

# Demography of the cycad *Ceratozamia mirandae* (Zamiaceae) under disturbed and undisturbed conditions in a biosphere reserve of Mexico

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Received: 22 July 2004 / Accepted: 1 March 2006 / Published online: 30 March 2006  
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**Abstract** The cycad *Ceratozamia mirandae* is endemic to Chiapas, Mexico. Demographic studies were made in two of its populations in the *Sepultura Biosphere Reserve* under different conservation conditions; in the nucleus zone “Tres Picos” (conserved) and buffer zone “La Sombra” (disturbed and under management). Spatial distribution of *C. mirandae* was aggregated, showed a clumped local distribution on shallow soils on steep slopes and male and female cones appear to be synchronous in both populations. The population structure was of type I (Bongers) for both sites. Individuals between the sites showed differences in growth pattern. The oldest plants (80–90 cm tall) were estimated to be about 490 years at “La Sombra”. The finite growth rate ( $\lambda$ ) in the buffer zone population showed a tendency for decrease whilst in the nucleus zone this estimate remained stable. The highest elasticity values lied in the transition of the first three classes of the “La Sombra” population, in “Tres Picos” this corresponded to adult plants between 20

and 30 cm tall. Given the above, it is proposed that in the nucleus zone, reproductive adults should be of highest conservation priority, whereas in the buffer zone seedling reintroduction should be carried out regularly until the population increases. We recommend an IUCN Red List category of Vulnerable (VU C, 2a), largely due to difficult-to-control destructive annual forest fires that occur in this Reserve.

**Keywords** Chiapas · Conservation biology · Cycadales · Endangered species · Finite growth rate · Mexico · Matrix modelling

## Introduction

Cycads are considered worldwide as threatened and endangered (IUCN 2003) and it is estimated that there are about 300 species of cycads worldwide (Donaldson 2003; Hill et al. 2004). Many workers believe the number may reach as many as 400 species when all potential cycad habitats have been investigated and taxonomic studies are completed (Osborne personal communication). Based on the world cycad census (Osborne 1995; Osborne et al. 1999; Hill et al. 2004) Mexico is second worldwide in cycad diversity (Vovides 2000). Cycads are considered a national conservation priority (INE-SEMARNAP 2000; CONABIO 2000) and are protected by national and international laws (Diario Oficial 2000; IUCN 2003). The threats

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to their survival are caused by multiple factors, most of which are anthropogenic: (a) uncontrolled fires, (b) human demographic expansion, (c) illegal collecting and (d) habitat transformation.

*Ceratozamia mirandae* is a medium to large sized under-story cycad in pine-oak forests with trunks up to one meter long which are erect or prostrate topped with an ascending to spreading crown of up to 23 pinnate leaves approximately 1.5 m long and 70 cm wide (Vovides et al. 2001). The species is entomophilous which accords with that reported for other Neotropical cycads (Tang 1987; Norstog and Fawcett 1989; Vovides 1991; Vovides et al. 1997b).

There are not more than four populations in its known range in Chiapas and the total number of individuals in these four populations is estimated between 1000 and 1500 plants. The immediate threats to the survival of *C. mirandae* are habitat destruction and or transformation (coffee plantations), periodic fires and illegal trade. Leaf predation of this cycad on leaves and cones presents a similar pattern by insect herbivores (larvae of *Eumaeus* spp. Lepidoptera) as in the majority of Neotropical cycads, and total defoliation does not appear to kill or affect cycads as reported by Vovides (1990) for *Dioon edule* and González (2004) for the Colombian *Zamia encephalartoides*.

The wild peccari *Tayassu pecari* was observed directly and indirectly (excrement and tracks near the mother plant) to eat and disperse the cycad seeds (Pérez-Farrera et al. 2000). The seeds of this species are covered by a creamy coloured fleshy sweet sarcolemma, which emits a fruity fragrance that attracts these animals. Other small mammals such as squirrels, opossum, raccoon and mice, though not observed during the study, may also act as dispersal agents (Pérez-Farrera and Vovides 2004).

Donaldson (1995) points out that the presence of specific pollinators in the cycad habitats is indicative of the populations state of conservation, and is of vital importance to the cycads survival (Norstog and Fawcett 1989; Norstog and Nicholls 1997; Vovides et al. 1997b).

