

Effect of reproductive modes and environmental heterogeneity in the population dynamics of a geographically widespread clonal desert cactus

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Received: 7 July 2006 / Accepted: 16 November 2006 / Published online: 2 February 2007
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Abstract The dynamics of plant populations in arid environments are largely affected by the unpredictable environmental conditions and are fine-tuned by biotic factors, such as modes of recruitment. A single species must cope with both spatial and temporal heterogeneity that trigger pulses of sexual and clonal establishment throughout its distributional range. We studied two populations of the clonal, purple prickly pear cactus, *Opuntia macrocentra*, in order to contrast the factors responsible for the population dynamics of a common, widely distributed species. The study sites were located in protected areas that correspond to extreme latitudinal locations for this species within the Chihuahuan Desert. We studied both populations for four consecutive years and determined the demographic consequences of environmental variability and the mode of reproduction using matrix population models, life table response experiments (LTREs), and loop and perturbation analyses. Although both populations seemed

fairly stable (population growth rate, $\lambda \sim 1$), different demographic parameters and different life cycle routes were responsible for this stability in each population. In the southernmost population (MBR) LTRE and loop and elasticity analyses showed that stasis is the demographic process with the highest contributions to λ , followed by sexual reproduction, and clonal propagation contributed the least. The northern population (CR) had both higher elasticities and larger contributions of stasis, followed by clonal propagation and sexual recruitment. Loop analysis also showed that individuals in CR have more paths to complete a life cycle than those in MBR. As a consequence, each population differed in life history traits (e.g., size class structure, size at sexual maturity, and reproductive value). Numerical perturbation analyses showed a small effect of the seed bank on the λ of both populations, while the transition from seeds to seedlings had an important effect mainly in the northern population. Clonal propagation (higher survival and higher contributions to vital rates) seems to be more important for maintaining populations over long time periods than sexual reproduction.

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Keywords Cactaceae · Clonal growth · Demography · Life history traits · Loop analysis · LTRE analysis · Matrix models · *Opuntia*

Introduction

The relative importance of sexual versus clonal propagation differs among clonal species and populations, from those where both processes occur repeatedly, to those where one or the other mode is uncommon or absent (Eriksson 1989, 1994; Eriksson and Bremer

1993; Mandujano et al. 2001; Eckert 2002). Some studies have quantitatively compared the magnitude of each reproductive mode within or among clonal plants and identified the ecological factors underlying the demographic consequences of each type of reproduction (Mandujano et al. 1998, 2001; Eckert 2002; Liston et al. 2003; Clark-Tapia et al. 2005).

Opuntia macrocentra Engelm. (purple prickly pear, Cactaceae) is a species that can produce both sexual and clonal offspring. It is one of the few cactus species that displays a wide geographical distribution across the Chihuahuan Desert, the largest warm desert in America (Bravo-Hollis 1978; MacMahon 1988). Because of its wide elevation and latitudinal span, this desert comprises a variety of vegetation types (Bravo-Hollis 1978; MacMahon 1988). Despite the general characteristics, which allow its classification as a distinct physiognomic province (i.e., geology, climate, and the presence of dominant species such as *Agave lechugilla* and *Flourensia cernua*; MacMahon 1988), differences at regional and local scales affect the widely distributed plant and animal species. Some of these differences are the limitations imposed by low and unpredictable precipitation and high temperature fluctuations, which have fostered the suggestion that desert populations are primarily limited by abiotic factors (Noy-Meir 1973). However, interactions among species (for example, nurse–protégé relationships and herbivory in the Cactaceae) can also be important determinants of population structure (Brown et al. 1972; Briones et al. 1996; Flores-Martínez et al. 1994; Burger and Louda 1995; Mandujano et al. 1998).

Both biotic (e.g., nurse–plant interaction and herbivores) and abiotic factors (e.g., precipitation and temperature, including variation along elevation gradients) contribute to environmental heterogeneity in arid environments (Zavala-Hurtado 1982). Both biotic and abiotic factors can differentially affect the vital rates (survival and fecundity) of recruits (sexual and clonal), which, in turn, determine population growth rates (Noy-Meir 1973; Huenneke and Sharitz 1990; Mandujano et al. 2001). Previous studies in cacti have explored the relative contributions of sexual and clonal propagation to population dynamics using elasticity analysis, and they all suggest that population growth rates are less sensitive to sexual recruitment than they are to clonal propagation (Mandujano et al. 2001; Rosas Barrera and Mandujano 2002; Godínez-Alvarez et al. 2003). Rosas Barrera and Mandujano (2002), using elasticity analysis, have shown in cacti that the influence of clonality in determining life history strategy places these species in areas of the Growth

(G)–Longevity (L)–Fecundity (F) triangular space (Silvertown et al. 1993; Caswell 2001), where $G > L > F$.

Our study aims to compare the effect of reproductive mode and environmental heterogeneity on the population dynamics of the clonal purple prickly pear (*O. macrocentra*) in two sites located at the extremes of its distribution in the Chihuahuan Desert, where it is the dominant succulent species (Bravo-Hollis 1978; Guzmán et al. 2003). Using matrix population models, we estimated the rate of population increase and life history traits (Lefkovich 1965; Caswell 2001). We assessed the sensitivity of λ to each demographic process (i.e., growth, stasis, fecundity, and clonal propagation) by means of elasticity analysis. Loop and numerical perturbation analyses were also performed to explore the effect of reproductive mode on the population growth rate (Caswell 1996). Finally, we compared the influence of time (years) and space (site) on the finite rate of population increase using life table response experiments (LTREs) and loglinear analysis to compare the counts of observed transitions between years and sites (Caswell 1996, 2001).

Methods

Study species and populations

The purple prickly pear, *O. 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 fruit is oblong, 3–6 cm long, reddish to purplish-red when mature. The distribution of *O. macrocentra* encompasses southern AZ, NM, and TX in the USA and Chihuahua, Coahuila, Durango, Nuevo León, and the northern parts of Baja California and Sonora in Mexico, within the Chihuahuan and Sonoran deserts (Benson 1982; Bravo-Hollis 1978; Pinkava 1997). Although the species can dominate the succulent 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 *Opuntia* (i.e., 100 ind/ha, M.C. Mandujano, unpublished data). The life form of *O. macrocentra* resembles that of other trunk-less prickly pears, such as *O. rastrera* and *O. microdasys*.

