

## ABORTED FRUITS OF *OPUNTIA MICRODASYS* (CACTACEAE): INSURANCE AGAINST REPRODUCTIVE FAILURE<sup>1</sup>

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New individuals in clonal populations arise through the recruitment of sexual or clonal offspring. The predominance of one type of regeneration over the other has been correlated with different selective environmental pressures. We compared the reproductive mode (sexual through seeds and vegetative through plantlets or detached cladodes) of *Opuntia microdasys* from three desert habitats of the Chihuahuan Desert: bajada (BH), hill-piedmont (HPH), and an interdune (IDH). Successful establishment and growth of plantlets were determined in two experiments: (1) the effect of light (three levels of photosynthetically active radiation [PAR]: full, low, and medium) and two levels of watering and (2) maternal effects and provenance of plantlets. Adult plant densities did not differ among habitats (639 individuals/ha), but the number of offspring and fruit production increased significantly at BH. Plantlets (94.3%) dominated the form of recruitment for all habitats, followed by cladodes (3.1%) and seedlings (2.6%). A higher proportion of plantlets established in the low and medium PAR treatments (76%) in comparison to full exposure (39%). Maternal factors affected survival and growth, but plantlet provenance did not. The high fruit abortion rate resulting from environmental and maternal effects provided suitable conditions for establishment of plantlets.

**Key words:** clonal propagation; fruit abortion; *Opuntia*; prickly pear; pseudovivipary; plantlet; sexual recruitment.

The maintenance of populations depends on some form of recruitment that replenishes the loss of individuals through time. The modular construction of plants has in some cases (i.e., clonal plants) provided a means of propagating individual modules (ramets) that can potentially become detached and live independently (Herben et al., 1994). Clonal plants can replenish individuals through sexual reproduction and/or vegetative propagation (Cook, 1985; Eriksson, 1989; Arizaga and Ezcurra, 2002). However, recruitment via sexual reproduction is infrequent in harsh conditions such as those found in arid environments (Eriksson, 1989; Mandujano et al., 2001). For example, the establishment of cacti seedlings is rare because of the extremes in temperature, humidity, and herbivory, but it is mediated by nurse plants that diminish these environmental pressures (Shreve, 1911; Valiente-Banuet and Ezcurra, 1991; Callaghan et al., 1992; Mandujano et al., 1998; Jiménez-Sierra and Jiménez-González, 2002).

In clonal plant species, the production of vegetative propagules, which ends with the formation of ramets with the same genetic information of the parent plant, is an important ecological strategy for the rapid colonization of suitable habitats (Anthony, 1954; Cook, 1985; Auge and Brandl, 1997; Reusch et al., 1998). In some cases, vegetative propagation can be the most frequent form of recruitment (Frego and Staniforth, 1985; Eriksson, 1989; Mandujano et al., 1997; Mandujano et al., 1998; Hicks and Mauchamp, 1999; Arizaga and Ezcurra, 2002).

New clonal offspring can be produced by three pathways. (1) Asexual formation of unfertilized seeds (agamospermy) is common in some *Opuntia* (Pimienta-Barrios and Del Castillo, 2002) and has mostly a genetic consequence (Cook, 1985), but these seeds can be ecologically equivalent to sexual seeds (Cook, 1985). (2) The development of new plants from vegetative structures such as stems, bulbs, rhizomes, and stolons, that have higher establishment probabilities and can eventually give rise to independent but genetically identical individuals (Callaghan et al., 1992; Arizaga and Ezcurra, 1995; Mandujano et al., 1998; Bobich, 2005). (3) In a number of families (Crassulaceae, Oxalidaceae, Polygonaceae, Saxifragaceae, Agavaceae, Bromeliaceae, Cactaceae, Poaceae, Juncaceae, Liliaceae, and Gesneriaceae), reproductive structures (e.g., a pericarpel or the apex of an inflorescence) can give origin to new clonal individual plants (i.e., pseudovivipary) by means of clonal propagules such as bulbils or plantlets in place of sexual reproductive structures (Youngner, 1960; Elmquist and Cox, 1996; Diggle et al., 2002; Wang and Cronk, 2003; Cota-Sánchez, 2004; Wang et al., 2004). This last type of vegetative propagation that incorporates sexual structures that fail to produce sexual seeds to produce plantlets has been described as insurance against sexual reproductive failure (Arizaga and Ezcurra, 1995).

In particular, pseudovivipary has been reported for very few species in the Cactaceae such as *Opuntia rufida*, *O. phaeacantha*, *O. monacantha*, *O. salmiana*, *Cylindropuntia imbricata*, *C. fulgida*, *C. kleiniae*, *C. leptocaulis*, *C. tunicata*, *C. prolifera* (Buxbaum, 1950; Anthony, 1954), *O. echios* (Hicks and Mauchamp, 1999), and in some members of the Agavaceae (*Agave marmorata*, *A. fourchroydes*, and *A. macroacantha*; Arizaga and Ezcurra, 1995, 2002; Gentry, 1998). Clonal reproduction has ecological advantages: (1) fast population growth rates increase the potential survival and future reproduction (Mandujano et al., 2001); (2) established plants have an opportunity to inhabit current favorable sites; (3)

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space can be foraged, and plants can have further access to resources (Harper, 1981); and (4) ramets, in general, have a higher probability of survival than seedlings in harsh environments (Mandujano et al., 1998; Hicks and Mauchamp, 1999; Arizaga and Ezcurra, 2002). In the short term, environments that maintain clonal propagation provide greater benefits, but the presence of ramets with the same genetic information that remain relatively close to the parent plant may drastically affect the mating system through an increase in inbreeding (Handel, 1985; Trame et al., 1995; Charpentier, 2002), which can eventually lead to the evolution of different reproductive strategies (Lovett-Doust, 1989).

In the southern Chihuahuan Desert, *Opuntia microdasys* vegetatively propagates by the establishment of one or several detached cladodes or by the fall of unripe fruits that produce plantlets. Propagation through cladodes appears to be less frequent than propagation through plantlets, the most frequent form of recruitment (M. Mandujano, unpublished data). Unlike the rest of the angiosperms, the fruits in the Cactaceae are composed of stem tissue (pericarpel) with embedded sexual structures, surrounded by viable areoles, which are true lateral meristems of caulinar origin (Buxbaum, 1950; Bravo-Hollis, 1978; Mauseth, 1984).

