**CLONAL DIVERSITY AND DISTRIBUTION IN *STENOCEREUS ERUCA* (CACTACEAE), A NARROW ENDEMIC CACTUS OF THE SONORAN DESERT**

RICARDO CLARK-TAPIA,² CECILIA ALFONSO-CORRADO,³ LUIS E. EGUIARTE,⁴ AND FRANCISCO MOLINA-FREANEY²,⁵

³Instituto de Ecología-UNAM, Departamento de Ecología de la Biodiversidad, Estación Regional del Noroeste, Apartado Postal 1354, C.P. 83000, Hermosillo, Sonora, Mexico; ²Instituto de Ecología-UNAM, Departamento de Ecología Funcional, Apartado Postal 70-275, México, D.F. C.P. 04510, Mexico; and ¹Instituto de Ecología-UNAM, Departamento de Ecología Evolutiva, Apartado Postal 70-275, México, D.F. C.P. 04510, Mexico

*Stenocereus eruca* (Cactaceae), a prostrate cactus endemic to the Sonoran Desert, is thought to be highly clonal. We examined its clonal diversity and distribution: (1) at the population level, in four distinct populations along its distribution range; and (2) at a micro scale level, within a single population. Our objective was to evaluate the importance of sexual versus clonal recruitment through the use of RAPD markers. Contrary to previous field observations, clonal diversity was relatively high across the distribution range. This finding suggests that sexual recruitment is an important regeneration mechanism. The proportions of distinguishable genotypes ($G_{IN} = 0.83$) and genotypic diversity ($D = 0.987$) were greater than in other clonal cacti, suggesting that clonal propagation is not the major regeneration mechanism. Autocorrelation analyses revealed a spatial genetic structure that may be the result of restricted gene flow (via pollen or seeds) and clonal propagation. A molecular variance analysis (AMOVA) indicated that most of the variation (66.3%) was found within and not across populations. Future studies on pollen and seed dispersal are needed to understand the role of the clonal habit in the mating system of *S. eruca*.

**Key words:** Baja California; Cactaceae; clonal diversity; RAPD; spatial genet structure; Sonoran Desert; *Stenocereus eruca*.

Many perennial plants combine sexual reproduction and clonal propagation as population regeneration mechanisms (Abrahamson, 1980; Richards, 1997). In some clonal species the success of sexual vs. clonal recruitment often varies geographically in response to ecological and genetic factors that limit one regeneration mechanism or the other (Eckert, 2002). The demographic balance between sexual and clonal recruitment is likely to have important consequences for the clonal diversity and genetic structure of plant populations (Ellstrand and Roose, 1987; Eckert and Barrett, 1993). Seedling recruitment strategies in clonal species range from repeated seedling recruitment, or the establishment of seedlings on a regular basis, to initial seedling recruitment, their establishment only during the initial colonization of a site (Eriksson, 1993, 1997). The pattern of seedling recruitment influences the maintenance of genotypic diversity, as clonal diversity rapidly declines in the absence of new seedling input and selection (Watkinson and Powell, 1993). In contrast, even low rates of seedling recruitment are enough to maintain relatively high levels of genotypic variation within plant populations (Soane and Watkinson, 1979; Watkinson and Powell, 1993). For this reason, studies that document clonal diversity can be used to draw inferences about the role of sexual as compared to clonal recruitment in the regeneration of plant populations.

In arid environments, the population dynamics of many plant species vary considerably because of extreme temperatures and unpredictable rainfall events (Polis, 1991). In these environments, seedling recruitment of succulent species may occasionally be restricted to pulses during rare heavy rainfalls (Jordan and Nobel, 1979; Turner, 1990; Pierson and Turner, 1998), even when viable seeds are consistently produced (Fleming et al., 1996; Mandujano et al., 1998). In contrast, clonal propagation is often a successful mechanism of regeneration in populations of succulent species (Parker and Hamrick, 1992). Nonetheless, our knowledge about the clonal structure and the relative importance of clonal vs. sexual recruitment in clonal cacti is poor.