The study was conducted in two populations of *O. macrocentra* located near the extremes of its latitudinal distribution within the Chihuahuan Desert. The northern population was located on the eastern bajada slope below Mount Summerford in the New Mexico

State University Chihuahuan Desert Rangeland Research Center (formerly known as College Ranch, CR) NM, USA (32°25′–32°50′N and 106°30′–106°55′W, at 1,500 masl). Mean annual rainfall is 273 mm, with 52% occurring in the summer, between June and October; the mean temperature is 28°C (data from the Jornada Basin Long-Term Ecological Research weather station). The southern population was located at Ejido La Flor, close to Cerro Coronas in the Mapimi biosphere reserve (MBR), Durango, Mexico (26°29′–26°52′N and 103°32′–103°58′W, at 1,100 masl; Montaña and Breimer 1988). Rainfall averages 227 mm per year (80.2% between June and October), and the mean temperature is 20.8°C (Montaña 1990). Over an 11-year period (1989–2000), the rainfall did not differ between sites ($t=1.4897$, $P=0.1505$), but the variation was greater at MBR (MBR CV=33.35% and CR CV=27.22%). The study sites at both MBR and CR were established on bajadas (slope 2–4%) within *Larrea–Opuntia*-dominated scrublands, where the dominant cactus species was *O. macrocentra*. The study sites share dominant plant life forms, although species composition differed between sites (see Allred 1988; Montaña 1990).

Six and five 20×50-m permanent plots were established at MBR and CR, respectively. *O. macrocentra* individuals were first tagged in spring 1997, and both populations were surveyed annually every summer until 2000. The total number of cladodes and the number of flowers and fruits were counted for each individual. In addition, seedling establishment, plant mortality, and vegetative propagation by cladode establishment were recorded. Recruitment via clonal propagation was measured by counting individual detached ramets near (<5 m distance) the presumed parent plant. In cases where no single parent plant could be identified or assigned with certainty, clonal propagation was attributed equally to all nearby plants larger than two cladodes. Plant density was estimated in each population using an area method and compared between sites and among size classes. A sample of 100 randomly selected fruits from each population was collected and the seeds were counted to calculate the mean number of seeds per fruit. In order to compare potential seed germination, we conducted an experiment with seeds from both populations, in which ten Petri dishes per population with 1% bacteriological agar containing 50 seeds each were followed for 6 months. In addition, to describe the degree of disturbance in these habitats, we used the methodology described by Martorell and Peters (2005) that combines human activities, livestock raising, and land degradation into a relative index that varies from 0 to 100 (0 being less disturbed). To quantify disturbance,

five sets of two orthogonal 50-m transects were made at each site next to the studied populations of *O. macrocentra*. In addition to the disturbance index, we assessed plant cover by species establishing five 50×1-m transects at each site.

Population analyses

Annual stage size transition matrices for the MBR and CR populations were constructed. Seeds were the first stage class and the remaining nine size classes were defined by size limits (number of cladodes) as follows: 1, 2–5, 6–10, 11–15, 16–25, 26–35, 36–45, 46–65, and ≥66 (see Mandujano et al. 2001). We used these class limits as *O. macrocentra* shows a similar life form to that of *O. rastrera* and several analyses demonstrate that these categories adequately describe fecundity, growth, and survival rates in this and other similar prickly pears (M.C. Mandujano, unpublished data). The demographic parameters for each population were calculated using both annual and mean matrix population models, which assume that the growth of the population over one time interval is: $\mathbf{n}_{t+1}=\mathbf{A}\mathbf{n}_t$ (Caswell 2001). The mean matrix $\mathbf{A}=\{a_{ij}\}$ corresponded to the average from the three annual transition matrices. We assumed a 10% probability of annual survival and permanence in the seed bank for the matrix projections ($a_{11}=0.1$; see Montiel and Montaña 2000). The matrix entries corresponded to a_{1j} sexual fecundity, $a_{i=j}$ stasis, $a_{i<j}$ regression and clonal propagation, and $a_{i>j}$ growth (Mandujano et al. 2001).

The program MATLAB-PC (The MathWorks, Natick, MA) was used for the matrix analyses. We calculated the finite rate of population increase (λ), stable size structure (\mathbf{w}), and reproductive value (\mathbf{v}) for each population and year (Caswell 2001). Confidence intervals for λ using the percentile method (Efron 1979; Caswell 2001) were calculated for all annual matrices after 1,000 bootstraps for both CR and MBR populations, and the values of fecundity were compared between populations with generalized linear models (GLIM, Royal Statistical Society 1993; Crawley 1993). We performed elasticity and loop analyses to determine the sensitivity of λ to different demographic processes (Caswell 2001; de Kroon et al. 1986), based on the mean matrix from each population (average of the three transition matrices constructed for each site).

In order to determine the effect of population and time (years) on the transition frequencies per size class as well as on mortality, we fitted a loglinear model for multiple treatments (Bishop et al. 1975; Caswell 2001; Golubov et al. 2004). The data set was organized as a four-way state (S , class at time t) × fate

(F , class at time $t+1$) \times time (T , year) \times population (P , MBR vs. CR) contingency table and we tested the null hypothesis (see Caswell 2001): STP , SF : $\log m_{ijkl} = u + u_{P(i)} + u_{F(j)} + u_{T(k)} + u_{S(l)} + u_{SF(ij)} + u_{ST(ik)} + u_{SP(it)} + u_{TP(kl)} + u_{STP(ikl)}$. Models were then fitted to determine the effect of year, population, and the population \times year interaction term (Caswell 2001).

Loop analysis

In order to identify the importance of clonal propagation and sexual reproduction in each population, we used loop analysis (van Groenendael et al. 1994). For each population, we first calculated the number of loops using $L=b-n+c$, where b is the number of arcs in the life cycle graph (transitions), n is the number of nodes (size classes), and c is the number of components (always 1 for demographic life cycles; Wardle 1998; Caswell 2001). Loops (paths followed by individuals in the population) were identified for each population from the life cycle graph. The characteristic elasticity of each loop was then assigned as the elasticity of the unique arc in the loop and multiplied by the number of arcs in the loop. Because loop elasticities are additive and sum to 100% (van Groenendael et al. 1994), we added the loops that involved sexual reproduction and those that involved clonal propagation for each population to express the importance of each type of reproduction.

