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Reproductive Ecology of *Opuntia macrocentra* (Cactaceae) in the Northern Chihuahuan Desert

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ABSTRACT.—We studied the floral biology, floral visitors, levels of florivory, and mating system of *Opuntia macrocentra* in a population of ca. 300 individuals in order to describe what factors affect flower/fruit ratios. Blooming for the species occurred once a year during spring. Flowers were hermaphroditic, produced nectar, and remained open 6 to 9 h during a single day. Anther dehiscence starts at flower aperture and stigma receptivity starts approximately 1 h later. The most important floral visitors were solitary bees from the Anthophoridae family (genus *Diadasia*). Open-pollinated control and cross-pollination treatments had the highest fruit set ($96.8 \pm 3.2\%$ and $83.9 \pm 6.7\%$, respectively), but fruit set for forced self-pollination treatment ($77.4 \pm 7.6\%$) did not differ from the cross-pollination treatment. Seed production was also highest in the open-pollinated treatment; the average number of seeds per fruit in the open-pollinated treatment was 40% higher than the cross-pollinated treatment and 64% higher than the self-pollinated treatment. The flowers were self-compatible and did not require a visitor to set fruit. Flower/fruit ratio was slightly above one over all pollination treatments (fruit ratios between 1.0–1.3), suggesting that almost all flowers turned into fruits. Outcrossing rates suggest a mixed mating system, but inbreeding depression was found for both fruit and seed set. Developing fruits were consumed by the caterpillar (Lepidoptera: *Olycella subumbrella*) and decreased fruit set from 20% to 100%. Florivory and inbreeding depression were the major factors that decrease fruit set for this species.

INTRODUCTION

Flower and fruit production are two closely related processes that determine reproductive success in angiosperms, but the factors as well as sources of variation that determine either flower or fruit production can be very different across species. Angiosperms consistently produce many more flowers than fruits and understanding what factors control fruit/flower ratios in plants and the adaptive significance of such ratios has been an active area of research since the 1980s (e.g. Lloyd, 1980; Lloyd *et al.*, 1980; Stephenson, 1981; Sutherland and Delph, 1984; Sutherland, 1986a, b; Agren, 1988; Campbell, 1989; Guitian, 1994; Martínez-Peralta and Mandujano 2011). Fruit set depends on environmental conditions and resources (*i.e.*, precipitation, temperature) (Trueman and Wallace, 1999; Bowers, 1996; Piña *et al.*, 2007) and biotic factors such as pollinator availability (Rathcke, 2001), pollinator behavior, and specificity (Marr *et al.*, 2000; Schiestl and Schluter, 2009) plant size (Bowers,

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1996; Mandujano *et al.*, 2001) florivory, and mating system (Holsinger, 1992; Bowers, 1997; McCall, 2008; Piña *et al.*, 2010). The latter will largely depend on genetic factors such as self-incompatibility (Elam *et al.*, 2007) and inbreeding depression (Bellusci *et al.*, 2009; Strong and Williamson, 2007).

Flowering plants exhibit a variety of sexual systems (Darwin, 1859; Lloyd, 1979; Schemske and Lande, 1985; Holsinger, 1992; Richards, 1997; Barrett, 2003). Reproduction through seeds vs. clonal reproduction can affect opportunities and selection pressure for selfing vs. outcrossing (Bowers, 1996). Compared to nonclonal species, plant species with clonal reproduction can have more opportunities for selfing due to spatial clustering of clones (Carrillo-Angeles *et al.*, 2011). Developing a more complete database on mating systems of clonal plant species would help address whether selfing rates or selection pressures against selfing (such as inbreeding depression) are actually lower in clonal species. Even though clonality is widespread in vascular plants and found in several genera in the Cactaceae (*e.g.*, *Backebergia*, *Cylindropuntia*, *Echinocereus*, *Lophophora*, *Mammillaria*, *Opuntia*, *Stenocereus*), the importance and effect on the breeding and mating systems has only recently been explored (Carrillo-Angeles *et al.*, 2011).