Endangered plant species listings of Mexico are so far subjective and differ according to the criteria of each specialist (Vovides 1981; Malda 1990; Hernández 1994; Vovides et al. 1997a). This is mostly due to a poor and partial knowledge of the

country's flora. Nevertheless these listings were instrumental in achieving a national official listing along with protective legislation (Diario Oficial 2000). Some authors have proposed more precise threat evaluations by using quantitative methods to estimate the degree of threat (Green and Young 1993) and to estimate extinction probabilities within a specified period of time (Mace and Lande 1991), as well as analysis of population viability (Schaffer 1981; Menges 1991). Population analysis of threatened plants, especially cycads, based on these methods, will not only enable us to propose more precise IUCN listing categories but also to recommend management plans and in situ conservation strategies which will hopefully lead to maintenance and preservation of their diversity. Sustainable utilization strategies have been implemented for in situ management of some Mexican cycad species including *C. mirandae*, aimed at discouraging illegal collecting, and to provide incentive to conserve their habitats by local farmers (Vovides and Iglesias 1994; INE-SEMARNAP 2000; Vovides et al. 2002). This activity fits in well with the missions of regional botanic gardens as assessors to biosphere reserves, thus implementing various articles of the Convention on Biological Diversity (Given 1997).

The *Sepultura Biosphere Reserve*, created in June 1995 owing to its high levels of biodiversity, consists of over 167,309 ha situated in the north east of the "Sierra Madre de Chiapas". The region consists of largely of Palaeozoic gneiss and granite with Tertiary sediments. Eight different vegetation types are found on the Reserve and the cycad species *Dioon merolae*, *C. mirandae* and *C. alvarezii* occur in three; tropical dry forests, oak/cloud-forest and pine-oak forests, respectively, (Kobelowsky-Sosa 2003; INE-SEMARNAP, 1999). Three of the known populations of *C. mirandae* occur in this Reserve.

The purpose of this study was to analyse the situation of *C. mirandae* by using the following ecological parameters: density, spatial distribution, population structure, growth pattern, age and fecundity. These demographic characteristics were contrasted and analysed in two different habitats, with and without noticeable disturbance. The demography and growth rate in these habitats were compared and contrasted as stage-transition matrix modelling for

both sites. It is hoped that the results obtained will permit efficient long-term conservation action plans for the species, as well as a precise IUCN listing.

## Methods

The study area consists of two sites. ‘La Sombra’, is located within the buffer zone of the *Sepultura Biosphere Reserve*, municipality of Villaflores (INEGI 1982c), at an altitude of 950 m. The climate is hot, sub-humid with rainfall in the summer. The rainy season extends through the months of May to October, with an annual rainfall from 1400 to 1600 mm; and average temperature 24.3°C (INEGI 1982b). Geologically the locality is composed of Palaeozoic bedrock (INEGI 1982) and the predominant soils types are lithosols (associated with regosols and luvisols) under agricultural use and present a relative heterogeneity (INEGI 1982a). The vegetation type at the locality is *Quercus* forest, or ‘Bosque de Encino’ according to the Rzedowski (1978) nomenclature. This site is subject to cattle grazing, induced fires and firewood extraction during the dry season.

The other site at ‘Tres Picos’ is located inside the nucleus zone of the *Sepultura Biosphere Reserve*, at an altitude of 1320 m. It has a semi-hot humid climate with rainfall in the summer. The rainy season extends from May to October, with an annual precipitation of 300–400 mm and a mean temperature of 24.3°C (INEGI 1982b). The locality is composed of Cenozoic bedrock (INEGI 1982) with predominant soil types are heterogeneous lithosols, associated with regosols and chromics (INEGI 1982a). The vegetation type is also a *Quercus* forest but a little more humid, owing to its proximity to cloud forest, or ‘Bosque Mesófilo de Montaña’ (*sensu* Rzedowski 1978). This site is free from human disturbance.

At both sites four contiguous permanent quadrats of 20 × 20 m were established on a transect of 20 × 80 m, and all plants were labelled. Since the populations studied are relatively small, transects were determined arbitrarily by bisecting the populations through their centres thus including the maximum number of individuals. A total of 376 individuals from both populations were analysed during this study. Each quadrat was subdivided

into sub-quadrats of 5 × 5 m. Height, diameter and number of leaves per trunk, number of leaf bases and reproductive condition were recorded. Sex was determined by the presence of cones or remnants inside the leaf crown and amongst the cataphylls.

Detection of non-randomness was determined by comparing the number of observed plants in 100 randomly distributed 1 m quadrats against the random expectation by use of the Poisson distribution as a mathematical model for randomness. The departure of the expected from the observed number for this quadrat size was subjected to the  $\chi^2$  test. The scale at which non randomness occurs (spatial distribution) was determined by analysis of a contiguous grid of quadrats technique for the detection of pattern by plotting variance against block size according to Greig-Smith (1983) and Kershaw and Looney (1985). Spatial distribution analysis and age estimation were done at the ‘La Sombra’ site only. Class structure and growth patterns were obtained from both sites following the method described by Krebs (1978), Begon et al. (1990) and Vovides (1990). Density and fecundity were determined for each site. Regression analysis was carried out to determine associated variables and growth patterns. Age estimation was calculated according to Chamberlain (1919) modified by Vovides and Peters (1987) and Vovides (1990). This was based on the division of mean annual leaf production by total number of persistent leaf bases present on trunks per height class.