The purpose of this study was to determine the relative importance of vegetative propagation through plantlets or detached cladodes of the bunny-ears prickly pear, *Opuntia microdasys*, in three different populations (habitats) in the Mapimi Biosphere Reserve (MBR) in the southern part of the Chihuahuan Desert in Mexico and to determine the relation of vegetative propagation to some of the factors (light, water, and provenance) that have been reported as being important for the recruitment of individuals in other species of Cactaceae (Shreve, 1911; Gibson and Nobel, 1986; Valiente-Banuet and Ezcurra, 1991; Altesor et al., 1992; Mandujano et al., 1998, 2002; Jiménez-Sierra and Jiménez-González, 2002).

## MATERIALS AND METHODS

**Study plant**—*Opuntia microdasys* (Lehmann) Pfeiffer is a short plant approximately 60–80 cm tall, erect to sprawling shrubs and circular to elliptic-ovate, bright green pads without spines, with many reddish brown or usually yellow or whitish glochids. The flowers have bright yellow inner perianth segments and are ca. 2.5–3 cm long. The outer perianth segments are sometimes reddish tinged. The fruits are red, fleshy, and globose to obovate ca. 2–2.5 cm long. They are usually found in sandy to loamy calcareous soils of desert hills and uplands at 1700–2100 m a.s.l. The species is distributed in the states of Coahuila, Zacatecas, Nuevo León, Tamaulipas, San Luis Potosí, and Hidalgo and apparently hybridizes with *O. rufida* near Saltillo, Coahuila, and Concepción del Oro, Zacatecas, Mexico (Bravo-Hollis, 1978). The flowering period is from April to mid-May (Cornet, 1985), and fruits ripen from June to August.

**Study site**—The study was conducted in the Mapimi Biosphere Reserve (MBR) located in the southern Chihuahuan Desert (26°29'–26°52' N, 103°32'–103°58' W, 1100 m a.s.l., 264 mm mean annual rainfall [80.2% between June and October], 20.8°C mean temperature; Cornet, 1988). The observations were made in populations of *O. microdasys* in three sites that differ in their biotic and abiotic characteristics: bajada, hill-piedmont, and interdune habitats (Fig. 1).

The bajada (BH) is a physiographic unit formed by coalescent alluvial fans with an average slope of 2%; drainage is confined to channels near mountains, which give rise to laminar flows that drain to playas (Fig. 1A2). The soils are deep, usually a mixture of gravel and sand, but can present secondary accumulation of clay. Shrubs of *Larrea tridentata* and *Fouquieria splendens* are common, although sometimes *F. splendens* can be replaced by *Opuntia rastrera* (Montaña, 1988) as the most common species. Individuals of *O. microdasys*, *Jatropha dioica*, and *Agave asperrima* can also be found as the dominant succulent life forms (Montaña, 1988). Hill-piedmont is a habitat

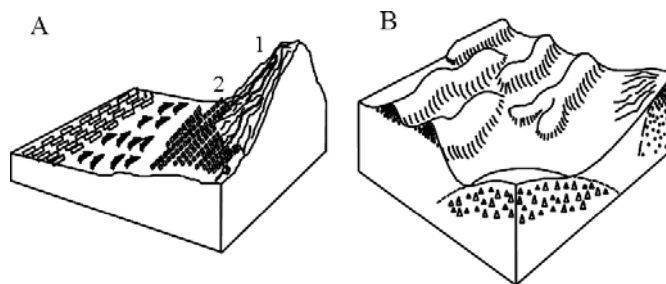


Fig. 1. Schematic of the geological formations of the three studied habitats of *Opuntia microdasys* in the Chihuahuan Desert. (A) 1: Bajada habitat (BH), 2: Hill-piedmont habitat (HPH), and (B) Interdune flat habitat (IDH). Modified from Montaña (1988).

(HPH) of igneous rock, with an average slope of >10% and a shallow stony soil having scarce vegetation (Fig. 1A1; Montaña, 1988). The dominant species in this habitat are *F. splendens*, *L. tridentata*, and *Yucca rigida*, with other secondary succulents such as *Opuntia microdasys*, *O. rastrera*, *A. asperrima*, and *A. lechugilla*, as well as hemicyptophyts (e.g., *Selaginella lepidophylla*; Montaña, 1988). Extensive sandy plains, found between sandy dunes, constitute the interdune flats habitat (IDH) where the average slope is <1% (Fig. 1B). The dunes form a dense network of hills, that are connected by flat interdune plains. Flood plains are absent, because the sandy substrate facilitates fast infiltration and lateral water movement is mainly underground. The typical vegetation of dunes is dominated by *Dalea scoparia* and *Yucca elata* in the high sections of dunes and by different combinations of *Acacia greggii*, *A. constricta*, *L. tridentata*, and *Lycium berlandieri* in the lower parts of the dunes. Areas between the dunes constitute plains that present a moderately deep ground, with a secondary accumulated layer of lime (Montaña, 1988). These plains are largely covered by vegetation of shrubbery communities dominated by *Prosopis glandulosa* and *Flourensia cernua*, sometimes having a dense layer of grass dominated by *Hilaria mutica*. In some cases, *O. rastrera* and *O. microdasys* can be found as the dominant species in the interdune habitats, along with *Zinnia acerosa* (Montaña, 1988).

