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# How important is clonal recruitment for population maintenance in rare plant species?: The case of the narrow endemic cactus, *Stenocereus eruca*, in Baja California, México

Ricardo Clark-Tapia [a], Maria C. Mandujano [b], Teresa Valverde [c], Ana Mendoza [d], Francisco Molina-Freaner [a,*]

[a] *Departamento de Ecología de la Biodiversidad, Instituto de Ecología-UNAM, Estación Regional del Noroeste, Apartado Postal 1354, Hermosillo, Sonora, C.P. 83000, Mexico*
[b] *Departamento de Ecología de la, Biodiversidad, Instituto de Ecología-UNAM, Apartado Postal 70-275, México D.F. C.P. 04510, Mexico*
[c] *Departamento de Ecología y Recursos Naturales, Facultad de Ciencias-UNAM, México D.F. C.P. 04510, Mexico*
[d] *Departamento de Ecología Funcional, Instituto de Ecología-UNAM, Apartado Postal 70-275, México D.F. C.P. 04510, Mexico*

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**Abstract**

*Stenocereus eruca* is a postrate columnar cactus whose regeneration seems to occur mainly through clonal propagation. It is a narrow endemic species of the Sonoran desert in Baja California Sur and currently considered as threatened under Mexican legislation. In this paper we describe the demography of ramets in four populations along its distribution range and the demography of genets in one population during a 3-year-study period in order to evaluate its conservation status. We also analyze the relative contribution of sexual reproduction and clonal propagation to population maintenance and provide guidelines for the formulation of conservation programs. Elasticity analyses were used to explore the relative contribution of sexual and clonal recruitment to projected population growth rate ($\lambda$). During the three years of study, regeneration occurred only through clonal propagation while sexually derived seedlings were not detected within or outside the permanent plots. Our demographic data showed that the four population of *S. eruca* are in equilibrium ($\lambda \approx 1$), and elasticity analyses showed that the relative contribution to $\lambda$ of clonal recruitment was larger than sexual recruitment, at least during the analyzed ecological time scale. Simulations showed that removing sexual recruitment had a minor impact on $\lambda$, but the absence of clonal propagation alone was sufficient to keep below unity. We propose the establishment of at least one reserve with adequate protection from human disturbance to conserve *S. eruca*.
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*Keywords:* Clonal propagation; Demography; Rare species; Sonoran desert; *Stenocereus eruca*

## 1. Introduction

The population dynamics of many clonal plants is often dominated by the birth and death of ramets produced by vegetative reproduction, whereas the recruitment of new seedlings of sexual origin is relatively rare or sporadic (Jordan and Nobel, 1979; Jelinski and Cheliak, 1992; Eriksson, 1993). This is especially true in arid environments, where the population dynamics of many plant species is highly variable due to extreme temperatures and unpredictable rainfall events (Polis, 1991). These conditions often lead to low rates of seedling recruitment even when viable seeds are seasonally available, whereas clonal propagation is

* Corresponding author. Tel.: +662 213 9303.
*E-mail addresses:* freaner@servidor.unam.mx (F. Molina-Freaner).

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often a successful mechanism of population regeneration (Parker and Hamrick, 1992; Mandujano et al., 2001). Thus, the relative importance of sexual and clonal recruitment varies in response to diverse environmental conditions, and their contribution to population growth rate is expected to differ (McFadden, 1991; Mandujano et al., 2001). However, our knowledge about the role of sexual vs. clonal recruitment in the maintenance and growth of plant population in arid environments is still quite limited.

Demographic studies of clonal species that consider the dynamics of both genets and ramets are exceptionally valuable for our understanding of plant population dynamics, as inferences about the relative importance of sexual and clonal recruitment through time can be made (Hartnett and Bazzaz, 1985a; Damman and Cain, 1998). The dynamics of ramets and genets may be different within a population (Eriksson, 1993), yet our knowledge about the dynamics and demography of clonal plants has been restricted mainly to ramets (Dickerman and Wetzel, 1985; Mandujano et al., 2001), due to the difficulty of identifying genets in the field. However, the use of molecular markers has been extremely useful in this context as they can be used to identify genets (Jonsson et al., 1996) making the study of demography at both the genet and ramet level possible (Suzuki et al., 1999).

