

Population Dynamics of *Pterocereus gaumeri*, a Rare and Endemic Columnar Cactus of Mexico¹

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ABSTRACT

We conducted a demographic examination of *Pterocereus gaumeri*, a rare and endemic columnar cactus of the Yucatan peninsula, Mexico. Growth, survival, and fecundity of individuals were recorded in two populations from 1997 to 1999. Size-based population projection matrices were constructed to document the population dynamics. Seed germination and seedling establishment experiments were conducted in the field to estimate the rate of seed and seedling survival. Our results show that *P. gaumeri* did not reproduce by asexual means or vegetative growth and thus relies wholly on sexual reproduction for population growth. Low reproductive success, seed predation, and low seedling survival appear to be important factors that contribute to the rarity of this species. The population growth rate (λ) varied between 0.9545 and 1.0316. According to the matrix elasticity values, population dynamics of this species depend mainly on adult survival, with low values in fecundity and survival for the lowest size categories. Our results did not indicate that the population size of *P. gaumeri* was decreasing; however, increasing pressure on land use transformation is one of the most important factors that may threaten the persistence of this species.

RESUMEN

Se presenta un estudio demográfico de *Pterocereus gaumeri*, un cactus raro, y endémico columnar de la Península de Yucatán, México. Desde 1997 a 1999, se registró el crecimiento, la sobrevivencia y la fecundidad de individuos en dos poblaciones. Se construyeron matrices de proyección basadas en tamaño poblacional para documentar la dinámica de las poblaciones. Se realizaron experimentos de germinación de semillas y establecimiento de plántulas en condiciones naturales, para estimar la tasa de sobrevivencia de semillas y plántulas. Nuestros resultados sugieren que *P. gaumeri* no se reproduce asexualmente o por crecimiento vegetativo, por lo tanto el crecimiento poblacional depende completamente de la reproducción sexual. El bajo éxito reproductivo, la depredación de semillas y la baja tasa de sobrevivencia parecen ser factores importantes que contribuyen a la rareza de esta especie. La tasa de crecimiento poblacional (λ) varía entre 0.9545 y 1.0316. De acuerdo con los valores de la matriz de elasticidad, la dinámica poblacional de esta especie depende principalmente de la sobrevivencia de los adultos, con valores bajos en fecundidad y sobrevivencia de las categorías de tamaños menores. Nuestros resultados no indican que el tamaño poblacional de *P. gaumeri* esté decreciendo, sin embargo, el incremento de presión por el cambio de uso de la tierra es uno de los factores más significativos que puede amenazar la continuidad de esta especie.

Key words: elasticity analysis; endemic cacti; plant demography; population dynamics; *Pterocereus gaumeri*; rare species.

THE CONCEPT OF RARITY is associated with abundance, distribution, habitat specificity, and taxon persistence (Harper 1981, Rabinowitz 1981, Fielder & Ahouse 1992, Gaston 1994). The study of rarity is important because the risk of extinction for rare species is generally high (Wilson 1988, Fielder & Jain 1992, Harrison 1993) and the number of species at such risk is increasing as the rate

of disturbance and destruction of natural ecosystems intensifies.

Demographic studies are an important tool to evaluate the current status of rare species and their populations because the processes of birth, mortality, reproduction, and migration allow us to quantify the regenerative potential of a species (Schemske *et al.* 1994, Martínez-Ramos & Alvarez-Buylla 1995). Information on variation in population size can be used to determine which is the most vulnerable stage in the life cycle and predict the fate

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of the population in time and under different ecological conditions (Schemske *et al.* 1994, Olmsted & Alvarez-Buylla 1995, Esparza-Olguín *et al.* 2002). Demography and population dynamics of many plants have been studied intensively in the last 20 years (Oyama 1993, Silvertown *et al.* 1993, Olmsted & Alvarez-Buylla 1995). Most of these studies, however, have focused on dominant, abundant, or common species (Franco & Silvertown 1990). Due to the limited number of demographic studies on rare species, life history patterns of related common species are sometimes used to make generalizations about unstudied rare species (Byers & Meagher 1997).

Among vascular plants, the Cactaceae has a high proportion of rare and endangered species. The entire family has been included in the Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) and 45.7 percent of total cactus species are listed in the Red Data Book as rare, threatened, or in danger of extinction (Walter & Gillett 1998). Many cactus species have very low recruitment rates via seeds or ramets; also, they possess low growth rates, long life cycles (Steenberg & Lowe 1983, Valiente-Banuet & Ezcurra 1991, Nobel 1994), restricted geographic distribution, and small population sizes (Hernández & Godínez 1994). Mexico is the most important center of diversification for Cactaceae; 850 of the almost 2000 total species are found in Mexico and 84 percent of them are endemic to Mexico (Bravo-Hollis & Sánchez-Mejorada 1978, 1991; Arias-Montes 1993). Surprisingly, there have been few demographic studies of cactus species even though there is great interest in conserving and managing these species.