*Stenocereus eruca*, a clonal columnar cactus of the Sonoran Desert (Gibson, 1989; Turner et al., 1995), is an extremely narrow endemic species restricted to coastal areas of the Magdalena Plains in Baja California Sur, Mexico (Gibson, 1989), as shown in Fig. 1. The flowers of *S. eruca* are self-incompatible. Fruit set is generally low and highly variable in space and time because of pollinator limitation associated with variations in sphingid abundance (Clark-Tapia and Molina-Freaney, 2004). Because seedling recruitment has seldom been observed in natural populations of *S. eruca*, clonal propagation is thought to be the major regeneration mechanism (Gibson, 1989; Turner et al., 1995). A 3-yr demographic study of *S. eruca* suggests that sexual recruitment’s relative contribution to population growth rate ($\lambda$) is less important than that of clonal propagation (Clark-Tapia et al., in press). *Stenocereus eruca* is considered the “most extreme case of clonal propagation in the cactus family” (Gibson and Nobel, 1986). Clonal propagation occurs by detachment of branches from the major shoot as the base of the branch dies and rots. In *S. eruca*, the ramets (vegetatively produced modular units, Harper, 1977) of a genet (set of all products from a particular zygote) thus tend to detach and fragment. Therefore the genetic similarity among ramets can only be studied using genetic markers, namely iso-

---

¹ Manuscript received 2 March 2004; revision accepted 21 September 2004. The authors thank Teresa Valverde, Daniel Filoño, and two anonymous reviewers for critical comments on earlier versions of the manuscript, and Daniel Morales, Rocio Esteban, and Oscar Rodriguez for their lab and field assistance. Financial support was provided by SEMARNAT-CONACYT (0665/A1), PAPIIT-DGAPA-UNAM (IN-211997 and IN-205500), and a CONACYT and DGEP scholarship to Ricardo Clark-Tapia.

² Author for correspondence (E-mail: freaney@servidor.unam.mx).
zymes or DNA based markers. A previous isozyme study on the clonal diversity of *S. eruca* suggested that both sexual and clonal recruitment are important (mean $G/N = 0.53$) in the regeneration of its populations (Clark-Tapia, 2000). Isozyme evidence also showed moderate levels of genetic variation ($H_e = 0.158$, $P = 46.2$); substantial deviation from Hardy-Weinberg expectations ($f = 0.739$); low genetic differentiation among populations ($\theta = 0.069$); and no evidence of isolation by distance (Clark-Tapia, 2000). DNA-based markers usually have higher resolution power than isozymes. DNA-based markers thus allow a more precise characterization of genotypic diversity in clonal plant populations (Peaukkal et al., 1995; Ayres and Ryan, 1997). To analyze *S. eruca*’s clonal diversity and genetic structure, the present study used RAPD markers to: (1) evaluate the importance of sexual versus clonal recruitment in four populations of this clonal columnar cactus; and (2) describe the spatial distribution of genotypes in a single population and explore whether they have a random or aggregated distribution; and (3) describe the genetic structure of four populations.

**MATERIALS AND METHODS**

**Collection of genetic material**—To investigate the importance of sexual vs. clonal recruitment across populations, we selected four populations in the Magdalena Plains of Baja California. These specific populations were chosen in an effort to cover the entire distribution range of *S. eruca* (Fig. 1). For population-level surveys, we sampled 30 ramets along a 1200 m long transect in each of these four sites, collecting tissue samples every 30–40 m in order to cover each population in its entirety. To assess the spatial distribution of clones within a single population, we selected the Estero Salinas site because it had by far the largest population density (ca. 4500 ramets/ha), much than at the other sites. For a demographic study, all ramets within a 10 × 60 m plot at Estero Salinas have been tagged, numbered and mapped (Clark-Tapia et al., in press). All ramets within this plot ($N = 282$) were sampled and their exact locations recorded by measuring their distances from the plot margins.

With a cork borer, small (2–3 cm$^3$) samples of rib chlorenchyma were extracted from each selected ramet. Tissue samples were collected during November 2001 and were stored on ice for two d and then in a −70°C freezer for 30 d prior to DNA extraction.