Life table response experiments

This approach was used to estimate the impact of the year and site and to decompose each factor and its effect on λ into contributions due to the influence of size- or stage-specific survival and reproductive rates. Life table response experiments (LTREs) have n treatments, yielding population projection matrices $\mathbf{A}^{(m)}$ and rates of increase $\lambda^{(m)}$ for $m=1, \dots, n$. The main effects of each factor and the interactions among factors in two-way cross-classified treatments can be decomposed. $\mathbf{A}^{(m)} = \mathbf{A}^{(ij)}$ was the transition matrix resulting from the i th level of time (years, with three levels 1997–1998, 1998–1999 and 1999–2000) and the j th level of site (CR or MBR), and $\lambda^{(ij)}$ was its eigenvalue. $\mathbf{A}^{(r)}$ was the reference population projection matrix (mean matrix) with corresponding rate of increase $\lambda^{(r)}$. The effect of a treatment m on λ was then decomposed into contributions from each of the matrix entries (Caswell 1996):

$$\lambda^{(m)} - \lambda^{(r)} \approx \sum \left(a_{ij}^{(m)} - a_{ij}^{(r)} \right) \frac{\partial \lambda}{\partial a_{ij}} \Big|_{\mathbf{A}^\dagger}$$

where $\mathbf{A}^\dagger = (\mathbf{A}^{(m)} + \mathbf{A}^{(r)})/2$. Each term in the summation portion of the equation defined the effect of treatment m on λ . The contributions depended on the effect of the treatment on the matrix entry and on the sensitivity of λ to that effect. Following Caswell (1989, 2001) for notation, the model for the experiment was:

$$\lambda^{(ij)} = \lambda^{(\cdot)} + \alpha^{(i)} + \beta^{(j)} + \alpha\beta^{(ij)}$$

where $\lambda^{(\cdot)}$ was the overall mean finite rate of population increase, $\alpha^{(i)}$ and $\beta^{(j)}$ the main effects, and $\alpha\beta^{(ij)}$ the interaction effect. Estimates of the treatment effects were given by:

$$\bar{\alpha}^{(i)} = \lambda^{(i)} + \lambda^{(\cdot)},$$

$$\bar{\beta}^{(j)} = \lambda^{(j)} + \lambda^{(\cdot)},$$

$$\bar{\alpha}\bar{\beta}^{(ij)} = \lambda^{(ij)} - \bar{\alpha}^{(i)} - \bar{\beta}^{(j)} - \lambda^{(\cdot)}.$$

These effects were decomposed as follows:

$$\bar{\alpha}^{(i)} = \sum_{k,l} \left(a_{kl}^{(i)} - a_{kl}^{(\cdot)} \right) \frac{\partial \lambda}{\partial a_{kl}} \Big|_{\frac{(\mathbf{A}^{(i)} + \mathbf{A}^{(\cdot)})}{2}},$$

$$\bar{\beta}^{(j)} = \sum_{k,l} \left(a_{kl}^{(j)} - a_{kl}^{(\cdot)} \right) \frac{\partial \lambda}{\partial a_{kl}} \Big|_{\frac{(\mathbf{A}^{(j)} + \mathbf{A}^{(\cdot)})}{2}},$$

$$\bar{\alpha}\bar{\beta}^{(ij)} = \sum_{k,l} \left(a_{kl}^{(ij)} - a_{kl}^{(\cdot)} \right) \frac{\partial \lambda}{\partial a_{kl}} \Big|_{\frac{(\mathbf{A}^{(ij)} + \mathbf{A}^{(\cdot)})}{2}} - \bar{\alpha}^{(i)} - \bar{\beta}^{(j)}.$$

Each of these equations approximated an observed change in λ as a linear function of the changes in the entries of the matrix; the slope of the linear approximation was evaluated at the midpoint of the two matrices being compared (Caswell 1989, 2001). The sensitivities in the equation $\lambda^{(m)} - \lambda^{(r)} \approx \sum \left(a_{ij}^{(m)} - a_{ij}^{(r)} \right) \frac{\partial \lambda}{\partial a_{ij}} \Big|_{\mathbf{A}^\dagger}$ were evaluated at a midway matrix \mathbf{A}^\dagger between the two matrices $\mathbf{A}^{(m)}$ and $\mathbf{A}^{(r)}$ (Caswell 2001).

Numerical perturbation analysis

We modified three processes (i.e., seed survival in the seed bank, transition from seed to seedling, and clonal propagation) in the mean matrix for each population to investigate the effect of changes in these vital rates on λ (Horvitz and Schemske 1995; Horvitz et al. 1997). Stasis in the seed bank (i.e., matrix entry a_{11}) was gradually increased from 0 to 1 in 0.05 intervals for each time step. To analyze the transition from seed to

seedling (a_{21} cell), each seed produced was made to germinate until all possible seeds became established seedlings (i.e., 1/16,897 to 16,897/16,897 in CR and 1/8,866 to 8,866/8,866 in MBR). To assess clonal propagation, cell entries (contributions a_{19} – a_{89} , a_{18} – a_{78} , a_{17} – a_{76} , a_{16} – a_{56} , a_{15} – a_{45} , a_{14} – a_{34} , a_{13} – a_{23} , and a_{12}) were changed, adding a single clonal offspring in one matrix entry during each simulation and the value of λ was calculated. When appropriate, the assumption of an increase in clonal recruitment was compensated by biomass loss (retrogression) in those classes contributing to clonal growth (i.e., clonal growth in this species occurs when cladodes detach from the parent plant and eventually establish).

Results

Study populations

Disturbance indices differed between sites; MBR (mean for five sites=29.5, range 18.62–42.83) had a higher disturbance index than CR (mean for five sites=15.99, range 12.29–23.51). This disturbance could also be seen in plant cover and diversity. Plant cover at CR was nearly twice that of MBR (44.1% and 27.4%, respectively). The most striking difference between sites was species composition. The CR community included three grass species (*Scleropogon brevifolius*, *Muhlenbergia porteri*, and *Dasyochloa pulchella*), three subshrubs (*Parthenium incanum*, *Xanthocephalum microcephalum*, and *Zinnia acerosa*), four shrubs (*Prosopis glandulosa*, *Larrea tridentata*, *Flourensia cernua*, and *Lippia graveolens*), and three succulents (*O. macrocentra*, *Yucca baccata*, and *Echinocereus triglochidiatus*), while MBR had only five succulents (*O. macrocentra*, *O. leptocaulis*, *Echinocereus merckeri*, *Jatropha dioica*, and *Polianthes variegata*) and two woody shrubs (*L. tridentata* and *F. cernua*). We found no species of subshrubs or grasses at MBR.

