

Demographic analysis of a rare columnar cactus (*Neobuxbaumia macrocephala*) in the Tehuacan Valley, Mexico

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Received 15 April 2001; received in revised form 15 May 2001; accepted 1 June 2001

Abstract

In this study we used population projection matrices to evaluate the conservation status of *Neobuxbaumia macrocephala*, a columnar cactus endemic to a small region in the Tehuacan Valley, in central Mexico. Demographic data included 2-year observations on growth, fecundity and survival of individuals classified by size. Our results indicate that the population is comprised of 70% juveniles. Population growth rate was 0.979 and 0.994 for the 1997/1998 and the 1998/1999 periods, respectively. The slight increase in λ in 1998/1999 was a result of increased fecundity and seedling survival. The highest elasticity values correspond to the survival of large/old individuals. Numerical simulations were performed by changing the value of particular matrix entries and directly evaluating their effect on λ . Population growth rate reached values above unity only when either fecundity or seedling survival probability were increased 10-fold. Given these limitations for population growth, along with its limited distribution range and low population densities, we propose *N. macrocephala* to be classified as a rare species and to promote its conservation by favoring management practices aimed to increase germination and seedling establishment success. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Population dynamics; Columnar cacti; Population projection matrices; Tehuacan Valley; Rare species

1. Introduction

Currently, the Cactaceae is one of several plant families with a very high proportion of species included in the IUCN (International Union for the Conservation of Nature) red list of endangered taxa (Hunt, 1992; Hernández and Godínez, 1994; Nobel, 1994). This may be explained by the fact that many cacti are specific to particular kinds of habitats and/or they tend to support relatively small populations, which accounts for the high level of endemism found in this family (Hernández and Godínez, 1994). These features appear to be intrinsic to the biology of this group and may be determined in part by their low relative growth rates and their low survival probability during the early phases of establishment (Steenbergh and Lowe, 1969; Valiente-Banuet and Ezcurra, 1991; Valiente-Banuet et al., 1991a, 1991b; Nobel, 1994). Additionally, in recent years habitat destruction and illegal trade have severely threatened

the persistence of many cacti species which, given their biological features, appear to be particularly vulnerable to disturbance.

Mexico is one of the most diverse countries with respect to cacti. Of the nearly 2000 cacti species currently recognized by taxonomists, 850 are found in Mexico, 84% of which are endemic (Bravo-Hollis and Sánchez-Mejorada, 1978, 1991; Arias-Montes, 1993). Although efforts are being made by academic and government organizations to protect some of these species, many of them are vulnerable because conservation and management plans are almost non-existent given the lack of information regarding their population biology. In addition, the social problems involved in the nature preservation politics of third-world rural areas are particularly complex, which makes conservation practices even more difficult. Population studies are urgently needed in order to provide the tools necessary to evaluate the current status of existent populations, detect vulnerable stages in the species' life cycle and project the populations' fate under different ecological scenarios. This study addresses these issues through the demographic

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analysis of a rare columnar cactus, *Neobuxbaumia macrocephala* (Weber) Dawson, whose distribution range is restricted to a small valley in the Tehuacán area in central Mexico.

The study of plant demography has grown tremendously in the past couple of decades. A wealth of demographic information has been generated since the use of transition matrices was adapted to the complex life cycles characteristic of plant populations (Lefkovich, 1965; Caswell, 1989). The introduction of matrix analysis, along with sensitivity and elasticity analyses, has given the possibility to address important aspects of the biology of populations including evolutionary, ecological and conservation issues. Much of the demographic information that has been generated is now being used for all kinds of purposes, from management plans (Olmstead and Alvarez-Buylla, 1995) to life history analysis and conservation policies (Crouse et al., 1987; Silvertown et al., 1993, 1996).

The search for demographic patterns in nature is still a central issue in plant ecology (Horvitz and Schemske 1995). Some attempts have been made to systematize the available knowledge on plant demography and interesting trends have arisen (Silvertown et al., 1993). However, little is known regarding the demography of long-lived plant species given the complications involved in dealing with large, slow-growing individuals in which population changes may occur in the scale of decades. In the case of columnar cacti, the knowledge on both life histories and population dynamics is rather limited (but see Steenberg and Lowe, 1969, 1977, 1983; Zavala-Hurtado and Díaz-Solís, 1995; Godínez-Alvarez et al., 1999), which represents a drawback when trying to evaluate the conservation status of rare species that might be facing significant threats to their persistence. Thus, the contribution of this paper is to: (1) increase our understanding of demographic patterns in nature, in particular within a plant group for which little is known regarding population dynamics; (2) contribute to the knowledge of the life-histories of long-lived cacti species; and (3) offer insight into the species' demographic features that determine its rarity, which in turn will allow us to evaluate the potential impact of different conservation strategies upon the species long-term persistence.

2. Methods

2.1. Study area

The demographic analysis of *N. macrocephala* was carried out in the Valley of Zapotitlan Salinas, in the Mexican state of Puebla (18°20' N, 97°28' W). This small valley forms a sub-system within the larger Tehuacan Valley, which is well known for its high cacti diversity (Hernández and Godínez, 1994; Zavala-Hur-

tado and Díaz-Solís, 1995; Valiente-Banuet et al., 1997). The Valley of Zapotitlan Salinas has a sub-arid climate with mean annual temperature oscillating between 18 and 22°C (minimum annual temperature = 11°C, occurring in January; maximum annual temperature = 34°C, occurring in June), and total annual rainfall of ca. 400 mm; nearly 85% of the total annual precipitation falls during the summer rainy season between June and September. The soils in this area are calcareous, shallow and rocky and support a xerophitic vegetation dominated by columnar cacti (e.g. *N. macrocephala*, *N. tetetzo*, *Cephalocereus columna-trajani*), globular cacti (i.e. *Mammillaria* sp., *Echinocactus* sp., *Ferocactus* sp.) and other elements such as *Agave macroacantha*, *Yucca periculosa*, *Lippia graveolens*, *Hechtia podantha*, *Cercidium praecox*, *Beucarnea gracilis*, *Acacia* spp. and *Mimosa* spp.