**RAPD analysis**—Total genomic DNA was extracted using a modification of the Qiagen Plant Minikit method (Qiagen, Inc., Valencia, CA, USA; M. Sánchez-Hernández and R. Esteban-Jiménez, Instituto de Ecología UNAM, unpublished data). Tissue from rib chlorenchyma was frozen briefly in liquid nitrogen and ground with a mortar and pestle to a fine powder. Amplification reactions of the target DNA were carried out in a total volume of 23.3 mL $10 \times$ GibcoBRL buffer minus Mg (a mixture of 1.38 mL GibcoBRL buffer minus Mg at pH $= 8.4$, 0.05 mL of 1 mol/L MgCl$_2$, and 0.26 mL [0.1 mmol/L] of each Pharmacia (Uppsala, Sweden) dNTP). PCRs (polymerase chain reactions) were performed in a Techgene (Bethesda, Maryland, USA) thermal cycler programmed for one cycle of 5 min at 94°C, followed by 44 cycles of 1 min at 94°C, 1 min at 38°C, 30 s at 54°C and 2 min at 72°C. After the last cycle, a final extension step of 13 min at 72°C was carried out. Amplification products were separated electrophoretically on a 1.4% agarose gel with 0.5X TBE running buffer at 120 V for 2.5 h. Gels were stained with ethidium bromide and visualized under UV light. A digital camera recorded the images.

Using DNA test samples from the four different populations of *S. eruca*, 40 primers were screened with Operon Technologies, Inc. Kits A and G for reproducible amplification patterns. For each primer, the reproducibility and repeatability of the amplification profiles were tested three times with four random DNA samples from each population. Six informative and reproducible primers (A01, A10, A15, G03, G16 and G18) were identified, and only strong polymorphic bands between 350 and 2036 bp were used for data analysis. Control samples containing all the reaction materials except DNA were used to ensure that no self-amplification or DNA contamination had occurred. In the construction of the data matrix, all RAPD bands were scored as present (1) or absent (0).

**Data analysis**—Clonal diversity—Based on the scored RAPD banding patterns, putative genets were identified. To estimate clonal diversity, the following parameters were calculated for both the population-level and Estero Salinas surveys. (1) The proportion of distinguishable genotypes (Ellstrand and Roose, 1987) was measured as $G/N$, where $G$ is the number of genets and $N$ is the total number of individuals (ramets) sampled. (2) Simpson’s diversity index ($D$) modified for finite sample size by Pielou (1969), measures the probability that two ramets selected at random from a population of $N$ plants will be from different multilocus genotypes. This index thus yields a measure of multilocus genotype diversity. $D$ ranges from 0 to 1, with 1 being the maximum diversity. Each index value was calculated as:

$$D = 1 - \sum \frac{n_i(n_i - 1)}{N(N-1)}$$

where $n_i$ is the number of individual ramets of genotype $i$, and $N$ is the sample size. (3) Genotypic evenness (Fager, 1972) was measured as:

$$E = \frac{(D_{max} - D_{min})}{(D_{max} - D_{mean})}$$

where

$$D_{max} = \frac{(G-1)(2N-G)}{N(N-1)}$$

and

$$D_{mean} = \frac{(G-1)(N)}{[G(N-1)]}$$

where $G$ is the number of clones, and $N$ is the sample size. Index values can range from 0 for a population dominated by one genotype, to 1 for a population in which all genotypes are represented by the same number of ramets.

**Spatial genetic structure**—The data concerning band presence/absence in the RAPD analysis were used to determine genetic identity and examine the spatial distribution of genets at Estero Salinas. The spatial distribution in this population was evaluated by constructing a detailed map that identified the genet of each ramet and enabled the distribution and spatial extent of genets to be determined. Spatial autocorrelation analysis was performed on the basis of genetic similarity/dissimilarity in the RAPD banding patterns found among single ramets. The spatial autocorrelation was examined with a distance measure, namely the geographical distance, and Tanimoto’s genetic distance ($D_{tg}$), which is typically used with binary data such as fingerprints. This analysis was performed on 10 geographical distance classes (see Results section), using Spatial Genetic Software v.1.0c (Degen, 2001). To assess statistical significance and control the overall probability that we would mistakenly declare $D_{tg}$ significant, we used the 99% confidence intervals generated from 5000 permutations (Degen et al., 2001). We visually examined the spatial autocorrelation in the form of a correlogram that plotted $D_{tg}$ values, mean genetic distances, and the 99% confidence intervals as a function of geographic distance. If $D_{tg}$ (observed) is greater than the $D_{tg}$ (99% CI), then there is a significant autocorrelation at that distance class and therefore significant genetic structure (Degen et al., 2001). In addition, we analyzed the spatial genetic structure within Estero Salinas as a result of clonal propagation or isolation by distance through limited gene flow. Spatial Genetic Software v.1.0c (Degen, 2001) was used to perform spatial autocorrelations at both the genet and ramet levels (Reusch et al., 1999; Hangelbroek et al., 2002). At the ramet level, all 282 samples were included, while at the genet level only one ramet of each genet was taken at random from the field plot.

