

Population dynamics of the Mexican cycad *Dioon edule* Lindl. (Zamiaceae): life history stages and management impact

PABLO OCTAVIO-AGUILAR¹, JORGE GONZÁLEZ-ASTORGA^{1*} and ANDREW P. VOVIDES²

¹Laboratorio de Genética de Poblaciones, Departamento de Biología Evolutiva, Instituto de Ecología, A. C. Km 2.5 Antigua Carretera a Coatepec, Congregación el Haya no. 351, C. P. 91070, Xalapa Veracruz, México

²Laboratorio de Biología Evolutiva de Cycadales, Departamento de Biología Evolutiva, Instituto de Ecología, A. C. Km 2.5 Antigua Carretera a Coatepec, Congregación el Haya no. 351, C. P. 91070, Xalapa Veracruz, México

Received 18 April 2007; accepted for publication 21 September 2007

The demographic dynamics of three populations of *Dioon edule* Lindl. (Zamiaceae) were studied in a fragmented landscape using projection matrix modelling. Compared with other plant species, *D. edule* behaves like a tree life-form species. Density and spatial distribution patterns varied among populations according to models for animal-dispersed tree species. In all scenarios, λ was most sensitive to changes in abundance of adult plants. The elasticity reproductive component (F) for the three populations was zero and stasis values (L) were higher, this being a function of the permanence of non-reproductive individuals. It was detected that disturbance influences the population dynamics of *D. edule* as a function of adult plant persistence. This observation suggests that the conservation of adult plants is critical for *D. edule* and perhaps for all cycads species. Adult plant decapitation should be halted at the 'Monte Oscuro' population, subjected to sustainable management since 1990, if higher seed production is needed in rural nurseries. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 157, 381–391.

ADDITIONAL KEYWORDS: conservation biology – demography – elasticity analysis – leaf-crown removal – projection modelling – survival.

INTRODUCTION

Cycads are long-lived perennial plants, most of which are considered as Threatened, Rare or Endangered and are listed in the IUCN (2004) Red List. This is a result mainly of their being affected by habitat destruction and illegal trade as well as represented, in some cases, by unique and relatively small populations or narrow distribution (Donaldson, 2003). The approximately 300 species known to date (Hill, Stevenson & Osborne, 2004) vary in aspects such as

size, habitat, growth–form and species relationships (Norstog & Nicholls, 1997; Treutlein & Wink, 2002; Raimondo & Donaldson, 2003). These aspects are important in that they define the plant's response to periodic environmental changes, habitat destruction (Negrón-Ortiz & Gorchoy, 2000; Pérez-Farrera *et al.*, 2000, 2006) and management under *in situ* sustainable cultivation (Vovides *et al.*, 2002).

A useful method for analysing population dynamics and structure are projection matrices (Manly, 1990; Silvertown, Franco & Menges, 1995; Caswell, 2001; Caswell, Lensink & Neubert, 2003). This type of research has become greatly relevant in population ecology studies, as it is possible to incorporate

*Corresponding author.

E-mail: jorge.gonzalez@inecol.edu.mx, dionastorga@yahoo.es

seasonal or annual variation, associated to demographic parameters, and projection of long-term population behaviour in the matrix models. It is also possible to define factors such as susceptibility to management practices, habitat reduction or fragmentation (Crowse, Crowder & Caswell, 1987; Groenendael, De Kroon & Caswell, 1988; Caswell & Trevisan, 1994; Olmsted & Alvarez-Buylla, 1995; Benton & Grant, 1999; Heppell, Caswell & Crowder, 2000), as well as permanence probabilities and/or the extinction of the species (Lande, 1988). In addition, the identification of life history stages that have the highest influence on population growth would make it possible for conservation programmes to target these vulnerable stages.

The analysis of elasticity and sensitivity of finite population growth rate (λ) were developed from these transition matrices (Caswell, 2001). Models derived from these matrices are also used in evolutionary ecology studies, as population growth rates can be interpreted as mean measures of fitness and, thus, reflect the evolutionary potential of the populations (Lande, 1999). In order to develop these projections, it is necessary to know certain traits of the individuals that differ between genotypes, classes and populations, such as seedling establishment, survival and reproduction costs (De Kroon *et al.*, 1986; Benton & Grant, 1999).

Transition matrices have been used in plant demography studies with different reproductive strategies and life forms (e.g. Bullock, 1980; Piñero, Martínez-Ramos & Sarukhán, 1984; Olmsted & Alvarez-Buylla, 1995; Silvertown *et al.*, 1995; Valverde & Silvertown, 1998; Sánchez-Velásquez *et al.*, 2002; Valverde *et al.*, 2004; Pérez-Farrera *et al.*, 2006). In these studies it has been observed that life history attributes combined with environmental variability (biotic and abiotic) determine the population dynamics. However, these attributes affect long-lived plants differently, making it necessary to consider diverse historic events in order to explain the present population structure in these cases (Martínez-Ramos, Alvarez-Buylla & Sarukhán, 1989). Population dynamics for long-lived woody perennials have been determined where variation in time has been considered with factors such as age structure, size and/or sex ratio (Enright, Franco & Silvertown, 1995), as well as processes associated with habitat disturbance and fragmentation (Martínez-Ramos *et al.*, 1988, 1989; Hoffmann, 1999). Silvertown *et al.* (1995) and Franco & Silvertown (2004) used the same methods to compare 84 and 102 species of plants, respectively, with a wide range of life histories. Their results showed that long-lived woody plant species all have very high composite elasticity values for stasis (measured by the composite elasticity of stasis and retro-

gression, L), and low relative importance of seed recruitment (measured by the composite fecundity elasticity, F) and transition (growth, G).

Although general population studies on various species of cycads exist (e.g. Tang, 1989; Vovides, 1990; Watkinson & Powell, 1997; Negrón-Ortiz & Gorchov, 2000; Pérez-Farrera *et al.*, 2000; Keppel, 2001). Matrix projection models were used in only three studies (Negrón-Ortiz, Gorchov & Breckon, 1996; Raimondo & Donaldson, 2003; Pérez-Farrera *et al.*, 2006). In these the matrices based on life history transitions of the plants showed that the determinant factor for population survival is the permanence of reproductive adults. This is in agreement with other studies on long-lived plants (Silvertown *et al.*, 1995).