2.2. The species

Neobuxbaumia macrocephala is a branching columnar cactus that may reach between 7 and 15 m in height. The number of branches in an adult plant may vary from one to 10. Plants bear a reddish cephalium at the tip of each branch from which purple-red flowers emerge during the end of the dry season (May–June). Flowers are pollinated by bats (Valiente-Banuet et al., 1997). Fruits ripen during June and July and are consumed by bat and bird species that presumably act as seed dispersers.

N. macrocephala has a narrowly restricted distribution that comprises only a small area within the Tehuacan Valley in central Mexico (the Tehuacan Valley itself is roughly 80×50 km). Within this region the species may be found on calcareous soils in xerophitic shrublands and tropical dry forests at an altitude of 1600–2300 m above sea level (Bravo-Hollis and Sánchez-Mejorada, 1991; Arias-Montes et al., 1997). Within its distribution *N. macrocephala* is consistently found at relatively low densities (ca. 130–200 plants/ha) compared with other columnar cacti from the same area (e.g. *Neobuxbaumia tetetzo*: 1500–2000 plants/ha—Valiente-Banuet and Ezcurra, 1991).

2.3. Field methods

All *N. macrocephala* plants found within four 200×20 m permanent transects were located, numbered and tagged in June 1997. Length-wise and cross-wise coordinates within each transect were recorded for each plant for relocation purposes. The total stem length of each plant was measured with the aid of a measuring tape, or with a leveling rod (for plants taller than 2 m). When a plant had several branches, the length of each branch was measured separately and then added up together to give a measure of total stem length.

Plants were tagged with the aid of metal plaques attached to the stem through a metal wire ($n = 206$ juvenile and adult plants). The purpose of these tags was to identify each individual (or each branch) with a number, and to mark the spot from which individual (or branch) length would be re-measured a year after. Thus, in June 1997 two measures were taken per plant (or per branch): total stem length, and the length from the tags to the stem tips. Subsequently, in June 1998 and June 1999 only the length from the tag to the tip was re-measured to obtain total length increments. In this way we were able to measure yearly individual growth for a 2-year period.

During the fruiting season of 1997, 1998 and 1999 we recorded the number of fruits produced per plant. This was done with the aid of a mirror attached to the tip of a leveling rod, which was maneuvered until the number of fruits (or fruit marks) could be counted with binoculars in the mirror's image from the ground. Additionally, a fruit sample was collected in 1997 ($n = 50$) to obtain an estimate of the mean number of seeds per fruit. These data were used to calculate a component of plant fecundity, as detailed later.

Seed germination and seedling establishment experiments were carried out in the field in order to obtain estimates of survival and transition probabilities during these life-cycle phases. These estimates had to be experimentally obtained because no seeds or seedlings were found in the field that could be followed directly to determine their fate. Seeds were introduced to the field at the beginning of the rainy season, in June 1997 and June 1998, in small open boxes ($15 \times 10 \times 5$ cm) made of plastic mesh and half-filled with soil. Eight boxes, each with 100 seeds, were placed on the ground, four in completely open conditions (full sunlight), and four under the cover of *Lippia graveolens* shrubs, which appears to be the nurse plant for *N. macrocephala* seedlings and juveniles.

In *N. macrocephala* seed germination takes place within the first week after sowing, given enough moisture is provided. If moisture conditions are maintained, most seeds germinate within 2 weeks. In 1997 germination was recorded monthly in our field experiment; the first record was taken 1 month after seed sowing, and only in this first observation did we observe germinated seeds. In 1998 germination was recorded daily for the first 8 days, and then monthly until no further germination was observed. The data resulting from these observations, along with the information on seed production, was used to calculate plant reproductive success, which was incorporated as a fecundity measure ($F = \text{no. of seedlings/plant} = \text{no. of seeds per plant} \times \text{seed germination probability}$) in subsequent matrix analyses. In this case fecundity was given in seedling units because it was assumed that this species does not form a long-term seed bank in the soil. Since seeds are produced

during the rainy season and are readily viable after dispersal, it is reasonable to suppose that dispersed seeds either germinate or die within a relatively short time after dispersal, as appears to be the case for other columnar cacti (Godínez and Valiente-Banuet 1998; Godínez et al., 1999). Thus, the seed stage was not included in the population projection matrix.

Seedling establishment experiments were carried out in 1997 and 1998. Seedlings were obtained by germinating 1-month-old seeds in a greenhouse at Mexico City in June 1997 and June 1998. Seeds were placed in Petri dishes with an agar (2%) substrate. Seed germination reached an average of 85% within the first 8 days; no further germination was recorded after this date. One week after germination seedlings were transplanted to small plastic containers with soil and agrolite and left in the greenhouse for 6 weeks. During this period they were watered every 2 weeks. In 1997, seedlings were introduced to the field in September; eight groups of 30 seedlings each were planted in small areas (30×30 cm) marked on the ground with wooden sticks. Four of these groups were placed in open conditions and four under the cover of *Lippia graveolens* shrubs. In 1998 the same procedure was followed and approximately the same dates were used, with the exception that this time only 25 seedlings were planted per group. Both in 1997 and 1998 seedling survival was monitored monthly for 1 year.

2.4. Data analysis

2.4.1. Germination and seedling establishment

Within each season we obtained a mean germination percentage in each of the two conditions analyzed (i.e. open and shaded); these percentages (arcsin transformed for linearity) were compared through a Student *t*-test. We built seedling survivorship curves ($\log l_x$) for each of the periods analyzed (1997–1998 and 1998–1999); within each period, curves obtained in different conditions were compared through the Peto and Peto analysis (Pyke and Thompson, 1986) to test the significance of the effect of the nurse plant on establishment probability.

2.4.2. Matrix analysis

We subdivided the population into 10 size classes according to plant total stem length. Each size class had a minimum of 10 individuals from which to calculate matrix transitions (Table 1). We estimated transition probabilities among size classes by calculating the relative frequencies of each observed transition (including death) from 1 year to the next. Since no deaths were observed in the largest size class, the probability of dying in this class was estimated as the inverse of the length of the class, in years (Enright and Ogden, 1979), estimated from an age-based analysis of plant growth rate (Vilchis-Anaya 2000), as detailed in Section 3.