**Description and frequency of clonal propagation**—Several transects (15 in BH, 14 in HPH, and 16 in IDH) were made during May in each site to obtain a sample of at least 100 adult plants. From each plant, we measured height at the tip of the highest cladode, diameter in two orthogonal directions, and total number of cladodes (including lignified cladodes). We also counted the number of plantlets, floral buds, and aborted fruits found underneath each adult individual as well as fruits that were still connected to the adult to obtain a rate of abortion by plant and by habitat. In addition, the number of juveniles associated to the parent plant (directly under the canopy of the adult), which were produced by plantlets (i.e., rooted aborted fruits) or detached cladodes were registered. Of all the detached plantlets found on the ground we evaluated whether they were the product of immature floral buds that did not complete anthesis or aborted fruits (i.e., flowers that completed anthesis and were aborted post-pollination). We also assessed the development of a root system, which allowed us to establish the rate of recruitment of plantlets. The size of each plantlet was measured longitudinally (tip to point of abscission from cladode, in centimeters), and we counted the number of cladodes and measured the distance from each plantlet to the base of the parent plant (in centimeters). Finally, the frequency of fallen fruits with or without the development of seeds was estimated from a sample of 90 randomly collected fruits at each site and dissected to confirm the absence of seeds. Statistical analyses include chi-square test, residual analyses, and ANOVAs (SAS Institute, 1995). Photosynthetically active radiation (PAR, in micromoles per second per square meter) was measured from eight cardinal points around four focal plants in open space (100 cm from parent plant) and under the shade of focal plants (50 cm, 16 measurements per plant). Light measurements were made in May 1999 at a randomly selected site (HPH) and were taken every three hours (from 0800 to 2000) using a steady state porometer quantum sensor (Model LI 1600; LICOR, Lincoln, Nebraska, USA).

**Effect of radiation in the vegetative propagation by aborted fruits**—We estimated the establishment of *O. microdasys* plantlets in a greenhouse at MBR using a completely randomized 2 × 3 split-plot design. The greenhouse is

protected along all four edges and top with metallic mesh to prevent the entrance of vertebrates, but is exposed to the same weather conditions as study sites in MBR. Two factors were tested: (1) light (the main treatment assigned to whole plots) with three levels: full sunlight (high solar radiation); medium solar radiation (representing 43% PAR extinction, measured with a LI-COR sensor Q15494, achieved by a covering of a single layer of nylon mesh) and low solar radiation (70% PAR extinction with two layers of mesh), and (2) two soil moisture regimes (with or without watering). The experimental unit for each treatment was a pot with four fruits, with 20 pots for each light level and humidity combination of treatments. Soil moisture was kept at field capacity (every 4 days, each pot was watered with either 0.4 L for low solar radiation treatments, 0.5 L for medium, and 1 L for high). Therefore, two pots in each replicate were exposed to the same light conditions, but received different amounts of water. Plantlets were grown from May until November 2000, when surviving individuals were then counted, harvested, oven dried at 60°C, and weighed.

Data were analyzed using nested ANOVAs for split plot designs and Tukey honestly significant difference (HSD) tests (Zar, 1996). The response variables were the proportions of survivors (arcsine transformed; Zar, 1996) and dry mass (in grams) of plantlets. All statistical analyses were made with the JMP statistical program (SAS, 1995).

**Site and parental effects**—We experimentally assessed the possible effects of the parent plants over their progeny and verified the possible relationship between the habitat and the size of the parent plant on the quality of plantlets in a greenhouse at the Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM), Mexico, in a completely randomized 3 × 10 factorial design with three replicates. In each of the three habitats, 10 focal plants were chosen, and 12 fruits were taken from each plant (N = 360 fruits). The development of fruits in each habitat was compared within the same watering conditions to evaluate the parental effect on survival. Fruits from each habitat (N = 120) were measured (length and width, in centimeters) and weighed, and four fruits were placed in each of 8 × 8 × 8 cm jiffy pots. Pots were watered every 4 d to keep field capacity, and survival was followed for 6 mo. At the end of the experiment, all remaining plantlets were oven dried and weighed to constant mass. Data analysis were carried out using ANOVAs, having survival percentage and dry mass as response variables for each treatment and the initial mass (in grams) as a covariable (Zar, 1996).

The magnitude of selection on fruit size was determined by means of regression analysis on the relationship between maternal clonal success (number of aborted fruits × probability of establishment) and the size of the propagule (aborted fruit). Absolute fitnesses were transformed to relative fitnesses by dividing each absolute value by the mean absolute fitness (mean = 1; Lande and Arnold, 1983; Arnold and Wade, 1984a, b).

RESULTS

**Description and importance of the modes of clonal propagation**—The density of adult plants did not differ between habitats (BH = 666, HPH = 785, and IDH = 637 individuals/ha; mean = 693.3 individuals/ha; P = 0.73), but when vegetative (plantlets and cladodes) and sexual recruitment are included, the density of individuals increased 3.9 times in BH (2620 individuals/ha), 1.3 times in HPH (1042 individuals/ha), and 1.8 times in IDH (1175 individuals/ha; Table 1). The HPH and IDH habitats were less favorable for the recruitment of plantlets ( $F_{2,309} = 25.46, P < 0.001$ ; Tables 1, 2), while the IDH was also unsuitable for seedlings and the BH habitats were unsuitable for seedlings and cladodes. All differences in the density of sexual and clonal recruitment were highly significant ( $\chi^2 = 591, 4 \text{ df}, P < 0.0001$ ; Tables 1, 2). The percentage of aborted fruits (amount of fruits on the ground/total of fruits per habitat) was significantly higher in the BH (40%) and in the HPH (36%) than in the IDH (19%,  $F_{2,309} = 14.63, P < 0.01$ ; Table 2). However, the percentage of plantlets with respect to aborted fruits was significantly higher in BH (22.6%,  $P < 0.001$ ) than in the other two habitats (IDH = 10.9%, HPH = 4.4%). In general, the number of aborted

TABLE 1. Density (individuals per ha) and percentage per site of sexual (seedlings) and vegetative offspring (cladodes and plantlets) of *Opuntia microdasys* from three habitats in the Chihuahuan Desert, Mexico.

Habitat	Type of offspring							
	Cladode		Aborted fruits		Seedlings		Total	
	No./ha	%	No./ha	%	No./ha	%	No./ha	%
Bajada (BH)	6.7–*	0.3	1953.3	99.3	6.7–*	0.4	1966.7	67.5
Hill-piedmont (HPH)	14.3	4.3	257.1–*	76.6	64.3+*	19.1	335.7	11.5
Interdune (IDH)	68.8+*	11.2	537.5–*	87.8	6.3–*	1.0	612.6	21.0
Total	89.8	3.1	2747.9	94.3	77.3	2.6	2915	100

Note: An asterisk indicates cells that differ with residual analyses according to normal distribution values at  $\alpha = 0.05$ . A plus (+) or minus (–) symbol indicates whether there are more or less individuals recruited by each mode of reproduction.

fruits was positively correlated to the number of plantlets ( $R^2 = 0.22; P < 0.01$ ) under individual plants.