In order to understand the present situation of *Dioon edule* Lindl., some knowledge of the localities' histories is necessary: At 'Rancho del Niño' there is a remnant population of the cycad of a once much wider distribution that has become reduced over the last century by agricultural expansion (Chamberlain, 1919, 1935). 'Monte Oscuro' has a long history of disturbance, deforestation for agricultural expansion as well as decapitation of adult individuals. The 'El Farallón' population has a very limited extension and is undisturbed by human activities; it is also unique in that it is the only coastal *D. edule* population known.

We consider the present study important as information generated will be complementary to the long-term management and conservation of the species and its habitat by addressing the following questions: (1) to what extent do different disturbance patterns of the three populations effect their population dynamics?; (2) what is the actual situation of the three populations, as well as that through projected time – increasing, stable or decreasing?; (3) can disturbed populations recover from loss of adult individuals?

To answer these questions the following was carried out: plants were divided into six classes, density and spatial distribution were calculated for each of the three populations studied; transition, sensitivity and elasticity matrices were constructed, growth until stable structure reached was also projected for the three populations. For the 'Monte Oscuro' population, an additional hypothetical projection was made assuming no plant decapitation had occurred. Finally, comparison with other cycads and a long-lived tree species was made.

MATERIAL AND METHODS

STUDY SPECIES

Dioon edule Lindl. (Zamiaceae) is a cycad endemic to Mexico. It is an arborescent, dioecious and pan-

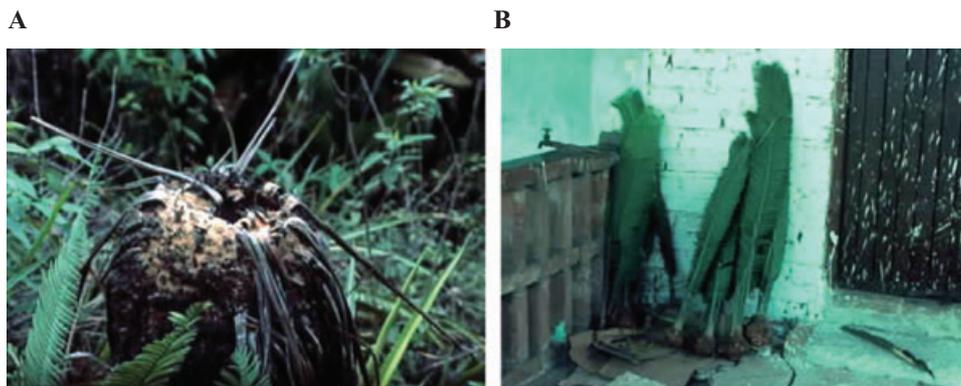


Figure 1. A, decapitated adult plant of *Dioon edule*. B, leaf crowns awaiting transport.

chronic plant up to 5 m tall, often branching with age (Vovides, Rees & Vázquez-Torres, 1983), distributed in eastern Mexico, central Veracruz state, the states of Queretaro, Hidalgo, San Luis Potosi and Tamaulipas (González-Astorga, Vovides & Iglesias, 2003a, González-Astorga *et al.*, 2003b). It is listed as Near Threatened in the CITES Appendix 2 of the IUCN (2004) Red Data Book and as Endangered in the Mexican Norm listings (INE-SEMARNAP, 2000; Official Norm). This species is subjected to illegal extraction by decapitation of the leaf crowns of large adults for sale as ornamental plants by street peddlers (Fig. 1A, B). This practice occurs only at the 'Monte Oscuro' population (one of the sites studied), where a project aimed towards sustainable management has been established since 1990 as an alternative conservation strategy in order to discourage plant decapitation and removal (Vovides & Peters, 1987; Vovides & Iglesias, 1994; Vovides *et al.*, 2002).

STUDY SITES

The three localities in central Veracruz chosen for the study were: (1) 'Monte Oscuro' at 19°22'12"N, 96°47'35"W; (2) 'El Farallón' beach at 19°36'50"N, 96°22'41"W; and (3) 'Rancho del Niño' at 19°43'20"N, 96°29'-W (Fig. 2).

POPULATION SAMPLING

Two transects of variable length were placed at each locality and were divided into contiguous rectangle blocks of 200 m² (10 × 20 m). All the *Dioon* plants were measured and mapped to scale. This process was repeated twice between the years 2002–2004 for each site. The population density was estimated by calculating the mean dispersal area (area/no. of plants)^{1/2} (Muller-Dombois & Ellenberg, 1974). Spatial

distribution pattern analysis was carried out using the formula: $I = \sigma^2/X$, where σ^2 and X are the variance and mean distance per block, respectively. To verify if the spatial distribution coefficient (I) differed significantly from one, a t -test was used, where $t = (\sigma^2/X - 1)/(v2/n - 1)$ and d.f. are the number of blocks minus one (Smith, 1996; González-Astorga & Núñez-Farfán, 2000).

DATA ANALYSIS

The plants were assigned to one of the following classes according to their life-cycle stage: seeds, seedlings, juveniles, adults₁ (non-reproductive plants) and adults₂ (reproductive plants) (*sensu* Negrón-Ortiz *et al.*, 1996). The number of seeds for generation t_0 was calculated with the minimum number of seeds per female cone multiplied by the number of coning female plants. In order to estimate survival for plants that would have changed size class during the monitoring period, the following steps were carried out: (1) each individual was assigned to an initial stage class using trunk height, presence/absence of reproductive structures and state of maturity; (2) individuals were moved through stage classes using calculated growth transition probabilities; and (3) any mortality was proportioned among individuals in each stage.

The 2 years of data were combined to obtain reliable estimates of stage-specific survival. Also, Lefkovich sensitivity and elasticity matrices for each population were then constructed from the data obtained. The proportion of individuals at stable structure (w) was compared with the observed structure under natural conditions with a χ^2 test with $k-1$ d.f. (Sokal & Rohlf, 1995).