**Genetic variation**—The following estimates of variation were obtained using Tools for Population Genetic Analysis (TFPGA) software v.1.3 (Miller, 2000): percentage polymorphic loci ($P_s$), and expected heterozygosity ($H_e$). Because co-dominant markers (isozymes) revealed significant deviations from
Fig. 1. Distribution range (shaded area) of *Stenocereus eruca* in Baja California Sur, Mexico and locations of the four populations sampled in this study. Modified from Turner et al. (1995).

Hardy-Weinberg equilibrium predictions (Clark-Tapia, 2000), a molecular variance analysis, or AMOVA (Excoffier et al., 1992), was used to describe population structure where the variance was partitioned within and among populations. AMOVA determined the pair-wise genetic distances ($\phi_{st}$) among the four populations, as well as the significance levels of these distances. All the molecular variance analyses were performed with AMOVA-PREP v. 1.01 (Miller, 1998) or WINAMOVA v.1.55 (Excoffier et al., 1992; Excoffier, 1993). WINAMOVA generates $\phi_{st}$, a parameter analogous to Wright $F_{st}$ (an indicator for the degree of differentiation among populations), and thus facilitates comparison of results with those from other studies. $\phi_{st}$ was used to calculate the number of migrants per generation entering each population ($N_m$), using the formula $N_m = ((1/\phi_{st}) - 1)^{1/2}$, where $\alpha = (n\theta - 1); and $n$ is the number of subpopulations (Crow and Aoki, 1984). The TFPGA implementation of the Mantel test (Mantel, 1967; Miller, 2000) was used to correlate genetic and geographic distances among the four cacti populations in order to test for isolation by distance.

RESULTS

**Clonal diversity**—The population-level survey detected high clonal diversity. In the 30 ramets that we examined from each population, we obtained RAPD banding pattern variations that indicated a large number of distinct genets. The number of putative genets within each population ranged from
24 to 26 (Table 1). The proportions of distinguishable genets (G/N), genotypic diversity (D), and evenness (E) were generally high as well as similar across populations.

In the microscale survey at Estero Salinas, the clonal diversity was lower than in the population-level survey (Table 1). The 282 sampled ramets yielded 109 different putative genets. The mean proportion of distinguishable genets (G/N) within this site was 0.39. Estimates of Simpson’s diversity index (D) and evenness (E) were 0.940 and 0.907, respectively (Table 1).

**Spatial distribution**—The spatial distribution of genets at Estero Salinas is shown in Fig. 2. These genets had from 2 to 41 ramets, with a mean number of 2.4 ± 5.1 ramets (±1 SD), and 32% of the ramets had a different and unique putative genet. Most of the sampled ramets from a particular genet were growing close to each other in a clumped distribution (Fig. 2). However, we found several genets with an extensive distribution. The largest genets (numbers 15 and 17) had spread throughout the entire plot (600 m²). The greatest numbers of ramet pairs with identical RAPD band patterns were separated by distances between 0 and 20 m and the number of identical genets decreased as distance among pairs increased.

The correlogram of the 282 ramets from Estero Salinas revealed a significant positive spatial autocorrelation over distances <7 m and negative spatial autocorrelation >approximately 29 m (Fig. 3a). The correlogram and the 99% confidence intervals of Dg for the 109 genets show a similar pattern (Fig. 3b). Although the correlograms show similar spatial patterns at both the ramet and genet levels, with positive correlations at smaller spatial scales, it is important to note that the degree of relatedness (for example, the magnitude of Dg) differed markedly between the two levels. Compared to the genet level, the ramet level had relatively small significant values of Dg for the first two distance classes (<11 m, Fig. 3).

**Genetic variation**—From a total of 75 reproducible bands analyzed, 57 (76%) were polymorphic at the species level. The average percentage of polymorphic loci (Pp) among the four populations was 71.98 ± 7.09 (ranging from 63.79 to 81.03%), whereas in the single population at Estero Salinas it was 98%. The average genetic variation (H) among populations was 0.27 ± 0.02 (ranging from 0.25 to 0.30), while in the plot at Estero Salinas the average H value was 0.36 (Table 1). Pair-wise AMOVA showed highly significant (ϕst = 0.337, P < 0.002) genetic differentiation among the four populations of *S. eruca* (Table 2). The average migration per generation (Nm) was estimated to be 0.30. The Mantel test detected no evidence of isolation by distance, as genetic and geographical distances (in kilometers) among populations were not significantly correlated (r = 0.808, P = 0.158).