One of the endangered species in Mexico is the rare and endemic columnar cactus *Pterocereus gaumeri* (Britton & Rose) MacDougall & Miranda (Walter & Gillett 1998). It has a very restricted distribution range on the Yucatan peninsula and low population densities (*ca* 100 adult plants/ha), compared with other co-occurring columnar cacti (*Stenocereus laevigatus*: 400 adult plants/ha; *Pilosocereus gaumeri*: 165 adult plants/ha [M. Méndez, pers. obs.]) and columnar cacti from different areas, (*Neobuxbaumia tetetzo*: 1500–2000 plants/ha in the Tehuacan Valley [Valiente-Banuet & Ezcurra 1991]). We conducted a demographic study to examine the dynamics of this rare species as a fundamental step toward the development of management and conservation programs for this species (Harvey 1985, Lande 1988, Mehrhoff 1989, Oyama 1993, Schemske *et al.* 1994). The main objec-

tives of this study were to: (1) contribute to the information base on rare plants by describing the demographic patterns of *P. gaumeri*; (2) define the importance of each stage of the life cycle and each demographic parameter of the population growth rate; and (3) determine the demographic traits that explain the rarity of this species.

MATERIALS AND METHODS

THE SPECIES.—*Pterocereus gaumeri* (Britton & Rose) MacDougall & Miranda is a rare and endemic columnar cactus with a restricted distribution in lowland deciduous forests in the northern portion of the Yucatan peninsula, Mexico. Individual height is up to 8 m and the trunks are ramified after reaching 2 m in height. Bravo-Hollis (1978) described this species as having four ribs, but we found individuals with up to seven ribs; when young, the plants have a single trunk with three ribs. Flowers are *ca* 5 cm long and are yellow-green or cream colored. The flowering peak is in March. Anthesis occurs at night and flowers are pollinated by bats. The red globose fruit is 3–4 cm in diameter with many black seeds and is presumably dispersed by birds.

The genus *Pterocereus* is at the base of the phylogeny of the columnar cacti of North America (Buxbaum 1958, Gibson & Horak 1978). *Pterocereus* has been assigned to the tribe Pachycereeae, and it has been suggested that extinct ancestors of that tribe may have been related to ancestors of the tribe Leptocereeae, which is distributed in the northern portion of South America, Central America, and the Antilles (Bravo-Hollis 1978).

STUDY AREA.—A 1 ha permanent plot was established in both Chumhabin (21° 18' N; 89° 10' W) and San Antonio (21° 18' N; 89° 19' W) localities in the northern part of the Yucatan peninsula, Mexico (Fig. 1). This area has an annual mean temperature of 26°C with a maximum of 40°C and a minimum of 11°C; the average annual precipitation is 528.5 mm. The dry season is from February to May and the rainy season is from June to January, which contributes 71 percent of the total annual precipitation. Litosol with redzina soils predominate with some calcareous rocks in a flat terrain; the elevation is below 10 m (Lugo & García 1999) and the soils are shallow and patchily distributed.

The vegetation of both study areas is low deciduous forest (*sensu* Holdridge 1967) or low deciduous forest with columnar cacti (Miranda & Her-

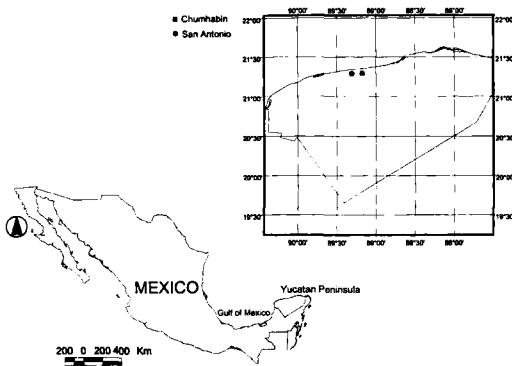


FIGURE 1. Location of study sites, in the northern part of the Yucatan Peninsula, Mexico. A 1 ha permanent plot was established in both Chumhabin and San Antonio.

nández-X. 1964). Dominant trees are *Acacia gauderi*, *A. pringlei*, *Bursera simaruba*, *Guaiacum sanctum*, *Lysiloma latisiliquum*, *Metopium brownei*, *Malpighia glabra*, and *Vitex gaumeri*. Many species in these forests are endemic and several other cactus species also occur, such as *Acanthocereus pentagonus*, *Stenocereus laevigatus*, *Nopalea gaumeri*, *N. inaperta*, *Mammillaria gaumeri*, *Opuntia stricta*, *Hylocereus undatus*, and *Selenicereus donkelaarii* (Durán *et al.* 1998).

At the end of the 19th century and during the first half of the 20th, a large portion of the dry tropical forest was used for cultivation of henequen (*Agave fourcroydes* Lem.). This activity has declined considerably and the fields have either been abandoned or burned prior to current use for cattle ranching (González-Iturbe *et al.* 2002). In Chumhabin, the forest is generally less than 8 m tall and the vegetation has not been cut for at least 40–50 years. The study area is surrounded with lands dedicated to cattle ranching; however, the forest has been protected from cattle perturbation and there is no sign of cattle presence within the forest.