Fecundities were estimated as the mean number of seedlings produced per adult individual in each size class. We first calculated the number of seeds produced per plant (obtained from its number of fruits times the mean number of seeds per fruit) and multiplied it by the germination probability (given by the results of the germination experiments averaged between treatments). As previously noted, fecundities were given in seedling units because our observations suggest that seeds do not remain viable in the soil for long periods of time.

Seedling establishment probabilities (i.e. the transition from the first to the second class) were calculated from the seedling establishment experiments described earlier, by counting the number of seedlings alive after 1 year of planting with respect to the initial number of seedlings introduced in the two experimental conditions considered.

The matrix limit properties (i.e. the dominant eigenvalue and the right and left eigenvectors, which correspond to population growth rate, the stable stage distribution and the stage-specific reproductive values, respectively) were obtained by iteration using an Excel worksheet especially designed for that purpose. The 95% confidence intervals for λ were calculated through the analytic method proposed by Alvarez-Buylla and Slatkin (1994; Valverde and Silvertown 1998).

From the right and left matrix eigenvectors we calculated the sensitivity of λ to changes in each matrix entry (Caswell, 1989); from these values we built elasticity matrices for both study periods (1997/1998 and 1998/1999). Elasticity evaluates the relative sensitivity of λ to relative changes in each matrix entry. Since all the elasticities in a matrix add up to unity, each elasticity value may also be interpreted as the contribution of each matrix entry to the population's finite rate of increase (de Kroon et al., 1986; Caswell, 1989). Thus, elasticities are a useful tool from a conservation point of view because they allow us to identify the most vulnerable

phases of the species' life cycle (de Kroon et al., 1986; Silvertown et al., 1996; Mills et al., 1999). Additionally, since elasticity values corresponding to different demographic processes (i.e. growth, persistence or stasis, and fecundity) may be added up to represent proportions, the relative contribution of each of these processes to population growth rate may be evaluated (Silvertown et al., 1993).

2.4.3. Matrix simulations

We used the population projection matrix obtained for the period 1997/1998 to carry out numerical simulations to evaluate the potential impact of specific changes in particular matrix entries on population growth rate (λ). We evaluated (1) the effect of changes in juvenile and adult mortality by increasing or decreasing the original mortality values in percentages from 5 to 30%; (2) the effect of modifying the fecundity values by multiplying or dividing the original values by different numbers ranging between 2 and 10; and (3) the impact of changes in seedling establishment success by increasing or decreasing that particular matrix entry in proportions ranging from 2 to 10 times. We chose to test the effect of these particular matrix modifications because we observed that those are the main sources of the variation in demographic behavior between years, and because they may throw light onto the potential success of particular conservation practices.

Additionally, we carried out simulations by modifying the value of the survival and persistence probability of size-class 9 individuals, since this matrix entry was estimated from growth rate analysis as the inverse of the number of years spent by individuals in this category. The simulations performed allowed us to evaluate the extent to which the potential errors in our estimate altered the results of our demographic analysis, in particular the λ value.

3. Results

3.1. Seed germination and seedling establishment

Seed germination in greenhouse conditions reached an average of 85%; however, in the field it was much lower. During the summer of 1997 only one out of 400 seeds was observed germinating in each treatment, i.e. the open and the shaded microsites, corresponding to 0.25% germination, and thus the *t*-test did not detect significant differences between treatments ($t=2.138$, d.f. = 2, $P=0.166$). In the summer of 1998 germination percentage was significantly higher in the shaded (4.75%) than in the open microsites (0.0%; $t=4.526$, d.f. = 2, $P=0.032$). These germination percentages were interpreted as germination probabilities (averaged between treatments) and were incorporated in the

Table 1
Size categories used to describe the demography of *Neobuxbaumia macrocephala*^a

Category	Total length (cm)	Life-cycle stage
0	0–1	Seedlings
1	1.1–5	Juveniles
2	5.1–15	
3	15.1–45	
4	45.1–135	
5	135.1–300	Adults
6	300.1–550	
7	550.1–850	
8	850.1–1050	
9	> 1050	

^a Total stem length refers to the sum of the length of all stems in a plant.

matrix model as part of the fecundity values. The average germination probability obtained in summer 1997 was used to build the 1997/1998 matrix, while the one obtained in summer 1998 was applied to the 1998/1999 matrix.

With regards to the seedling survival experiments, a significantly higher mortality was observed in the exposed microsites than in the shaded ones for both study periods (for 1997/1998: $LR = 9.056$, $d.f. = 1$, $P < 0.05$; for 1998/1999: $LR = 4.63$, $d.f. = 1$, $P < 0.05$; Fig. 1). In the exposed treatment, 100% mortality was reached by the 5th month in 1997/1998, while in 1998/1999 total mortality was attained within the 1st month after seedling transplant. In the shaded treatments some seedlings were still alive 1 year after their introduction to the field: 2.6 and 7.4% of seedlings reached the age of 1 year in 1997/1998 and 1998/1999 respectively (Fig. 1). Seedling survival probability was averaged between treatments for each study period and was incorporated in the matrix model as the transition probability from the first to the second size category.

3.2. Matrix analysis

Mortality of *N. macrocephala* individuals was found to be closely associated with size (Table 2); for both study periods the highest probability of dying was found among the seedling category, whereas all adult categories showed no mortality at all. To build the population projection matrices some adult mortality must be incorporated in the largest size category in order to have a defined matrix with real positive eigen-

values and to reflect the fact that old/large plants eventually die. The mortality of individuals in category 9 was estimated by calculating the time that an individual may spend in this category, i.e. the approximate time that elapses from the moment in which a plant reaches a total stem length of 1050 cm to the moment in which it reaches 2240 cm, which was the largest total stem length measured. According to a study on *N. macrocephala* growth rates, this time was estimated to be around 25 years (Vilchis-Anaya, 2000). Thus, mortality of category 9 individuals was estimated as the inverse of this value (i.e. $1/25 = 0.04$). Therefore, to calculate the persistence probability of individuals in category 9, we took into account both the probability of decreasing in size towards category 8 (i.e. retrogression), and the mortality value. These persistence probabilities turned out to be 0.869 for 1997–1998 and 0.883 for 1998–1999; the difference between years was given by a small difference in the retrogression probability. As detailed later, numerical simulations were carried out by modifying this matrix entry in order to evaluate the extent to which the observed λ value may depend on these estimates.