The Cactaceae is a large plant family that is essentially restricted to the New World (Gibson and Nobel, 1986). Mexico is one of the most important centers of species diversity in the continent, possessing almost 850 species (42% of the family) of which more than 700 are endemic (Arias-Montes, 1993). However, many Mexican cacti are being threatened by habitat destruction, illegal collection and trade, and land-use change toward farming and cattle ranching (Arias-Montes, 1993). Despite the importance of this plant family to the biological diversity of Mexico, our knowledge about the population dynamics and conservation status of the vast majority of Mexican cacti is extremely poor. Demographic studies of cacti have been previously employed to evaluate the current population status and to detect vulnerable stages in their populations (Contreras and Valverde, 2002; Esparza-Olguín et al., 2002), as well as other aspects of their population biology (Steenbergh and Lowe, 1983; Pierson and Turner, 1998). Additionally, the development of prospective analysis (i.e., elasticity) and numerical simulations has opened the possibility of addressing important problems on population biology and conservation issues (Caswell, 2001). In particular, elasticity values – that compare the relative contribution of different demographic process (i.e., fecundity or clonal propagation) to $\lambda$, have been used across taxa to evaluate which demographic process is proportionally more relevant to overall population growth and is also a valuable tool for conservation and management as it helps to determine the most vulnerable phases of a species' life cycle (de Kroon et al., 1986).

*Stenocereus eruca* is a clonal columnar cactus endemic to the Sonoran desert (Gibson, 1989; Turner et al., 1995). The flowers of *S. eruca* are self-incompatible; fruit set is low and highly variable in space and time as a consequence of pollinator limitation (Clark-Tapia and Molina-Freaner, 2004). Clonal propagation occurs in this case by detachment of branches from the major shoot as the base of the branch dies and rots. Thus, in *S. eruca*, the ramets (the vegetative production of modular units) of a genet (all products of a zygote) tend to detach and fragment. Field records have been unable to detect establishment of seedlings of sexual origin, and it is thought that population regeneration occurs mainly through clonal propagation (Gibson, 1989; Turner et al., 1995). However, a previous study of the clonal diversity of *S. eruca* populations using isozymes suggested that both sexual and clonal recruitment are important mechanisms of population regeneration (Clark-Tapia, 2000). Due to the fact that seedlings are extremely rare in natural conditions, the evidence of clonal diversity suggests that seedling recruitment is restricted to "narrow windows of opportunity" (Jelinski and Cheliak, 1992) during rare events of favorable conditions (e.g., heavy rainfall in the area). Therefore, detailed and long-term demographic studies are necessary in order to understand the regeneration mechanisms and the relative role of sexual and clonal recruitment in the maintenance and growth of *S. eruca* populations.

*S. eruca* is also an extremely narrow endemic species, restricted to coastal areas of the Plains of Magdalena in Baja California Sur (Gibson, 1989; Fig. 1) and is listed as a threatened species by the Mexican legislation (NOM-059-ECOL-2001). Major threats to the persistence of *S. eruca* populations include habitat loss associated with land-use change towards farming and illegal collection (Cancino et al., 1995). In consequence, it is critical to understand the population dynamics and its current status in order to design conservation strategies. For instance, analyzing how anthropogenic disturbance and restricted seedling recruitment affect the population growth rate is of paramount importance in order to develop appropriate management plans.

In this study, we used demographic analysis to explore the relative importance of sexual and clonal recruitment for population growth rate in *S. eruca*. To this end, we describe the demography of ramets in four populations along its distribution range and the demography of genets (identified with molecular markers) at Estero Salinas and used elasticity analyses to evaluate the relative contribution of life history traits to projected finite population growth rate. Finally, all demographic