Within the Cactaceae the reproductive biology for approximately 2% of the 2,000 species has been studied (Mandujano *et al.*, 2010), and these studies suggest that most species seem to have relatively high fruit sets in comparison to other angiosperms (Mandujano *et al.*, 1996; Piña *et al.*, 2007). Some of the factors that have been shown to affect cactus fruit production are the environmental variation found in their habitats (Mandujano *et al.*, 1996; Bowers, 1996; Bowers, 2002; Mandujano *et al.*, 2001; Piña *et al.*, 2007), genetic factors (Boyle, 2003; Negrón-Ortiz, 1988), and even florivory by beetles or moths (Bowers, 1997; Piña *et al.*, 2007, 2010; Martínez-Peralta and Mandujano, 2011). The mating system has been studied in at least 52 species within the Cactaceae and of these outcrossers are highly represented (39 species) followed by mixed mating systems (19 species) and one agamosperous species. Even in relatively well studied groups such as the Opuntioideae only 11 species out of *ca.* 300 have had their mating system determined (Mandujano *et al.*, 2010). In this study we describe the reproductive ecology of *Opuntia macrocentra*, a prickly pear cactus common to the Chihuahuan and Sonoran deserts. The specific issues addressed were: to describe the mating system of *O. macrocentra*, determine the pattern of floral visitors, and to assess if pollinators, florivores or inbreeding depression affects flower/fruit ratios.

METHODS

STUDY SPECIES

The purple prickly pear cactus, *Opuntia macrocentra* Engelm. (= *O. violacea* Engelm.) is a short shrub (up to 1 m tall), with orbiculate or obovate cladodes, 10–20 cm long, 6–18 cm wide. The segments of the perianth are yellow with bright red bases, and the fruits are oblong, 3–6 cm long, reddish to purplish-red when mature. The distribution of *O. macrocentra* encompasses southern AZ., NM., and TX. in the U.S.A and Chihuahua, Coahuila, Durango, Nuevo Leon, and the northern parts of Baja Ca. and Sonora in Mexico, within the Chihuahuan and Sonoran deserts (Benson, 1982; Bravo-Hollis, 1978; Anderson, 2001). Although the species can dominate the low shrub stratum in some areas, sharing dominance with microphyllous shrubs such as *Larrea tridentata* or *Fouquieria splendens*, in most localities, its population density is low compared with other species of *Opuntia* (*i.e.*, 100 ind/ha, Mandujano *et al.*, 2007). *Opuntia* floral attributes are evolutionarily conservative and retain bee-adapted traits (*e.g.*, anthesis, nectar production and anther dehiscence are diurnal, segments of the perianth are predominantly yellow, and flowers display radial symmetry, Bravo-Hollis, 1978; Mandujano *et al.*, 2010).

STUDIED POPULATION

The population of *Opuntia macrocentra* is located on the eastern bajada slope below Mount Summerford in the New Mexico State University Chihuahuan Desert Rangeland Research Center (hereafter CDRRC) N.M., U.S.A. The CDRRC is located at 32°25' to 32°50'N and 106°30' to 106°55'W, 1500 m altitude, 230 mm rainfall, 52% occurs in summer between Jun. and Oct.; 28°C mean temperature (data from the Jornada LTER weather station). All *O. macrocentra* individuals ($N = 278$) in five 20 m \times 50 m permanent plots were tagged in spring 1997. Size at first reproduction occurs in plants having more than 5 cladodes and fruit production varies among years from 30 fruits/plant to less than one (Mandujano *et al.*, 2007). We counted the number of cladodes (plant size), flower, and fruit production over a 2 y period (1997–1998). Fruit/flower ratios were estimated and plant size was correlated with number of fruits to establish possible differences in reproductive output between years.

FLORAL BIOLOGY AND NECTAR PRODUCTION

The floral cycle was determined using individuals in one 20 \times 50 m² plot using all the buds that opened in one day ($n = 46$). Corolla diameter was measured every other hour throughout anthesis. The activity of the antheridium was determined by visually inspecting anther dehiscence every hour and stigma receptivity was estimated by direct observation of pollen adhesion to the surface. Nectar production was quantified by bagging 32 flower buds with bridal veil to avoid the removal of nectar by floral visitors. Accumulated nectar was sampled using calibrated 5 μ l micropipettes every 2 h covering the entire floral cycle from 0800–2000 (Kearns and Inouye, 1993).