Table 2 shows the transition matrices obtained in this study for the 1997/1998 and the 1998/1999 periods. Along with the matrices we present the population finite rate of increase (λ) and the right and left eigenvectors of the matrices, which correspond to the stable size structure (w) and the size-specific reproductive values (v). The matrices for both periods are similar to some

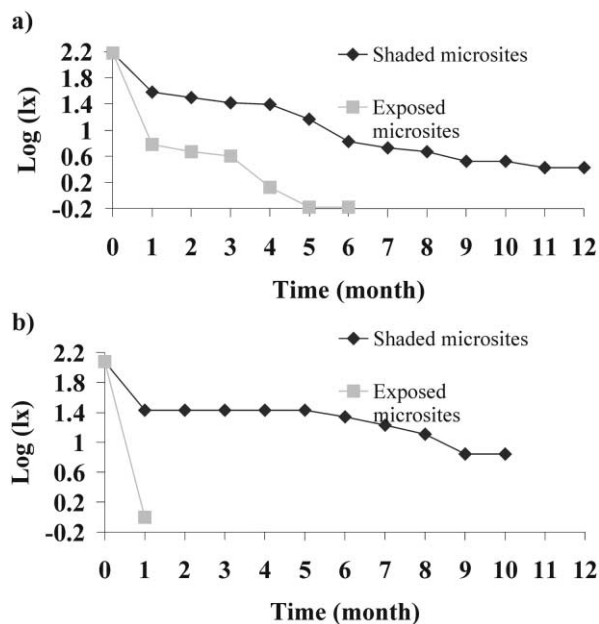


Fig. 1. Survivorship curves ($\log I_x$) for the seedlings introduced to the field in shaded and exposed microsites in (a) summer 1997 and (b) summer 1998.

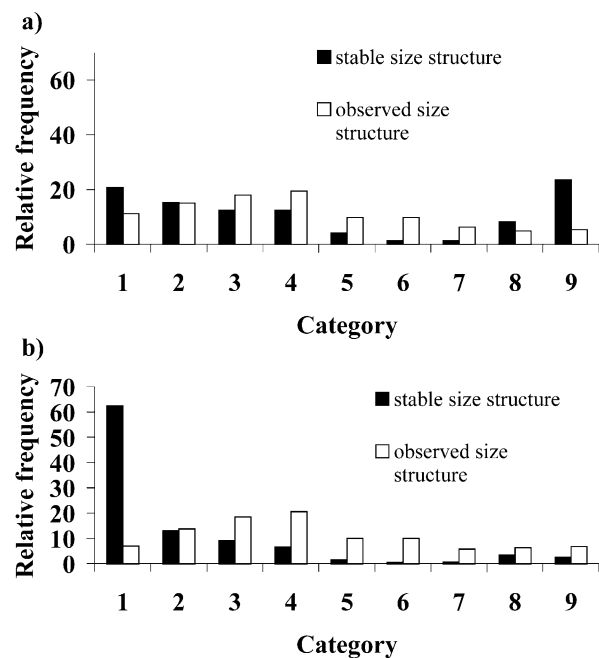


Fig. 2. Relative frequency (%) of individuals in each size category according to the observed population structure (in summer 1997 and summer 1998) and the calculated stable size distribution for (a) the 1997–1998 and (b) the 1998–1999 matrices. Category 0 is not shown in these graphs because no seedlings were observed in the field; thus, the stable size distribution vectors were standardized accordingly.

extent, with the exception of seedling establishment and fecundity, which were higher in the second compared with the first period. In both cases we observed, in general, higher fecundity values with increasing plant size. Only a small number of plants decreased in size from 1 year to the next; these were in category 7 in 1997/1998 and in category 2 in 1998/1999. These types of transitions correspond to either the loss of branches, or the loss of plant tips due to injury by peasants and/or cattle. Both matrices are characterized by higher values corresponding to stasis or persistence in the same plant category compared to values corresponding to growth.

The λ value of the two matrices was slightly below unity (Table 2), although the 95% confidence intervals (calculated through the analytical method proposed by Alvarez-Buylla and Slatkin, 1994) do not allow us to consider them as significantly different from one: the low and high limits of λ for 1997/1998 were 0.860–1.098, and for 1998/1999 they were 0.879–1.109. The slight increase in λ during the second study period was associated with an increase in both fecundity and seedling

establishment probability compared with the values recorded during the first period.

The population's size structure observed in 1997 and 1998 was characterized by a relatively high frequency of plants in the first four categories, with an increasing number of individuals towards category 4 (Fig. 2). Individuals in categories 6–9 (i.e. adults) represent approximately 30% of the population, with a decreasing number of individuals towards the largest categories. These population structures differ significantly from those expected at equilibrium, i.e. vector w in Table 2 (for 1997/1998: $G = 68.811$, d.f. = 9, $P < 0.05$; for 1998/1999: $G = 190.457$, d.f. = 9, $P < 0.05$). Stable population structures for both periods were characterized by a high proportion of individuals in the first and the last categories (Fig. 2), particularly for the matrix corresponding to 1997/1998. Note that Fig. 2 does not include the seedling category since no seedlings were observed in the field during the study period due to their small size and their low survival probability; thus the transitions corresponding to this category had to be estimated through

Table 2
Population projection matrices corresponding to (a) 1997–1998 and (b) 1998–1999^a