In San Antonio, the vegetation is *ca* 12 m high and probably had not been cut for previous henequen cultivation. This area has been dedicated to cattle ranching for *ca* 100 years. A common practice of the ranching activity consists of letting the animals graze in open areas while providing access to forested areas where they can browse and find shade.

DEMOGRAPHIC DATA.—Each plot was divided into quadrats of 100 m² (10 × 10 m) and all individual plants were located, tagged, mapped, and monitored for three years (1997–1999). The total length

of each plant was determined with a measuring tape. When a plant had a several branches, the length of each branch was measured from its point of attachment and then added to the length of the main stem to give a measure of total stem length. Growth and survivorship were recorded on March 1997, 1998, and 1999. During the reproductive seasons (January–June) of 1998 and 1999, every two weeks, the numbers of flowers and immature and mature fruits produced per plant were recorded. The probability of reproduction for both populations was defined as the proportion of individuals that reproduced each year in relation to the total. Fruit set was defined as the number of mature fruits in relation to the number of flowers produced and reproductive success was defined as the proportion of individuals that produced mature fruits. To estimate the mean number of seeds produced per fruit, 30 fruits outside of the study site were collected in 1997. Fruits were produced at the beginning of the rainy season in June. After dispersal seeds were difficult to find, and because they have around five months of viability (M. Méndez, pers. obs.), the seed stage was not included in the population projection matrix; it seems that *Pterocereus gaumeri* does not form a long-term seed bank as is the case for other columnar cacti (Godínez-Alvarez *et al.* 1999, Esparza-Olguín *et al.* 2002).

GERMINATION AND SEEDLING ESTABLISHMENT.—In August 1998 during the rainy season, seed germination experiments were conducted in the field. For 200 replicate plots, 30 one-month old-seeds were placed on the ground in 10 cm quadrats on a side and locations were tagged and mapped. Half of the seed plots were protected from predators with 5 mm wire mesh cages (15 × 15 × 10 cm), which were partially buried in the soil. To exclude ants in the protected plots, chlordane was applied to the soil on the periphery of each plot every week. The remaining 100 plots were sown without protection, and no insecticide was applied. During the first month, germination was recorded weekly, and then every two weeks until no further germination occurred. Five additional groups of 30 seeds each were simultaneously germinated in a germination chamber to test viability; the seeds were placed in petri dishes with expanded perlite as the substrate. The chamber's day/night temperature was 35/30°C with a 12-hour photoperiod and the perlite was kept moist with weekly watering.

Seedlings from the unprotected germination experiment were followed for one year in the field.

TABLE 1. Size categories used to describe the population dynamics of *Pterocereus gaumeri*.

Size category	Total length (cm)
1	0.1–1.0
2	1.1–5.0
3	5.1–10.0
4	10.1–25.0
5	25.1–50.0
6	50.1–100
7	100.1–200
8	200.1–300
9	300.1–400
10	>400

During the first month, seedling survival was recorded weekly, and then every 50 days.

POPULATION PROJECTION MATRICES.—For the construction of population projection matrices, we defined ten size categories according to the total length of the plant (Table 1). Four Lefkovich (1965) transition matrices were constructed, one for each time period (1997–1998 and 1998–1999) and one per population, to estimate probabilities of survival, growth, and fecundity (Caswell 1989). The permanence and transition probabilities for each size class were estimated by calculating the relative frequencies of each observed transition, including regressions to smaller size categories and death.

We used the probability of germination in the unprotected treatment with the information of seed production to calculate the fecundity matrix component, which we defined as the mean number of seedlings produced per adult plant in each size class ($F = \text{number of seeds per plant} \times \text{seed germination probability}$).

The survival and transition probabilities from the first to the second size category were calculated from the unprotected germination experiment by counting the number of seedlings alive after one year with respect to the initial number.

Finite population growth rate (λ) along with the stable size structure (w) and the reproductive value associated with each of size categories (v) were estimated by iteration using the computer program Gauss. The analytical method proposed by Alvarez-Buylla and Slatkin (1994) was used for estimating the 95 percent confidence intervals for λ .

A sensitivity analysis ($s_{ij} = \partial\lambda/\partial a_{ij}$) was performed to measure how the changes in each matrix entry could modify the rate of population growth. A measure of the proportional sensitivity was given

by the elasticity ($e_{ij} = a_{ij}/\lambda \times s_{ij}$), which determines what the relative effect of a proportional change in any matrix element may be on the population growth (de Kroon *et al.* 1986). Four elasticity matrices were constructed, one for each study period (1997–1998 and 1998–1999), and one per population (Chumhabin and San Antonio). To determine the relative importance of each demographic process to the maintenance and growth of the studied populations, the elasticity values for each demographic process were summed following the criteria of Silvertown *et al.* (1996).

DATA ANALYSIS.—Two log-linear analyses were used to test the demographic differences between populations and among different times by comparing the complete transition matrices (Caswell 1989, Ehrlen 1995, Horvitz & Schemske 1995, Valverde & Silvertown 1998). A three-way contingency table was constructed to compare the observed size class structures between the two populations (Chumhabin and San Antonio) and among the three census dates (March 1997, 1998, and 1999); a four-way contingency table was constructed to examine the effects of year, population, and initial size category on the fate of the individuals, where death was included as a fate, fecundity was excluded, and a 0.5 constant was added to all of the entry cells of the table (Silva *et al.* 1990).