The projection matrices contained the transition probabilities from one class to the next, the resilience probability, the retrogression of a reproductive to a non-reproductive individual and fecundity. This

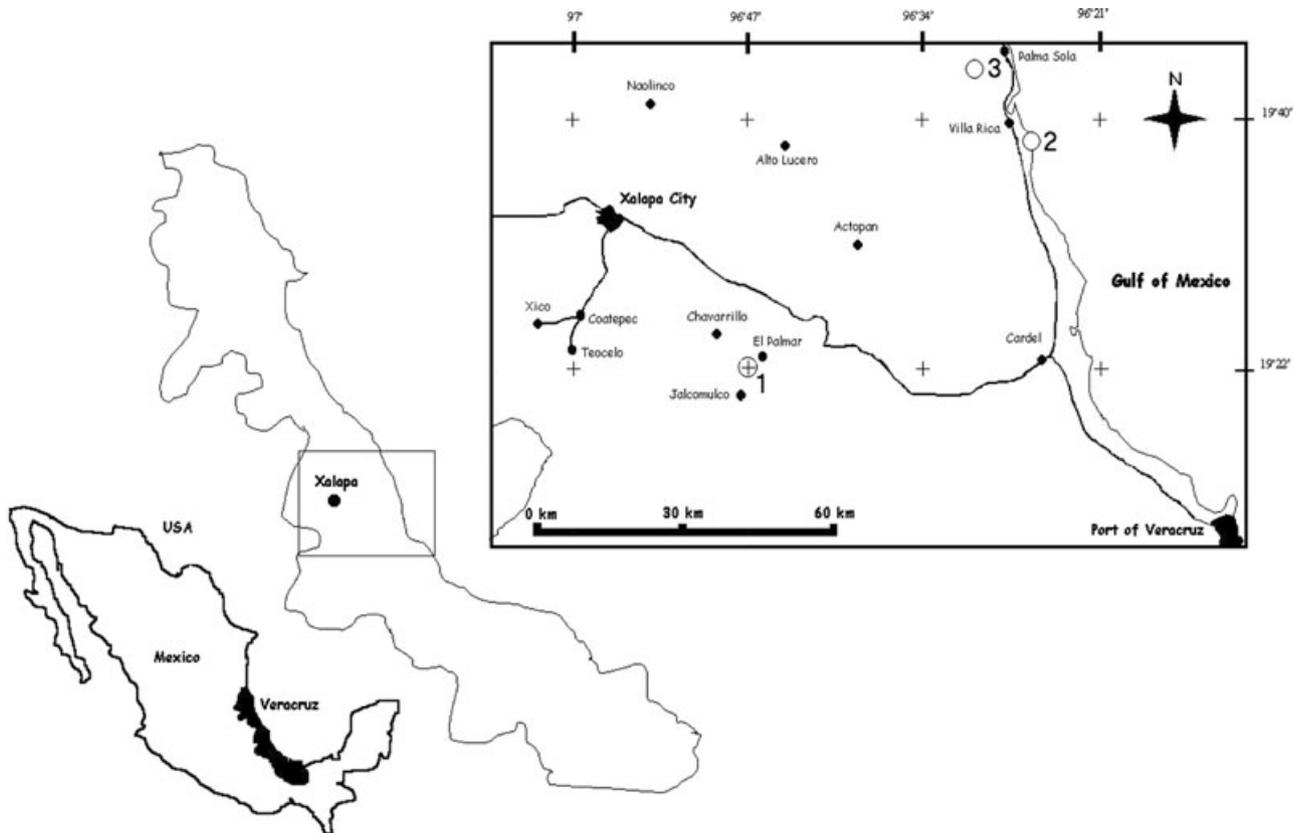


Figure 2. Geographical location of study sites in Veracruz. 1, 'Monte Oscuro'; 2, 'El Farallón'; 3, 'Rancho del Niño'.

was calculated as the number of seedlings produced per female plant in 2 years, estimated by the algebraic product of the observed proportion of reproductive female plants, minimum number of seeds per female cone, germination rate (Vovides, 1990) and survival of seedlings during the monitoring period (Raimondo & Donaldson, 2003; Pérez-Farrera *et al.*, 2006).

The population size after one generation was determined by the product of the transition matrix L by the N_0 vector where $L = [l_{ij}]$ for $i, j = \{1, 2, \dots, 5\}$ and N_0 is the vector containing the number of individuals per class at t_0 . This process was repeated until the proportion of individuals per class remained stable, represented by the right vector (w). The expected λ was also obtained for the matrix model: (N_t/N_{t-1}) , where N_t is the total number of individuals at time t and N_{t-1} is the number of individuals at time $t - 1$ (Caswell & Trevisan, 1994; Caswell, 2001).

The sensitivity matrices were constructed with the vectors w and v , that represent the proportional reproductive value in each class and are obtained by iteration of the transposed L matrix and N_0 until stability. The scalar value vw , was obtained with these two vectors, which is: $v_1w_1 + v_2w_2 + \dots + v_5w_5$.

Sensitivity matrix values were obtained from the equation: $S_{ij} = v_iw_j/vw$.

The elasticity matrix was constructed with the following equation: $E_{ij} = (L_{ij}/L)S_{ij}$, where E_{ij} is the ij^{th} element of the elasticity matrix, L_{ij} is the ij^{th} element of matrix L , S_{ij} is the ij^{th} element of the sensitivity matrix and λ is the finite population growth rate, obtained by initial iteration of the L matrix (De Kroon *et al.*, 1986; Caswell, 2001). The elasticity value of a matrix element is defined as the proportional change in the population growth rate for a proportional change in the matrix element (De Kroon *et al.*, 1986; Benton & Grant, 1999). A useful attribute of elasticity analyses is that elasticity values of all matrix elements sum to one.

Owing to plant decapitation at 'Monte Oscuro' that does not occur at the other two localities, a matrix was generated simulating non-decapitation at this population, implicating an increase in the elasticity values for fecundity in this population, by assigning a proportion of the decapitated individuals to the reproductive females class; this assignment was proportional to the number of females expected. The population growth rate (λ) and elasticity values of this population were estimated.

RESULTS

DENSITIES AND SPATIAL DISTRIBUTION

The area sampled in the populations was variable: 2400 m² at 'Rancho del Niño', 4800 m² at 'El Farallón' and 16 200 m² at 'Monte Oscuro'; even although individuals were not distributed uniformly. The proportion of reproductive adults with respect to total number of individuals is not proportional to the area sampled (8.3, 21.58 and 15.71% for 'Monte Oscuro', 'El Farallón' and 'Rancho del Niño', respectively). Plant density is highest in 'Rancho del Niño' (0.44 ind/m²) with respect to 'Monte Oscuro' (0.21 ind/m²) and 'El Farallón' (0.31 ind/m²) populations. On the one hand, the 'Monte Oscuro' and 'Rancho del Niño' populations showed a contagious spatial distribution in all classes. However, at 'El Farallón', seedlings and juveniles plants showed a random distribution (*I*-values: 0.76–0.59, respectively, $P > 0.05$) whilst the adults were found to be contagious (*I*-value: 1.41, $P < 0.01$). On the other hand, the seed production in the three populations varied from 103 ± 54 ('El Farallón') to 203 ± 74 ('Rancho del Niño') seeds per cone.