Population dynamics

The population density was much lower at MBR (140 ind/ha) than at CR (596 ind/ha) ($F=17.52$, $P<0.001$), and the populations differed in size class distributions ($F=2.26$, $P=0.017$). The population at CR mainly consisted of small plants, whereas that at MBR was skewed towards larger plants (Fig. 1). We fitted the unsaturated model in order to test the assumption of conditional independence of the initial state on fate (STP , F : $\log m_{ijkl}=u+u_{P(i)}+u_{F(j)}+u_{T(k)}+u_{S(l)}+u_{ST(ik)}+$

$u_{SP(ij)}+u_{TP(kl)}+u_{STP(ikl)}$). The significant result ($\chi^2=1783$, $df=315$, $P<0.001$) suggested that fate was conditional on the initial state; however, when adding the state×fate interaction (STP , FS), the lack of significance ($\chi^2=119.32$, $df=243$, $P>0.05$) suggested that the fate of individuals depended only on their initial state, and was independent of both population and year. The finite rate of population increase (λ) calculated for the annual and mean matrices for both CR and MBR populations did not differ from unity (Table 1).

Fecundity (fruit and seed production) was, on average, significantly higher in CR than at the MBR population ($\chi^2=6,701$, $df=1$, $P<0.001$; Fig. 1), except for the largest size class ($P<0.05$, Fig. 1). However, there were no differences in germination percentages observed between seeds from MBR and CR ($\bar{x}=2.2\pm 0.004SE$ and $3\pm 0.005SE$, respectively; $\chi^2=0.95$, $df=1$, $P=0.33$). Sexual maturity occurred one size class earlier at CR than at MBR (Fig. 1). Reproductive value increased at four points in the life history at MBR (from size class 1 to 2 and from size classes 6 to 7, 7 to 8, and 8 to 9), while in CR, it increased continuously with plant size (Fig. 1), except in the last size class.

Recruitment and demographic processes

Sexual recruitment was observed every year at CR, but occurred only once at MBR (Table 2). The observed seedlings at CR were established under *Larrea tridentata* (4.5%), *Yucca elata* (9.1%), *Prosopis glandulosa* var. *glandulosa* (13.6%), and *Bouteloua eriopoda* (72.7%). At MBR, the only observed seedling was established under *Jatropha dioica*. Clonal propagation was four times more frequent in CR than at MBR (Table 2), and ramets were located close to putative parent plants at MBR, whereas in 30% of the cases at CR, we were unable to assign parenthood. This was because clonal recruits (ramets) established in bare areas without near neighboring conspecifics. The size of new ramets was, on average, close to three cladodes in both populations.

In general, elasticities by demographic processes were the highest for stasis (0.73417 for CR and 0.9994 for MBR), followed by growth. The elasticity of growth was much higher for the CR population than that of MBR (0.26573 and 0.00055, respectively). The elasticity of clonal propagation was higher than that of sexual reproduction at CR (0.00145 and 0.00010, respectively), while in the MBR population, the elasticity of clonal propagation was the lowest (0.00001), followed by sexual reproduction (0.00005). Therefore, contributions of clonal and sexual recruitment and growth for the CR population were relatively higher than that of MBR.

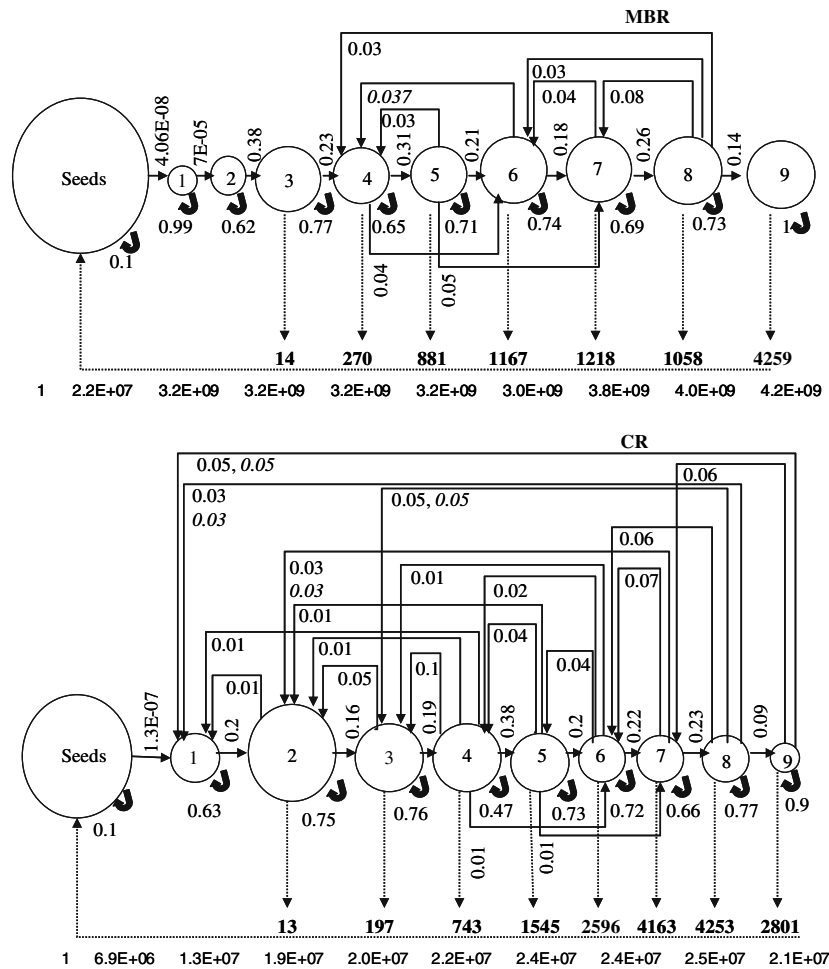


Fig. 1 Life cycle diagram of *Opuntia macrocentra* obtained from five and six 1,000-m² plots in a bajada of the southern (Mapimi biosphere reserve, MBR, $\lambda=1.0000$) and northern (College Ranch, CR, $\lambda=0.9982$) Chihuahuan Desert populations, respectively. The values shown correspond to the mean matrix (1997–1998, 1998–1999, and 1999–2000). The figure at the center of each circle indicates the size classes from 1 to 9, corresponding to: 1, 2–5, 6–10, 11–15, 16–25, 26–35, 36–45, 46–65, and ≥ 66 cladodes. The diameter of each circle approximately represents the number of individuals in each size class. The lower figure is the probability of stasis in the same size class. The average individual fecundity (number of seeds individual⁻¹ year⁻¹) is indicated by

the lower dotted arrows connecting reproductive classes to the seed stage (figures in bold). The upper arrows connecting nodes and the middle arrows between them are both the probabilities of retrogression to smaller size classes and the average individual contributions to vegetative propagation (clonal recruits individual⁻¹ year⁻¹, in italics). The shorter straight line arrows between nodes contain the probabilities of growth to the next class and the lower arrows represent probabilities of growth to classes beyond the next one in a 1-year interval. The reproductive value per size class for each population is shown below the life cycle graph