CONTROLLED POLLINATION EXPERIMENTS

We set up a hand-pollination experiment following a completely randomized block design to determine the mating system. In each of 31 plants (blocks), six 12 \times 12 cm bridal veil bags were used to cover sufficient floral buds so as to have all treatments within a plant ($n = 155$ flowers). All pollination treatments were performed at the time of highest stigma receptivity (1000–1500 h). During May 1998, once a flower opened, it was randomly assigned to one of the following treatments: (1) Automatic self-pollination: bagged flowers with no further manipulation, (2) Forced self-pollination: flowers manually self-pollinated, (3) Cross-pollination: pollen from ten plants was applied to previously emasculated flowers, the average distance of pollen source was approximately 50 m and none of the 31 plants (block) were included and (4) Open-pollination (control): mature flowers left open and bagged at the end of the day. We also attempted to set up an apomixis treatment, but to implement the treatment, flowers needed to be emasculated and left un-pollinated and covered with a mesh bag to prevent access by floral visitors. However, almost all plants when opened showed contact between stigma surface and anthers, so any further manipulation would immediately cause some degree of selfing. For each treatment, the fruit set (fruits/flowers) and flower/fruit ratios were determined once fruits were fully developed in Jul. 1998. Fruits were then collected, dried at room temperature in the laboratory, and seeds counted. Each collected fruit was bagged independently and labeled indicating plant number and treatment. Every fruit was opened with a cutter and all seeds counted. Data were analyzed using generalised-linear models using a binomial error structure for fruit set and a Poisson error structure for seed set in JMP ver. 7 (SAS Institute, Cary NC). Treated flower/fruits that were attacked by the caterpillar (Lepidoptera, Pyralidae: *Olycella subumbrella*) were counted to estimate florivory and the pollination treatment was repeated

on a new flower. The percentage of eaten flowers was calculated per plant to estimate the intensity of flower predation.

In addition we estimated the outcrossing rate (te) using the fruit set for selfing (w_s) and outcrossing treatments (w_x) following Mandujano *et al.* (2010): $te = 1 - s$ where s is the selfing rate estimated by: $s = w_s / (w_x + w_s)$. Outcrossing rates varies from 0–1, 0 in species with selfing and 1 in species with outcrossing and 0.5 for species with mixed mating systems. So values >0.5 tend towards outcrossing and <0.5 to selfing (Brown, 1990).

INBREEDING DEPRESSION

We used the ratio between selfed produced progeny (fruits and seeds) and the value for outcrossed produced progeny to estimate inbreeding depression (Charlesworth & Charlesworth, 1987): $\delta = 1 - (w_s / w_x)$ where w_s is the average fitness of selfed progeny and w_x is the average fitness of outbred progeny. Values from 0.5 to 1 indicate inbreeding depression.

FLORAL VISITORS

The abundance and diversity of floral visitors were evaluated during the 1998 flowering peak (May–Jun.). Thirty minute observation periods were conducted seven times a day (0800, 1000, 1200, 1400, 1600, 1800 and 2000 h) for 2 d during anthesis. In addition presence/absence of floral visitors were recorded in two 500 m transects in which all flowers were observed every 2 h ($n = 964$ flowers). Total observation time of visitors activity was 19 h. Bee activity with respect to time of day was analyzed using generalised linear models in R (R Development Core Team, 2010). Expected values were calculated using contingency table analysis that compared presence/absence of floral visitors and time of day (Everitt, 1977). Finally, a sample of floral visitors was collected for identification.

RESULTS

STUDY POPULATIONS

Flower and fruit production and flower/fruit ratios were very similar in the two studied years (Table 1). Precipitation was also similar (260.35 mm 1996 and 262.59 mm 1997, data from the Jornada LTER weather station) and is important to consider because prickly pears tend to grow before the rainy season using rain that fell in the previous year. This fact suggests that the same rain input may result in the same amount of flower production. There was a significant correlation between plant size with both flower and fruit production (only for reproductive plants), which suggests that bigger plants produced more flowers and the number of fruits increased with plant size (Table 1). However, the regression coefficients explained a small proportion (0.128 to 0.222) of the total variance (Table 1), indicating that other factors have an effect on flower and fruit production.