MATRIX MODELS

The iteration of the Lefkovich matrix for the 'Monte Oscuro' population showed a stable structure value λ of 0.995 (Fig. 3A). The elasticity matrix for this population showed that the reproductive component (F) did not contribute to the population elasticity, the increment (G) contributed to 3.45% and stasis (L) to 96.55% (Table 1, Fig. 3B). The class with the highest

elasticity value was the non-reproductive adults class (96.46%). The matrix analysis was also run assuming that adult-plant decapitation did not occur and these adults could pass to the reproductive adults class. The population increment rate value λ of 0.999 (Fig. 3A) and population growth rate components were distributed thus: L = 83.87%, G = 16.13%, F = 0 (Table 1).

The matrix iteration for the 'El Farallón' population showed a finite population growth rate at stable structure, λ -value of one (Fig. 3A). The elasticity matrix indicated that the reproductive component (F) did not contribute to the elasticity, growth (G) contributed to 17.54% and stasis (L) accounts for 82.46% (Table 1, Fig. 3B).

The iteration of the matrix for the 'Rancho del Niño' population estimated a stable structure λ -value of one (Fig. 3A). The elasticity matrix values indicated that component F represented 0% of the elasticity, G 13.41% and L 86.59% (Table 1, Fig. 3B).

The low rate of positive increase is largely a result of high seed and seedling mortality; however, in these categories a unique value of growth in the transition matrices was observed. High levels of survival amongst adults resulted in a population profile dominated by persistence of individuals (Table 2). The elasticity of non-reproductive adult stasis is substantially higher than for any other stage (Table 3).

The eigenvector (*w*) was significantly different from the observed proportion of individuals in all three populations studied. ('Monte Oscuro': $\chi^2 = 21.55$, $P < 0.001$, d.f. 4; 'El Farallón': $\chi^2 = 30.48$, $P < 0.001$, d.f. 4; 'Rancho del Niño': $\chi^2 = 33.37$, $P < 0.001$, d.f. 4).

Table 1. Comparison of finite population growth rates for various cycad species and elasticity components: stasis (L), growth (G) and fecundity (F)

Species	λ	Elasticity		
		L	G	F
<i>Encephalartos villosus</i> *	1.047	0.806	0.173	0.021
<i>Encephalartos cycadifolius</i> *	1.000	0.986	0.014	0
<i>Zamia amblyphyllidia</i> (1982–1983)†	0.966	0.958	0.042	0
<i>Z. amblyphyllidia</i> (1983–1984)†	0.999	0.95	0.05	0
<i>Zamia loddigesii</i> ‡	0.780	0.953	0.039	0.008
<i>Dioon edule</i> ('El Farallón')§	1.000	0.825	0.175	0
<i>D. edule</i> ('Rancho del Niño')§	1.000	0.866	0.134	0
<i>D. edule</i> ('Monte Oscuro' decapitated)§	0.995	0.966	0.034	0
<i>D. edule</i> ('Monte Oscuro' not decapitated)§	0.999	0.839	0.161	0

*Raimondo & Donaldson (2003).

†Negrón-Ortiz *et al.* (1996).

‡González-Astorga, unpublished data.

§This study.