Differences between the population structures were tested using the log-likelihood ratio G , which is a more robust test than χ^2 (Zar 1999). To compare the mean germination percentage, we used an ANOVA after an arcsine transformation for linearity. Seedling survivorship curves for each condition were compared through the Peto and Peto analysis (Pyke & Thompson 1986, Esparza-Olguín *et al.* 2002) to test the significance of predation on the probability of germination.

RESULTS

GERMINATION AND SEEDLING ESTABLISHMENT.—The mean percentage of germination obtained in the laboratory was 97.3 percent; all seeds germinated within two weeks after sowing. Germination in the field was much lower. During August and September 1998, germination in the protected treatment was significantly higher (33.7%) than in the exposed treatment (1.7%; $F_{1, 198} = 110.97$, $P < 0.001$). After one year, 88 percent of the seedlings died in the exposed treatment as opposed to 64 percent in the protected treatment (Fig. 2; $LR = 11.90$, $df = 1$, $P < 0.01$). One-year-old seedlings

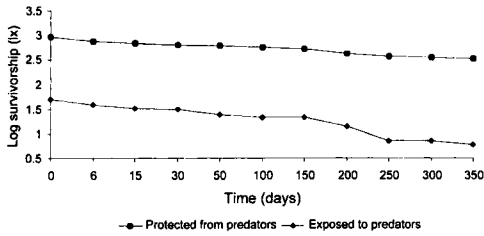


FIGURE 2. Survivorship curves (log I_x) for seedlings in protected and unprotected treatments.

in both treatments grew to an average height of 38 mm.

DEMOGRAPHIC PARAMETERS.—The Chumhabin population, which had 701 individuals in the first census (1997), had a density 3.2 times greater than that of San Antonio (222 initial individuals). Population structures of both areas, however, were very similar ($\chi^2 = 9.8692$, $df = 8$, $P = 0.7256$). Also, population structures did not change significantly during the three-year study ($\chi^2 = 10.826$, $df = 16$, $P = 0.1799$). Almost 80 percent of the individuals were concentrated in the first four size categories (Fig. 3).

During 1997–1998 and 1998–1999 for both populations, the highest probability of death was for newly germinated seedlings (seedlings up to 1 cm height, size category 1; Table 1), followed by categories 2 and 3. After plants reached more than 10 cm height (category 4), the probability of dying was lower (Fig. 4). The mortality pattern was similar for both populations ($\chi^2 = 0.105$, $P > 0.05$) and both years ($\chi^2 = 0.12$; $P > 0.05$).

The smallest plants that reproduced were 110 cm tall (category 7). In Chumhabin during 1998, only plants in size categories 8 and 10 reproduced; however, all adult plants (categories 7–10) produced mature fruits the following year. In contrast, in San Antonio, only plants in category 10 reproduced during both years (Table 2). Of the 132 flowers censused during 1998 in Chumhabin, 73 produced immature fruits and only 11 produced mature fruits, resulting in a fruit set of 8.3 percent relative to the total number of flowers produced. In the same year, of the 108 flowers produced in San Antonio, 84 produced immature fruits but only 2 fruits attained maturity, resulting in a fruit set of 1.9 percent. For 1999 in Chumhabin, the number of flowers produced was 254, more than double that of 1998; from this, 174 become immature fruits and 61 reached maturity, resulting in a fruit set of 24.0 percent. In San Antonio, of 83

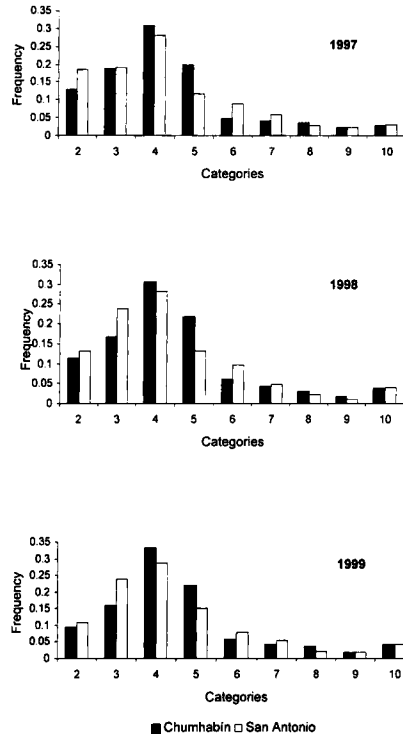


FIGURE 3. Frequency (%) of individuals observed in each size category for 1997, 1998, and 1999, in Chumhabin and San Antonio. Category 1 is not included because few seedlings were observed in the field during the study period.

flowers produced, 27 became immature fruits and only 2 fruits reached maturity, resulting in a fruit set of 2.4 percent. The mean number of seeds per fruit was *ca* 350.