Slope and soil depth were also determined. The slope was determined with a clinometer while the soil depth was obtained by introducing a 0.5 in diameter galvanized steel rod beside each plant until this struck rock.

The localities were visited monthly for 4–5 days during 3 years to determine the number of seeds produced inside the transect according to Krebs (1978).

The plants were assigned into height classes at 10 cm intervals in order to obtain survival per class:  $l_x = n_x/n_{x-1}$ , the reproductive component:  $m_x$ , which represents the number of reproductive females in the class  $x$ ; the net reproductive rate:  $R_0 = \sum l_x m_x$ , the intrinsic population growth rate:  $r = [\ln R_0] / [x l_x m_x / R_0]$ , the finite rate of population increment:  $\lambda = e^r$ , the reproductive value:  $V_x = \sum e^{-rx} l_x m_x [e^{rx} / l_x]$

and life expectancy:  $Ex=Lx/Tx$ , where  $Lx=[l_x+l_{x+1}]/2$  and  $Tx=\sum Lx$  (Silvertown 1984; Manly 1990).

The Lefkovich matrices were used to estimate the population dynamics through time until stability. The matrices contain the transition probabilities from one class to the following ( $n_x/n_{x-1}$ ), probability of permanence ( $n_x-n_{x-1}/n_x$ ) and fecundity for each class, estimated from the algebraic product of the mean number of seeds per cone, the germination rate, seedling survival and proportion of reproductive female plants in each class (Raimondo and Donaldson 2003).

The population size after one generation was determined by the product of the Lefkovich matrix ( $L$ ) by the vector  $n_0$ , where  $L=[L_{ij}]$  for  $i,j=\{1,2,\dots,n\}$ , and  $n_0$  is the vector that contains the number of individuals at zero time ( $t_0$ ). This process was repeated until the expected proportion of individuals per class remained stable, represented by the right vector ( $w$ ) and was compared with the observed structure under natural conditions using the Chi-squared test  $\chi^2$ ,  $k-1$  d.f. (Sokal and Rohlf 1995). The expected estimate of  $\lambda$  was also obtained for the matrix model  $n_t/n_{t-1}$  (Caswell 2001; Caswell and Trevisan 1994; Silvertown et al. 1995; Franco and Silvertown 2004).

The standard deviation of  $\lambda$  was estimated using the analytical method, which assumes that the errors of the  $L_{ij}$ th elements are small and of a normal distribution,  $\lambda$  will also have a normal distribution (Alvarez-Buylla and Slatkin 1991, 1994). Thus the transition probability variances were estimated with the formula:  $V(\lambda) = \sum_{ij} [(S_{ij})^2 V(L_{ij})]$ , where  $S_{ij}$  are the  $ij$ th elements from the sensitivity matrix and  $V(L_{ij})=(L_{ij}[1-L_{ij}])/N$ , where  $L_{ij}$  is the probability of transition from state  $i$  to state  $j$ , in the matrix  $L$  and  $N$  is the number of individuals used to estimate such transition (Contreras and Valverde 2002; Jiménez-Lobato and Valverde 2006).

Sensitivity matrices were constructed with the vectors  $w$  and  $v$ , where  $v$  represents the proportional reproductive value for each class and was obtained through iteration of the transposed matrix  $L$  and  $n_0$  until stability. The scalar value of the algebraic product of  $vw$ , which is:  $v_1w_1+v_2w_2+\dots+v_iw_i$ . The values of the elasticity matrix were obtained from the equation  $E_{ij} = (L_{ij}/\lambda)S_{ij}$ , 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 sensibility

matrix and  $\lambda$  is the finite rate of population growth obtained by the initial iteration of matrix  $L$  (Caswell 2001), these results are represented by transition graphics for each population (de Kroon et al. 1986; Benton and Grant 1999).