Table 1 Values of the finite rate of population increase (λ and 95% confidence intervals) for two populations of *Opuntia macrocentra* in the Chihuahuan Desert

Study period	Population		Precipitation (mm)	
	MBR	CR	MBR	CR
1997–1998	1.0002 (0.999–1.0005)	1.0000 (0.800–1.0501)	210.4	263.1
1998–1999	1.0000 (0.999–1.002)	1.0000 (0.9001–1.0332)	157	211.7
1999–2000	1.0000 (1.000–1.0330)	1.0000 (0.999–1.0145)	177.8	213.36
Mean	0.9997 (0.9993–1.000)	0.9789 (0.9327–1.096)	181.7	229.4

The mean value was obtained from 1,000 bootstrap estimates on the original data. Observed precipitation during the study period is reported for both locations

MBR=Mapimi biosphere reserve, CR=Jornada College Ranch

Table 2 Population traits of *Opuntia macrocentra* for College Ranch (CR) and Mapimi Biosphere Reserve (MBR) populations in the Chihuahuan Desert. Data from five and six 20x50-m plots, respectively

Trait	CR				MBR			
	1997	1998	1999	2000	1997	1998	1999	2000
No. adults/ha	628	608	592	592	138	138	137	138
No. new seedlings/ha	2	6	14	22	2	0	0	0
Probability of seedling survival	1	0.94	0.86	0.62	1	0	0	0
Clonal offspring/ha	0	6	0	2	0	0	0	2
Probability of clonal offspring survival	0	1	0	1	0	1	0	1
Fruits/ind	30	27	8	0.31	32	4	6	6
New cladodes/ind	8	2	5	2	11	0.2	11	8

Loop analysis

Based on the life cycle graph, we identified 25 loops for MBR and 37 loops for CR. For MBR, 17 loops corresponded to processes of survival (ten self-loops, five retrogressions, and two associated to rapid growth), seven to sexual reproduction, and one to clonal propagation. In CR, 26 loops were associated to survival (ten self-loops, 14 retrogression, and two associated to individuals that jumped size classes), eight to sexual reproduction, and three to clonal propagation. Loop analysis gave similar results to those of elasticity summed by demographic process. In both populations, loops that involved survival had the highest elasticities. In CR, the elasticity of loops associated to clonal propagation were more important than sexual reproduction (6.6% and 0.1%, respectively), whilst the elasticity of paths associated to sexual reproduction in MBR were higher than those of clonal propagation (0.046% and 0.003%, respectively).

Life table response experiment

The LTRE allowed us to identify which demographic process contributed most to the value of λ on a yearly basis compared to the corresponding $\lambda^{(r)}$ or reference rate of increase for each population. The contribution by size class differed across yearxsite combinations. In general, the contribution of size class 1 was not important relative to other size classes (Fig. 2a, b). Further analyses indicated that the growth rate was highly influenced by size classes 2 and 9 during 1997–1998 for CR, and all but size class 7 for MBR for the same time period. In addition, contributions in MBR were positive for all size classes except in size classes 7–9, which had negative contributions in some years (Fig. 2a). On the contrary, the contributions were highly variable between size classes and years for CR (Fig. 2b). When the effect of vital rates is decomposed by population, sexual fecundity had a positive and

higher contribution in CR than in MBR (Fig. 3a). The largest positive contributions towards survival were for MBR, while the contribution in CR was low and negative (Fig. 3b). Clonal propagation was positive in CR and negative in MBR (Fig. 3b), and, finally, the contribution of growth was negative for both populations (Fig. 3b).

In general, contributions of fecundity were very low and there was no clear interaction between site and year for fecundity. Sexual reproduction contributed

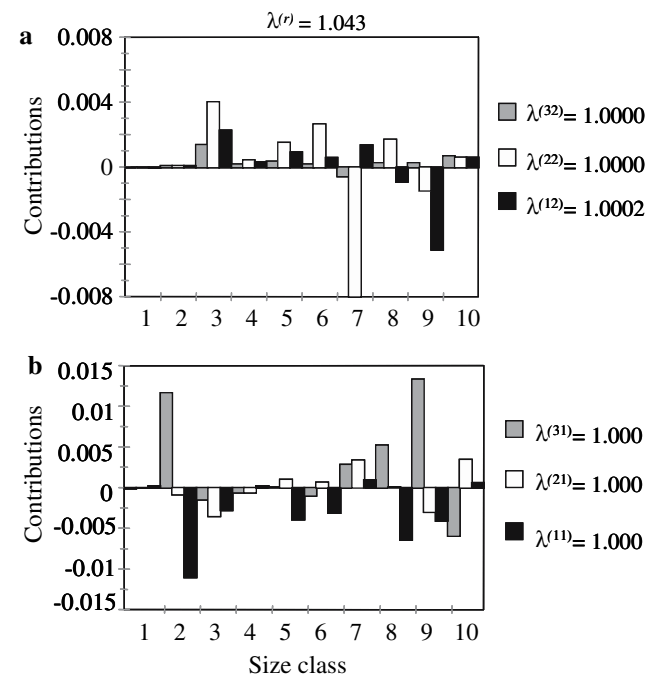


Fig. 2a, b Analysis of the life table response experiment (LTRE) of *Opuntia macrocentra* comparing the *i*th level of the first treatment (time=studied periods, with three levels 1997–1998 (gray bars), 1998–1999 (white bars), and 1999–2000 (black bars)) and the *j*th level of the second treatment (site with two levels **a** Mapimi Biosphere Reserve (MBR) or **b** College Ranch (CR)). The finite rate of population increase for the relevant average matrix is given at the top ($\lambda^{(r)}$) and the annual values are given on the right-hand side ($\lambda^{(ij)}$). Contributions were grouped by size classes