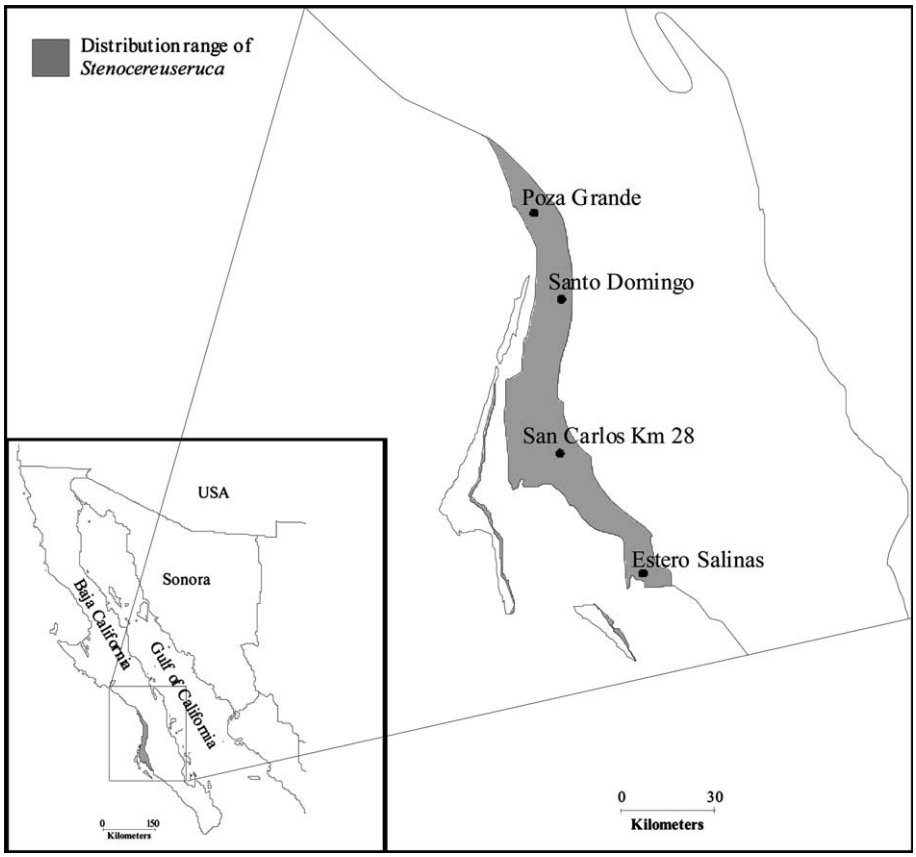


Fig. 1. Range of distribution (shaded area) of *Stenocereus eruca* in Baja California Sur and the location of the studied populations. Modified from Turner et al. (1995)).

evidence and our field observations were used to propose conservation strategies.

## 2. Material and methods

### 2.1. Study area

This study was conducted in the Plains of Magdalena, in the Sonoran desert of Baja California Sur (B.C.S.), Mexico (Fig. 1). The Plains of Magdalena have an arid climate with mean annual rainfall of around 100 mm, and nearly 80% of the total rainfall occurring between July and September (1988–2001 data from Comisión Nacional del Agua, La Paz, B.C.S.). *S. eruca* has a patchy distribution in the area with densities of 300 to 4700 ramets/hectare.

### 2.2. Studied populations

In August 1999 we selected four populations of *S. eruca* along its distributional range in the Plains of Magdalena (Fig. 1). In each population a permanent plot of 600 $m^2$ ($10 \times 60$ m) was established in order to record at least 250 individual plants. All individuals inside the plots were identified with a numbered metal tag. The length of the major stem of each plant was measured with a flexible pocket tape. When a ramet had several branches, the length of each branch was measured and then added up to estimate total stem length.

### 2.3. Demographic parameters

All plants within the plots were recorded and measured again in August of 2000, 2001 and 2002. In each census the following data were recorded: (1) length increase, (2) mortality, (3) seedling recruitment, and (4) detachment or fragmentation events (clonal propagation). During the fruiting season (from September to November) of 1999, 2000, 2001, and 2002 the number of fruits produced per plant was also recorded. Mature fruits outside the plots were collected every year ($n \approx 25$) in order to estimate the mean number of seeds per fruit, which was used to calculate plant fecundity.

### 2.4. Seedling recruitment

Each year we searched for new seedlings of sexual origin within plots and in the area surrounding each plot in every population of *S. eruca* during and after

the rainy season. However, no sexual recruitment has been observed in any population. Therefore, field experiments of seed germination and seedling survival were carried out to determine the probability of recruitment. Field experiments were performed at the Estero Salinas population, because this was the only population where seeds were systematically available during the study period. To evaluate seed germination, seeds were sown in the field during the summer rainy seasons of August 2000 and August 2001, using $10 \times 10$ cm experimental plots. Each experimental plot contained 100 seeds distributed in the ground in two microhabitats: 12 replicates were placed in open spaces and 12 beneath the cover of shrubs acting as nurse plants. To estimate the probability of seedling survival in the field, we germinated seeds in a greenhouse and seedlings were transplanted to the field in August 2001, after six months of growth (watered every 2–3 weeks) in the greenhouse. We used experimental plots containing 150 seedlings in two microhabitats: three plots in open spaces and three under the cover of shrubs, and watered after transplant. Seed germination and seedling survival were recorded during two months, following their status until all seeds or seedlings died or disappeared. Additionally, a seed germination and seedling survival experiment under controlled condition was conducted at the Institute of Ecology (UNAM) in Mexico City during the years of 1999, 2000, and 2001, using batches of 10,000, 5000 and 8000 seeds, respectively. This experiment was necessary as field evidence showed that no seedling established after several years of experimentation. Seeds of *S. eruca* were placed in petri dishes with an agar substrate (2%) in germination chambers at 25 °C. Seed germination was scored every day; two weeks after germination seedlings were transplanted to individual trays filled with homogenized soil from the study site and kept in the greenhouse. The trays were watered every two weeks and seedling survivorship was recorded every month for one year to estimate the transition probability under controlled conditions.

### 2.5. Genet determination

Random amplified polymorphic DNA (RAPDs) were used to identify genets and ramets within the plot at Estero Salinas due to difficulty of identifying individual genotypes in the field. Estero Salinas was selected because it had the smallest degree of human disturbance and the regularity of sexual reproduction events of this population. Each plant within the plot was mapped in a $x$–$y$ coordinate for later relocation. All ramets inside the plot ($n = 282$) were sampled and small (2–3 $cm^3$) samples of rib chlorenchyma were extracted using a cork borer and stored at −80 °C for later analysis. DNA was extracted using a modification of the Quiagen Plant Minikit extraction method and six informative and reproducible primers (A01, A10, A15, G03, G16 and G18) were used for RAPD analysis. The separation and scoring of amplification products was done on 1.4% Agarose gels using 0.5× TBE (Clark-Tapia et al., 2005).