MATRIX ANALYSIS.—Only one population's finite rate of increase (λ) was above unity (1.032; Chumhabin 1998–1999); the other three values were slightly below unity (Table 3). The 95 percent con-

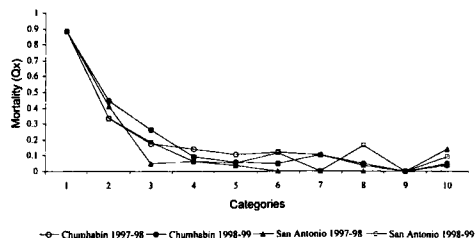


FIGURE 4. Mortality (Q_x) for each size category during 1997–98 and 1998–99 in Chumhabin and San Antonio.

TABLE 2. Reproductive behavior of *Pterocereus gaumeri*. Reproductive success was defined as the proportion of adults that contributed seeds (mature fruits) to the population.

Size categories	Chumhabin				San Antonio			
	7	8	9	10	7	8	9	10
1998								
Adults in each category (<i>N</i>)	30	26	16	20	13	6	5	7
Reproductive individuals (%)	10	42	75	40	8	50	40	100
Reproductive success	0	0.36	0	0.25	0	0	0	0.14
1999								
Adults in each category (<i>N</i>)	30	21	13	27	13	6	3	11
Reproductive individuals (%)	13	38	77	74	31	0	100	73
Reproductive success	0.5	0.38	0.5	0.4	0	0	0	0.13

fidence intervals of the four matrices (Chumhabin for 1997–1998 and 1998–1999; San Antonio for 1997–1998 and 1998–1999) indicated that the λ values did not differ significantly from 1 (Table 3). The lowest λ value (0.954) occurred in San Antonio during 1998–1999.

The log-linear analysis of the complete transition matrices indicated that the effect of the population ($\chi^2 = 74.82$, $df = 180$, $P = 0.99$) and the year ($\chi^2 = 46.09$, $df = 180$, $P = 0.99$) on the fate of individuals was not significant; however, the initial size category had a significant effect on the fate of individuals ($\chi^2 = 3280.79$, $df = 390$, $P < 0.001$).

For Chumhabin during 1998–1999, the stable size category structure indicated that most individuals were concentrated in the seedling stage (size category 1), whereas for Chumhabin during 1997–1998 and for San Antonio during both periods, the distribution of individuals was concentrated in both the first (seedling) and the last (adult) size categories (Fig. 5). The observed population structures differed significantly from the stable structures for both Chumhabin (1997–1998: $G = 609.83$, $df = 9$, $P < 0.005$; 1998–1999: $G = 748.15$, $df = 9$, $P < 0.005$) and for San Antonio (1997–1998: $G = 130.69$, $df = 9$, $P < 0.005$; 1998–1999: $G = 247.54$, $df = 9$, $P < 0.005$). For Chumhabin during both time periods and for San Antonio during 1998–1999, the lowest size-specific reproductive values occurred for the smallest size categories, and the highest values occurred for size categories 7–10 (reproductive individuals).

ELASTICITY ANALYSIS.—The highest values of elasticity corresponded to the survival of categories 7–10 (reproductive individuals). For all four elasticity matrices, category 10 had one of the two highest values, the other corresponding to category 7, 8, or

9, depending on the year or site, whereas categories 1–3 had the lowest values (Table 4). Fecundity had the lowest values in all four elasticity matrices. For both populations and both years, the demographic process of greatest importance in the determination of the population growth rate was survival of the individuals (Fig 6).

DISCUSSION

In its narrow sense, rarity implies limited abundance or distribution (Gaston 1994); however, species that are considered rare can exist within a vast range of abundance and distribution. Rabinowitz (1981) identified seven forms of rarity distinguished by differences in local abundance, geographical range, and habitat specificity whereas Fiedler and Ahouse (1992) proposed an alternative scheme with four classes of rare plants based upon differences in spatial distribution and taxon persistence. *Pterocereus gaumeri* has a limited distribution (restricted to the low deciduous forest with columnar cacti of Yucatan, Mexico) and a lower density (*ca* 100 plants/ha) than other columnar cacti from the same area (*e.g.*, *S. laevigatus* with 400 plants/ha and *Pilosocereus gaumeri* with 165 plants/ha).

In contrast to other columnar cacti such as *S. laevigatus* and *Pilosocereus gaumeri*, *Pterocereus gaumeri* did not reproduce by asexual means or vegetative growth and thus relies wholly on sexual reproduction for population growth. In both populations, *Pterocereus gaumeri* lost immature fruits by abortion and predation. Consequently, plants of *Pterocereus gaumeri* had very low reproductive success. The fruit set (1.9–24%) was lower than that reported for other columnar cacti such as *Carnegiea gigantea* (48%; McGregor *et al.* 1962), *Pilosocereus mortizianus* (46%), *Subpilosocereus horrispinus* (50%), *Stenocereus griseus* (76 and 82%), *Subpi-*

TABLE 3. Population projection matrices and results of the matrix analysis for *Pterocereus gaumeri*; w is the stable size structure and v is the size-specific reproductive value; number of individuals in each size category is given. Diagonal matrix elements are in bold and fecundity entries are in script to facilitate reading.