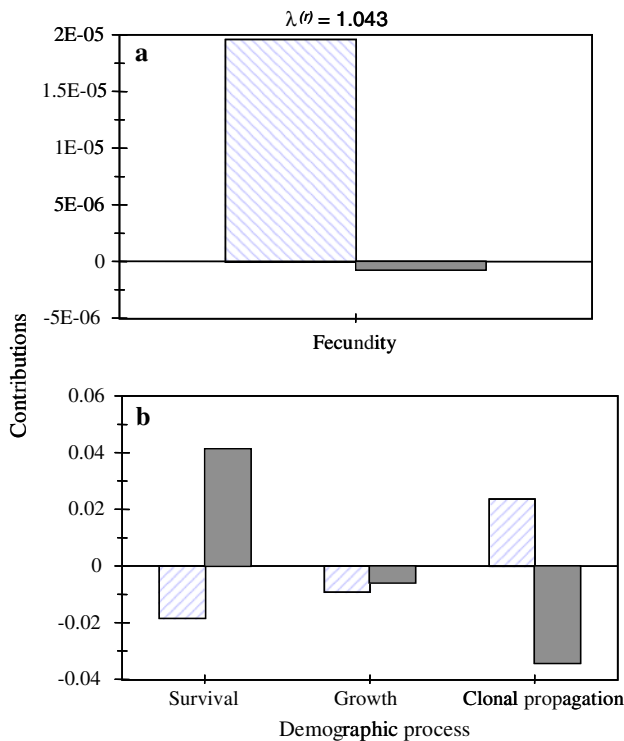


Fig. 3a, b Results of the LTRE for *Opuntia macrocentra* comparing the effect of sites (MBR and CR). The finite rate of population increase for the relevant average matrix is given at the top ($\lambda^{(\theta)}$). Contributions were grouped by demographic process. **a** Contributions of fecundity to $\lambda^{(i)}$. **b** Survival, growth, and clonal propagation. Contributions of MBR (solid bars) and CR (hatched bars)

positively in both populations in 1997–1998, and negatively in both populations in 1999–2000; the effect differed between the populations in 1998–1999 (Fig. 4a). The contribution of growth varied from positive to negative contributions between years in both MBR (Fig. 4b) and CR (Fig. 4c), and was not consistent among years and populations. Stasis (plants that remain in the same size class) had a negative contribution in both populations in 1998–1999 (Fig. 4b, c), and showed the highest overall contributions to λ (Fig. 4b, c), although there were substantial differences among sites and years. Clonal propagation differed markedly between populations, having more positive contributions in CR (Fig. 4c). The contributions of clonality were very important for all of the studied years (Fig. 4b, c) and different size classes were responsible for this pattern throughout the study period (data not shown).

Numerical simulations

Simulated heterogeneity in the probability of survival of seeds in the seed bank showed a positive correlation

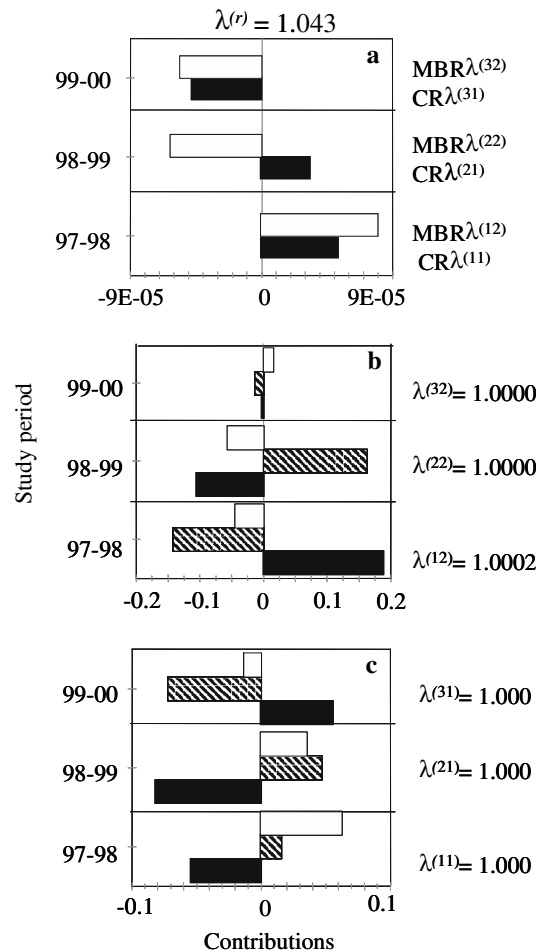


Fig. 4a–c Results of the LTRE for *Opuntia macrocentra* comparing the *i*th level of the first treatment (time=studied periods, with three levels 1997–1998=97–98, 1998–1999=98–99, and 1999–2000=99–00) and the *j*th level of the second treatment (site with two levels CR or MBR). The finite rate of population increase for the relevant average matrix is given at the top ($\lambda^{(r)}$), and the annual values are given on the right-hand side ($\lambda^{(ij)}$). Contributions were grouped by demographic process. **a** Contributions of fecundity to $\lambda^{(i)}$. **b** MBR and **c** CR. Contributions of survival (black bars), growth (hatched bars), and clonal propagation (white bars) to $\lambda^{(ij)}$

between survival and λ , but this effect does not increase λ substantially (CR $\lambda=0.9942\pm0.009$; MBR $\lambda=1.0001\pm0.001$). In contrast, the simulated increase in the probability of the recruitment of new seedlings showed an important effect on λ (Fig. 5a, b). The effect was greatest in the CR population ($\lambda=1.4711\pm0.4447$), but less pronounced in MBR ($\lambda=1.0567\pm0.0486$). When the entries for clonal propagation were changed, the projected effect on λ was the highest among all simulations; adding just one clonal offspring increased λ for both populations (average over all size classes, CR $\lambda=1.0915\pm0.0652$; MBR $\lambda=1.1135\pm0.0844$). There is also an important effect of the size of offspring; the