Reproductive plants have more cladodes in HPH ( $F_{2,309} = 5.086, P = 0.02$ ; Table 2), but contrary to expected, they produced significantly fewer fruits than plants in the BH and IDH habitats. Total production of fruits per habitat was higher at BH and IDH habitat than at the HPH ( $F_{2,309} = 2.45, P = 0.08$ ; Table 2), a similar response was found with the fruits that were still attached to the parent plant, mature, and therefore had completed seed development ( $F_{2,309} = 3.50, P < 0.03$ ; Table 2). All plantlets found on the ground came from flowers that completed anthesis (i.e., aborted fruit, N = 315); not a single plantlet came from flower buds.

The size of fruits is dependent on the origin of the detached fruit; aborted floral buds were significantly smaller than aborted fruits (1.36 ± 0.02 cm, 1.93 ± 0.07 cm respectively;  $P < 0.001$ ). Similarly, the average distance of the nonrooted fruits from the parent plant (63.55 ± 1.076 cm) was greater than between plantlets and parents (44.93 ± 2.64 cm,  $P < 0.001$ ; Table 2), probably due to the protection provided by the parent plant against excessive solar radiation. We found that

TABLE 2. Trait values per capita (mean ± SE) for reproductive plants of *Opuntia microdasys* in three contrasting habitats in the Chihuahuan Desert (N indicates sampled plants in each site). BH = Bajada habitat, HPH = Hill-piedmont habitat and IDH = Interdune flat habitat.

Plant trait	Site		
	BH N = 100	HPH N = 110	IDH N = 102
Number of cladodes	96.26 <sup>a</sup> (10.54)	129.43(14.27)	78.28 <sup>a</sup> (8.88)
Fruits still attached to the plant	13.14 <sup>a</sup> (2.47)	6.93(1.43)	18.55 <sup>a</sup> (4.73)
Total fruit production	26.11 <sup>a</sup> (3.95)	14.60(2.39)	26.26 <sup>a</sup> (6.05)
Abortion (%)	40.32 <sup>a</sup> (3.62)	36.95 <sup>a</sup> (3.73)	19.38(2.51)
Number of plantlets	2.93(0.46)	0.33 <sup>a</sup> (0.07)	0.62 <sup>a</sup> (0.18)
Number of seedlings (sexual origin) <sup>b</sup>	0.01#	0.08	0.01#
Number of clonal offspring (cladodes) <sup>b</sup>	0.01#	0.02#	0.10
Mean distance of plantlet to parent plant (cm)	44.61(0.76)	88.80(2.67)	57.79(1.58)

<sup>a</sup> Indicates groups that did not differ with Tukey honestly significant difference (HSD) test at  $\alpha = 0.05$  (JMP, SAS 1995).

<sup>b</sup> Chi-squared test. A pound sign (#) indicates groups that did not differ with residual analyses.

TABLE 3. Results of the experiment to determine the parental effect on survival, dry mass, and vegetative characteristics of fruits of *Opuntia microdasys* from three habitats in the Chihuahuan Desert under controlled conditions: BH = Bajada habitat, HPH = Hill-piedmont habitat, and IDH = Interdune flat habitat.

Characteristic	BH	HPH	IDH
Survival (%)	50.07	54.17	66.67
Dry mass (g)	0.41 ± 0.17	0.40 ± 0.16	0.44 ± 0.14
Average number of roots produced	2.18 ± 2.54	2.21 ± 2.26	2.85 ± 2.08
Average of areoles that produce root	2.04 ± 2.4	2.09 ± 2.12	2.85 ± 2.03
Average of cladodes per plantlet	0.88 ± 1.25	1.08 ± 1.35	1.48 ± 1.51

the most suitable habitat for the establishment of plantlets was the BH ( $P < 0.0001$ ; Tables 1, 2). Plantlets did not differ between habitats in the number of cladodes produced (mean =  $1.68 \pm 0.08$  cladodes), but rooted fruits were significantly larger ( $1.93 \pm 0.038$  cm;  $N = 315$ ) than nonrooted fruits ( $1.81 \pm 0.016$  cm,  $P = 0.002$ ;  $N = 2613$ ), suggesting that the probability of rooting is related to the size of the propagules, their location relative to a potential nurse plant, as well as the resources that can be acquired once established.

**Effect of radiation on the vegetative propagation by aborted fruits**—Survival percentages were dependent on light conditions. Plantlets under shade conditions had higher survival rates (77.5% and 74.4% for 70% and 43% PAR extinction, respectively) than those exposed to direct sunlight (39.4% for 0% PAR extinction;  $F_{2,57} = 19.01$ ,  $P < 0.001$ ). The average number of cladodes on plantlets depends on exposure to light, because growth, measured in terms of cladode production, significantly increased as light decreased ( $0.55 \pm 0.08$  cladodes/fruit at 0% extinction PAR;  $1.61 \pm 0.09$  cladodes/fruit at 43% extinction PAR;  $1.81 \pm 0.09$  cladodes/fruit at 70% extinction PAR;  $F_{2,57} = 50.01$ ,  $P < 0.001$ ). As a consequence, accumulated biomass was also dependent on light conditions as well as on the initial fruit size. The cladodes from fruits in shade were significantly heavier than those exposed to direct sunlight ( $0.04 \pm 0.01$  g at 0% extinction PAR;  $0.16 \pm 0.01$  g at 43% extinction PAR;  $0.18 \pm 0.01$  g at 70% extinction PAR;  $F_{2,57} = 33.92$ ;  $P < 0.001$ ). Survival between watering regimes ( $F_{1,57} = 2.06$ ,  $P = 0.156$ ) and the interaction term ( $F_{2,57} = 0.03$ ,  $P = 0.96$ ) were not significant.