## 3. Data analyses

### 3.1. Matrix analysis and construction

Once identified, genets and ramets were grouped in seven size classes according to total stem length (Table 1). Total stem length for each genet was obtained as the sum of individual length of each ramet (that shared the same banding pattern), in such a way that the selection of each size category was conditioned to the number of ramets and to stem length of each ramet. To categorize ramets we only included the total stem length of each individual in the populations. Based on measurements of annual ramet growth and the spatial expansion of clones, the age of genets of *S. eruca* were estimated according to Steinger et al. (1996). Fecundity was estimated by calculating the mean number of seeds produced per size class, multiplied by germination probability (i.e., proportion of germinated seeds). Additionally, these values were multiplied by the probability that a seedling survives for one year. As no seedling survival has been detected in the field, the transition probabilities from seed to seedling were calculated using greenhouse experiments during 3-year-study periods (1999–2000, 2000–2001 and 2001–2002). The seed class was not included in the demographic model because there is no persistent seed bank (i.e., seeds do not remain in the soil for more than one year.) and field observations suggest that seeds are consumed by rodents and lizards and are rapidly depleted from the population (Clark-Tapia, pers. obs.).

Table 1
Size classes used in the projection matrices for genet and ramet level of *Stenocereus eruca*

| | Total length (cm) | |
|---|---|---|
| Stage classes | Ramet level | Genet level |
| 1 – Seedling | 0–3 | 0–3 |
| 2 – Non-reproductive | 3.1–30 | 3.1–60 |
| 3 – Reproductive I | 30.1–60 | 60.1–120 |
| 4 – Reproductive II | 60.1–90 | 120.1–180 |
| 5 – Reproductive III | 90.1–120 | 180.1–240 |
| 6 – Reproductive IV | 120.1–150 | 240.1–300 |
| 7 – Reproductive V | >150 | >300 |

*Notes*: Reproductive status is determined by remnants of flowers or fruits.

The population models used in this study were straightforward applications of the projection Lefkovitch matrix models (Caswell, 2001)

$$n_{t+1} = \mathbf{A}n_t,$$

where $n$ denotes a column vector whose elements $n_i$ are the number of individuals in each category at time $t$ or $t + 1$, and **A** represents a square matrix with the transition probabilities among life cycle categories from one period to the next. Demographic processes fell into the following regions within the matrix **A**: (a) fecundity values were in the first row; (b) stasis or the probability of remaining in the same category were in the main diagonal; (c) retrogression in size or clonal propagation in the upper diagonal; and (d) growth to larger stages occupy the sub diagonals (Fig. 2). We estimated $\lambda$ (finite rate of population increase), **v** (left eigenvector, reproductive value) and **w** (right eigenvector, stable size distribution) for all annual matrices as well as the mean matrix.

Annual matrices (1999–2000, 2000–2001 and 2001–2002) and a mean matrix were built for genets (only for Estero Salinas) and ramets (all four sites). The transition probabilities among classes were calculated by the relative frequencies of each estimated transition from one year to the next or by going backwards from a group to another of smaller size (retrogression or decrease in size). Whenever the value of stasis was equal to 1.00 (no mortality occurred in individuals of the last size classes), the coefficients $a_{77}$ for genets ($0 < a_{77} > 1$) and $a_{77}$ for ramets ($0 < a_{77} > 1$) were calculated in a way that $a_{77}{}^{x} < 0.00005$, where $x$ = the estimated time of permanence in such size classes.

$$A = \begin{vmatrix} S_{11} & 0 & F_{13} & F_{14} & F_{15} & F_{16} & F_{17} \\ G_{21} & S_{22}+C_{22} & C_{23}+R_{23} & C_{24}+R_{24} & C_{25}+R_{25} & C_{26}+R_{26} & C_{27}+R_{27} \\ 0 & G_{32} & S_{33}+C_{33} & C_{34}+R_{34} & C_{35}+R_{35} & C_{36}+R_{36} & C_{37}+R_{37} \\ 0 & 0 & G_{43} & S_{44}+C_{44} & C_{45}+R_{45} & C_{46}+R_{46} & C_{47}+R_{47} \\ 0 & 0 & 0 & G_{54} & S_{55}+C_{55} & C_{56}+R_{56} & C_{57}+R_{57} \\ 0 & 0 & 0 & 0 & G_{65} & S_{66}+C_{66} & C_{67}+R_{67} \\ 0 & 0 & 0 & 0 & 0 & G_{76} & S_{77}+C_{77} \end{vmatrix}$$