Category n_{t+1}	Category (n_t)										w	v
	0	1	2	3	4	5	6	7	8	9		
$(a) \lambda = 0.979 \pm 0.119$												
0							4.130	11.456	10.238	31.73	0.896	0.000
1	0.013	0.435									0.022	0.003
2		0.217	0.677								0.016	0.009
3			0.097	0.865							0.013	0.029
4				0.108	0.875						0.013	0.035
5					0.025	0.900					0.004	0.152
6						0.050	0.850	0.077			0.002	0.240
7							0.150	0.615			0.001	0.200
8								0.308	0.700	0.091	0.009	0.173
9									0.300	0.869	0.024	0.158
n	300	23	31	37	40	20	20	13	10	12		
q_x	0.987	0.348	0.226	0.027	0.100	0.050	0	0	0	0.040		
$(b) \lambda = 0.994 \pm 0.115$												
0							7.364	35.615	33.425	76.77	0.775	0.000
1	0.023	0.857	0.038								0.141	0.002
2		0.071	0.654								0.030	0.004
3			0.115	0.829							0.021	0.010
4				0.086	0.872						0.015	0.019
5					0.026	0.842					0.003	0.090
6						0.053	0.895				0.001	0.259
7							0.105	0.909			0.002	0.239
8								0.091	0.917	0.077	0.008	0.205
9									0.083	0.883	0.006	0.173
n	300	14	26	35	39	19	19	11	12	13		
q_x	0.977	0.072	0.193	0.085	0.102	0.105	0	0	0	0.040		

^a Only non-zero entries are included to facilitate reading. Above each matrix the population growth rate ($\pm 95\%$ confidence intervals) is given. w = stable-size structure; v = size-specific reproductive value; n = number of individuals in each size category; q_x = mortality. The mortality reported for plants in category 9 was estimated for both matrices.

experimental analyses. Therefore, the stable population structures represented in Fig. 2 were standardized after eliminating the seedling category in order to compare them with the observed population structure. Table 2 shows that the stable population structure including the seedling category comprises almost 90% seedlings and 2.4% category 9 adults for the 1997/1998 matrix, and 78% seedlings and 0.6% category 9 adults for the matrix corresponding to 1998/1999.

The vector describing the size-specific reproductive values for both study periods (i.e. vector v in Table 2) shows very low values for the seedling and juvenile categories, with the exception of category 5, which presents a relatively high reproductive value compared with the other non-reproductive categories. Within the adults, despite the increasing fecundity towards larger sizes, the reproductive value decreases with increasing size, which must be related to the gradual approach to the end of life.

The elasticity matrices show that the demographic events that contribute the most to population growth rate are the persistence (i.e. stasis) of category 8 and 9 individuals (Table 3). The elasticities of stasis entries were consistently higher than those representing plant growth. In both periods the lowest elasticity values corresponded to fecundity entries. The elasticity of the matrix entry corresponding to seedling establishment was low in both the 1997/1998 and the 1998/1999 periods. The results of adding up the elasticity values associated to each of the different demographic processes

are presented in Fig. 3. Note that in this case we considered the transitions corresponding to a decrease in size as part of the stasis component. In both periods stasis contributed with 88–90% of total elasticity, followed by growth (9–10%) and fecundity (1–2%).

3.3. Matrix simulations

Although the λ values obtained in this study were not significantly different from unity according to their 95% confidence intervals, we considered it interesting to simulate the absolute effect on λ of potential changes in the values of particular matrix entries to analyze the type of demographic behavior that would result in higher or lower λ values. This is precisely the aim of sensitivity and elasticity analyses; however, these analyses do not consider the actual range of potential variations in matrix entries; thus, by directly manipulating matrix values simulating different ecological scenarios, we could explore the way in which particular changes would affect population dynamics. Although the magnitude of the resulting changes in λ might not be meaningful in an absolute sense (because they occur mostly within the confidence intervals for λ), this approach allows us to detect those conservation strategies that would render relatively better results.

Although mortality was found to be fairly constant during our study period, we used our matrix model (for 1997/1998) to simulate changes in mortality because this is one of the most important demographic components

Table 3
Elasticity matrices for the *Neobuxbaumia macrocephala* population studied^a

Category n_{t1}	Category (n_{t0})									
	0	1	2	3	4	5	6	7	8	9
(a)										
0							5.2E-05	6.1E-05	0.001	0.005
1	0.005	0.004								
2		0.006	0.012							
3			0.006	0.043						
4				0.006	0.051					
5					0.006	0.070				
6						0.006	0.057	0.002		
7							0.008	0.015		
8								0.006	0.142	0.050
9									0.056	0.440
(b)										
1	0.008	0.053	0.000							
2		0.008	0.016							
3			0.008	0.040						
4				0.008	0.056					
5					0.008	0.043				
6						0.008	0.070			
7							0.008	0.079		
8								0.007	0.327	0.021
9									0.025	0.201

^a (a) 1997–1998 and (b) 1998–1999. The five highest values in each matrix are bold. Only non-zero entries are represented to facilitate reading.

that may vary as a result of changes in land use, for instance. We modeled the effect of changes on juvenile and adult mortality independently because we considered that survival probabilities of both groups are quite distinct and that the mortality factors that affect each of them might be different. When increasing juvenile mortality up to 30%, λ varies from 0.979 to 0.974 (Fig. 4a), which represents a very slight change. However, when adult mortality was increased 30% the effect on λ was more dramatic (i.e. varying from 0.979 to 0.931—Fig. 4a).

The results concerning the effect of potential variations in the fecundity entries (F =seed production \times seedling germination probabilities) showed interesting trends. When fecundities were given values 10 times lower than the original ones the effect on λ was only slight (i.e. varying from 0.979 to 0.974—Fig. 4b). However, when fecundity values were increased up to 10 times their original value, we obtained a λ above unity (i.e. 1.002—Fig. 4b). Note that these simulations were carried out with the 1997/1998 matrix, which showed lower fecundities compared with the 1998/1999 matrix. When simulations of potential increases in fecundity entries were carried out with the 1998/1999 fecundity values, only a 3-fold increase was necessary to obtain a $\lambda=1$ value (results not shown).