FLORAL BIOLOGY

The entire floral cycle was diurnal and lasted approximately 9–11 h. The flowers started to open in the morning (0800 h) and reached maximum aperture at midday (1200 h) and gradually closed a little after 1800 h (Fig. 1). There is no dichogamy in the species as the anthers released pollen as soon as the flower opened. Stigmas were receptive shortly after anthesis (0900 h, 15%; 1000h, 41.3% of total flowers). The remaining flowers were receptive approximately 2 h later (1100 h). Herkogamy was also absent in the species as anthers and stigmas are found at the same height within the flower. Flowers produce large amounts of nectar every 2 h (mean = $5.74 \mu\text{l} \pm \text{SE} = 0.9$) with two peaks of production: at 1000 h and

TABLE 1.—Reproductive traits *Opuntia macrocentra* individuals. Data set from 5 (20 × 50 m) permanent plots at the Chihuahuan Desert Rangeland Research Center, the Northern Chihuahuan Desert, New Mexico. Correlation coefficients (r^2) represent the proportion or fraction of the total variance explained by the proposed relationship among involved factors. The number between parentheses in the first two rows is the standard error. 1997 = * $P < 0.0001$; 1998 = + $P < 0.0001$

Trait	Year	
	1997*	1998+
Mean (SE) number of flowers per plant in reproductive size	26.18 (2.5)	25.86 (2.1)
Mean (SE) number of fruits per plant per plant in reproductive size	26 (2.5)	23.73 (1.9)
Flower/fruit ratio	1.1	1.02
Reproductive Plants: Total plants	173 : 278	158 : 278
Plant size vs. number of flowers (r^2 , df = 1, 172)*+	0.220	0.128
Plant size vs. number of fruits (r^2 , df = 1, 157)*+	0.222	0.144

1400 h, and between 1000 h and 1600 h the production is equal or higher than the average (Fig. 2). The rate at which nectar is generated diminished rapidly at the end of the day.

CONTROLLED POLLINATIONS

The fruit set percentages differed between pollination treatments ($\chi^2 = 15.39$, df = 3; $P < 0.001$, Fig. 3A). Orthogonal contrasts showed that the open pollinated control (96.77%) and outcrossing (83.87%) treatments differed from the automatic self-pollination (58.1%) and forced selfing (77.41%; $P < 0.001$; Fig. 3A). In terms of seed set, (Fig. 3B), the self-pollination experiments were not statistically different from each other and the cross-pollinated treatment produced significantly more seeds than either self-pollination treatment. Open-pollinated flowers produced significantly more seeds per fruit than the manual pollination treatments and automatic self-pollination treatment (Fig 3B). The flower/fruit ratio for *Opuntia macrocentra* population (Table 1) as well as for the experimental sample was close to one (mean = 1.31 SE = 0.15). Outcrossing rate was *te*

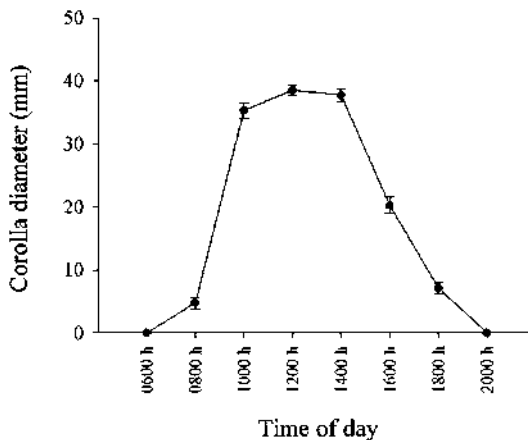


FIG. 1.—Corolla diameter (mm \pm SE) over time of *O. macrocentra* flowers ($n = 46$) in the Chihuahuan Desert Rangeland Research Center, the Northern Chihuahuan Desert, New Mexico

