.58$ n.s.	-0.04	$F_{1,56} = 1.77$ n.s.	-0.11
Rainfall 3w	$F_{1,56} = 1.06$ n.s.	-0.14	$F_{1,56} = 1.21$ n.s.	-0.10
Rainfall 6w	$F_{1,56} = 0.05$ n.s.	0.03	$F_{1,56} = 2.58$ n.s.	-0.21

Both variables were transformed to meet the assumption of a normal distribution. Temperature and rainfall data come from the closest meteorological station (Xalapa or Actopan). Temperature and rainfall 1, 3, and 6 weeks prior to observation were used as fixed predictor co-variables; and region (Xalapa and Actopan) and year (2005 and 2006) are random effects factors in the two models, one per response variable. Three degrees of freedom are used in the grouping structure of random factors in addition to those used in coefficient calculation. Standardized coefficients of only fixed effects are shown in the table. Variance components of random effects (region + year in region) are 3.32×10^{-10} (open flowers) and 3.91×10^{-10} (proportion)

** $P < 0.01$

n.s. Non-significant

Table 3 Statistical summary of linear mixed-effects models to assess the relationship between plant size (height to top of main branch) and flowering phenology [start of flowering (Onset), duration of the flowering season (Duration), number of flowering pulses (Pulses), production of flowers per plant (Flowers), and synchrony index (Synchrony)]

Response variable	Predictor variable		
	Size		
	Statistic	Coefficient	Variance component
Onset	$F_{1,87} = 31.07^{**}$	-0.49	0.295
Duration	$F_{1,87} = 59.96^{**}$	0.62	0.054
Pulses	$F_{1,87} = 53.83^{**}$	0.62	0.018
Flowers	$F_{1,87} = 96.31^{**}$	0.72	0.036
Synchrony	$F_{1,87} = 0.73$ n.s.	-0.07	0.095

One model was fitted per phenological variable. All significant P values are still significant after a Bonferroni correction. Three degrees of freedom are used in the grouping structure of random factors in addition to those used in coefficient calculation. Standardized coefficients and variance components of random effects (region + year in region) are shown

** $P < 0.01$

n.s. Non-significant

models explained variation in fruit set nor did plant size explain variation in fruit set (Table 4).

Discussion

The high values of CV_p (0.95–1.31) and low values of synchrony (0.25–0.31) allow us to properly define the flowering phenology of *P. leucocephalus* as

asynchronous pulsed. Although we suspected that the phenology of this species was synchronous pulsed, the synchrony indexes in the two regions studied are lower than those previously reported by Michalski and Durka (2007) for nine species of *Juncus* with synchronous pulsed flowering (synchrony range 0.39–0.74). Possibly, synchrony among *P. leucocephalus* individuals is lower than in *Juncus* because some cacti only bloomed for 1 or 2 weeks, and this

Table 4 Results of linear mixed-effects models to assess the relationship between phenology descriptors [onset of flowering (onset), duration of flowering (Duration), number of pulses (Pulses), production of flowers per plant (Flowers), synchrony index (Synchrony), and plant size (Size)] with fruit set (response variable)

Source of variation	Statistics	Coefficient
Onset	$F_{1,83} = 4.12^*$	0.19
Duration	$F_{1,83} = 0.01$ n.s.	0.06
Pulses	$F_{1,83} = 0.43$ n.s.	-0.03
Flowers	$F_{1,83} = 0.04$ n.s.	0.09
Synchrony	$F_{1,83} = 0.85$ n.s.	0.11
Size	$F_{1,83} = 0.71$ n.s.	-0.16

Only one model was fitted. Three degrees of freedom are used in the grouping structure of random factors in addition to those used in coefficient calculation. Only fixed effects are shown in the table. The variance component of the random effects (region + year in region) is 0.161