	1	2	3	4	5	6	7	8	9	10	w	v
Chumhabin												
1997-1998	0.0000						0.0000	7.0895	0.0000	1.7281	0.4519	0.0016
$\lambda = 0.9626 \pm 0.067$	0.1176	0.3803	0.0687	0.0046	0.0216	0.0303					0.1003	0.0132
		0.2864	0.1504	0.0648							0.0413	0.0268
			0.6053	0.5026	0.0935	0.1212	0.0333				0.0749	0.0347
				0.2891	0.4989	0.0606	0.0333		0.0625		0.0530	0.0486
					0.2780	0.4829					0.0307	0.0685
						0.1838	0.6709	0.0769			0.0220	0.1378
							0.1624	0.5733	0.0625		0.0100	0.2305
								0.3113	0.3816		0.0054	0.2176
									0.4934	0.9500	0.02105	0.2208
N	51	90	131	216	139	33	30	26	16	20		
1998-1999	0.0000						1.5361	5.7602	37.6628	25.6009	0.6916	0.0008
$\lambda = 1.0316 \pm 0.140$	0.1176	0.3032	0.0869	0.0047	0.0067	0.0238					0.1165	0.0073
		0.2481	0.0639	0.0566	0.0333	0.0952	0.0333				0.0348	0.0214
			0.5883	0.3811	0.0800	0.1191	0.0333				0.0410	0.0342
				0.4633	0.4759	0.0667	0.0667				0.0413	0.0453
					0.3441	0.4631					0.0250	0.0630
						0.2512	0.5693	0.0370			0.0148	0.1062
							0.1973	0.7191	0.1539		0.0140	0.2176
								0.2333	0.4592		0.0057	0.2709
									0.3870	0.8889	0.0155	0.2333
N	51	90	131	216	139	33	30	26	16	20		
San Antonio												
1997-1998	0.0000						0.0000	0.0000	0.0000	1.6458	0.2857	0.0061
$\lambda = 0.9710 \pm 0.109$	0.1176	0.2576	0.0952	0.0484							0.0501	0.0503
		0.3278	0.1029	0.0484							0.0222	0.1095
			0.7543	0.6103	0.0385	0.1500					0.0593	0.1197
				0.2768	0.7724	0.6069					0.1202	0.1368
					0.1507	0.2431					0.0497	0.1498
							0.8800	0.07500			0.1329	0.1399
							0.1200	0.2500			0.0722	0.1060
									0.5100		0.0392	0.0937
									0.4900	0.8571	0.1686	0.0882
N	51	41	42	62	26	20	13	6	5	7		

TABLE 3. Continued.

	1	2	3	4	5	6	7	8	9	10	w	v
1998–1999	0.0000						0.0000	0.0000	0.0000	1.0473	0.3000	0.0049
$\lambda = 0.9545 \pm$	0.1176	0.3319	0.0154	0.0130							0.0582	0.0401
0.191		0.3347	0.0575	0.0520		0.0385					0.0262	0.0746
			0.7425	4461		0.0385					0.0419	0.0893
				0.4240	0.6153	0.0769					0.0632	0.0967
					0.3292	0.5200	0.7492				0.0479	0.0996
						0.2108	0.2508				0.0492	0.1401
								0.6333			0.0384	0.1147
								0.2033	0.6333	0.0909	0.1017	0.1812
									0.3666	0.8181	0.2734	0.1587
N	51	36	65	77	36	26	13	6	3	11		

losocereus repandus (49 and 100%; Petit 1995, Nasar *et al.* 1997), *Pachycereus pringlei* (50%; Fleming *et al.* 1994), and *Stenocereus stellatus* (71%; Casas *et al.* 1999).

Seed predation played a fundamental role in the low recruitment of new individuals of *Pterocereus gaumeri* to the population. Granivores removed a high percentage of seeds (*ca* 95%), similar to data reported for *Neobuxbaumia tetezzo* (Valiente-Banuet & Ezcurra 1991). In *Pterocereus gaumeri*, like other species in dry deciduous forests, flowering and fruiting of plants occur during the dry season, and fruit maturation and seed dispersal are synchronized at the beginning of the rainy season; however, the percentage of germination obtained in the field (33.7% for a predator-protected site and 1.7% in an unprotected site) was much lower than that under laboratory conditions (97.3%). In addition to high seed predation, high seedling mortality was another factor that contributed to the limited abundance of *Pterocereus gaumeri*. After one year, only 6 experimental seedlings of 3000 seeds sowed in the field survived. High solar radiation, extreme temperatures, and soil moisture evaporation may have contributed greatly to the low germination and survivorship of seedlings (Nobel 1980, 1994; Franco & Nobel 1989; Valiente-Banuet *et al.* 1991; Godinez-Alvarez *et al.* 1999; Esparza-Olguín *et al.* 2002). In *Pterocereus gaumeri*, low reproductive success, large seed predation, low seed germination, and low seedling survival appear to be strong factors that contribute to the rarity of this species, as in other rare cacti (Contreras & Valverde 2002, Esparza-Olguín *et al.* 2002).