## Results

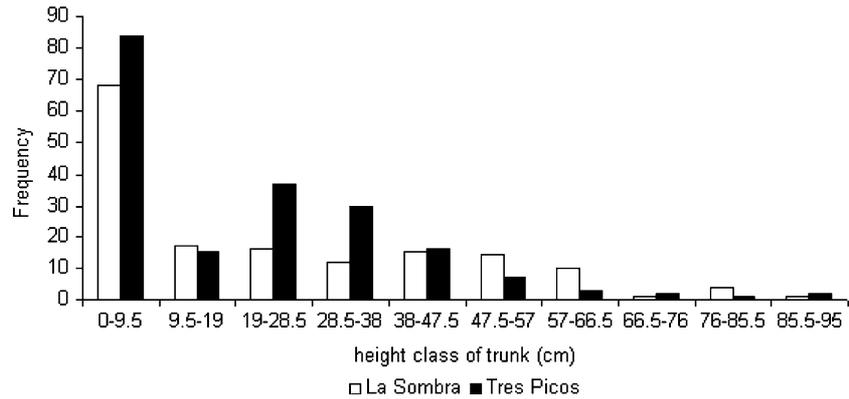
At ‘‘La Sombra’’ and ‘‘Tres Picos’’ 178 and 198 individuals were sampled, respectively. At ‘‘Ejido La Sombra de la Selva’’ the plants exhibited a non-random distribution  $\chi^2 = 24.84$ ; d.f.=6;  $P<0.05$ . The pattern analysis at ‘‘La Sombra’’ showed a grouped or aggregate distribution in one block which corresponds to 50 m<sup>2</sup>. The majority of the seedlings and juveniles were found around mother plants and under tree shade of *Pinus* and *Quercus*. Average slopes of 45–50° were found for both sites, which we consider a fundamental factor in seed dispersion. Many seeds were found at the bottom of these slopes when mother plants were present on the upper parts. Plants are established preferentially in soil depths of 10–25 cm at both sites.

The size based population structure present at both sites corresponds to a type I curve according to Bongers et al. (1998), that is to say a high frequency of seedlings and juveniles and a decrease in frequency of adults (Fig. 1) and the oldest plants of *C. mirandae* (80–90 cm tall) were estimated to be about 490 years (Table 1).

No significant difference was found for trunk height, diameter and sex of plants between both sites, but a significant difference was found among the number of plants at different life-cycle stages (seedlings, juveniles, adults;  $\chi^2 = 36.32$ ;  $P<0.001$ ; 1 d.f.). Differences in the number of leaf bases per plant between the two sites were found ( $\chi^2 = 15.35$ ;  $P<0.001$ ; 1 d.f.).

At ‘‘La Sombra’’ the plant reaches its maximum annual leaf production (20) when a trunk diameter of 20–30 cm is reached. Whilst at ‘‘Tres Picos’’ site, when the individuals reach a similar trunk diameter, the annual maximum leaf production is ten. The different rates of growth between the sites among these variables (trunk diameter versus height and trunk height versus leaf base number) appears to be due to the differences in leaf production per plant.

**Fig. 1** Height class population structure of the two populations of *Ceratozamia mirandae* in the *Sepultura Biosphere Reserve*



**Table 1** Age estimation of *C. mirandae* based on mean annual leaf production per size class and the mean total number of leaf bases present on trunks per height class

Height class (cm)	Mean total bases	Increment	Mean leaves/year	Residence	Age (year)
0–10	42.6		1.44	30	30
10–20	123.07	80.5	1	80.5	110.5
20–30	565.68	442.61	2.5	117	227.5
30–40	985.71	420.03	3.67	114	341.5
40–50	1408.17	422.46	7	60.4	401.9
50–60	1721.22	313.05	7.8	40.1	442
60–70	1984.99	263.77	12	22	464
70–80	1996.14	11.15	16	0.7	464.7
80–90	2523.47	538.48	21.6	24.9	489.6

Leaf production data obtained from 181 individuals in the transect over a period of 3 years at “Ejido La Sombra de la Selva”, Sepultura Biosphere Reserve, Chiapas, Mexico

Ten female and two male cones were found at the time of study and 12 female and 25 male cones appearing before the beginning of this study at “La Sombra”. At “Tres Picos” five female and three male cones were found. Twenty-five female and 35 male plants were coning before the beginning of this study. The female cones produced from 74 to 170 seeds (mean 118,  $n=14$ ).

Table 2 summarizes the demographic parameters from the static life tables. At “Tres Picos” the rates of population growth of *C. mirandae* are higher than at “La Sombra”, in that for one generation growth is

133% in comparison to 77% of the “La Sombra” population at this point in time. The reproductive value and life expectancy were highest in the first classes for both the populations. The proportion of individuals observed per height class differed significantly from the expected ( $\chi^2 = 0.047$ ,  $d.f=8$ ,  $p<0.05$ ) in the two populations, which means they are not structured according to height. Height therefore, is not an adequate life history indicator for the species, since during the first stages of growth there is no significant increase in height, causing stasis or arrest during these stages, though increase in diameter has been detected.