* $P < 0.05$

n.s. Non-significant

significantly affects the overlap (e) term in Augspurger's synchrony index (see formula in Methods). Whether pulsed flowering is synchronous or asynchronous, might be determined by the pollen vector. The *Juncus* species studied by Michalski and Durka (2007) are wind pollinated. In contrast to animal-pollinated species, in wind-pollinated plants, male reproductive success increases linearly with the increase in the reproductive function (Charnov 1982). *P. leucocephalus* might have fewer synchronous flowering pulses because synchrony is less important for animal-pollinated species. However, because other cases of animal-pollinated species with pulsed flowering did not report synchrony or a CV_p (*Myrica rhodosepala*, *Blepharocalyx salicifolius*, Proença and Gibbs 1994; *Myrica tomentosa*, Torezan-Silingardi and de Oliveira, 2004), this explanation requires further study to be tested properly. The number of pulses previously recorded ranges from 2 to 8 for *Juncus* species and up to 3 in the animal-pollinated species listed above, which does not contrast very strongly with the 1–7 pulses we observed for *P. leucocephalus*.

Although the synchrony index of *P. leucocephalus* and those of the *Juncus* species are not very different from the synchrony values calculated for plants with unimodal flowering such as *Pulsatilla vulgaris* [0.76; calculated by Michalski and Durka (2007); data from

Kratochwil (1988)], there is a substantial difference in CV_p between pulsed (e.g., *Juncus*: 0.89–2.78; *P. leucocephalus*: 0.95–1.31) and unimodal flowering phenologies (e.g., *Pulsatilla vulgaris*: 0.70). Our study supports the suggestion that the coordinated use of one synchrony index and CV_p is an effective approach for describing pulsed phenologies (Michalski and Durka 2007); otherwise, flowering pulses can be obscured by the traditional descriptors of flowering phenology. The flowering phenology for most of the columnar cactus species studied to date is unimodal and, for just a few species, bimodal or multimodal (Table 1). In these studies (Ruiz et al. 2000; Petit 2001; Bustamante and Búrquez 2008) the authors did not mention pulsed phenology nor did they use the appropriate method—only developed recently—to identify pulsed phenology. Although not focused on phenology, in her study Figueredo (2007) claimed that *Pilosocereus tillianus* shows pulsed phenology. It would be interesting to look at the phenology of this and other species in *Pilosocereus* and assess whether there is any phylogenetic inertia in this genus of columnar cacti.

In tropical dry forest, rainfall is expected to have a major influence on the flowering phenology of plants (Borchert et al. 2004). However, our results suggest that only temperature triggers flowering while rainfall does not affect the phenology of *P. leucocephalus*. The influence of temperature in previous studies on columnar cacti ranges from null to positive (Table 1). The study species is sensitive to the most immediate temperature (1 week before data collection). This could be related to the faster development of flowers of columnar cacti in warmer temperatures (Holland and Fleming 2002). Flowering in other species of columnar cacti such as *Cereus repandus*, *Pilosocereus lanuginosus* and *S. griseus* is related to rainfall, with a positive relationship in the first two species and a negative relationship in the others (Table 1). Apparently, for *P. leucocephalus* blooming during the rainy or dry season does not confer any advantage or disadvantage in terms of flower production. Variation in the capacity of species to store water could explain the variation in sensitivity to rainfall in succulent plants (Bertiller et al. 1991; Nobel 1977).

Cactus size was strongly related to nearly all phenological descriptors: the onset of flowering, flowering duration, number of pulses, and number of flowers. However, size was unrelated to synchrony and

fruit set. Size consistently affects the phenology of other columnar cactus species (Table 1), barrel cacti (*Ferocactus*; McIntosh 2002), and some non-succulent plants (e.g., *Lotus corniculatus*; Ollerton and Lack 1998). In columnar cacti, larger individuals have more branches and probably a greater capacity for water or energy storage (Bustamante and Búrquez 2008) and that may be influencing flowering phenology.

The onset of flowering affects the fruiting success of *P. leucocephalus*. In other plants, phenological traits are correlated with reproductive success which usually suggests that phenology has some adaptive value (Rathcke and Lacey 1985, but see Ollerton and Lack, 1992). The onset of flowering has an adaptive value in several plant species (e.g., Widén 1991; Ollerton and Díaz 1999; Parra-Tabla and Vargas 2004). Although the role of biotic interactions (pollination and predispersal seed predation) has been particularly emphasized, resource storage and time to fruit maturation are also recognized as important explanatory factors of the fine tuning of flowering time to maximize reproductive success in several species (Reviewed by Elzinga et al. 2007).