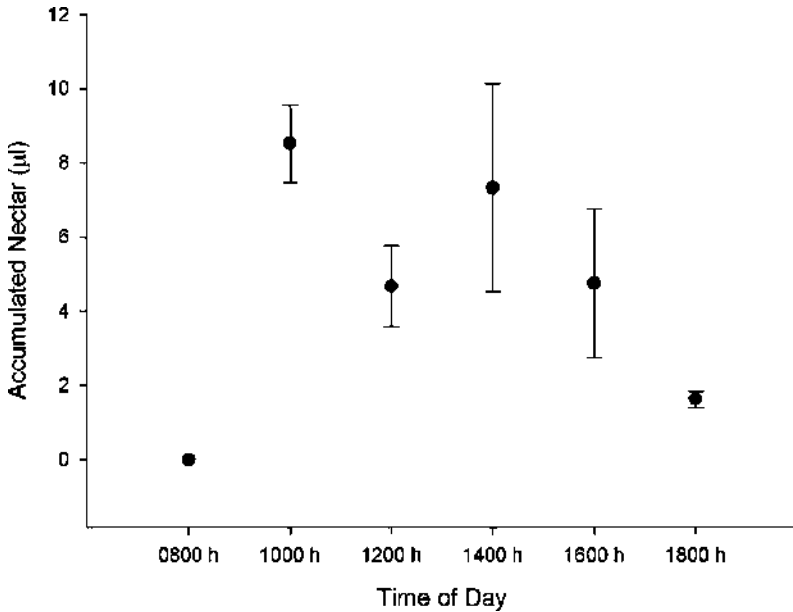


FIG. 2.—Accumulated nectar (mean $\mu\text{l} \pm \text{SE}$) of *O. macrocentra* flowers ($n = 32$) over time in the Chihuahuan Desert Rangeland Research Center, the Northern Chihuahuan Desert, New Mexico

= 0.53 (selfing rate estimated: $s = 0.714 / (0.8064 + 0.7141)$). Inbreeding depression was lower for fruit set than for seed set ($\delta = 0.08$ and 0.48 , respectively).

We found a high incidence of flowers attacked by the larvae of *Olycella subumbrella* Dyar, which reduced individual fruit set from 20% to 100% (Fig. 4). From the 155 flowers used in the pollination experiments, 30 were consumed (19.3%). Most plants did not show evidence of florivory (54.84%) and just one individual had all flowers consumed (Fig. 4) suggesting an aggregated larval feeding behavior.

FLORAL VISITORS

Flowers were only visited by solitary bees: *Diadasia* aff. *rinconis*, *Melissodes* sp. and an unidentified Antophorid. We found no differences between days so data were pooled ($\chi^2 = 16.09$, $df = 12$, $P = 0.19$). Time of day and presence/absence of visitors were both significant ($\chi^2 = 46.14$, $df = 5$, $P < 0.001$; $\chi^2 = 68.57$, $df = 1$, $P < 0.001$; Fig. 5). Visitors were present at higher than expected frequencies during the first two sampling times (0800 h and 1000 h), less than expected at 1400 h, and no different than expected values at midday and the last two afternoon sampling times. At the end of the day all censused flowers had been visited at least once.

DISCUSSION

Flower/fruit ratio for *Opuntia macrocentra* was close to one and it is high in comparison with other flowering plants (Stephenson, 1981; Sutherland, 1987), suggesting an efficient system for setting fruit in which allocated resources to produce flowers in a harsh environment are fully harnessed. There are two groups of factors that determined flower production and fruit set. On one hand, plant resources ultimately depend on