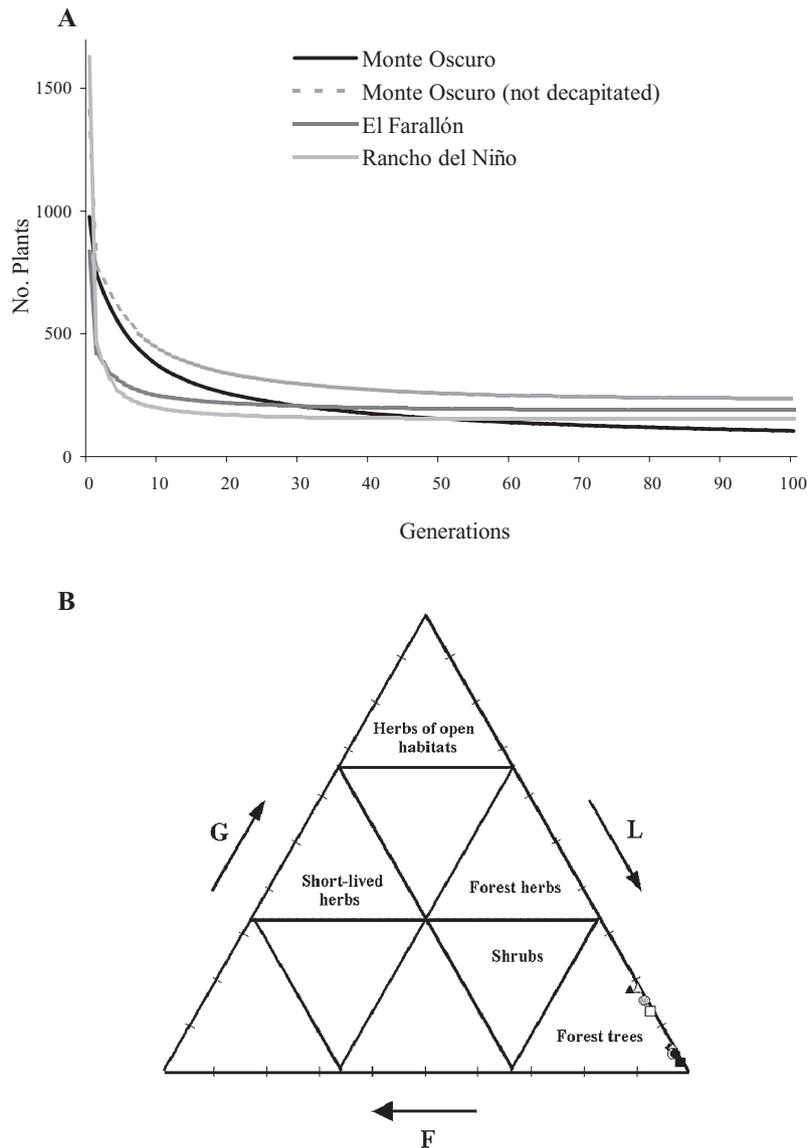


Figure 3. A, iteration to 100 generations from three populations of *Dioon edule* and hypothetical not-decapitated condition in 'Monte Oscuro'. B, comparative triangle of elasticity for various cycad species: *Encephalartos villosus* (\blacktriangle); *Encephalartos cycadifolius* (\blacksquare); *Zamia amblyphyllidia* (82–83, \diamond); *Z. amblyphyllidia* (83–84, \blacklozenge); *Zamia loddigesii* (\circ); *D. edule* ('Monte Oscuro', \bullet ; non-decapitation analysis, \oplus); *D. edule* ('El Farallón', \triangle); *D. edule* ('Rancho del Niño', \square). Figure and legends from Silvertown *et al.* (1995) for comparison of 84 plant species.

DISCUSSION

DENSITY AND SPATIAL DISTRIBUTION

The results of this study show that populations of *D. edule* have an aggregated spatial distribution pattern, excepting seedlings and juvenile plants at the 'El Farallón' population. This pattern repeats for other long-lived plants in tropical forests (Alvarez-Buylla *et al.*, 1996a), which can be as a result of historical and ecological variation of the populations (Olmsted & Alvarez-Buylla, 1995; Freckleton *et al.*,

2003) and principally of biological factors related to dispersal (Fleming, Breitwisch & Whitesides, 1987; Caswell *et al.*, 2003). Seed dispersal can also be reduced in habitat fragments owing to the local extinction of dispersal agents (Santos & Telleria, 1994). Additionally, seedling establishment diminishes as a result of altered environmental conditions (Martínez-Ramos *et al.*, 1989; Bruna, 1999), depression because of inbreeding (Menges, 1991) or to natural selection pressures upon individuals with least genetic diversity (Ellstrand & Elam, 1993).

Table 2. Transition matrices for the study sites

	0	1	2	3	4
(a) 'Monte Oscuro'					
0	–	–	–	–	1.5669
1	0.3566	0.8125	–	–	–
2	–	0.0074	0.95402	–	–
3	–	–	–	0.9595	0.9661
4	–	–	–	0.0357	0.0271
(b) 'Monte Oscuro' not decapitated					
0	–	–	–	–	2.1622
1	0.1337	0.8125	–	–	–
2	–	0.0074	0.95402	–	–
3	–	–	–	0.8049	0.9314
4	–	–	–	0.1951	0.0686
(c) 'El Farallón'					
0	–	–	–	–	1.5514
1	0.0809	0.7046	–	–	–
2	–	0.0231	0.94624	–	–
3	–	–	–	0.7838	0.9307
4	–	–	–	0.2162	0.0693
(d) 'Rancho del Niño'					
0	–	–	–	–	2.7594
1	0.0782	0.5926	–	–	–
2	–	0.0073	0.90164	–	–
3	–	–	–	0.8438	0.9459
4	–	–	–	0.1563	0.0541

Classes: 0, seeds; 1, seedlings; 2, juveniles; 3, non-reproductive adults; 4, reproductive adults.

Table 3. Elasticity values for each stage class in the study populations

Classes	'Monte Oscuro'	'Monte Oscuro' not decapitated	'El Farallón'	'Rancho del Niño'
0	0	0	0	0
1	0	0	0	0
2	0	0	0	0
3	0.9645	0.827	0.811	0.858
4	0.0355	0.173	0.189	0.142

Classes: 0, seeds; 1, seedlings; 2, juveniles; 3, non-reproductive adults; 4, reproductive adults.

At 'El Farallón', all plants were located on steep slopes (> 50°), which suggests that gravity is the major cause of seed dispersal, where a differential spatial distribution pattern exists between cohorts. At 'Monte Oscuro' and 'Rancho del Niño', the aggregated spatial distribution of seedlings around the mother plants indicated poor dispersion (cf. Pérez-Farrera *et al.*, 2000, 2006). In which case the distribution pattern could be as a result of previous harvesting

(Olmsted & Alvarez-Buylla, 1995) and the absence of seed dispersers (Ballardie & Whelan, 1986), or that a potential disperser avoids the seeds owing to their high concentration of toxins such as cycasins, mac-rozamins, neocycasins and β -*N*-methylamine-alanine propionic acid (Vovides *et al.*, 1993; Schneider *et al.*, 2002; Brenner, Stevenson & Twigg, 2003). Nevertheless, Vovides (1990) reported the rodent *Peromyscus mexicanus* predating *D. edule* seeds in an adjacent population of 'Monte Oscuro' and the presence of these along with other seeds and leguminous seed pods in the rodents' nests in the rocky parts of the habitats. It is also expected that periodic forest fires would have an effect on the differential distribution of plants in the population and at class level, as well as fecundity (cf. Vovides, 1990; Negrón-Ortiz & Gorchova, 2000; Goubitz, Werger & Ne'eman, 2003).

There are a number of theoretical studies (Harper & White, 1974; Antonovics & Levin, 1980; Venable, 1984) as well as empirical studies (e.g. Baskin & Baskin, 1972; Martínez-Ramos *et al.*, 1988; Alvarez-Buylla *et al.*, 1996b; Broncano, Riba & Retana, 1998) that have valued the effect of plant density on the survival of seeds and seedlings. In long-lived perennial species there is a density-dependent mortality during the early stages of the life cycle (Bullock, 1980; Alvarez-Buylla & Martínez-Ramos, 1990; Alvarez-Buylla *et al.*, 1996b; García, 2003; Pino, Picó & de Roa, 2007). In the *D. edule* populations, survival decreases during the first-stage class. The main reason for this pattern is the high mortality of seed as a result of water deficit, which is indicative of a density-independent mortality effect in these classes. Our studies are in agreement with Vovides (1990), who demonstrated a Deevey (1947) type III survival curve for this species in a nearby population, with high mortality in seeds and plants in the early stages of the life cycle. Similar patterns were reported in the cycads: *Zamia amblyphyllidia* (Negrón-Ortiz *et al.*, 1996), *Encephalartos cycadifolius* (Raimondo & Donaldson, 2003), *Ceratozamia matudai* (Pérez-Farrera *et al.*, 2000) and *Ceratozamia mirandae* (Pérez-Farrera *et al.*, 2006). Even although in *Encephalartos villosus* mortality decreases proportionally to the increment in plant size (Raimondo & Donaldson, 2003) and in *C. mirandae* the mortality was of type I (Pérez-Farrera *et al.*, 2006), these studies indicate that no definite pattern exists for cycads in general, as diverse factors determining mortality can be expected (cf. Venable, 1984).