With respect to potential changes in seedling establishment probability, we found that a 10-fold decrease in this matrix entry produced a change in λ from 0.979 to 0.976. However, an equivalent increase in the same matrix entry resulted in a change in λ from 0.979 to 1.002 (Fig. 4b). Thus, the only potential changes that

resulted in λ values above unity were those corresponding to fecundity and seedling establishment. Yet, it is likely that these values do not vary independently but are affected in the same way by weather conditions, for instance. Thus, during favorable years both seed germination (which is a component of fecundity values) and seedling establishment may vary in a correlated way. We carried out simulations that included changes in both fecundity and seedling establishment values simultaneously, and found that only a 3-fold increase in these matrix entries was necessary to obtain a λ value above unity (i.e. 1.02).

As noted earlier, the matrix entry corresponding to the survival and persistence of size-category 9 individuals was estimated by assuming that plants spend 25 years in this size category. However, the time lapse spent in this category may vary and an error in this estimate may have an effect on λ . To address this issue we carried out simulations assuming that individuals may spend from 20 years to 50 years in size-category 9, thus the value of the relevant matrix entry varied from 0.859 to 0.889, respectively (Table 4). As a result, λ changed from 0.974 to 0.991. Thus, λ did not reach a value above unity even when the estimated time spent in size-category 9 was doubled (i.e. from 25 to 50 years). Population growth rate reached a positive value ($\lambda=1.0001$) only when the survival probability of the largest adults was 0.905, which would mean a persistence

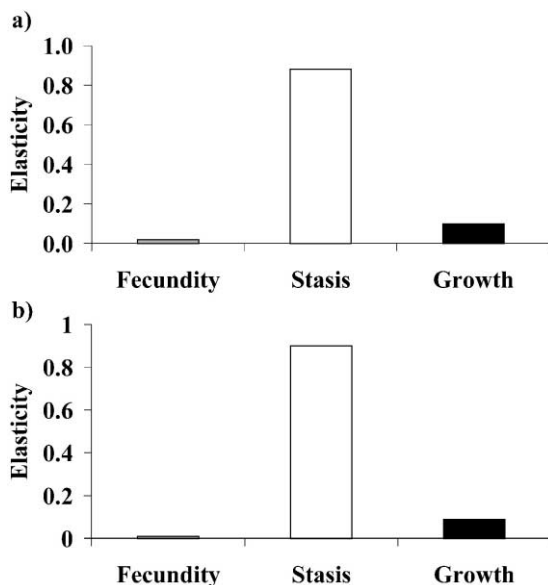


Fig. 3. Relative contribution of the different demographic processes (i.e. fecundity, stasis and growth) to the value of λ according to the elasticity matrices obtained for (a) the 1997–1998 and (b) the 1998–1999 periods.

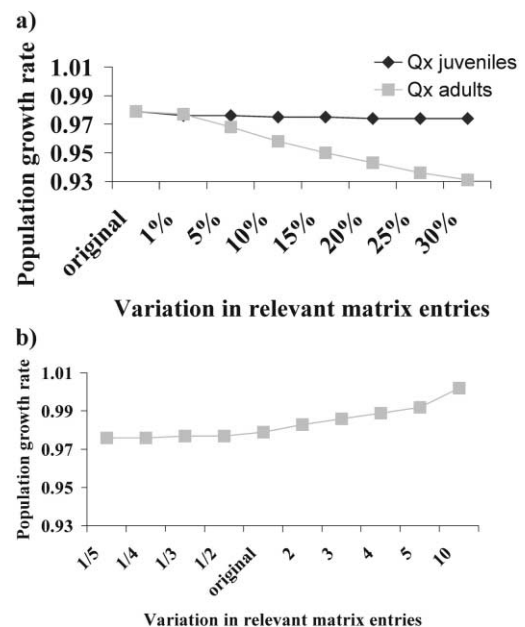


Fig. 4. Variation in population growth rate (λ) that results from modifications in matrix entries corresponding to (a) juvenile and adult mortality (increase in mortality by the given percentages); and (b) fecundity and seedling establishment probability. The latter graph displays only one curve, since the results for both simulation yielded completely overlapping trends. The projection matrix for 1997–1998 was used to perform these simulations.

Table 4

Results of the simulations performed by changing the estimated duration of size-class 9, from 20 to 50 years

Duration of size-class (years)	Value of matrix entry	λ	e_{ij}^a
20	0.859	0.974	0.437
25 ^b	0.869	0.979	0.440
30	0.876	0.983	0.442
50	0.889	0.991	0.445

^a e_{ij} refers to the elasticity value of the matrix entry corresponding to the persistence probability of size-class 9 individuals.

^b The conditions of the original projection matrix.

time of 250 years for adult 9 individuals in their own category.

4. Discussion

It has been estimated that *N. macrocephala* individuals may reach a maximum age of approximately 200 years, and the age at first reproduction may be close to 90 years (Vilchis-Anaya, 2000). It is clear that in the case of this and other such long-lived species a 2-year demographic data set is rather limited to address its long-term population dynamics, since population changes occur in the scale of decades. Thus, the evaluation of extinction risks for these species becomes a particularly complicated task (Alvarez-Buylla et al., 1996; Schwartz et al., 1999, 2000). However, until long-term studies are performed we must do our best to use the available information to understand the population processes of rare taxa, like *N. macrocephala*. In this sense, the use of matrix simulations may throw light onto this and other aspects of the biology of rare species.

The results of this study showed a population growth rate slightly below unity in both years. Yet, λ confidence intervals do not allow us to distinguish it from a numerically stable population. For a long-lived species it is expected that λ would be very close to unity for most years. Additionally, it has been recognized that in plant populations from semi-arid regions recruitment is favored during rainy years, thus increasing population numbers, while the rest of the time the lack of recruitment gives the impression of a slowly decreasing population. In fact, other columnar cacti populations appear to be performing well despite wide fluctuations in population numbers and periods of poor seed production and seedling recruitment. Such is the case for *Neobuxbaumia tetetzo* in the Tehuacan Valley (Godínez-Alvarez et al., 1999) and *Carnegie gigantea* in the Sonoran desert (Steenbergh and Lowe, 1969, 1977, 1983; Pierson and Turner, 1998). Thus, the case of *N. macrocephala* might be somewhat similar and the population might be maintaining itself through occasional high

recruitment events followed by several years in which almost no recruitment might be taking place, which in fact may be suggested by the observed size-frequency distribution (Fig. 2).