**Table 2** Demographic parameters of the two populations of *C. mirandae* in the *Sepultura Biosphere Reserve*

Population	$r$	$R_0$	$\lambda$	$V_x$	Ex
“La Sombra”	0.57	5.85	1.77	20–30 cm=11.27	10–20 cm=4.95
“Tres Picos”	0.84	8.2	2.33	10–20 cm=13.18	10–20 cm=4.06

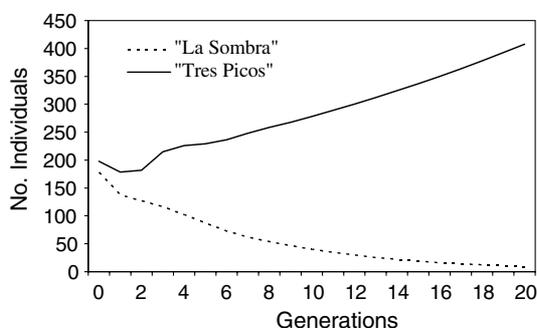
$r$ , intrinsic population growth rate;  $R_0$ , net rate of population turnover;  $\lambda$ , finite population growth rate estimated from life table data;  $V_x$ , reproductive value (individuals per female); Ex, life expectancy

Iteration matrix for the “La Sombra” population showed a  $\lambda$  value at stable structure of  $0.86 \pm 0.09$  (Fig. 2) indicating a significant population decrement. The  $w$  vector differs significantly from the observed proportion of individuals ( $\chi^2 = 0.002$ ; 8 d.f.  $P < 0.05$ ). This present population is not in equilibrium because the observed structure differs from the expected structure by iteration (Table 3a, b). Elasticity matrix for this population (Table 4) showed that the reproductive component ( $F$ ) contributed 16.91% of the total elasticity of the population, the plant growth increment ( $G$ ) 78.26% and stasis ( $L$ ) 4.83%. Highest elasticity value (57.41%) corresponded to the survival of adult individuals between 20 and 30 cm tall (Fig. 3).

Iteration with the Lefkovitch matrix for “Tres Picos” gave a stable structure  $\lambda$  value of  $1.039 \pm 0.046$  indicating a non-significant difference to unity, but apparent relative population growth (Fig. 2). Significant differences were obtained ( $\chi^2 = 5.59 \times 10^{-9}$ , 8 d.f.  $P < 0.05$ ) upon comparison of the  $w$  vector with the proportion of individuals observed. The elasticity matrix for this population (Table 4) showed that the reproductive component ( $F$ ) contributed 30.61% of the total elasticity of the population, the plant growth increment ( $G$ ) 49.94% and stasis ( $L$ ) 19.45%. The highest elasticity value (57.41%) corresponded to the survival of adult individuals between 20 and 30 cm tall (Fig. 3).

## Discussion

The spatial distribution pattern present in *C. mirandae* can be the result of interaction of various factors. Most seedlings, juveniles and seeds were located at



**Fig. 2** Population projection of two the populations of *C. mirandae* in the *Sepultura Biosphere Reserve*

the bases of steep slopes of over  $40^\circ$ , where we assume to be related to dispersal by gravity. In some relatively flat areas inside the study transect, seedlings and seeds were found located around the mother plant and under tree canopy providing shade. This suggests poor dispersion and/or seedling survival associated with tree and mother plant shade, which is a principal factor to the first phases of establishment and development (Pérez-Farrera et al. 2000; Pérez-Farrera and Vovides 2004).

The high seedling and juvenile plant frequency present in the population structure of this species can also suggest disturbance during past years, such as fire. This situation was observed in some individuals at both sites, where a high cone production, and therefore seeds, after a forest fire occurred. It has been shown that in several species of cycads fire is an important factor in the stimulation of cone production (Dyer 1965; Grove et al. 1980; Ornduff 1991, 1996; Negrón-Ortiz & Gorchoy 2000). Fire has two consequences: higher cone production resulting in higher recruitment in the population, and a high mortality amongst seedlings tantamount to the removal of the previous year's cohort. This reflects the population's history of interaction with environmental factors (Martínez-Ramos and Alvarez-Buylla 1995).