MATRIX MODELS

Demographic components of elasticity vary systematically amongst plant species with different life cycles (Franco & Silvertown, 2004). Elasticity in tree species

is mainly explained by persistence (L), whilst, for annual plants, the major component is explained by fecundity (F) (Silvertown *et al.*, 1993, 1995; Franco & Silvertown, 2004). With respect to long-lived plants, λ is more sensitive to the L component, in particular the survival of seeds, seedlings and non-reproductive individuals, such as *Podococcus barteri* (Bullock, 1980), *Astrocaryum mexicanum* (Piñero *et al.*, 1984), *Cecropia obtusifolia* (Alvarez-Buylla & Martínez-Ramos, 1990), *Calathea ovoidensis* (Horvitz & Schemske, 1995), *Primula vulgaris* (Valverde & Silvertown, 1998), *Mammillaria magnimamma* (Valverde *et al.*, 2004), *Borderea chouardii* (García, 2003) and the Mexican palms *Coccothrinax readii* and *Thrinax radiata* (Olmsted & Alvarez-Buylla, 1995). Notwithstanding, in *Zea diploperennis* (Sánchez-Velásquez *et al.*, 2002) and the tree *Bertholletia excelsa* (Zuidema & Boot, 2002), the observed contribution relative to demographic components (i.e. persistence, sexual reproduction and vegetative growth) varies relative to the level of habitat disturbance. Thus, in disturbed sites, the contribution to the sexual reproduction component is relatively high, whilst, in relatively conserved sites, a consistently high contribution occurs in the plants' persistence, generating a significant decrease in sexual reproduction. In long-lived species, the extremely slow capacity for recovery following disturbances renders habitat preservation essential. This pattern is similar in other cycad species, and explains their behaviour as long-lived trees in the context of the Elasticity Triangle (Fig. 3B; Negrón-Ortiz *et al.*, 1996; Raimondo & Donaldson, 2003; González-Astorga, unpublished data). Following this pattern, the populations behave as long-lived trees (Silvertown *et al.*, 1995; Franco & Silvertown, 2004), with a high contribution to the finite stable state to stasis or persistence, but a low reproductive component and growth.

A similar pattern was detected in the cycads: *Z. amblyphyllidia* (Negrón-Ortiz *et al.*, 1996) for two consecutive years; in *E. cycadifolius* and *E. villosus* (Raimondo & Donaldson, 2003). The 'Monte Oscuro' population of *D. edule* behaves like *E. villosus*, *Z. amblyphyllidia* and *Zamia loddigesii* (González-Astorga, unpublished data), whilst populations at 'El Farallón' and 'Rancho del Niño' behave like *E. cycadifolius*. These differences in population behaviour can be attributed to the environmental stochasticity impact (cf. Pfister & Stevens, 2003) or by human disturbance that mainly affects the adult cohort (Martínez-Ramos *et al.*, 1988; Olmsted & Alvarez-Buylla, 1995). The magnitude of this impact depends on the species longevity, as well as the variation in fecundity and mortality of the population and explains why population growth rate shows population stability in disturbed habitats (Olmsted & Alvarez-Buylla, 1995;

García, 2003). This indicates that population behaviour can vary in time, depending on the differences between cohorts (González-Astorga & Núñez-Farfán, 2000).

When the population dynamics of *D. edule* at 'Monte Oscuro' under the assumption of non-decapitation of reproductive adults (thus allowing for sexual reproduction) is considered, then the population will grow and will approach a position similar to the other two populations shown in the Elasticity Triangle (Fig. 3B). This future scenario can be envisaged if plant decapitation is stopped, thus permitting recruitment (Cardoso da Silva & Tabarelli, 2000).

It is strongly recommended that decapitation be stopped as part of the management plan in order to strengthen population management at 'Monte Oscuro'. It is therefore necessary to continue with the work initiated by Vovides *et al.* (2002), with reintroduction of *D. edule* plants since 1997, at sites where populations of the cycad once existed, as well as to discourage plant removal and decapitation. This is in collaboration with the subsistence farmers running the sustainable management nursery of this species (Vovides & Iglesias, 1994; Vovides *et al.*, 2002).

In this sense, studies that embark on dynamics of diversity and genetic structure using age classes or stages can help define the magnitude of disturbance, in function of life history, geographical distribution and speciation processes. We consider these studies particularly important for the successful long-term sustainable management of *D. edule* and especially important for cycads in general. These plants of ancient lineage that are phylogenetically basal to the living seed plants are an important plant conservation issue (Norstog & Nicholls, 1997).

ACKNOWLEDGEMENTS

This study was financed by CONACyT grant nos 34077-N and CONACyT-SEMARNAT 2002-C01-0183 to APV and JG-A. We are grateful to Carlos Iglesias, Concepción Díaz Villa and Daniel Aguirre Fey for assistance in the field. We would like to thank Daniel Piñero, Luis Eguiarte, Fabián Vargas and Francisco Ornelas for helpful comments on the manuscript. The present study was also supported by a PhD grant from CONACyT to PO-A.

REFERENCES

- Alvarez-Buylla ER, García-Barrios R, Lara-Moreno C, Martínez-Ramos M. 1996a. 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.