Although our results do not point in the direction of a clearly declining population, we can think of a number of factors that might threaten the long-term persistence of this and other highly restricted, slow-growing, long-lived species. Many of these factors arise from both the dynamics of its natural environment and from human activities. In the first category we may consider the low water availability and high solar radiation, which characterize semi-arid regions and impose serious limitations to population growth, mainly because they induce high seedling mortality and constrain the establishment of new individuals. With regards to the human-induced environmental threats, perhaps one of the most significant is the increasing pressure on land-use transformation, especially in the region where *N. macrocephala* lives, which is a relatively densely populated and very poor rural area in central Mexico. As agriculture is tremendously unproductive in this region due to its high aridity, steep slopes and poor soils, peasants must rely mainly on goats to make their living. These animals do not need much tending and are capable of moving around on uneven terrain and feeding on almost any plant species; these features make them a convenient, yet precarious, productive activity in the region.

The widespread presence of goats on semi-arid lands in Mexico affects populations of columnar cacti by: (1) reducing recruitment probability by directly killing recently established seedlings; (2) limiting seedling establishment success by reducing the shade provided by nurse plants; and (3) causing mortality among adult plants, since peasants frequently sever cactus stems for thirsty goats, thus producing injuries that may result in infections and eventual plant death. The increased adult mortality and the absence of seedling establishment are slowly creating a sparse landscape in which the lack of vegetation combined with strong summer showers are resulting in significant soil erosion.

In *N. macrocephala*, seed germination and seedling recruitment appear to be strong population bottlenecks, even when compared with other columnar cacti (Valiente-Banuet et al., 1991a; Godínez-Alvarez and Valiente-Banuet, 1998). These features may constitute important limitations to population growth. Yet, elasticity values of seed germination (an element of fecundity entries) and seedling establishment are low, which coincides with what has been found for other columnar cacti (Silvertown et al., 1993; Godínez-Alvarez et al., 1999). In general, many long-lived species with λ values close to unity show this kind of elasticity pattern in which the population dynamics appears to depend mainly on juvenile and adult survival rather than on seed production and seedling establishment (Enright and Odgen,

1979; Oyama, 1993; Silvertown et al., 1993; Alvarez-Buylla et al., 1996).

The result of the elasticity matrices appears to suggest that potential changes in matrix entries representing fecundity or seedling survival may have a negligible effect on population growth rate. However, our matrix simulations showed that λ values were larger than unity when either seedling establishment or fecundity (or both) were significantly increased. On the other hand, introducing changes in other matrix entries with relatively higher elasticity values did not result in positive population growth rates. Note however, that the magnitude of the changes that may occur in both fecundity and seedling establishment is much larger than that of other matrix entries. Although the variations in λ resulting from matrix simulations are only slight and are within the confidence intervals of the original λ value, the comparison of the different simulation results offer a relative evaluation of the way in which the population may respond to changes in alternative demographic pathways.

The results presented here suggest that the interpretation of elasticity values for conservation purposes must be cautious since they may provide a limited tool for decision making (de Kroon et al., 2000). In addition to elasticity analysis, the use of numerical simulations using population matrix models may provide a deeper insight into the actual limitations for population growth (Crouse et al., 1987; Olmstead and Alvarez-Buylla, 1995; Schwartz et al., 1999, 2000). Using this methodology we were able to show that *N. macrocephala* is limited by restrictions in seed germination and seedling establishment. Thus, if it is eventually necessary to implement management practices aimed to the conservation of the *N. macrocephala* populations, they must concentrate on these particular aspects of the species life cycle.

The definition of a rare species differs among classification systems. The IUCN classification emphasizes that rare taxa show small population numbers and are generally restricted to remote habitats; although they are not at present endangered or vulnerable, they are at risk given their population characteristics (Hunter, 1996). According to the CITES classification, rare species have small total numbers of individuals, often due to limited geographical ranges or low population densities; these populations do not face any immediate danger but are candidates to become endangered (Primack, 1993). Both descriptions fit *N. macrocephala*, which shows a small distribution range, low population densities (ca. 130–200 plants/ha) and intrinsic limitations for population growth given by low seedling recruitment. Therefore, we suggest that *N. macrocephala* should be formally classified as a rare species, since at the moment it does not hold any conservation protection status (Hunt 1992). If long-term demographic data eventually reveals that populations are in fact declining,

then it would be adequate to classify it as a vulnerable species. In any case, an appropriate management plan should favor the recruitment of new individuals to the population, either by actively introducing seedlings and juveniles or by increasing the survival probabilities of naturally established ones. In this context, the widespread presence of goats in the region should be somehow regulated in order to give both the human communities and the native vegetation a chance to coexist.

Acknowledgements

We are grateful to CONABIO (project No. R129) for economic support during the development of the present study. The first author was given a grant by Fundación UNAM to carry out this project. We wish to thank Pedro Eloy Mendoza, Mariana Hernández, Marco Antonio Romero, Sandra Quijas, Marcela Ruedas, Cinthya Contreras, Ariel Arias and Jerónimo Reyes for valuable help in the field. The comments of two anonymous reviewers greatly improved the manuscript.