**Site and parental effects in controlled conditions**—Even though plantlets and unrooted fruits were statistically different in size, we explored the effect of habitat and parent on the size of progeny. Our results suggest no statistical differences in the fruit attributes as a result of the parental habitat ( $P > 0.5$ ). However, percentage survival ( $F_{2,29} = 3.5$ ,  $P < 0.001$ ), dry mass ( $F_{2,29} = 6.91$ ,  $P < 0.01$ ), mean number of roots ( $F_{2,29} = 3.63$ ,  $P < 0.01$ ), mean number of cladodes ( $F_{2,29} = 2.27$ ,  $P < 0.01$ ), and mean number of areoles that produced roots ( $F_{2,29} = 3.53$ ,  $P < 0.01$ ) were strongly influenced by the parent (Table 3). The characteristics associated with the parent plant strongly influenced the probability of survival of fallen fruits in all three habitats.

**Quantitative analysis of selection**—The selection analysis suggests a strong influence of size on the probability of establishment. The estimated probability for successful establishment of aborted fruits was 0.142 with a mean absolute

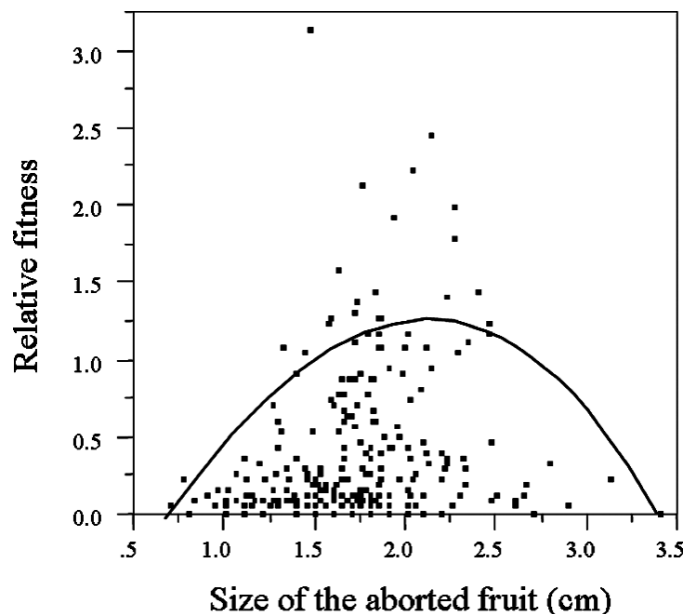


Fig. 2. Polynomial regression of relative fitness values and propagule size (measured longitudinally from tip to point of abscission from cladode) for *Opuntia microdasys* in the Chihuahuan Desert.

fitness of  $4.09 \pm 0.18$  plantlets (mean  $\pm$  SE). Regression analysis indicated that natural selection did act on propagule size ( $F_{2,258} = 10.50$ ,  $P < 0.0001$ ), specifically, a stabilizing selection, as shown by the standardized selection coefficients obtained in the analysis (plantlet size =  $2.984573 \pm 0.834059$  cm,  $P = 0.0004$ ; plantlet size =  $-0.701748 \pm 0.225578$  cm<sup>2</sup>,  $P = 0.0021$ ; Fig. 2).

## DISCUSSION

Understanding the mechanisms and environmental conditions that favor the establishment of different types of newborns is crucial in plant ecology. This is especially so, because 75% of angiosperms have the ability to reproduce sexually and clonally (Tiffney and Niklas, 1985). We found that the ability of facultative species to switch from one strategy to another allows species to survive in a wide range of habitats (Eckert, 2002); arid environments are one of the most important areas to explore. In arid environments the successful establishment of sexual offspring for Cactaceae as well as for other succulent species is restricted by biotic factors such as predation (e.g., granivory, herbivory, and the absence of nurse plants) and the inability of seedlings to withstand the harsh abiotic conditions (e.g., light, temperature, water availability; Nobel, 1988; Mandujano et al., 1998). Vegetative structures, on the other hand, permit the growth of selected genotypes in an environment adequate for their survival (Anthony, 1954; Cook, 1985), are more resistant because they are generally more developed (e.g., developed root system, larger leaf surface; Miao et al., 1998), and can even differ in metabolic pathways (C<sub>3</sub> in seedlings, crassulacean acid metabolism [CAM] in adults; Altesor et al., 1992). These characteristics provide more resources, protective structures, changes in predator preference, and adequate metabolism (e.g., spines, secondary metabolites, CAM), which allow vegetative structures to circumvent the critical seedling stage (Holthe and Szarek, 1985; Arizaga, 1998; Mandujano et al., 1998).

Like other succulent plants and some species of the same subfamily (*Cylindropuntia imbricata* and *C. bigelovii*), *O. microdasys* presents clonal propagation through two mechanisms: pseudovivipary and cladodes (i.e., stems; Johnson, 1918; Anthony, 1954; Arizaga, 1998; Gentry, 1998; Mandujano et al., 1998). Although the clonal establishment of new plants has been reported for other species by a number of authors (Anthony, 1954; Mandujano et al., 1998, 2001; Arizaga and Ezcurra, 2002; Bobich, 2005), little has been done in terms of field research to evaluate the real demographic significance of the phenomenon. Clonality assures offspring establishment, a trait especially important to colonize the bare areas common in arid environments and other extreme habitats where the conditions for sexual reproduction are not always appropriate and organisms depend on stored resources for survival (Lee and Harmer, 1980; Nobel, 1988; Elmqvist and Cox, 1996; Mandujano et al., 2001; Pierce et al., 2003). Given the low probability of sexual establishment (through seeds) for *O. microdasys* and for other clonal species (Wang et al., 2004), pseudovivipary is a benefit that enhances the permanence of species in extreme habitats (Youngner, 1960; Lee and Harmer, 1980; Arizaga and Ezcurra, 1995; Elmqvist and Cox, 1996; Pierce et al., 2003; Wang and Cronk, 2003). In particular, pseudovivipary in *O. microdasys* is favored by three factors in all three studied habitats: (1) high fruit abortion that increases the number of fruits on the ground that may develop a root system and become established, (2) parental traits that increase the probability of surviving fruits, and (3) the parent plants generate adequate microenvironmental conditions for the establishment of plantlets.