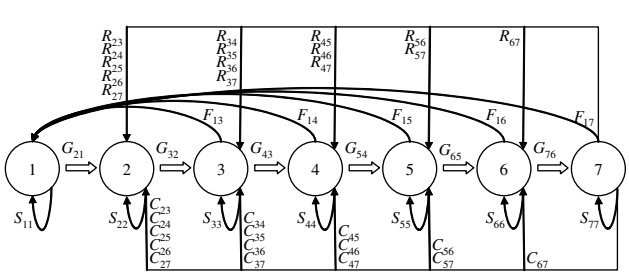


Fig. 2. Life cycle diagram and the projection matrix model corresponding to *Stenocereus eruca*. The elements inside the matrix **A** have the following regions: fecundity ($F$, in the first row); stasis ($S$, in the main diagonal); retrogression in size or clonal propagation ($R$ and $C$, respectively in the upper diagonal); and finally growth to later stages ($G$, in the sub diagonals). See Table 1 to identify the corresponding nodes.

### 3.2. Elasticity analysis

Elasticity and sensitivity analyses of projection matrices are prospective analyses, since they quantify the expected degree of perturbation to population growth given a specific change in one (or more) elements of the matrix (Horvitz et al., 1997; Caswell, 2001).

Based on sensitivity values ($S_{ij} = v_i w_j / vw$), we calculated the corresponding elasticity matrices ($e_{ij} = a_{ij}/\lambda)(S_{ij})$ (de Kroon et al., 1986; Caswell, 2001) for the 3-year-study period (1999–2000, 2000–2001, and 2001–2002). The elasticity evaluated the relative contribution of matrix entries ($a_{ij}$) to the population finite rate of increase ($\lambda$) and is scaled so that the sum of all values equals unity (Caswell, 2001).

### 3.3. Simulations excluding clonality and fecundity

The contribution of sexual reproduction or clonal propagation to the finite rate of population increase ($\lambda$) was evaluated by means of simulations. Clonal propagation or fecundity values were excluded from the ramet matrices for the 3-year-study period. To evaluate the importance of sexual reproduction the corresponding values of clonal propagation were eliminated, and to assess the importance of clonal propagation, the entries in the matrices associated to sexual reproduction were eliminated. All matrix models and elasticity analyses were carried out using MATLAB, version 5.2.0 (The MathWorks, Natick, MA, USA) and 95% confidence intervals for $\lambda$ values were calculated through Monte Carlo simulations as proposed by Alvarez-Buylla and Slatkin (1993).

## 4. Results

### 4.1. Sexual and clonal recruitment

*S. eruca* produced on average over all populations (mean over the 3-year-study period ± 1 SD) from 0.003 ± 0.490 to 0.130 ± 0.490 fruits per ramet, and fruits produced from 211 ± 87 to 336 ± 186 seeds. Reproductive individuals (at both the ramet and genet level) were found from size-class 3 to 7 (Table 1) and the highest fecundity values were detected among individuals in size classes 6 and 7 (Fig. 3(a)). No major differences were detected in fecundity (fruit production) between ramets and genets ($\chi^2 = 0.07$, $P = 0.89$). In addition, only a small percentage of reproductive individuals were found at the ramet level (16%), whilst the genet level showed a higher percentage of reproductive individuals (26%), the largest genets showing higher reproduction (Fig. 3(b)).

Although seeds were produced every year, seedling recruitment was not observed during the study period

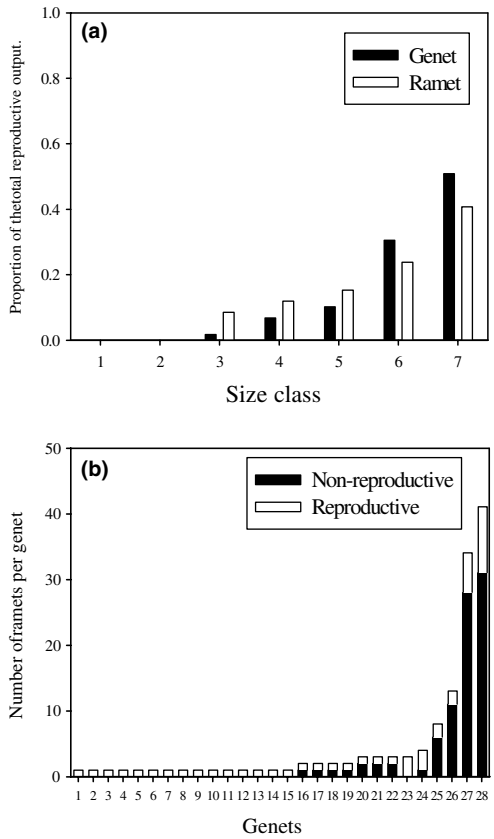


Fig. 3. Pattern of sexual fertility among genets and ramets of *Stenocereus eruca* at Estero Salinas. (a) Proportion of genets or ramets among size classes at Estero Salinas ($N_{genet} = 109$ and $N_{ramet} = 282$). (b) Distribution of reproductive and non-reproductive ramets among fertile genets. Only 28 genets from 109 detected were reproductive.