The highest mortality rates in seedlings and saplings (categories 1–4) were recorded during the dry season (February–May) when plants are subjected to extreme temperatures (35.5–43.5°C) and drought (< 61 mm of rain). During this period, almost all tree species lose their foliage in these forests (Olmsted *et al.* 1999). Once an individual has reached more than 10 cm height, its chance of survival is high. Although they have the capacity to regenerate a portion of the stem or new branches, stem damages by insects can transmit bacterial or fungal infections that may damage and kill a plant within a few months (M. Méndez, pers. obs.). Similar causes of death have been reported in the “pitaya” (*H. undatus*) when areoles are infected by the fungus *Dothiorella* sp. The fungal infection combined with a bacterial infection by *Erwinia carotovora*, transmitted by a hemipteran *Leptoglossus* sp., can damage the vascular bundles and kill the plant (Chi-May 1998).

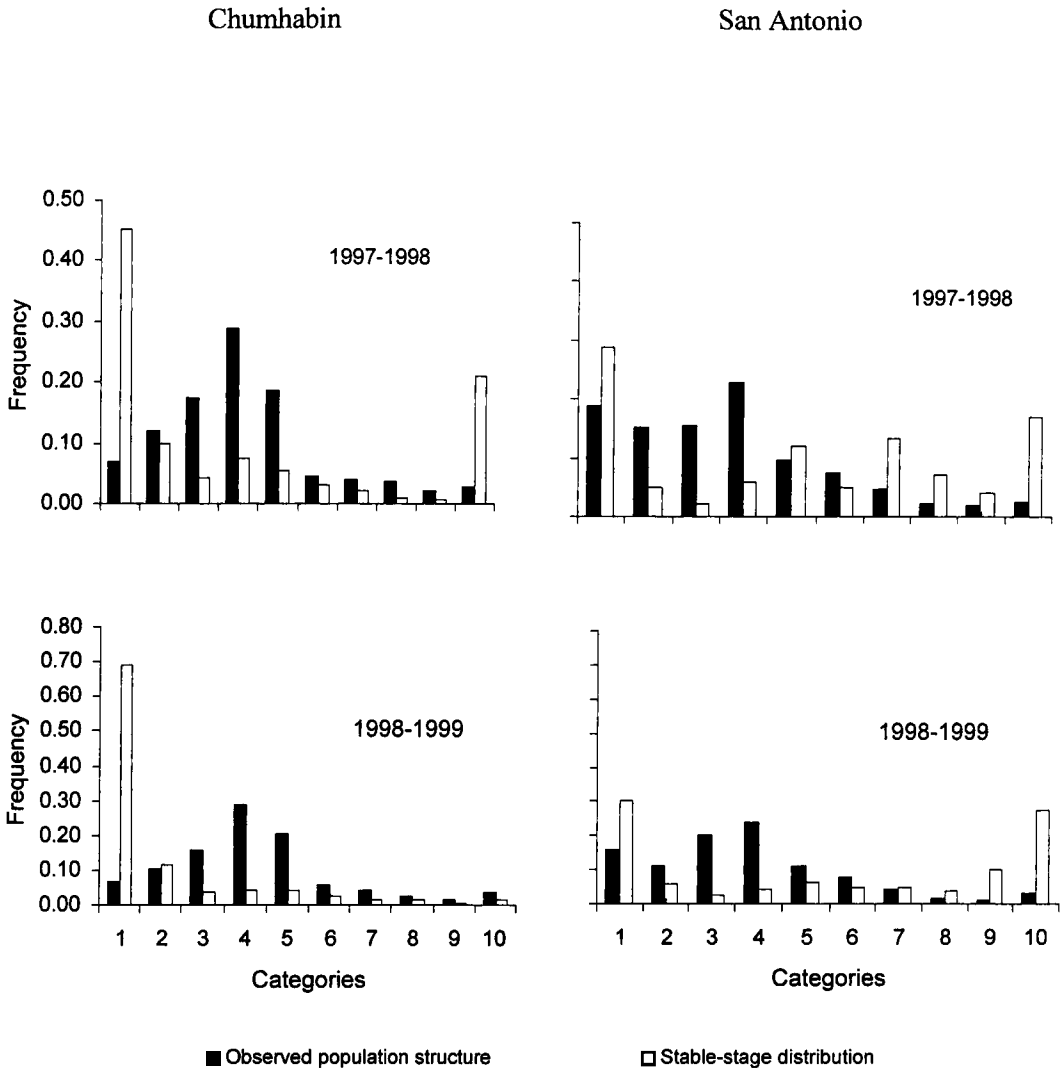


FIGURE 5. Observed population structures and calculated stable-stage distributions during 1997–98 and 1998–99 for Chumhabin and San Antonio.