The prevalence of fruit abortion in plants has been thought to be a consequence of excess flower production followed by abortion of fruits, which guarantees adequate resources to support viable seeds (Stephenson, 1981; Lee, 1988). Excess of flower production has been said to (1) increase male function (Sutherland and Delph, 1984; Bertin, 1988), (2) attract more pollinators (Podolsky, 1992), (3) increase fruit set during occasional but unpredictable years of resource or pollinator abundance (Lloyd, 1980), (4) provide reproductive assurance (whereby sufficient ovaries are available for maturation after losses from biotic and abiotic stresses; Ehrlén, 1991), and (5) provide variation in fruit quality (that can be selectively acted upon to maximize fitness; Burd, 1998). We can add that the excess of flowers in *O. microdasys* and possibly in other species that are able to produce plantlets is also a trait that can be favored by selection to produce clonal offspring. Even though *O. microdasys* produces a large number of flowers during its reproductive season at the beginning of May, many of these fruits are aborted (aborted fruits are the products of flowers that were pollinated). Fruit abortion in *O. microdasys* seems to result of two different processes: a high incidence of parasitism and the consequences of self-incompatibility (H. Piña, Instituto de Ecología A. C., UNAM, personal communication). Even though the causes behind abortion are still being investigated, the generation of plantlets is clearly the main contribution to vegetative propagation for this species in the MBR by at least one order of magnitude over sexual reproduction and other forms of clonal propagation, even for other species of *Opuntia* (Mandujano et al., 1998, 2001). The success of vegetative reproduction is constrained by the amount of resources available to develop a root system and is therefore a reflection of the amount of stored resources, which produce a higher probability of survival and establish-

ment (Hicks and Mauchamp, 1999) and are especially important when vegetative structures are subject to high soil and wind temperatures. Survival, size, and development of fallen fruits were strongly influenced by the parental plant, possibly suggesting a maternal effect (Donohue, 1998) that increases the success of plantlet establishment. For *O. microdasys*, the size of the parent plant affects the size of fruits, increasing the probability of recruitment with higher resources provided to fruits (Mandujano et al., 1998, 2001; Hicks and Mauchamp, 1999), a similar effect found in other species for germination percentage, seed mass, seedling survival, and plant growth, fruit characteristics, and seed/fruit dispersal (Kahn et al., 1994). The environmental characteristics generated by the parent plants (Shreve, 1911; Mandujano et al., 1998) and habitat (Van Zandt, et al., 2003) also favor vegetative propagation. For seedlings in Cactaceae, the presence of nurse plants increases and in some cases determines the establishment of individuals (Steenberg and Lowe, 1969; Nobel, 1988; Valiente-Banuet and Ezcurra 1991; Mandujano et al., 2002). In other species of *Opuntia*, intermediate shade (approximately 40% of PAR extinction) doubled the survivorship of vegetative propagules (i.e., cladodes; Mandujano et al., 1998). For *O. microdasys*, the drastic reduction in solar radiation and temperature generated by the parent plant creates a favorable microenvironment under which the probability of establishment increases. Even though we found no effect of the habitat on the survival and establishment of plantlets in the common garden, similar to what has been found in other clonal species (Eckert, 2002; Clark-Tapia et al., 2005), characteristics of the habitats affected the rates at which sexual recruitment and vegetative propagation occur. The HPH habitat favors sexual recruitment, suggesting that the fruits that are produced by plants at HPH generate seeds that can establish successfully and that the mechanisms that lead to fruit abortion are less influential (e.g., more resources, diminished self-pollination) than in the other two habitats. On the contrary, both the BH and IDH habitats produce more fruits and abortion is higher, leading to an increased probability of establishment through pseudovivipary. Even though these two habitats have higher fruit set, which could potentially lead to higher seed availability for sexual recruitment, environmental conditions needed for successful seedling establishment are not found. The environmental causes of seedling establishment and vegetative propagation of *O. microdasys* in all habitats have not been explored; however, environmental effects have been shown to affect the type of recruitment (Callaghan et al., 1992; Arizaga and Ezcurra, 1995; Mandujano et al., 1998; Bobich, 2005).

The timing of fruit abortion seems to be crucial for establishment. Small fruits tend to have lower probabilities of establishment, and it seems as though the first strategy followed by *O. microdasys* is the abortion of floral buds that did not complete anthesis. The production and final abortion of floral buds do not contribute to sexual or vegetative propagation. The second strategy followed by *O. microdasys* is pseudovivipary that can be considered a means of reproductive insurance (Wang and Cronk, 2003; Wang et al., 2004).

For *O. microdasys*, abortion soon after the beginning of development has become a strategy to avoid wasting resources (formation of seeds, fruit growth, sugar or reserve substances), insurance against the loss to predation and quite possibly an effect of the mating system (self-incompatibility and/or inbreeding depression). Even though the cost of flower

production in the Cactaceae has not been explored, resources that have been invested in their production can be channeled to pseudovivipary when conditions are not adequate for seed development (environmental stochasticity, which leads to variable resource availability over time as well as pollinator limitations). These “empty fruits” are providing vegetative recruitment for the genotype and can be considered an insurance against reproductive failure as has been suggested for other species (Arizaga and Ezcurra, 1995). However, this form of recruitment may lead to other ecological limitations (Honnay and Bossuyt, 2005). The establishment of plantlets in close proximity to the parent plant due to the lack of adequate dispersal mechanisms (limited to gravity and superficial water movements) and the fact that the species is self-incompatible may lead to a positive feedback in abortion by increasing geitonogamous pollination and therefore setting a spatial constraint to the mating system (Charpentier, 2002). The high abortion of fruits that occurs postpollination could be an indication of the problems that *O. microdasys* is facing through sexual reproduction. In the short term, pseudovivipary is a mechanism that is ensuring the survival of established genotypes and promoting colonization. However, this type of recruitment can lead to decreasing sexual reproduction over longer time periods, with a positive feedback for pseudovivipary that can lead to other ecological problems in the long term, such as diminished fitness and loss of genetic variability.