within the permanent plots nor in the area surrounding the plots in each population. No seedling established in the seed germination experiments performed in the field due to seed removal by animals and seedling mortality. Similarly, seedling transplant experiments showed that no seedling survived for more than two months, presumably due to desiccation, even when found under shade of shrubs. Since no seed or seedling survived in the field, the values of germination and seedling survival used to build the matrices were those obtained from greenhouse experiments. Under controlled conditions, germination reached values of 35% to 55%, however, the probability of seedling survival after one year was extremely low (average 0.002) even under the controlled conditions of a greenhouse.

In contrast, clonal propagation reached a rate of $1.88 \pm 1.33$ ramets/year and varied from $1.1 \pm 0.22$ to $2.57 \pm 2.07$ among years and populations, respectively. Ramet production showed temporal variation as significant differences were detected among years ($\chi^2 = 6.99$, $df = 2$, $P < 0.0302$), but no regional differences were observed as populations exhibited similar rates of ramet production ($\chi^2 = 5.07$, $df = 3$, $P = 0.166$). Ramet mortality rate was relatively low among populations and years, with a mean death rate of $0.011 \pm 0.19$/year varying from $0.002 \pm 0.04$ to $0.012 \pm 0.20$ among years.

Based on the scored presence/absence of RAPD bands, putative genets and their ramets were identified and their spatial distribution within the Estero Salinas plot was recorded. DNA amplification from the 282 ramets within the plot using 52 polymorphic bands yielded a total of 109 genets. Of all ramets found in the plot, 192 belonged to fragmented genets having 2 to 41 ramets (mean number of ramets per genet ± 1 SD: $2.4 \pm 5.1$) while 90 ramets (32%) belonged to a single unique putative genet. No genet mortality was recorded in this population during the 3-year-study period. Annual stem elongation rates of *S. eruca* ranged between 1.04 (±4.04) and 9.97 (±32.69) cm and, based on the size distribution of genets at Estero Salinas, an average genet may be $223 \pm 433$ years old. Age and fecundity of genets (fruits/genet) was strongly positively correlated (Spearman's rank-correlation coefficients $r = 0.541$, $n = 109$, $P < 0.001$) suggesting that fecundity increases with age.

### 4.2. Population growth rate ($\lambda$) and stable stage distribution (**w**)

Based on the 95% confidence intervals, population growth rates ($\lambda$) did not exhibit significant differences between years for each population, at both the ramet and genet level (Table 2). Growth rates at the ramet level varied from 1.002 (San Carlos, 2000–2001) to 1.034 (Santo Domingo, 2001–2002), while at Estero Salinas, $\lambda$ values for genets ranged from 0.965 to 1.030. In all cases, growth rates were not statistically different from unity for the different years and populations (Table 2). The observed population structure and the stable stage distribution (**w**) of each population for both the ramet and genet analyses were similar and were not statistically different (log likelihood ratio $G^2 = 0.069$, $df = 6$, $P = 0.999$ for ramet level and $G^2 = 0.048$, $df = 6$, $P = 0.999$ for the genet level).

### 4.3. Elasticity analysis

The elasticity analysis showed that survival ($S$) was the most important determinant of $\lambda$ in all years and for the two levels of study, followed by growth ($G$) and clonality ($C$) at the ramet level, and fecundity ($F$) at the genet level (Fig. 4). Fecundity and retrogression were of lesser importance in the matrices that considered the ramet level. The relative variation in the magnitude of the different demographic processes between years is very likely attributable to temporal variation in rainfall, which influences the interaction between the demographic processes.

Table 2
Mean and annual values (95% confidence intervals) of the finite rate of population increase ($\lambda$) calculated for four populations of *S. eruca* at the ramet level, and for one population (Estero Salinas) at the genet level, during the three study periods

| Population | Study period | | | |
|---|---|---|---|---|
| | 1999–2000 | 2000–2001 | 2001–2002 | Mean |
| *Ramet level* | | | | |
| Estero Salinas | 1.016 (0.989–1.043) | 1.014 (0.982–1.046) | 1.027 (0.990–1.064) | 1.021 (0.987–1.055) |
| San Carlos | 1.010 (0.984–1.037) | 1.002 (0.974–1.029) | 1.031 (0.993–1.069) | 1.020 (0.986–1.054) |
| Santo Domingo | 1.024 (0.995–1.053) | 1.023 (0.996–1.051) | 1.034 (0.996–1.071) | 1.028 (0.992–1.065) |
| Poza Grande | 1.013 (0.984–1.042) | 1.020 (0.988–1.051) | 1.019 (0.982–1.055) | 1.017 (0.989–1.045) |
| *Genet level* | | | | |
| Estero Salinas | 1.030 (1.00–1.061) | 0.985 (0.961–1.010) | 0.965 (0.930–1.000) | 1.004 (0.968–1.040) |