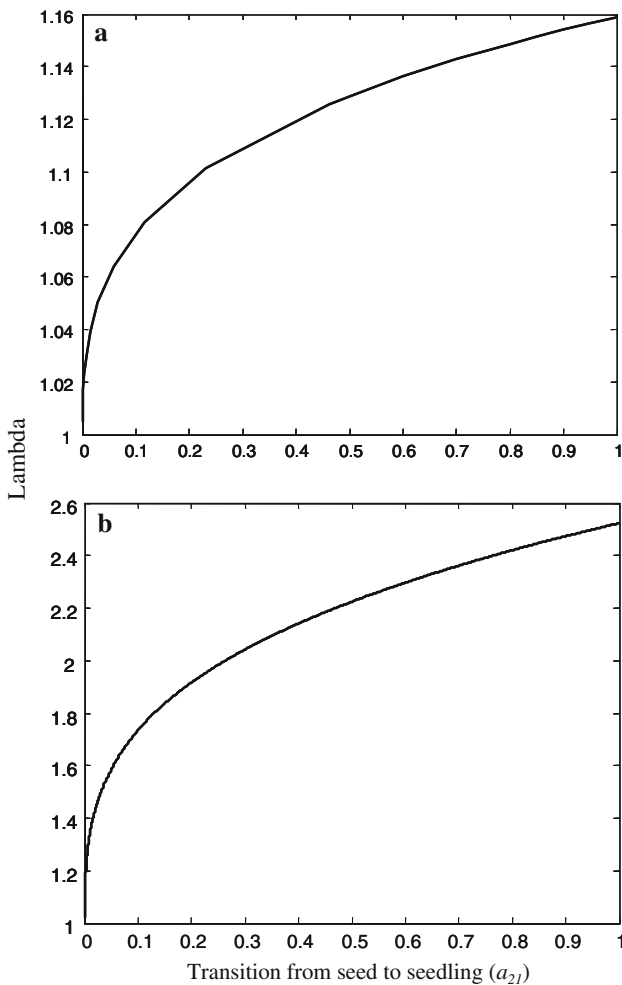


Fig. 5a, b Results from numerical simulations to estimate the effect of seedling recruitment on λ in two populations of *Opuntia macrocentra* in the Chihuahuan Desert. **a** MBR. **b** CR. The λ values were calculated changing the probability of transition from seed to seedling (a_{21} cell), adding one offspring per simulation until the total of the possible seeds produced were established (i.e., 1/16,897 to 16,897/16,897 in CR and 1/8,866 to 8,866/8,866 in MBR)

recruitment of an offspring in the larger size classes increased λ to a higher extent in comparison to smaller sized offspring (Table 3).

Discussion

In general, it is accepted that clonal propagation can be one of the most important demographic processes affecting population dynamics, but there are still relatively few quantitative assessments in the literature (e.g., Eriksson 1985, 1989; Huenneke and Marks 1987; Eckert and Barrett 1993; Mandujano et al. 1998, 2001; Bobich and Nobel 2001a, 2001b). Contrary to all previously published research (i.e., Eriksson 1985, 1989;

Table 3 Results of the numerical perturbation analyses to estimate the effect of clonal propagation on λ in two populations of *Opuntia macrocentra* in the Chihuahuan Desert. The finite rate of population increase, $\bar{\lambda}$ (95% confidence interval) indicates the contribution of clonal propagation of a given size class. $\bar{\lambda}$ was obtained from averaging the λ s resulting from the simulations in which the following entries were changed in the mean matrix: for size classes 1: $a_{19}, a_{18}, a_{17}, a_{16}, a_{15}, a_{14}, a_{13}$, and a_{12} . 2: $a_{29}, a_{28}, a_{27}, a_{26}, a_{25}, a_{24}$, and a_{23} . 3: $a_{39}, a_{38}, a_{37}, a_{36}, a_{35}$, and a_{34} . 4: $a_{49}, a_{48}, a_{47}, a_{46}$, and a_{45} . 5: a_{59}, a_{58}, a_{57} , and a_{56} . 6: a_{69}, a_{68} , and a_{67} . 7: a_{79} and a_{78} . 8: a_{89} and a_{88}

Size class of a new offspring (no. of cladodes)	$\bar{\lambda}$	
	CR	MBR
1 (1)	1.0459 (0.0445)	1.0010 (0.0021)
2 (2–5)	1.0651 (0.0489)	1.1266 (0.0806)
3 (6–10)	1.0855 (0.0376)	1.1192 (0.0473)
4 (11–25)	1.1223 (0.0811)	1.1448 (0.0609)
5 (26–35)	1.1174 (0.0607)	1.1457 (0.0456)
6 (36–45)	1.1320 (0.0523)	1.1483 (0.0296)
7 (46–55)	1.1606 (0.0637)	1.2237 (0.0345)
8 (56–66)	1.1588 (0)	1.2759 (0)

Huenneke and Marks 1987; Eckert and Barrett 1993; Mandujano et al. 1998, 2001; Bobich and Nobel 2001a, 2001b), we found that clonal propagation in *O. macrocentra* is less frequent than sexual reproduction, but these clonal offspring have a higher probability of survival, faster growth, and, also, faster reproduction than sexual offspring. In addition, we found that clonal propagation has a marked effect on λ in *O. macrocentra*. The production of different types of new offspring (i.e., newborns of different sizes, Caswell 1985), with associated differences in fecundity (sexual and clonal) and probability of survival, showed slightly different effects on λ . Clonal offspring in small size classes increased λ by 8%, while the production of large clonal offspring (classes 6–9) resulted in a 19% increase of λ . Furthermore, numerical simulations showed that adding 56 seedlings or a single clonal offspring (from size class 6 to size class 8) are equivalent in terms of the impact on λ ($\lambda=1.2$).

Environmental heterogeneity has been shown to have important consequences on population dynamics (Sarukhán and Harper 1973; Bierzychudek 1982; Huenneke and Marks 1987; Moloney 1988; van Groenendael and Slim 1988; Svensson et al. 1993; Mandujano et al. 2001; Kiveniemi 2002; Jongejans and de Kroon 2005; Morris and Doak 2005), but few studies have found differences between sites in population dynamics (Morris and Doak 2005; Jongejans and de Kroon 2005). Indeed, it is interesting to note how contrasting life history patterns (i.e., differing population structures, fecundities, size at first reproduction, survival, and clonal propagation) resulted in similar population growth rates for the two populations of this species. If