#### LITERATURE CITED

- ALTESOR, A. E., E. EZCURRA, AND C. SILVA. 1992. Changes in the photosynthetic metabolism during early ontogeny of four cactus species. *Acta Oecologica* 13: 777–785.
- ANTHONY, M. 1954. Ecology of the Opuntiae in the big bend region of Texas. *Ecology* 35: 334–347.
- ARIZAGA, S. 1998. Biología reproductiva de *Agave macroacantha* Zucc. en Tehuacán, Puebla. Ph.D. thesis, Universidad Nacional Autónoma de México, México City, Mexico.
- ARIZAGA, S., AND E. EZCURRA. 1995. Insurance against reproductive failure in a semelparous plant: bulbil formation in *Agave macroacantha* flowering stalks. *Oecologia* 101: 329–334.
- ARIZAGA, S., AND E. EZCURRA. 2002. Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette. *American Journal of Botany* 89: 632–641.
- ARNOLD, S. J., AND M. J. WADE. 1984a. On the measurement of natural and sexual selection: theory. *Evolution* 38: 709–719.
- ARNOLD, S. J., AND M. J. WADE. 1984b. On the measurement of natural and sexual selection: applications. *Evolution* 38: 720–734.
- AUGE, H., AND R. BRANDL. 1997. Seedling recruitment in the invasive clonal shrub, *Mahonia aquifolium* Pursh (Nutt.). *Oecologia* 110: 205–211.
- BOBICH, E. C. 2005. Vegetative reproduction, population structure, and morphology of *Cylindropuntia fulgida* var. *mamillata* in a desert grassland. *International Journal of Plant Sciences* 166: 97–104.
- BRAVO-HOLLIS, H. 1978. Las cactáceas de México, vol. 1. Universidad Nacional Autónoma de México, Mexico City, Mexico.
- BERTIN, R. I. 1988. Paternity in plants. In J. L. Lovett-Doust and L. Lovett-Doust [eds.], *Plant reproductive ecology: patterns and strategies*, 30–59. Oxford University Press, Oxford, UK.
- BURD, M. 1998. “Excess” flower production and selective fruit abortion: a model of potential benefits. *Ecology* 79: 2123–2132.
- BUXBAUM, F. 1950. Morphology of cacti. Section III. Morphology of fruits and seeds. Abbey Garden Press, Pasadena, California, USA.
- CALLAGHAN, T. V., B. A. CARLSSON, I. S. JÓNSDÓTTIR, B. M. SVENSSON, AND S. JONASSON. 1992. Clonal plants and environmental change: introduction to the proceedings and summary. *Oikos* 63: 341–347.
- CHARPENTIER, A. 2002. Consequences of clonal growth for plant mating. *Evolutionary Ecology* 15: 521–530.
- CLARK-TAPIA, R., C. ALFONSO-CORRADO, L. E. EGUIARTE, AND F. MOLINA-FREANER. 2005. Clonal diversity and distribution in *Stenocereus eruca* (Cactaceae), a narrow endemic cactus of the Sonoran Desert. *American Journal of Botany* 92: 272–278.
- COOK, R. E. 1985. Growth and development in clonal plant populations. In J. B. C. Jackson, L. W. Buss, and R. E. Cook [eds.], *Population biology and evolution of clonal organisms*, 259–296. Yale University Press, New Haven, Connecticut, USA.
- CORNET, A. 1985. Las Cactáceas de la Reserva de la Biosfera de Mapimí. Instituto de Ecología A.C., Mexico City, Mexico.
- CORNET, A. 1988. Principales características climáticas. In C. Montaña [ed.], *Estudio integrado de los recursos vegetación, suelo y agua en la Reserva de la Biosfera de Mapimí. I. Ambiente natural y humano*, 45–76. Instituto de Ecología A.C., Xalapa Veracruz, Mexico.
- COTA-SÁNCHEZ, J. H. 2004. Vivipary in the Cactaceae: its taxonomic occurrence and biological significance. *Flora* 199: 481–490.
- DIGGLE, P. K., M. A. MEIXNER, A. B. CARROLL, AND C. F. ASCHWANDEN. 2002. Barriers to sexual reproduction in *Polygonum viviparum*: a comparative development analysis of *P. viviparum* and *P. bistortoides*. *Annals of Botany* 89: 145–156.
- DONOHUE, K. 1998. Maternal determinants of seed dispersal in *Cakile edentula*: fruit plant and site traits. *Ecology* 79: 2771–2788.
- ECKERT, C. G. 2002. The loss of sex in clonal plants. *Evolutionary Ecology* 15: 501–520.
- EHRLEN, J. 1991. Why do plants produce surplus flowers? A reserve-ovary model. *American Naturalist* 138: 918–933.
- ELMQVIST, T., AND P. A. COX. 1996. The evolution of vivipary in flowering plants. *Oikos* 77: 3–9.
- ERIKSSON, O. 1989. Seedling dynamics and life histories in clonal plants. *Oikos* 55: 231–238.
- FREGO, K. A., AND R. J. STAINFORTH. 1985. Factors determining the distribution of *Opuntia fragilis* in the boreal forest of southeastern Manitoba. *Canadian Journal of Botany* 63: 2377–2382.
- GENTRY, H. S. 1998. Agaves of continental North America. University of Arizona Press, Tucson, Arizona, USA.
- GIBSON, A. C., AND P. S. NOBEL. 1986. The cactus primer. Harvard University Press, Cambridge, Massachusetts, USA.
- HANDEL, S. N. 1985. The intrusion of clonal growth patterns on plant breeding systems. *American Naturalist* 125: 367–384.
- HARPER, J. L. 1981. Modules, branches, and the capture of resources. In J. B. C. Jackson, L. W. Buss, and R. E. Cook [eds.], *Population biology and evolution of clonal organisms*, 1–34. Yale University Press, New Haven, Connecticut, USA.
- HERBEN, T., T. HARA, C. MARSHALL, AND L. SOUKOPOVÁ. 1994. Plant clonality: biology and diversity. *Folia Geobotanica Phytotax (Praha)* 29: 113–122.
- HICKS, D., AND A. MAUCHAMP. 1999. Population structure and growth patterns of *Opuntia echios* var. *gigantea* along an elevation gradient in the Galápagos Islands. *Biotropica* 32: 235–243.
- HOLTHE, P. A., AND S. R. SZAREK. 1985. Physiological potential for survival of propagules of crassulacean acid metabolism species. *Plant Physiology* 79: 219–224.
- HONNAY, O., AND B. BOSSUYT. 2005. Prolonged clonal growth, escape route or route to extinction. *Oikos* 108: 427–432.
- JIMÉNEZ-SIERRA, C., AND C. JIMÉNEZ-GONZÁLEZ. 2002. Heterogeneidad ambiental y distribución de cactáceas en una zona semiárida. *Cactáceas y Suculentas Mexicanas* 48: 4–17.
- JOHNSON, D. S. 1918. The fruit of *Opuntia fulgida*. A study of perennation and proliferation in the fruits of certain Cactaceae. Carnegie Institution of Washington, Washington, D.C., USA.
- KAHN, T. L., C. J. ADAMS, AND M. L. ARPAIA. 1994. Paternal and maternal effects on fruit and seed characteristics in cherimoya (*Annona cherimola* Mill.). *Scientia Horticulturae* 59: 11–25.
- LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- LEE, J. A., AND R. HARMER. 1980. Vivipary: a reproductive strategy in response to environmental stress? *Oikos* 35: 254–265.
- LEE, T. D. 1988. Patterns of fruit and seeds production. In J. Lovett-Doust