- Alvarez-Buylla ER, Chaos A, Piñero D, Garay A. 1996b.** Demographic genetics of a pioneer tropical tree species: patch dynamics, seed dispersal, and seed banks. *Evolution* **50**: 1155–1166.
- Alvarez-Buylla ER, Martínez-Ramos M. 1990.** Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* **84**: 314–325.
- Antonovics J, Levin DA. 1980.** The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics* **11**: 411–452.
- Ballardie RT, Whelan RJ. 1986.** Mating, seed dispersal and seed predation in the cycad *Macrozamia communis*. *Oecologia* **70**: 100–105.
- Baskin J, Baskin C. 1972.** Influence of germination date on survival and seed production in a population of *Leavenworthia stylosa*. *American Midland Naturalist* **88**: 318–323.
- Benton TG, Grant A. 1999.** Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution* **14**: 467–471.
- Brenner ED, Stevenson DW, Twigg RW. 2003.** Cycads: evolutionary innovations and the role of plant-derived neurotoxins. *Trends in Plant Science* **8**: 446–452.
- Broncano MJ, Riba M, Retana J. 1998.** Seed germination and seedling performance of two Mediterranean tree species, Holm oak (*Quercus ilex*) and Aleppo pine (*Pinus halepensis*): a multifactor experimental approach. *Plant Ecology* **138**: 17–26.
- Bruna EM. 1999.** Seed germination in rain forest fragments. *Nature* **402**: 139.
- Bullock SH. 1980.** Demography of an undergrowth palm in Littoral Cameroon. *Biotropica* **12**: 247–255.
- Cardoso da Silva JM, Tabarelli M. 2000.** Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* **404**: 72–74.
- Caswell H. 2001.** *Matrix population models*, 2nd edn. Sunderland, MA: Sinauer Associates Inc.
- Caswell H, Lensink R, Neubert MG. 2003.** Demography and dispersal: life table response experiments for invasion speed. *Ecology* **84**: 1968–1978.
- Caswell H, Trevisan MC. 1994.** Sensitivity analysis of periodic matrix models. *Ecology* **75**: 1299–1303.
- Chamberlain CJ. 1919.** *The living cycads*. New York: Hafner Press.
- Chamberlain CJ. 1935.** *Gymnosperms. Structure and evolution*. Chicago, IL: University of Chicago Press.
- Crowse DT, Crowder LB, Caswell H. 1987.** A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**: 1412–1423.
- De Kroon H, Plaiser A, Groenendael JV, Caswell H. 1986.** Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**: 1427–1431.
- Deevey ES. 1947.** Life tables for natural populations of animals. *Quarterly Review of Biology* **22**: 283–314.
- Donaldson JS. 2003.** *Cycads. Status survey and conservation action plan IUCN/SSC*. Gland: Cycad Specialist Group, International Union for the Conservation of Nature and Natural Resources.
- Ellstrand NC, Elam DR. 1993.** Population genetic consequences of small populations size: implications for plant conservation. *Annual Review of Ecology and Systematics* **24**: 217–242.
- Enright NJ, Franco M, Silvertown J. 1995.** Comparing plant life histories using elasticity analysis: the importance of lifespan and the number of life-cycle stages. *Oecologia* **104**: 79–84.
- Fleming TH, Breitwisch R, Whitesides GH. 1987.** Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics* **18**: 91–109.
- Franco M, Silvertown J. 2004.** A comparative demography of plants based upon elasticities of vital rates. *Ecology* **85**: 531–538.
- Freckleton RP, Matos DMS, Bovi MLA, Watkinson AR. 2003.** Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. *Journal of Applied Ecology* **40**: 858.
- García MB. 2003.** Demographic viability of a relict population of the critically endangered plant *Borderea chouardii*. *Conservation Biology* **17**: 1672–1680.
- González-Astorga J, Núñez-Farfán J. 2000.** Variable demography in relation to germination time in the annual plant *Tagetes micrantha* Cav. (Asteraceae). *Plant Ecology* **151**: 253–259.
- González-Astorga J, Vovides AP, Iglesias C. 2003a.** Morphological and geographic variation of the cycad *Dioon edule* Lindl. (Zamiaceae): ecological and evolutionary implications. *Botanical Journal of the Linnean Society* **141**: 465–470.
- González-Astorga J, Vovides AP, Ferrer M, Iglesias C. 2003b.** Population genetics of *Dioon edule* Lindl. (Zamiaceae, Cycadales): biogeographical and evolutionary implications. *Biological Journal of the Linnean Society* **80**: 457–467.
- Goubitz S, Werger MJ, Ne'eman G. 2003.** Germination response to fire-related factors of seeds from non-serotinous and serotinous cones. *Plant Ecology* **169**: 195–204.
- Groenendael JV, De Kroon H, Caswell H. 1988.** Projection matrices in population biology. *Trends in Ecology and Evolution* **3**: 264–269.
- Harper JL, White J. 1974.** The demography of plants. *Annual Review of Ecology and Systematics* **5**: 419–463.
- Heppell SS, Caswell H, Crowder LB. 2000.** Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* **81**: 654–665.
- Hill KD, Stevenson DW, Osborne R. 2004.** The world list of cycads. In: Walters TW, Osborne R, eds. *Cycad classification: concepts and recommendations*. Wallingford, Oxon: CABI Publishing, 219–235.
- Hoffmann WA. 1999.** Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* **80**: 1354–1369.
- Horvitz CC, Schemske DW. 1995.** Spatiotemporal variation in demographic transitions of a tropical understorey herb: projection matrix analysis. *Ecological Monographs* **65**: 155–192.
- INE-SEMARNAP. 2000.** *Prep 6: Protección, conservación y*