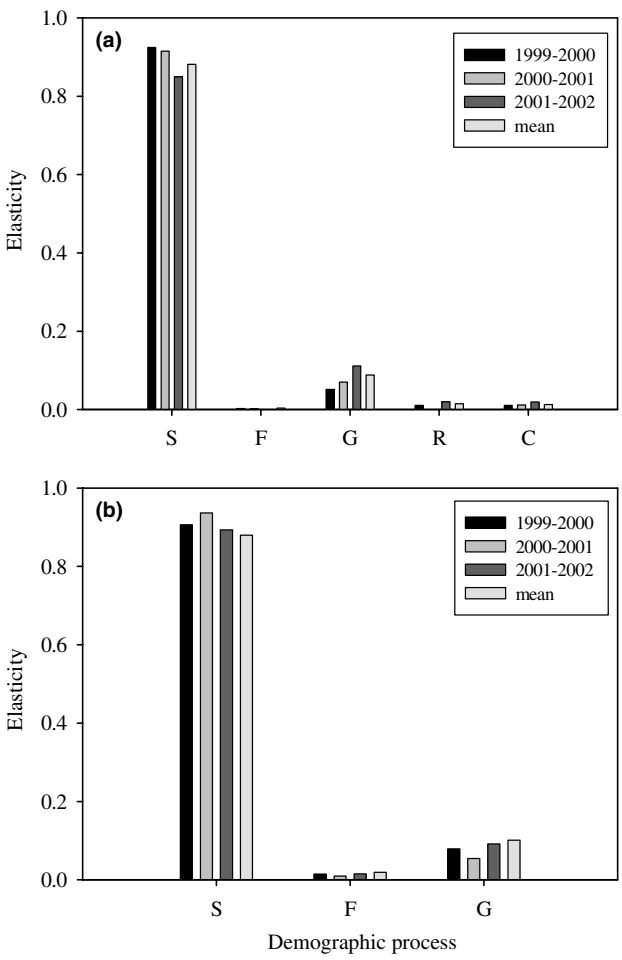


Fig. 4. Relative contribution of the different demographic processes (see Fig. 2) to the value of $\lambda$ from the elasticity matrices obtained for the census periods (1999–2000, 2000–2001 and 2001–2002). Elasticity values at the ramet (a) and genet level (b) in Estero Salinas. Elasticity values at the ramet level from San Carlos, Santo Domingo and Poza Grande were similar to Estero Salinas.

### 4.4. Matrix simulations without clonality or fecundity

Mean projection matrices for each population (available upon request to the corresponding author) were used to evaluate the relative importance of sexual reproduction and clonal recruitment, as no differences were detected between populations and years. The results indicate that clonal growth is more important than sexual reproduction as population growth rate was significantly affected by the elimination of clonal propagation. Without clonal propagation population growth rate varied from 0.96 to 0.98 whereas without sexual reproduction, rates varied from 1.01 to 1.03 among populations. Therefore, the influence of fecundity at the ramet level was insignificant within populations compared to clonal propagation.

## 5. Discussion

Our results indicate that populations of *S. eruca* exhibit stable rates of population growth that are not different from unity at either the genet and ramet level. During the three years of this study, regeneration of populations occurred only through clonal propagation, while seedlings of sexual origin were not detected within or outside the permanent plots. Elasticity analysis showed that the relative importance of clonal recruitment to $\lambda$ was greater than sexual recruitment and therefore the four populations of *S. eruca* are in equilibrium mainly due to clonal growth. According to our results, clonal growth is 3-times more frequent than sexual reproduction (282 ramets/109 genets = 2.6). Our data provide no evidence of declining populations or major threats to four populations of this species. However, if disturbance increase in the

region, we suggest the conservation of the Estero Salinas population.

Our demographic data were consistent with field observations that suggest that seedling recruitment is rare and regeneration is mainly by clonal propagation (Gibson, 1989; Turner et al., 1995), and different from what has been detected for other cacti, where seedlings have been observed to survive under field conditions (Steenbergh and Lowe, 1983; Mandujano et al., 2001; Contreras and Valverde, 2002; Esparza-Olguın et al., 2002). This pattern is similar to that observed in other clonal species where seedling recruitment is rare or restricted to "narrow windows of opportunity" even when seeds are regularly available (Jordan and Nobel, 1979; Eriksson, 1993; Mandujano et al., 2001). In contrast with demographic data, high levels of genotype diversity suggest that both sexual and clonal recruitment are important to the maintenance of populations of *S. eruca* (Clark-Tapia, 2000; Clark-Tapia et al., 2005). This apparent contradiction between demographic and genetic evidence is likely to result from the differences in time scales that are being sampled by ecological and genetic studies. Demographic studies usually sample brief periods of time while studies of the genotypic diversity usually capture events that occur at larger temporal scales. Thus, the available evidence suggests that on a regular basis, regeneration by sexual recruitment may be restricted to "narrow windows of opportunity" (i.e., decades or centuries) when seed escape to predation and favorable environmental conditions occur in the Plains of Magdalena.