Several explanations have been proposed to account for pulsed phenology. The advantage gained by spreading the risk of reproductive failure is the most likely (Michalski and Durka 2007), though no study has tested this hypothesis yet. We also speculate that competition for resources between flowers and developing fruit could be involved in the evolution of pulsed phenology. However, this and other questions can hardly be answered with such a limited number of cases properly documented. The study of the proximal and ultimate causes of pulsed flowering is without doubt a promising line of research. In conclusion, our results indicate that the flowering phenology of *P. leucocephalus* (1) is pulsed and asynchronous, (2) it is controlled by temperature and size, and (3) that the onset of flowering affects the reproductive success of this cactus.

Acknowledgments This study was financed by the Consejo Nacional de Ciencia y Tecnología which awarded a scholarship to MA Munguía-Rosas, by Bat Conservation International, and by the Instituto de Ecología, A. C. (INECOL). Comments by J. Ollerton, E. Bustamante, and two anonymous reviewers significantly improved the quality of our manuscript. We thank B. Torales-Herrera, E. Ruiz, JM Pech, A. Miranda-Jácome, A. Flores-Lepe, E. Testa, and LI Iñiguez for their help during the field work. Bianca Delfosse revised the English.

Appendix

See Table 5.

Table 5 Correlation matrix among temperature 1 (T1w), 3 (T3w), 6 (T6w), and rainfall 1 (P1w), 3 (P3w), and 6 (P6w) weeks before the phenological survey

	T1w	T3w	T6w	P1w	P3w	P6w
T1w						
T3w	0.093	n.s.				
T6w	0.68**	0.24	n.s.			
P1w	-0.13	-0.07	0.13	n.s.		
P3w	-0.24	0.30**	-0.10	0.02	n.s.	
P6w	0.29*	0.30*	-0.05	0.17	0.30*	n.s.

Values are Pearson product-moment correlation coefficients; numbers in *italics* are still significant after Bonferroni corrections

* $P < 0.05$, ** $P < 0.01$

n.s. Non-significant

References

- Anderson EF (2001) The cactus family. Timber Press, Portland
- Augsburger CK (1983) Phenology, flowering synchrony, and fruit set of six Neotropical shrubs. *Biotropica* 15:257–267
- Bertiller MB, Beeskov AM, Coronato F (1991) Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). *J Arid Environ* 21:1–12
- Borchert R, Meyer SA, Felger RS, Porter-Bolland L (2004) Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forest. *Glob Ecol Biogeogr* 13:409–425
- Bustamante E, Búrquez A (2008) Effects of plant size and weather on the flowering phenology of the organ pipe cactus (*Stenocereus thurberi*). *Ann Bot (Lond)* 102:119–1030
- Castillo-Campos G (2003) Biodiversidad de la selva baja caducifolia en un sustrato rocoso de origen volcánico en el centro del estado de Veracruz. PhD Dissertation, Universidad Autónoma Metropolitana
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, New Jersey
- Elzinga JA, Atlan A, Biere A, Gigord L, Weis AE, Bernasconi G (2007) Time after time: flowering phenology and biotic interactions. *Trends Ecol Evol* 22:432–439
- Fenner M (1998) The phenology of growth and reproduction in plants. *Perspect Plant Ecol* 1:78–91
- Figueredo CJ (2007) Biología de la polinización y el papel de los murciélagos en la reproducción sexual de *Pilosocereus tillianus* (Cactaceae). BSc Thesis, Universidad de los Andes