- recuperación de la familia Zamiaceae (Cycadales) de México. México D.F.: Instituto Nacional de Ecología.
- IUCN. 2004.** *IUCN red list of threatened species*. Available at <http://www.redlist.org> (accessed 17 April 2007).
- Keppel G. 2001.** Notes on the natural history of *Cycas see-mannii* (Cycadaceae). *South Pacific Journal of Natural Science* **19**: 35–41.
- Lande R. 1988.** Genetics and demography in biological conservation. *Science* **241**: 1455–1460.
- Lande R. 1999.** Extinction risks from anthropogenic, ecological and genetic factors. In: Landweber LF, Dobson AP, eds. *Genetics and the extinction of species*. Princeton, NJ: Princeton University Press, 1–22.
- Manly BF. 1990.** *Stage-structured populations sampling, analysis and simulation*. New York: Chapman & Hall Ltd.
- Martínez-Ramos M, Alvarez-Buylla ER, Sarukhán J. 1989.** Tree demography and gap dynamics in a tropical rain forest. *Ecology* **70**: 555–558.
- Martínez-Ramos M, Alvarez-Buylla ER, Sarukhán J, Piñero D. 1988.** Tree fall age determination and gap dynamics in a tropical forest. *Journal of Ecology* **76**: 700–716.
- Menges ES. 1991.** Seed germination percentage increases with population size in a fragmented prairie species. *Conservation Biology* **5**: 158–164.
- Muller-Dombois D, Ellenberg H. 1974.** *Aims and methods of vegetation ecology*. New York: J.T. Arthur.
- Negrón-Ortiz V, Gorchov DL. 2000.** Effects of fire season and postfire herbivory on the cycad *Zamia pumila* (Zamiaceae) in slash pine savanna, everglades national park, Florida. *International Journal of Plant Science* **161**: 659–669.
- Negrón-Ortiz V, Gorchov DL, Breckon GJ. 1996.** Population structure in *Zamia* (Zamiaceae) in northern Puerto Rico. II. Seed germination and stage-structured population projection. *International Journal of Plant Science* **157**: 605–614.
- Norstog KJ, Nicholls TJ. 1997.** *The biology of cycads*. Ithaca, NY: Cornell University Press.
- Olmsted I, Alvarez-Buylla ER. 1995.** Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. *Ecological Applications* **5**: 484–500.
- Pérez-Farrera MA, Quintanilla-Ascencio PF, Salvatierra BI, Vovides AP. 2000.** Population dynamics of *Ceratozamia matudai* Lundell (Zamiaceae) in the Triunfo Biosphere Reserve, Chiapas, Mexico. *Journal of the Torrey Botanical Club* **127**: 291–299.
- Pérez-Farrera MA, Vovides AP, Octavio-Aguilar P, González-Astorga J, de la Cruz-Rodríguez J, Hernández-Jonapá R, Villalobos-Méndez S. 2006.** Demography of the cycad *Ceratozamia mirandae* (Zamiaceae) under disturbed and undisturbed conditions in a biosphere reserve of Mexico. *Plant Ecology* **187**: 97–108.
- Pfister CA, Stevens FR. 2003.** Individual variation and environmental stochasticity: implications for matrix model predictions. *Ecology* **84**: 496–510.
- Piñero D, Martínez-Ramos M, Sarukhán J. 1984.** A population model of *Astrocaryum mexicanum* and sensitivity analysis of its finite rate of increase. *Journal of Ecology* **72**: 977–991.
- Pino J, Picó FX, de Roa E. 2007.** Population dynamics of the rare plant *Kosteletzkyia pentacarpus* (Malvaceae): a nine-year study. *Botanical Journal of the Linnean Society* **153**: 455–462.
- Raimondo DC, Donaldson JS. 2003.** Responses of cycads with different life histories to the impact of plant collecting: simulation models to determine important life history stages and population recovery times. *Biological Conservation* **111**: 345–358.
- Sánchez-Velásquez LR, Ezcurra E, Martínez-Ramos M, Alvarez-Buylla ER, Lorente R. 2002.** Population dynamics of *Zea diploperennis*, an endangered perennial herb: effect of slash and burn practice. *Journal of Ecology* **90**: 684–692.
- Santos T, Telleria JL. 1994.** Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniperus thurifera*. *Biological Conservation* **70**: 129–134.
- Schneider D, Wink M, Sporer F, Lounibos P. 2002.** Cycads: their evolution, toxins, herbivores and insect pollinators. *Naturwissenschaften* **89**: 281–294.
- Silvertown JW, Franco M, Menges E. 1995.** Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* **10**: 591–597.
- Silvertown JW, Franco M, Pisanty I, Mendoza A. 1993.** Comparative plant demography: relative importance of life-cycle components to the finite rate of increase in woody, herbaceous perennials. *Journal of Ecology* **81**: 465–476.
- Smith RL. 1996.** *Ecology and field biology*, 5th edn. New York: Harper Collins College Publishers, West Virginia University.
- Sokal RR, Rohlf FJ. 1995.** *Biometry*, 3rd edn. New York: W.H. Freeman.
- Tang W. 1989.** Seed dispersal in the cycad *Zamia pumila* in Florida. *Canadian Journal of Botany* **67**: 2066–2070.
- Treutlein J, Wink M. 2002.** Molecular phylogeny of cycads inferred from *rbcl* sequences. *Naturwissenschaften* **89**: 221–225.
- Valverde T, Quijas S, López-Villavicencio M, Castillo S. 2004.** Population dynamics of *Mammillaria magnimamma* Haworth. (Cactaceae) in a lava-field in central Mexico. *Plant Ecology* **170**: 167–184.
- Valverde T, Silvertown J. 1998.** Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *Journal of Ecology* **86**: 545–562.
- Venable DL. 1984.** Using intraspecific variation to study the ecological significance and evolution plants. In: Dirzo R, Sarukhán J, eds. *Perspectives on plant population biology*. Sunderland, MA: Sinauer Associates Inc., 166–187.
- Vovides AP. 1990.** Spatial distribution, survival, and fecundity of *Dioon edule* (Zamiaceae) in tropical deciduous forest in Veracruz, México, with notes on its habitat. *American Journal of Botany* **77**: 1532–1543.
- Vovides AP, Iglesias C. 1994.** An integrated conservation strategy for the cycad *Dioon edule* Lindl. *Biodiversity and Conservation* **3**: 137–141.

- Vovides AP, Iglesias C, Pérez-Farrera MA, Vázquez-Torres M, Schippmann U. 2002.** Peasant Nurseries: a concept for an integrated conservation strategy for cycads in Mexico. In: Maunder M, Clubbe C, Hankamer C, Groves M, eds. *Plant conservation in the tropics*. Kew: The Royal Botanic Gardens: The Cromwell Press Ltd., 422–444.
- Vovides AP, Norstog KJ, Fawcett PKS, Duncan MW, Nash RJ, Molsen DV. 1993.** Histological changes during maturation in male and female cones of the cycad *Zamia furfuracea* and their significance in relation to pollination biology. *Botanical Journal of the Linnean Society* **111**: 241–252.
- Vovides AP, Peters CM. 1987.** *Dioon edule*; la planta más antigua de México. *Ciencia y Desarrollo* **13**: 19–24.
- Vovides AP, Rees JD, Vázquez-Torres M. 1983.** Flora de Veracruz: (Zamiaceae). *INIREB, Xalapa Veracruz, México* **26**: 12–16.
- Watkinson AR, Powell JC. 1997.** The life history and population structure of *Cycas armstrongii* in monsoonal Australia. *Oecologia* **111**: 341–349.
- Zuidema PA, Boot RGA. 2002.** Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology* **18**: 1–31.