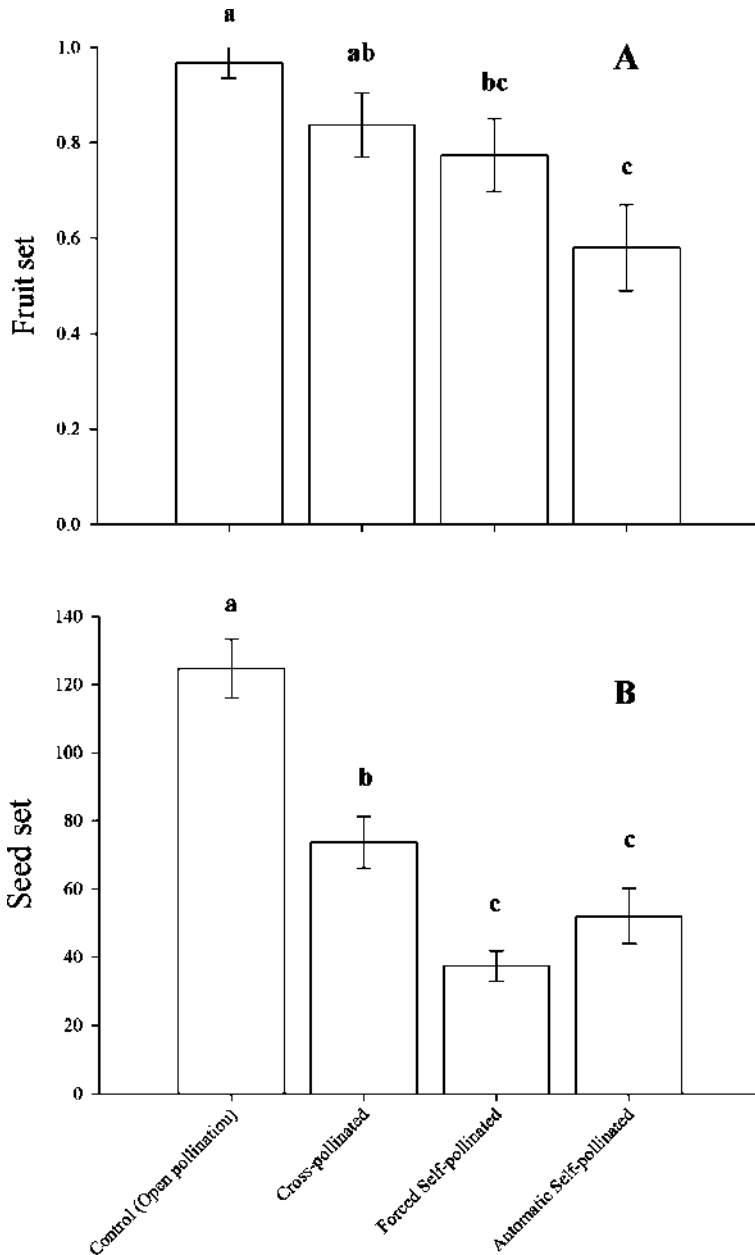


FIG. 3.—(A) Fruit set and (B) Seed set from controlled pollination treatments on *Opuntia macrocentra* in the Chihuahuan Desert Rangeland Research Center, the Northern Chihuahuan Desert, New Mexico. Different letters indicate significant differences between treatments ($\alpha = 0.05$)

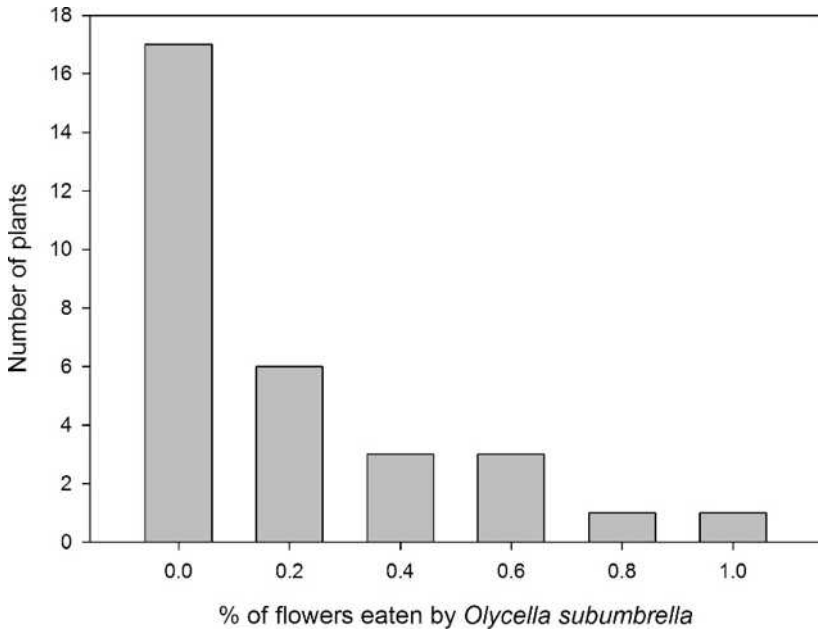


FIG. 4.—Number of *Opuntia macrocentra* plants ($N = 31$) with evidence of florivory as a percentage of flowers eaten ($N = 5$ flowers per plant) by *Olycella subumbrella* in the Chihuahuan Desert Rangeland Research Center, Northern Chihuahuan Desert, New Mexico