Our results show that clonal propagation has a greater influence on population dynamics, at least at an ecological time scale. The simulations showed that removing sexual recruitment had a minor impact on the finite rate of population growth and clonal propagation was sufficient to keep $\lambda$ at unity; however, eliminating clonal growth had a significant negative effect on $\lambda$. This result is consistent with other clonal species where the absence of clonal growth may increase the likelihood of extinction of populations (McFadden, 1991; Mandujano et al., 2001). The elasticity values of *S. eruca* are also consistent with the values reported for other clonal cacti (Mandujano et al., 2001) and show that clonal growth has a greater proportional increase in $\lambda$ than sexual reproduction.

Demographic studies at both the genet and ramet level support the view that both levels are reciprocally influenced (Hartnett and Bazzaz, 1985b; Mendoza, 1994; Zuidema, 2000). As other clonal plants species (Mendoza, 1994; Zuidema, 2000), *S. eruca* promotes the perpetuation of its most successful genets through clonal propagation. Thus, a genet might achieve a larger reproductive output through clonal propagation due to a prolonged longevity. The constant production of new ramets may be a more successful mechanism for population regeneration given the unpredictability of rainfall events that lead to successful seedling establishment in the Plains of Magdalena. Nevertheless, clonal propagation may have a cost, especially if clones spread over large areas, increasing the probability of geitonogamy and biparental inbreeding (Handel, 1985; Charpentier et al., 2000). Preliminary evidence indicate that the fecundity of genets is reduced when pollinators move pollen at distances below 20 m (Clark-Tapia, unpubl. data), and thus large genets may experience a reproductive cost.

Elasticity values of *S. eruca* at the genet and ramet level showed that $\lambda$ values were proportionally more sensitive to stasis and growth than the observed values for other cacti (Godınez-Alvarez et al., 1999; Esparza-Olguín et al., 2002). Silvertown et al. (1993) found that $\lambda$ values in long-lived plants were characteristically most sensitive to changes in stasis, followed by the growth of adult individuals. The high rate of survival of genets (100%) and ramets (99%) as well as continuous growth to later stages, is contributing to the importance of these two processes to population growth (as shown by elasticity analysis) in *S. eruca*.

*S. eruca* is considered as threatened under the Mexican legislation (NOM-059-ECOL-2001), and demographic studies can provide guidelines for conservation programs of this species. We did not record evidence of disturbance by illegal collection or habitat destruction due to agricultural development (the major threats according to Cancino et al., 1995) in our permanent plots, or in the area around each studied population. We did however observe evidence of plant burning and waste disposal in populations near human settlements (i.e., Poza Grande) and habitat destruction for agricultural development in the Villa Insurgentes-Ciudad Constitución agricultural area. Although these activities were not directly recorded in our demographic plots, we have observed evidence of disturbance that is very likely reducing and fragmenting the distribution of this narrow endemic species. *S. eruca* has a patchy distribution along a narrow coastal fringe ($20 \times 250$ km) and human disturbance is likely to be the major threat to these populations.

Molecular evidence (Clark-Tapia, 2000; Clark-Tapia et al., 2005) suggests that populations have moderate levels of genetic diversity and high levels of clonal diversity without any geographic pattern that could suggest the protection of particular areas of high diversity. Given that human disturbance is the major threat, and is likely to increase fragmentation in the near future, making *S. eruca* more vulnerable to extinction, we suggest the establishment of at least one reserve with protection from human disturbance. The Plains of Magdalena is one of CONABIO priority areas for conservation in Mexico (Arriaga et al., 2000). However, there is no current protection to any area in the

Plains of Magdalena (Breceda et al., 1995). Thus, we suggest that Estero Salinas could be a viable option for the conservation of *S. eruca* for two reasons: (1) It is the only large population (≈ 4700 ha) that is relatively isolated and where we have not observed human disturbance and (2) it is the only population where we have regularly observed sexual reproduction (fruit and seed production), and would therefore have the potential of generating new recombination, and maintaining genetic diversity. This population can be easily protected on a permanent basis and used as a source of plant material for restoration programs once disturbance has been reduced. Finally, we suggest the implementation of a program of environmental education in the region in order to reduce human disturbance and promote understanding of the Mexican legislation aimed at protecting threatened plants.

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