All tissues of cycads contain compounds such as cycasins, macrozamins and the powerful neurotoxin  $\beta$ -N-methylamine-alanine propionic acid (BMAA), that are highly toxic to mammals including humans (Duncan 1993; Norstog and Nicholls 1997; Monson et al. 2003). These toxins could be limiting factors to dispersal. Nevertheless predation and dispersion were observed by peccaries, but not quantified. However, it has been noted that the majority of seeds consumed, are destroyed through splitting of the sclerotesta, exposing the gametophyte and embryo to free atmosphere and thus to fungal contamination and desiccation leading to death. We believe that this mammal probably plays an important role during the first phases of habitat colonization by the cycad, even though few seeds survive the peccaries' digestive and elimination process. Cycad seed dispersal by this peccari species has also been reported for *C. matudae* (Pérez-Farrera et al. 2000; Pérez-Farrera and Vovides 2004).

Upon examining several seeds straight from a dehiscent cone, it was found that they presented immature embryos thus exhibiting physiological

**Table 3** Transition matrices for the two populations of *C. mirandae* in the Sepultura Biosphere Reserve (a) ‘‘Tres Picos’’, (b) ‘‘La Sombra’’

	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90
<b>(a)</b>									
0–10	–	–	0.4197	0.3731	0.1866	0.1955	0.0466	–	–
10–20	0.5667	–	–	–	–	–	–	–	–
20–30	–	1	0.5946	–	–	–	–	–	–
30–40	–	–	0.8919	–	–	–	–	–	–
40–50	–	–	–	0.3939	–	–	–	–	–
50–60	–	–	–	–	0.6923	–	–	–	–
60–70	–	–	–	–	–	0.3333	–	–	–
70–80	–	–	–	–	–	–	0.6667	–	–
80–90	–	–	–	–	–	–	–	0.5	–
<b>(b)</b>									
0–10	–	–	0.4064	0.4742	0.2033	0.4066	0.2033	–	0.6844
10–20	0.2639	–	–	–	–	–	–	–	–
20–30	–	1	0.05	–	–	–	–	–	–
30–40	–	–	0.85	–	–	–	–	–	–
40–50	–	–	–	1	0.0556	–	–	–	–
50–60	–	–	–	–	0.9444	–	–	–	–
60–70	–	–	–	–	–	0.4118	–	–	–
70–80	–	–	–	–	–	–	0.4286	–	–
80–90	–	–	–	–	–	–	–	1	0.4

Height class ranges in centimetres

**Table 4** Elasticity matrices for the two populations of *C. mirandae* in the Sepultura Biosphere Reserve (a) ‘‘Tres Picos’’, (b) ‘‘La Sombra’’. Height class ranges in centimetres

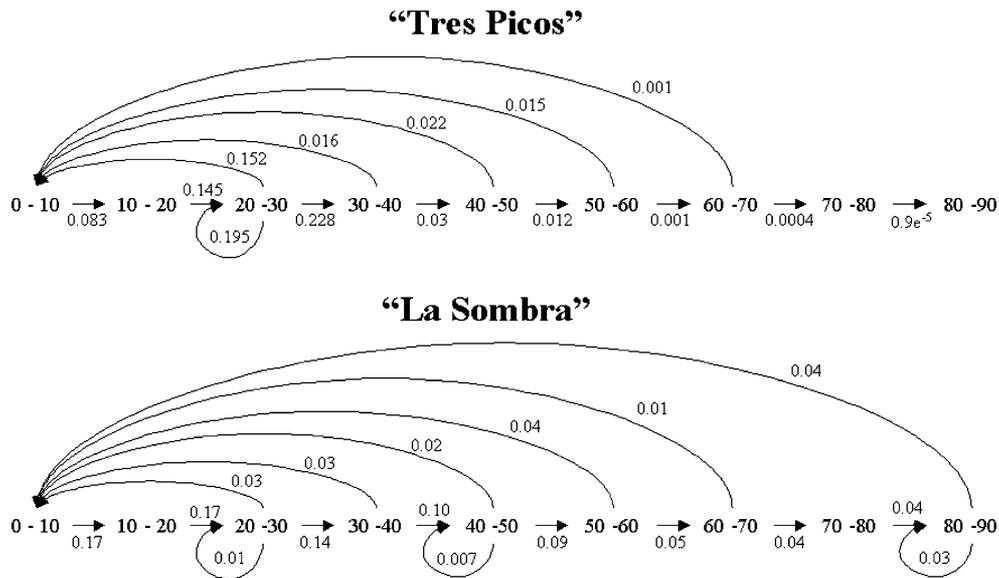
	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90
<b>(a)</b>									
0–10	–	–	0.1518	0.1158	0.022	0.0153	0.0012	–	–
10–20	0.0828	–	–	–	–	–	–	–	–
20–30	–	0.1454	0.1945	–	–	–	–	–	–
30–40	–	–	0.2278	–	–	–	–	–	–
40–50	–	–	–	0.0298	–	–	–	–	–
50–60	–	–	–	–	0.012	–	–	–	–
60–70	–	–	–	–	–	0.0011	–	–	–
70–80	–	–	–	–	–	–	0.0004	–	–
80–90	–	–	–	–	–	–	–	$9 \times 10^{-5}$	–
<b>(b)</b>									
0–10	–	–	0.0302	0.0348	0.0185	0.0406	0.0097	–	0.0353
10–20	0.1691	–	–	–	–	–	–	–	–
20–30	–	0.1691	0.0104	–	–	–	–	–	–
30–40	–	–	0.1389	–	–	–	–	–	–
40–50	–	–	–	0.1042	0.0072	–	–	–	–
50–60	–	–	–	–	0.0856	–	–	–	–
60–70	–	–	–	–	–	0.045	–	–	–
70–80	–	–	–	–	–	–	0.0353	–	–
80–90	–	–	–	–	–	–	–	0.0353	0.0307