**DISCUSSION**

This study has shown that populations of *S. eruca* are composed of a number of different genets (that is, they are multiclonal) and are characterized by high levels of clonal diversity. In general, ramets sharing the same genotype were spatially aggregated (<20 m), while only a few genets were spread over larger distances. Significant levels of genetic variation were found within a single population, while substantial differentiation was observed among populations. Overall, the available evidence indicates that *S. eruca* combines sexual recruitment and clonal propagation as mechanisms of regeneration.

Contrary to our expectations, which were based on field observations (Gibson, 1989; Turner et al., 1995), clonal diversity was relatively high across the distribution range of *S. eruca*. This is a surprising result, as seedling recruitment has not been detected in the field and a demographic study currently in progress suggests that clonal propagation is the most important mode of regeneration (Clark-Tapia et al., in press). However, our findings of high clonal diversity levels are consistent with results from other short-term studies of plant species in which seedling recruitment has not been observed (Jonsson et al., 1996; Verburg et al., 2000; Hangelbroek et al., 2002). Without seedling recruitment, clonal diversity is expected to rapidly decline and populations to become dominated by a few large genets (Eriksson, 1993; Watkinson and Powell, 1993). Thus our evidence for high clonal diversity suggests that sexual recruitment is a very important mechanism of regeneration in *S. eruca* populations. Seedling recruitment, however, may be restricted to “narrow windows of opportunity” (Jenkinson and Cheliak, 1992; Eriksson and Fröborg, 1996) when favorable conditions occur during rare heavy rainfalls. Those pulses might be rare temporal and spatial events that are difficult to detect on the ecological time scale of demographic studies.

The parameters of genotypic diversity and evenness found in *S. eruca* were within the value ranges detected in isozyme studies of other clonal species (Ellstrand and Roose, 1987; Widén et al., 1994) and RAPDs (Hangelbroek et al., 2002). Our estimates of population-level clonal diversity were greater

---

<table>
<thead>
<tr>
<th>Population</th>
<th>N</th>
<th>Hs</th>
<th>Pp</th>
<th>Gs</th>
<th>G/N</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Population-level survey</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Poza Grande</td>
<td>30</td>
<td>0.253</td>
<td>61.90</td>
<td>24</td>
<td>0.800</td>
<td>0.986</td>
<td>0.864</td>
</tr>
<tr>
<td>Santo Domingo</td>
<td>30</td>
<td>0.279</td>
<td>71.43</td>
<td>25</td>
<td>0.833</td>
<td>0.986</td>
<td>0.743</td>
</tr>
<tr>
<td>San Carlos</td>
<td>30</td>
<td>0.272</td>
<td>71.43</td>
<td>25</td>
<td>0.833</td>
<td>0.986</td>
<td>0.743</td>
</tr>
<tr>
<td>Estero Salinas</td>
<td>30</td>
<td>0.301</td>
<td>77.78</td>
<td>26</td>
<td>0.867</td>
<td>0.991</td>
<td>0.791</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>0.277</td>
<td>70.64</td>
<td>25</td>
<td>0.833</td>
<td>0.987</td>
<td>0.785</td>
</tr>
<tr>
<td>SD</td>
<td></td>
<td>0.020</td>
<td>6.55</td>
<td></td>
<td>0.027</td>
<td>0.003</td>
<td>0.057</td>
</tr>
<tr>
<td>B) Micro scale survey</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estero Salinas</td>
<td>282</td>
<td>0.359</td>
<td>98.0</td>
<td>109</td>
<td>0.387</td>
<td>0.940</td>
<td>0.853</td>
</tr>
</tbody>
</table>

**Note:** N = number of individuals sampled per population; Hs = expected heterzygosity; Pp (99% criteria) = percentage of polymorphic loci; Gs = observed number of genotypes; G/N = proportion of distinguishable genotypes; D = genotype diversity; and E = genotype evenness.
than those obtained from isozyme studies of *Lophocereus schottii* (Cactaceae) (Parker and Hamrick, 1992). Thus we suspect that *S. eruca* is not really the "most remarkable case of clonal propagation in the cactus family" (Gibson and Nobel, 1986). These differences in clonal diversity may be attributable to the differences in the resolution power of isozyme vs. RAPD analysis, such as those we have detected for *S. eruca* (G/N = 0.53 in Clark-Tapia, 2000, compared to G/N = 0.83 in the present study). The difference in clonal diversity observed between our population level survey (G/N = 0.83) and our smaller-scale analysis (G/N = 0.39) revealed a scaling effect associated with the sampling scheme. Clonal diversity usually shows an association with the sampling scale and the sampling grid's size. This is because collecting larger numbers of ramets at finer spatial scales increases the probability that the same genets will be sampled repeatedly (Cheliak and Pitel, 1984; Widén et al., 1994).