- Fleming TH (2007) Reproductive consequences of early flowering in organ pipe cactus, *Stenocereus thurberi*. *Int J Plant Sci* 167:473–481
- Fleming TH, Valiente-Banuet A (2002) Columnar cacti and their mutualists. Evolution, ecology and conservation. University of Arizona Press, Arizona
- Guzmán CU, Arias MS, Dávila P (2003) Catálogo de Cactáceas Mexicanas. Universidad Nacional Autónoma de México, Mexico City
- Holland JN, Fleming TH (2002) Co-pollinators and specialization in the pollinating seed-consumer mutualism between senita cacti and senita moths. *Oecologia* 133: 534–540
- Kochmer JP, Handel SN (1986) Constraints and competition in the evolution of flowering phenology. *Ecol Monogr* 56:303–325
- Kratochwil A (1988) Zur Bestäubungsbiologie von *Pulsatilla vulgaris* Mill. *Flora* 181:261–324
- McIntosh ME (2002) Flowering phenology and reproductive output in two sister species of *Ferocactus* (Cactaceae). *Plant Ecol* 159:1–13
- Michalski SG, Durka W (2007) Synchronous pulsed flowering: analysis of the flowering phenology in *Juncus* (Juncaceae). *Ann Bot (Lond)* 100:1271–1285
- Munguía-Rosas MA (2008) Interacciones interespecíficas positivas durante la polinización, dispersión y reclutamiento del cacto columnar *Pilosocereus leucocephalus*. PhD Dissertation, Instituto de Ecología A. C
- Munguía-Rosas MA, Sosa VJ (2008) Nurse plant vs. nurse object: The effects of woody plant and rocky cavities on the recruitment of *Pilosocereus leucocephalus*. *Ann Bot (Lond)* 101:175–185
- Munguia-Rosas MA, Sosa VJ, Jácome-Flores ME (2009b) Pollination system of the *Pilosocereus leucocephalus* columnar cactus (tribe Cereeae) in Eastern Mexico. *Plant Biol*. doi: 10.1111/j.1438-8677.2009.00254.x
- Munguía-Rosas MA, Jácome-Flores ME, Sosa VJ, Quiroz-Cerón ML (2009) Removal of *Pilosocereus leucocephalus* (Cactaceae, tribe Cereeae) seeds by ants and their potential role as primary seed dispersers. *J Arid Environ* 73:578–581
- Nassar JM, Beck H, Sternberg L, Fleming TH (2003) Dependence on cacti and agaves in nectar-feeding bats from Venezuelan arid zones. *J Mammal* 84:106–116
- Nobel PS (1977) Water relations of flowering of *Agave deserti*. *Bot Gaz* 138:1–6
- Ollerton J, Díaz A (1999) Evidence for stabilising selection acting on flowering time in *Arum maculatum* (Araceae): the influence of phylogeny on adaptation. *Oecologia* 119:340–348
- Ollerton J, Lack A (1992) Flowering phenology—an example of relaxation of natural selection? *Trends Ecol Evol* 7: 274–276
- Ollerton J, Lack A (1998) Relationships between flowering phenology, plant size and reproductive success in *Lotus corniculatus* (Fabaceae). *Plant Ecol* 139:35–47
- Ortega R (1981) Vegetación y flora de una corriente de lava (mal-país) al noreste del Cofre de Perote. *Biotica* 6:57–84
- Parra-Tabla V, Vargas F (2004) Phenology and phenotypic natural selection on the flowering time of a deceit-pollinated tropical orchid, *Myrmecophila christinae*. *Ann Bot (Lond)* 94:243–250
- Petit S (2001) The reproductive phenology of three sympatric species of columnar cacti on Curaçao. *J Arid Environ* 49:521–531
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-plus. Springer, New York
- Proença CEB, Gibbs PE (1994) Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytol* 126:343–354
- Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. *Annu Rev Ecol Evol Syst* 16:179–214
- Ruiz A, Santos M, Cavelier J, Soriano PJ (2000) Estudio fenológico de cactáceas en el enclave seco de la Tatacoa, Colombia. *Biotropica* 32:397–407
- Sosa VJ (1997) Dispersal and recruitment ecology of columnar cacti in the Sonoran Desert. PhD Dissertation, University of Miami
- R Development Core Team (2007) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org>
- Torezan-Silingardi HM, de Oliveira PEAM (2004) Phenology and reproductive ecology of *Myrcia rostrata* and *M. tomentosa* Myrtaceae in Central Brazil. *Phyton* 44:23–43
- Widén B (1991) Phenotypic selection on flowering phenology in *Senecio integrifolius*, a perennial herb. *Oikos* 61:205–215
- Wolf BO, Martínez del Río C (2003) How important are columnar cacti as sources of water and nutrients for desert consumers? A review. *Isot Environ Health Stud* 39:53–67
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed-effects models and extensions in ecology with R. Springer, New York