Height class ranges in centimetres

dormancy. These seeds remain ‘latent’ for a year in the soil seed bank whilst the embryo matures prior to germination, which is similar to *C. mexicana* (Sánchez-Tinoco et al. 2000). However, this period of

physiological latency also renders the seeds susceptible to predation and desiccation (Vovides 1990).

Coning appears to be synchronous between male and female plants of *C. mirandae*. The male plants



**Fig. 3** Simplified life-cycle graphs for the two populations of *C. mirandae* in the *Septulura* Biosphere Reserve with elasticity values

produce cones between March and April, whilst the female plants cone in February but are not receptive until March–April. The seeds of this species and of other cycads are recalcitrant and therefore perish when dehydrated (Pérez-Farrera and Vovides 1997).

The population structure present in both populations of *C. mirandae* is very similar to that of other cycad species in the genus such as *C. matudae* and also *Dioon edule* (cf. Vovides 1990; Pérez-Farrera et al. 2000) and suggests that for most populations optimum microhabitats exist in the first stages of the cycads' establishment (cf. González-Astorga et al. 2003). This is very typical of tropical species that grow under shade during the first phases of growth (Martínez-Ramos and Alvarez-Bullya 1995; Alvarez-Buylla et al. 1996; Franco and Silvertown 2004; Jiménez-Lobato and Valverde 2006), and is a possible explanation for seedlings and juvenile plants that are always associated with shade from the mother plants or the tree canopy. The growth pattern of *C. mirandae* is also similar to other cycads, i.e. *C. matudae* (Pérez-Farrera et al. 2000) and *Dioon edule* (Vovides 1990). Growth pattern is related to diameter increment during the first stages of the life cycle, and subsequently an elongation of the trunk (Stevenson 1980; Vovides 1990). When the plants age, the trunks become prostrate and branched that suggests presence of an active lateral meristem (Norstog and Nicholls 1997). The difference observed in height

growth of the cycads between the two sites suggests a response to the microenvironment and conservation conditions of these sites (Lande 1999). Presence of arborescent branches enables the production of various cones per plant. The association and growth of *C. mirandae* in forests of *Quercus*, appears to agree with the type III cycad life cycle of Donaldson (1995), a highly reproductive and persistent species with low recruitment from seedlings to juveniles (Raimondo and Donaldson 2003). This population structure was also reported for *Zamia amblyphyllidia*, in Puerto Rico by Negrón-Ortiz et al. (1996).

The weight of female cones and number of seeds that were found in this species is relatively high compared to other species of *Ceratozamia* such as *C. matudae*, which yields 35–56 seeds/cone and weighs 1–1.5 kg (Pérez-Farrera et al. 2000). The high productivity of *C. mirandae* can be explained by its branching habit since each branch has the potential of producing a cone. The presence of physiological dormancy of seeds as an adaptation to cold environments (Harper 1977) is present in *C. mexicana* (Sánchez-Tinoco et al. 2000) and apparently so for *C. mirandae*. Most *Ceratozamia* species occur in cool-moist cloud forests that have low (but not freezing) winter temperatures and can represent a disadvantage in germinating during the autumn when cones are dehiscent. Also, the early dehiscence of the cones may be advantageous to the mother plant in

saving energy, since the cool moist environment provides the released seed with sufficient humidity in order for the embryo to develop within the seed covered by moist soil humus independently from the mother plant. This is in contrast to *Dioon* where the majority of the species occur in seasonally dry forests with high dry-season temperatures and low precipitation. Female cones are maintained on the mother plant for 2 years after which germination occurs soon after cone dehiscence (Vovides 1990; Sánchez-Tinoco et al. 2000).