Our data on the distribution of genotypes at Estero Salinas suggest that, in general, the ramets sharing the same genotype show a clumped distribution, while a few genets are widely distributed. Most ramet pairs with identical genotypes were
located at distances of <20 m. This pattern probably occurs because the growth and detachment of branches that fragments genets. The evidence on the spatial genetic structure suggests restricted gene flow (via pollen or seeds) due to isolation by distance, or clonal propagation owing to the intermingling of ramets (Fig. 3a, b). Because S. eruca is self-incompatible (Clark-Tapia and Molina-Freaner, 2004), pollen movement within distances less than 20 m is likely to reduce fruit and seed set (Handel, 1985; Trame et al., 1995; Charpentier et al., 2000). Future studies should address the spatial scale of pollen and seed dispersal in order to evaluate the role that the clonal habit plays in the mating system of S. eruca.

The differentiation and estimated migration among populations (θst = 0.337, Nm = 0.30) suggest restricted gene flow. Our estimates of genetic differentiation for S. eruca fall within the range that isozyme studies have generated for columnar cacti (Hamrick et al., 2002). Our estimates are also similar to those reported for RAPD analyses of other plant species (Nyborg and Bartish, 2000; Navarro-Quesada et al., 2003). If sexual recruitment is restricted to narrow windows of opportunity, seed-mediated gene flow among populations of S. eruca may be episodic, occurring with rare heavy rainfalls. Because S. eruca’s major pollinators show high temporal variation in their abundance (Clark-Tapia and Molina-Freaner, 2004), pollen-mediated gene flow may also be episodic, occurring during years of high sphingid activity. Thus the considerable differentiation observed among populations could be due to the episodic, variable reproductive schedule of S. eruca.

Mexican law considers Stenocereus eruca an endangered species (NOM-059-ECOL-2001), and field studies have identified habitat destruction from agricultural development and illegal collection as major survival threats (Cancino et al., 1995). Our evidence from isozyme (Clark-Tapia, 2000) and RAPD analyses has revealed that populations have significant levels of genetic variation without a clear geographical pattern (Table 1). In the field, we have observed increasing human disturbance, which will likely increase S. eruca’s habitat fragmentation and vulnerability to extinction (R. Clark-Tapia, unpublished data). Because human disturbance is likely to intensify in the Magdalena Plains, we recommend permanent protection for at least one population. Estero Salinas is probably the best candidate for setting aside as a reserve. It is far from human settlements, and it is the only population where we have regularly observed flowers and fruits, the signs of sexual reproduction (Clark-Tapia and Molina-Freaner, 2004). It is demographically stable, and its ramet density is high (Clark-Tapia et al., in press).

In summary, our data provide evidence that sexual recruitment is important to the regeneration of S. eruca populations. Studies on pollen and seed dispersal, as well as age estimates of genets, could further increase knowledge of S. eruca’s spatial genetic structure and perhaps elucidate the clonal habit’s role in the mating system of this species.

**Table 2.** Molecular variance analysis (AMOVA) summary for four population of *Stenocereus eruca*. The significance (P) of the θst test was based on 5000 permutations.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>Variance component</th>
<th>% of total variance</th>
<th>θst</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among populations</td>
<td>3</td>
<td>264.05</td>
<td>2.75</td>
<td>33.71</td>
<td>0.337</td>
<td>&lt;0.002</td>
</tr>
<tr>
<td>Within populations</td>
<td>116</td>
<td>628.13</td>
<td>5.41</td>
<td>66.29</td>
<td>n/a</td>
<td>n/a</td>
</tr>
</tbody>
</table>

P: significance; n/a: not applicable.

**LITERATURE CITED**


Excoffier, L., P. D. Smouse, and J. M. Quattro. 1992. Analysis of mo-