References

- Alvarez-Buylla, E., Slatkin, M., 1994. Finding confidence limits on population growth rates: three real examples revisited. *Ecology* 75, 255–260.
- Alvarez-Buylla, E., García-Barrios, R., Lara-Moreno, C., Martínez-Ramos, M., 1996. Demographic and genetic models in conservation biology: applications and perspectives for tropical rain forest tree species. *Annual Review of Ecology and Systematics* 27, 387–421.
- Arias-Montes, S., 1993. Cactaceas: Conservación y Diversidad en México. In: *Diversidad Biológica en México*. In: Gío-Argáez, R., López-Ochotorena, E., Sociedad Mexicana de Historia Natural, Mexico, pp. 109–115.
- Arias-Montes, S., Gama-López, S., Guzmán-Cruz, L.U., 1997. Flora del Valle de Tehuacán-Cuicatlán, Fascículo 14, Cactaceae. Instituto de Biología, Universidad Nacional Autónoma de México, Mexico.
- Bravo-Hollis, H., Sánchez-Mejorada, H., 1978. Las Cactáceas de México, Vol. II. Universidad Nacional Autónoma de México, Mexico.
- Bravo-Hollis, H., Sánchez-Mejorada, H., 1991. Las Cactáceas de México, Vol. III. Universidad Nacional Autónoma de México, Mexico.
- Caswell, H., 1989. *Matrix Population Models*. Sinauer, Sunderland, MA.
- Crouse, D., Crowder, L., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 65, 1412–1423.
- Enright, N.J., Ogden, J., 1979. Applications of transition matrix models in forest dynamics: Araucaria in New Guinea, and Nothofagus in New Zealand. *Australian Journal of Ecology* 4, 3–23.
- Godínez-Alvarez, H., Valiente-Banuet, A., 1998. Germination and early seedling growth of Tehuacan Valley cacti species: the role of soil and seed ingestion by disperses on seedling growth. *Journal of Arid Environments* 39, 21–31.
- Godínez-Alvarez, H., Valiente-Banuet, A., Valiente-Banuet, L., 1999. Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacan Valley, Mexico. *Canadian Journal of Botany* 77, 1–6.

- Hernández, H.M., 1994. Godínez, A.H., Contribución al conocimiento de las cactáceas mexicanas amenazadas. *Acta de la Sociedad Botánica de México* 26, 33–52.
- Horvitz, C.C., Schemske, D.W., 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs* 65, 155–192.
- Hunt, D., 1992. CITES Cactaceae Checklist. Royal Botanical Gardens, Kew, UK.
- Hunter, M.L., 1996. *Fundamentals of Conservation Biology*. Blackwell Science, MA.
- de Kroon, H., Plaisier, H., van Groenendael, J.M., Caswell, H., 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67, 1427–1431.
- de Kroon, H., van Groenendael, J., Ehrlén, J., 2000. Elasticities: a review of methods and model limitations. *Ecology* 81, 607–618.
- Lefkovich, L., 1965. The study of population growth in organisms grouped by stage. *Biometrics* 21, 1–18.
- Mills, L.S., Doak, D.F., Wisdom, M.J., 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* 13, 815–828.
- Nobel, P.S., 1994. *Remarkable Agaves and Cacti*. Oxford University Press, Oxford, UK.
- Olmsted, I., Alvarez-Buylla, E.R., 1995. Sustainable harvesting of tropical trees: demography and matrix model of two palm species in Mexico. *Ecological Applications* 5, 484–500.
- Oyama, K., 1993. Conservation biology of tropical trees: demographic and genetic considerations. *Environment Update* 1, 17–32.
- Pierson, E.A., Turner, R.M., 1998. An 85-year study of Saguaro (*Carnegiea gigantea*) demography. *Ecology* 79, 2676–2693.
- Primack, R.B., 1993. *Essentials of Conservation Biology*. Sinauer, MA.
- Pyke, D.A., Thompson, J.N., 1986. Statistical analysis of survival and removal rate experiments. *Ecology* 67, 240–245.
- Schwartz, M.W., Hermann, S.M., van Mantgem, P.J., 1999. Population persistence in Florida Torreya: comparing modeled projections of a declining coniferous tree. *Conservation Biology* 14, 1023–1033.
- Schwartz, M.W., Hermann, S.M., van Mantgem, P.J., 2000. Estimating the magnitude of decline of the Florida torreya (*Torreya taxifolia* Arn.). *Biological Conservation* 95, 77–84.
- Silvertown, J.W., Franco, M., Pisanty, I., Mendoza, A., 1993. Comparative plant demography: relative importance of life cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81, 465–476.
- Silvertown, J., Franco, M., Menges, E., 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* 10, 591–597.
- Steenbergh, W.F., Lowe, C.H., 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at the Saguaro National Monument, Arizona. *Ecology* 50, 825–834.
- Steenbergh, W.F., Lowe, C.H., 1977. Ecology of the Saguaro: II Reproduction, germination, establishment, growth and survival of the young plant. *National Park Services Scientific Monograph Series No. 8*, USA.
- Steenbergh, W.F., Lowe, C.H., 1983. Ecology of the saguaro: growth and demography. *National Park Services Scientific Monograph Series No. 8*, 17, USA.
- Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisiana* in the Tehuacán valley, Mexico. *Journal of Ecology* 79, 961–971.
- Valiente-Banuet, A., Vite, G., Zavala-Hurtado, A., 1991a. Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. *Journal of Vegetation Science* 2, 12–14.
- Valiente-Banuet, A., Briones, O., Bolongaro-Crevenna, A., Ezcurra, E., Rosas, M., 1991b. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science* 2, 15–20.
- Valiente-Banuet, A., Rojas-Martínez, A., Arizmendi, M.C., Dávila, P., 1997. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. *American Journal of Botany* 84, 452–455.
- Valverde, T., Silvertown, J., 1998. Variation in the demography of a woodland understory herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *Journal of Ecology* 86, 545–562.
- Vilchis-Anaya, E., 2000. Estudio poblacional por edades de *Neobuxbaumia macrocephala* (Cactaceae) en Zapotitlán Salinas, Puebla. Bachelors Thesis. Universidad Nacional Autónoma de México. México D.F.
- Zavala-Hurtado, J.A., Diaz-Solis, A., 1995. Repair, growth, age and reproduction in the giant columnar cactus *Cephalocereus columna-trajani* (Karwinski ex. Pfeiffer) Schuman (Cactaceae). *Journal of Arid Environments* 31, 21–31.