the observed life history traits are representative of the long-term demographic behavior of these two populations, we must conclude that the values observed in these traits represent adaptive responses to the prevailing environmental and biotic conditions. In particular, *O. macrocentra* plants at the CR population were more precocious and had higher recruitment. These differences can be related to the fact that clonal propagation is more frequent in this population than at MBR (at least, during the study period), and, as has been shown, ingrow faster and survive better than sexual offspring (Fitter 1986; Mandujano et al. 1998, 2001). Differences in population structure (small plants at CR, large plants at MBR) may also be the result of very poor recruitment observed in the MBR population. Other clonal species also show infrequent seedling recruitment (Eriksson 1985, 1989; Eckert 2002). In contrast, sexual and/or clonal propagation was observed in all years at CR, resulting in an inverted “J” population structure, characteristic of populations with constant recruitment and often found in asexual species (Mendoza and Franco 1998). The differential pattern of recruitment in these populations could also be the result of browsing by herbivores and other factors associated with disturbance. MBR has a long history of cattle and goat grazing (more than 120 years), which reduces the herbaceous strata (subshrubs and grasses) and can lead to a complete absence of recruitment because of the lack of safe sites necessary for seedling survival (Mandujano et al. 1998). In contrast, livestock have not grazed the CR population since 1982, which has contributed to an increase in species abundance and diversity, especially grasses that could act as safe sites for sexual recruitment. Although in this study we did not assess the impact of herbivores, they have been shown to have important effects on the recruitment of plant species in desert environments (e.g., Brown et al. 1972; González-Espinosa and Quintana Asensio 1986; Mandujano et al. 1997, 1998; Montiel and Montaña 2000). These factors, coupled with the low precipitation observed during the study period, may account for low seedling establishment at MBR, despite having high seed production in some years (1997).

In CR, there was high retrogression (i.e., mortality of cladodes or clonal propagules), but there was also more sexual recruitment. Numerical perturbation analyses also support the importance of sexual recruitment in the CR population; in comparison, λ showed little response to sexual recruitment in MBR where the established plants are highly persistent (high stasis) and recruitment is infrequent. However, a slight increase in mortality would affect MBR populations drastically. The fragile balance between recruitment

and survival that resulted in population equilibrium ($\lambda \approx 1$) could easily be shifted towards population decline if either mortality increases or no recruitment occurs over a long time period.

In this context, sporadic sexual or clonal propagation for perennials may be the rule rather than the exception. Under these conditions, high seed output in the studied populations suggests that sporadic sexual recruitment is apparently sufficient to both maintain a stable population and to avoid the possible effects of inbreeding depression, which could occur under conditions of successive clonal propagation (Mandujano et al. 1996, 2001). The implication is that, in unpredictable environments, sexual establishment depends more on environmental heterogeneity (the biotic factors of nurse plants and herbivores, and abiotic resources such as rainfall) than on the intrinsic capacity for reproduction or investment in reproduction of the established adult plants. Similar to other desert perennials (e.g., *Larrea tridentata*, *Prosopis glandulosa*, *Coryphantha robbinsorum*, *O. rastrera*), there is great variability in flower, fruit, and seed production, although average reproductive values seem to be consistently high and increasing with plant size, suggesting a high allocation to seed reproduction over an individual's lifespan (Lee and Felker 1992; Franco et al. 1994; Schmalzel et al. 1995; Golubov et al. 1999). However, on short time scales (1–10 years), sexual recruitment is rarely successful in clonal plants (Eriksson 1996); for example, 60% of a sample of 68 clonal species did not show seedling recruitment in adult populations (Eriksson 1989). Adding to the logistic difficulty of these studies, populations of perennial species in arid environments must be followed for more than a year, as environmental conditions may not be appropriate in any given year and would, thus, give misleading results when modeled demographically (Golubov et al. 1999; Mandujano et al. 2001).

The loglinear analysis indicated that there were no significant differences in the frequency of observed transitions between populations. The conditional impact of the initial state must be reconsidered in a broad biological context. Populations depend on the initial state and, thus, they can differ in many traits. For example, population structures may reflect the frequency of successful types of recruitment (e.g., clonal over sexual). Our results indicated marked differences in fecundity, clonality, and retrogression. In addition to the demographic differences observed, the consequences of successful establishment in sexual and clonal offspring for the MBR and CR populations contrasted strongly. On one hand, the population at MBR produces large amounts of seeds; however,

though the soil seed bank is continuously being replenished, losses to granivory in *Opuntia* species can be quite high (e.g., González-Espinosa and Quintana Asensio 1986; Montiel and Montaña 2000). In addition, the low germination of seeds under controlled and relatively benign conditions suggests the presence of dormancy, which, in the short term, could also contribute to the low and variable seedling recruitment observed in this study (Mandujano et al. 1997; Rojas-Aréchiga and Vázquez-Yanes 2000; Baskin and Baskin 1998). Numerical simulations suggested that the persistence and amount of seed bank in this species (separate from the rate of seedling recruitment) did not affect λ ; however, persistent seed banks can enable populations to tolerate periods of reproductive failure (Kalisz and McPeck 1992; Mandujano et al. 2001). On the other hand, the population at CR has continuous establishment of individuals that contribute to maintaining genetic resources in the population. This continuous recruitment through clonal propagation is reflected in the size structure of the CR population and in the life history responses (i.e., precocity).

The elasticity of the *GLF* of both species is similar to that displayed by tolerant perennial species and other cacti (Silvertown et al. 1992; Rosas-Barrera and Mandujano 2002; Godínez-Alvarez et al. 2003), in which survival is the most important demographic process. However, fecundity and growth for CR is higher than for MBR, shifting the CR population into the group of many shrubs that increase *G* over *L*, and by cacti that have higher clonal propagation (Silvertown et al. 1993; Rosas-Barrera and Mandujano 2002).

The persistence of populations at MBR and CR depends largely on different pathways: MBR mainly depends on clonal propagation and CR on both sexual and clonal propagation. However, the end result is common to both populations ($\lambda \approx 1$). It has been suggested that the life cycle structure of long-lived species can often buffer the effects of environmental variability, resulting in rather stable dynamics of local populations (Eriksson 1996). In addition, reduced rates of sexual reproduction may be particularly common at the geographical margins of species ranges (Eriksson 1996).

Acknowledgments This research was supported by a grant from the USA Geological Survey, Biological Resources Division, to L.F.H.; by the NSF-funded Jornada Basin Long-Term Ecological Research (LTER) program; and by project 34980-V from CONACyT, 0350 Semarnat-Conacyt, and IN205500 from PAPIIT-DGAPA-UNAM to M.C.M., and PROMEP (2115–32637) and BBVA to J.G. We thank A. and F. Mandujano, L. Camarillo, R. Pérez-Ishiwara, S. Herrera, A. Herrera, M. Gronemeyer, Yup Verhulst, I. Carrillo, G. Aguilar, the wonder group, and J. Anderson for field assistance. M. Franco, P. Zuidema, and F. Mandujano provided constructive comments on the manuscript.

The Department of Biology, NMSU, New Mexico, gave us additional computer and logistic support. DGAPA-UNAM and CONACyT supported M.C.M. at NMSU.

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