environmental conditions (*i.e.*, precipitation, nutrients, temperature) and they may determine the amount of flower production and in some cases the amount of flowers that mature into fruits (*i.e.*, serial adjustment hypothesis and selective abortion hypothesis; Stephenson, 1981; Sutherland and Delph, 1984; Sutherland, 1986a, b; Nerd and Mizrahi, 1995; Bowers, 1997; Piña *et al.*, 2007). In our case precipitation was similar during both years, which was reflected in similar flower production and fruit sets. Flower production of *Opuntia rastrera* has been shown to be influenced by rainfall, in dry years in which flower production is >90% lower than in rainy years (Mandujano *et al.*, 2001). However, Bowers (1996) suggests that the cladodes produced during the previous year leads to a higher number of unused areoles that translated into a higher number of new cladodes and flowers that was not necessarily coupled with rainfall. In our study, factors such as plant size were correlated with flower production and explained up to 22% ($r^2 = 0.2$ and 0.128 in 1997 and 1998, respectively) of the total variance suggesting that a maternal component may be contributing to flower and fruit production (*i.e.*, resources or availability of meristems).

For *Opuntia macrocentra* biotic interactions were also important in determining fruit set. Predation of flowers by the larva *Olycella subumbrella* reduced individual fruit set by 20% to 100%, a role that has been largely ignored in the past but seems to be getting more attention recently (McCall, 2008; Piña *et al.*, 2007). Similar to our study, *Olycella junctolineella* reduced fruit set in *O. microdasys* by up to 100% in plants with severe attack, and on average was around 21% (Piña *et al.*, 2010). Other species with florivory reduce fruit set from 55 to 64% (Sánchez-Lafuente, 2007; Martínez-Peralta and Mandujano, 2011), and no reflowering has been reported for wild *Opuntia* species after the attack of florivores. In contrast cultivated species of *Opuntia* produce flushes of flowers in autumn after the manual

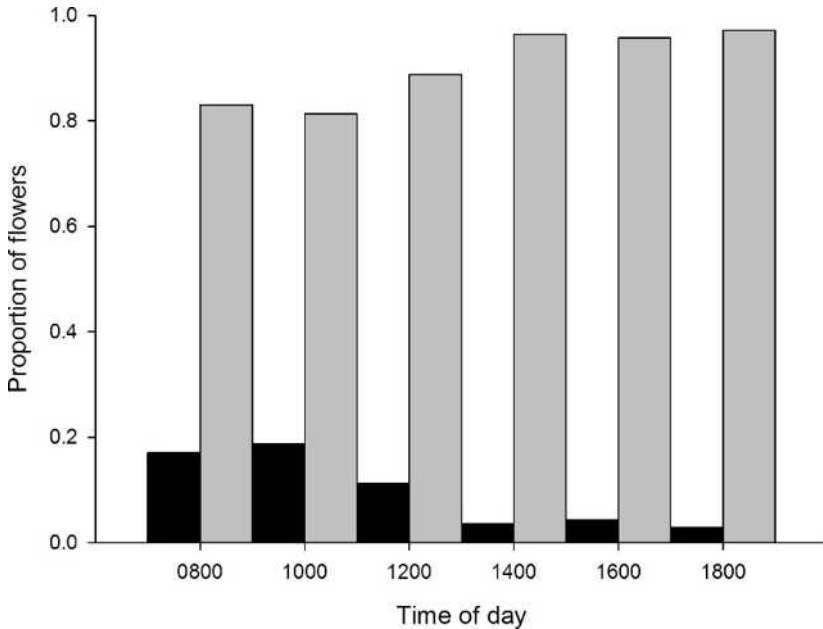


FIG. 5.—Frequency (presence/absence) of floral visitors observed on *O. macrocentra* flowers ($n = 964$) along 500 m transects in the Chihuahuan Desert Rangeland Research Center, Northern Chihuahuan Desert, New Mexico. Black bars = presence of visitor in a flower, Gray bars = absence of visitors in a flower

removing of floral or cladode buds during spring. This reflowering ability is widely exploited by farmers in Italy to obtain a late crop; this common practice is known as *scozzolatura* (Nerd and Mizrahi, 1995).