The results of the matrix analysis indicated that the population growth rates were not significantly different from unity and thus the population sizes were in equilibrium. In general, long-lived species have λ values close to unity, including columnar cacti like *C. gigantea* (Pierson & Turner 1998), *N. tetezo* (Godínez-Alvarez *et al.* 1999), *Neobuxbaumia macrocephala* (Esparza-Olguín *et al.* 2002), and other cactus species like *Coryphantha robbinsorum* (Schamalzel *et al.* 1995).

There were no significant differences between the matrices, which summarized the demographic parameters behavior even though there was a large

difference in population density. This may indicate that the observed similar demographic processes are a response to similar selective pressures on specific life cycle phases. On the other hand, there were large differences between the observed and the stable structures of both populations, which may be reasonable considering matrix models predict long-term stable population structures, something that may not be compatible with environments as variable as the low deciduous forests in which *Pterocereus gaumeri* occurs.

According to the matrix elasticity values, population dynamics of *Pterocereus gaumeri* depend

TABLE 4. Elasticity matrix of *Pterocereus gaumeri*. The highest values in each matrix are in bold. Only nonzero entries are represented to facilitate reading.

	1	2	3	4	5	6	7	8	9	10
Chumhabin										
1997-1998										
1	0.0000									
2	0.0115	0.0082	0.0006	0.0001	0.0003	0.0002		0.0019		0.0096
3		0.0126	0.0027	0.0021	0.0028	0.0021	0.0004			
4			0.0141	0.0212	0.0211	0.0015	0.0006		0.0003	
5				0.0172	0.0165	0.0166				
6					0.0127	0.0333				
7							0.0017			
8							0.0135	0.0217	0.0013	
9								0.0111	0.0073	
10									0.0096	
1998-1999										
1	0.0000									
2	0.0343	0.0149	0.0013	0.0001	0.0017	0.0007		0.0039		0.0190
3		0.0358	0.0028	0.0029	0.0010	0.0006				
4			0.0404	0.0308	0.0065	0.0047	0.0010			
5				0.0497	0.0514	0.0078	0.0026			
6					0.0517	0.0421				
7						0.0385	0.0517			0.0035
8							0.0367	0.1264	0.0110	0.0072
9								0.0511	0.0410	
10									0.0297	0.1851
San Antonio										
1997-1998										
1	0.0000									
2	0.0211	0.0081	0.0013							0.0211
3		0.0225	0.0031	0.0039						
4			0.0251	0.0541	0.0069					
5				0.0280	0.1587	0.0128				
6					0.0339	0.0565				
7						0.0211	0.2044			
8							0.0211	0.0717		
9								0.0211	0.0234	
10									0.0211	0.1591
1998-1999										
1	0.0000									
2	0.0159	0.0087	0.0002	0.0002						0.0159
3		0.0163	0.0013	0.0018						
4			0.0195	0.0187						
5				0.0421	0.0421	0.0015				
6				0.0192	0.0232	0.0019				
7						0.0278				
8						0.0159	0.0579	0.0313		
9							0.0159	0.0159	0.1307	0.0505
10									0.0663	0.3977

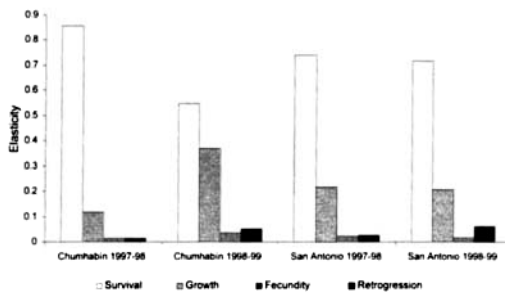


FIGURE 6. Relative importance of demographic processes in growth and maintenance of the populations studied.

mainly on adult survival, with low values in fecundity and survival of the lowest size categories (seedlings). In general, many long-lived species with λ values close to unity have this kind of elasticity pattern (Oyama 1993, Silvertown *et al.* 1993, Schamazel *et al.* 1995, Alvarez-Buylla *et al.* 1996, Esparza-Olguín *et al.* 2002). These results suggest that potential changes in matrix entries representing fecundity or seedling survival may have a negligible effect on population growth rate. The variance in these values, however, is high and these stages of the life cycle play a critical role in population regulation; therefore, the interpretation of these elasticity values for conservation purposes must be done with caution (de Kroon *et al.* 2000).

Fortunately, our results do not indicate that the population size for *Pterocereus gaumeri* is decreas-

ing, however, we should consider that increasing pressure on land use transformation is one of the most important factors that may threaten the persistence of this species. The increasing use of land for cattle ranching has fractured the habitat of this species and slash-and-burn agricultural practices continue with a current deforestation rate of 3000 ha/yr (Durán *et al.* 2000). Additionally, a major part of the populations of *Pterocereus gaumeri* are located on land within ranches or adjacent to them and the presence of livestock most likely reduces the probability of seedling survival. Plans for conservation of *Pterocereus gaumeri* should include restricting areas from potential invasion by livestock to protect both seedlings and adults and the introduction of laboratory-germinated seedlings to aid in increased recruitment of this highly restricted, scarce, and slow-growing but long-lived species.

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