- and L. Lovett-Doust [eds.], Plant reproductive ecology: patterns and strategies, 179–202. Oxford University Press, Oxford, UK.
- LOYD, D. G. 1980. Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive season. *New Phytologist* 86: 69–79.
- LOVETT-DOUST, J. 1989. Plant reproductive strategies and resource allocation. *Trends in Ecology and Evolution* 4: 230–234.
- MANDUJANO, M. C., A. FLORES-MARTÍNEZ, J. GOLUBOV, AND E. EZCURRA. 2002. Spatial distribution of three globose cacti in relation to different nurse-plant canopies and bare areas. *Southwestern Naturalist* 47: 162–168.
- MANDUJANO, M. C., J. GOLUBOV, AND C. MONTAÑA. 1997. Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the Chihuahuan Desert. *Journal of Arid Environments* 36: 259–266.
- MANDUJANO, M. C., C. MONTAÑA, M. FRANCO, J. GOLUBOV, AND A. FLORES-MARTÍNEZ. 2001. Integration of demographic annual variability in a clonal desert cactus. *Ecology* 82: 344–359.
- MANDUJANO, M. C., C. MONTAÑA, I. MÉNDEZ, AND J. GOLUBOV. 1998. The relative contributions of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. *Journal of Ecology* 86: 911–921.
- MAUSETH, J. 1984. Introduction to cactus anatomy. Part 11. Flower structure. *Cactus and Succulent Journal (USA)* 56: 250–255.
- MIAO, S. L., L. KONG, B. LORENZEN, AND R. R. JOHNSON. 1998. Versatile modes of propagation in *Cladium jamaicense* in the Florida Everglades. *Annals of Botany* 82: 285–290.
- MONTAÑA, C. 1988. Estudio integrado de los recursos vegetación, suelo y agua en la Reserva de la Biosfera de Mapimí. Instituto de Ecología, A.C. Mexico City, Mexico.
- NOBEL, P. S. 1988. Environmental biology of agaves and cacti. Cambridge University Press, Oxford, UK.
- PIERCE, S., C. M. STIRLING, AND R. BAXTER. 2003. Pseudoviviparous reproduction of *Poa alpina* var. *alpina* L. (Poaceae) during long-term exposure to elevated atmospheric CO<sub>2</sub>. *Annals of Botany* 91: 613–622.
- PIMIENTA-BARRIOS, E., AND R. F. DEL CASTILLO. 2002. Reproductive biology. In P. S. Nobel [ed.], Cacti: biology and uses, 77–90. University of California Press, Berkeley, California, USA.
- PODOLSKY, R. D. 1992. Strange floral attractors: pollinator attraction and the evolution of sexual systems. *Science* 258: 791–793.
- REUSCH, T. H. B., W. T. STAM, AND J. L. OLSEN. 1998. Size estimated age of genets in eelgrass, *Zostera marina*, assessed with microsatellite markers. *Marine Biology* 133: 519–525.
- SAS INSTITUTE. 1995. JMP statistics and graphics guide. SAS Institute, Cary, North Carolina, USA.
- SHREVE, F. 1911. The influence of low temperatures on the distribution of the giant cactus. *Plant World* 14: 136–146.
- STEENBERG, W. H., AND C. H. LOWE. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at the Saguaro National Monument, Arizona. *Ecology* 50: 825–834.
- STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12: 253–279.
- SUTHERLAND, S., AND L. F. DELPH. 1984. On the importance of male fitness in plants. *Ecology* 65: 1093–1104.
- TIFFNEY, B. H., AND K. J. NIKLAS. 1985. Clonal growth in land plants: a paleobotanical perspective. In J. B. C. Jackson, L. W. Buss, and R. E. Cook [eds.], Population biology and evolution of clonal organisms, 35–66. Yale University Press, New Haven, Connecticut, USA.
- TRAME, M. A., A. J. CODDINGTON, AND K. N. PAIGE. 1995. Field and genetic studies testing optimal outcrossing in *Agave schottii*. *Oecologia* 104: 93–100.
- VALIENTE-BANUET, A., AND E. EZCURRA. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and nurse plant *Mimosa luisana* in the Tehuacan valley, Mexico. *Journal of Ecology* 79: 961–971.
- VAN ZANDT, P. A., M. A. TOBLER, E. H. HASENSTEIN, AND S. MOPPER. 2003. Positive and negative consequences of salinity stress for the growth and reproduction of the clonal plant, *Iris hexagona*. *Journal of Ecology* 91: 837–846.
- WANG, C., AND Q. C. B. CRONK. 2003. Meristem fate and bulbil formation in *Trianostrichum* (Gesneriaceae). *American Journal of Botany* 90: 1696–1707.
- WANG, C., M. MOLLER, AND Q. CRONK. 2004. Aspects of sexual failure in the reproductive processes of a rare bulbiferous plant *Titanostrichum oldhami* (Gesneriaceae), in subtropical Asia. *Sexual Plant Reproduction* 17: 23–31.
- YOUNGNER, V. B. 1960. Environmental control of initiation of the inflorescence, reproductive structures, and proliferations in *Poa bulbosa*. *American Journal of Botany* 47: 753–757.
- ZAR, J. H. 1996. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey, USA.