The estimated age of *C. mirandae* plants between 50 and 60 cm tall is about 442 years and contrasts to that of *C. matudae* plants of similar size, estimated to be approximately 132 years (Pérez-Farrera et al. 2004) which is attributed to differences in the mean annual leaf production.

Matrix iteration for the ‘‘La Sombra’’ site gave a significantly decreasing population growth, whilst at ‘‘Tres Picos’’ population growth remains stable. The population growth figure at ‘‘La Sombra’’ is less than that of *Encephalartos villosus* and *E. cycadifolius*, although these species are subject to forest fires (Raimondo and Donaldson 2003). Our projection analysis of the population revealed that the ‘‘La Sombra’’ population could decline over time if human disturbance conditions persist. In addition, the period of forest fires is long and frequent here (cf. Negrón-Ortiz and Gorchoy 2000), which is typical of Pine-Oak forests in southern Mexico. Though the population growth value ( $\lambda$ ) is not significantly different from unity for *C. mirandae* at ‘‘Tres Picos’’, it is similar to that of the palm *Astrocaryum mexicanum* (Piñero et al. 1984), the long-lived endemic tree species *Borderea chouardii* (García 2003) and the cycads *Zamia amblyphyllidia* (Negrón-Ortiz et al. 1996) and *Encephalartos cycadifolius* (Raimondo and Donaldson 2003) which were subjected to studies over a number of years.

The population increase detected in the nucleus zone when compared with that of the buffer zone is relative. It may appear obvious that population increase should occur in the undisturbed nucleus zone; however, under certain conditions of disturbance the opposite might be true. It was found that in the Central American tropical rain forest cycad *Zamia skinneri*, cone production was correlated to canopy openness. Here, female plants in undisturbed primary

forest, produced cones only once in a 6.6 year period, whereas those in secondary forests coned more frequently (Clark and Clark 1987, 1988). Potentially reproductive adults were more actively reproducing in secondary forests than in primary. Light limitation is not surprising when one observes this forest understorey cycad with its long-lived leaves covered with lichens and mosses in the deep shade of primary wet forest. Further investigation is necessary to elucidate the effects of canopy openness on the reproduction of *C. mirandae* and hence its population behaviour. Correlation between the number of seeds per cone and the two localities could not be done due to a forest fire obliging us to discontinue the study.

Management activities in the buffer zone for the protection and propagation of *C. mirandae* aimed at sustainable utilization began in 1995. Conservation of the cycad in its buffer zone habitat has by and large been achieved with cash benefits to the peasant producers running small ‘‘patio’’ or ‘‘cottage industry’’ nurseries (Vovides et al. 2002). It is hoped that seedling reintroduction into habitat, as part of the management activities, will eventually arrest the estimated population decline at ‘‘La Sombra’’. At ‘‘Tres Picos’’ it is in the best interest to assure the survival of adult individuals between 20 and 30 cm tall. The survival of large reproductive adults has also been found to be the case for the cactus *Mammillaria crucigera* during a similar study (Contreras and Valverde 2002). On-going population studies and monitoring will eventually provide better resolution on population behaviour of *C. mirandae* over time.

## Conclusions

The differential behaviour of *C. mirandae* in the buffer zone compared to the nucleus zone has enabled us to recommend the following: (i) seedling introduction be continued in the buffer zone population (to compensate for seed removal and to stabilize the population); (ii) conservation of the reproductive adults in nucleus zone population and finally (iii) we recommend the following IUCN Red List classification; Vulnerable (VU C, 2a). We recommend this IUCN category in spite of the cycad’s presence in a protected area, largely because of its vulnerability to

uncontrolled annual forest fires. The year 1998 was particularly destructive leading to the total extinction of one known population of its congener *Ceratozamia miqueliana* in Chiapas, and also affected the populations of *C. mirandae* in the *Sepultura Biosphere Reserve* obliging us to discontinue these studies.

**Acknowledgements** Authors would like to thank Gunnar Keppel and Francisco González for their comments for improving the manuscript. The first author thanks: Fauna and Flora International Flora (96/64/15; MAPF); FMCN, A.C. (B2-134; MAPF); MAB-US through the Directorate Tropical Ecosystem US; Fish and Wildlife Service (G-350) who financed several phases of the project “Conservation of threatened palms and cycads of the Sierra Madre of Chiapas through sustainable use”. Also CONACyT-SEMARNAT-2002-C01-0183 to A. P.V and J. G-A. The authors give special thanks to Mr Luis Esquinca and his family who provided us all the facilities to carry out this work in the “Ejido La Sombra de la Selva”, Villaflores, Chiapas, Mexico.

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