Our results indicate that *Opuntia macrocentra* has a mixed mating system. Of the *Opuntia* species that have been studied most have a mixed mating system (Reyes Agüero *et al.*, 2006; Mandujano *et al.*, 2010). However, our outcrossed and control open-pollination treatments may have a confounding factor due to the impossibility of emasculating anthers before dehiscence and the overlap of male and female phases also provides suitable conditions for autogamy (Grant and Grant, 1979). The flowers of *O. macrocentra* are self-compatible and unlike other species of the genus, they do not require the pollinator to set fruit (Grant and Grant, 1979, Mandujano *et al.*, 1996). Fruit set by selfing only increased 17% if a vector is simulated (forced selfing pollination treatment). Visitors largely consisted of a *Diadasia* species a genus of solitary bees that has been suggested to have coevolved with *Opuntia* species (Trujillo-Argueta and Gonzalez-Espinosa, 1991). Despite autogamy (automatic self pollination), a visit of pollinators enhances pollination, increasing the number of fertilized ovules. Fruit set of species visited by solitary bees are always higher and they have been shown to be efficient pollinators (Grant and Grant, 1979). In addition we found the first peak nectar secretion and receptivity of reproductive structures coincide with peak pollinator activities, which suggest that floral visitors search for both nectar and pollen rewards.

Similar to other species of *Opuntia*, flowers of *Opuntia macrocentra* are slightly protandrous, and 27% are able to self-pollinate soon after anthesis, which suggest a degree of

pseudocleistogamy (Reyes Agüero *et al.*, 2006). In an effort to control the within-plant pattern of selective fruit retention in *O. macrocentra*, all hand-pollination treatments were performed in a block design. If the selective-fruit-abortion hypothesis accounts for the apparent overproduction of flowers and the subsequent low fruit set in *O. macrocentra*, then hand pollination of selected flowers within the plant should result in the selective retention of these flowers. That is, within a plant, selective fruit retention should result in an increase in fruit set for hand-cross pollinated flowers over naturally pollinated control. Results indicated no significant difference in fruit set for hand-cross pollinated flowers and naturally pollinated flowers, which is similar to other experiments on succulent species (*e.g.*, *Agave mckelveyana*, Sutherland, 1987). Inbreeding depression has been reported in four of the 11 studied species of *Opuntia* (Mandujano *et al.*, 2010). Self-compatibility has been thought to be a mechanism that ensures reproduction and could quite possibly be the case for clonal *Opuntia* and other species in arid environments. Fruit set for *O. macrocentra* at CDRRC was 10% lower than in other *Opuntia* species (Mandujano, *et al.*, 1996, Reyes-Agüero *et al.*, 2006). Seed production was 48% lower than those found in other *O. macrocentra* populations within the Chihuahuan desert (Mandujano *et al.*, 2007). Little is known of the Sonoran desert populations. It is clear though that the number of seeds produced by the self-pollination treatments were consistently lower than those from the cross pollination treatments and reproductive success would be better estimated by taking into account not only fruit and seed sets, but seed germination as well.

At CDRRC, sexual reproduction seems to play a minor role in the population dynamics of *Opuntia macrocentra*, while clonal propagation is significantly more frequent (Mandujano *et al.*, 2007). This means that selfing is more likely to occur in a population as individuals within the population are more likely to be genetically related and it is common in *Opuntia* plantations that are vegetatively propagated (Nerd and Mizrahi, 1995). Therefore, clonal species would benefit from being self compatible as relatedness increases. Other benefits of selfing have also been described such as to assure fruit set if there are variations in pollination success because of variations in pollinator densities or pollinator visitation rates (*i.e.*, reproductive insurance) and purging of deleterious mutations (Darwin, 1859; Lloyd, 1979) which give advantages to mixed mating systems. For *O. macrocentra*, high fruit sets seem to be guaranteed by selfing even under the high rates of loss to florivory, but the effects of inbreeding depression was evident during the seed set periods in the life cycle.

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