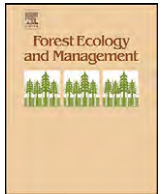




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Individual growth, reproduction and population dynamics of *Dioon merolae* (Zamiaceae) under different leaf harvest histories in Central Chiapas, Mexico

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ABSTRACT

Leaves of the long-lived *Dioon merolae* have been harvested intensively for decades (possibly for centuries) for ceremonial purposes by Zoque and mestizo groups inhabiting the Central Depression of Chiapas, Mexico. Over a period of four years, we evaluated vital rates (stem growth, leaf production, reproductive performance, and survival) and projected population growth rates in three populations (250 plants each, divided into eight size classes: new germinants, seedlings, saplings (S1, S2), and adults, A1–A4) with different leaf harvesting histories: non-defoliated by humans for at least 55 years (or very old harvest), defoliated annually until 15 years ago (recovering from harvest), and defoliated annually for at least the past 25 years (currently being harvested intensively). Population structure was affected by leaf harvest history. Stem growth was negatively affected by the annual harvest of leaves in size classes from seedlings up to A4 (ANOVA, $P < 0.003$); fewer leaves were produced by seedlings, saplings and adults at the annually harvested site (ANOVA, $P < 0.027$). Survival was high at all sites across all size classes; in the annually harvested site, A4 plants showed a decrease in survival (one dead out of four plants). Sex ratio of adults that produced cones during the four years of study was 61% males to 39% females. At the non-defoliated site, adult classes A2 and A4 produced >80% of the cones; no cones were produced by the A3 and A4 adult size classes at the annually harvested site. Asymptotic estimates of population growth indicated growing populations ($\lambda \geq 1$); the highest mean values of finite population growth rate were obtained in the non-harvested site ($\lambda = 1.0202$). Elasticity analysis with population projection matrices indicated that stasis (L, 9–38%) was the component that most contributed to λ , followed by growth (G, 1.2–2.9%), and fecundity (F, 0.2–1.1%). We observed detrimental effects on several vital rates due to continued long-term defoliation, although population growth parameters do not currently suggest a decreased trend as a result of the annual harvest of leaves. The duration of this study of a very long-lived plant species suggests caution when setting levels and frequency of leaf harvest. The results help pinpoint practical recommendations that could be implemented in a sustainable management plan for this species, particularly to increase seed production in the annually harvested site, and recruitment of new germinants and seedlings at all sites. However, sound practices will need to consider the interests of involved stakeholders (landowners, pilgrims, conservation organizations and authorities) to effectively reduce anthropogenic pressure on this endangered species.

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1. Introduction

Non-timber forest products (NTFP) are essential elements in the diet and in the religious and cultural life of rural communities worldwide (Marshall et al., 2006). Exploitation of these resources has been promoted due to the supposed low environmental impact

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involved in their utilization, when compared to other conventional practices such as cattle husbandry or extensive agriculture; their use has been accepted as an alternative to deforestation (Putz et al., 2001; Hiremath, 2004; Marshall et al., 2006), and as a viable way to foster biodiversity conservation (Rands et al., 2010). Sustainable harvest, generally speaking, involves extraction of a natural resource in such a manner that it is not depleted (Struhsaker, 1998; Martínez-Ballesté et al., 2005). Harvesting plant parts does not need to be effected at a commercial scale to have a negative impact on individual performance or on population viability; excessive clandestine harvest for ceremonial or commercial purposes often leads to deterioration of plant populations (Padoch, 1992; Young and Clarke, 2000; Endress et al., 2004). Experimental or observational studies indicate possible consequences on birth and death rates of plant populations due to negative effects on individual survival, reproduction and growth rates after over-harvesting of leaves (Mendoza et al., 1987; Oyama and Mendoza, 1990; Chazdon, 1991; Vanderklein and Reich, 1999; Ticktin et al., 2002; Anten et al., 2003), stems and fruits (Escalante et al., 2004; Holm et al., 2008), or entire individuals (Pinard, 1993; Olmsted and Álvarez-Buylla, 1995; Freckleton et al., 2003; Raimondo and Donaldson, 2003). Yet some studies have shown no effects (Endress et al., 2006) or positive effects on population growth when defoliation is not severe (López-Toledo, 2003). Recommendations from a sustainable harvest plan for a NTFP plant species depend on understanding the consequences of individual survival, and reproductive and vegetative performance on population parameter variations within mid- and long-term time frames (Martínez Ramos and Álvarez-Buylla, 1995; Olmsted and Álvarez-Buylla, 1995; Rodríguez-Buritica et al., 2005; Endress et al., 2006; Martínez Ramos et al., 2009).

Mexican species of Zamiaceae are protected by national laws (Diario Oficial, 1999; SEMARNAT, 2002) as well as by international criteria (IUCN, 2001); recently these organizations have considered Zamiaceae to be a NTFP. Current illegal trade and habitat destruction provoked by land-use change and uncontrolled frequent fires are considered the principal factors accounting for reduction in their populations worldwide (Donaldson, 2003; Golding and Hurter, 2003). In the case of *Dioon merolae*, the leaves are used in a traditional ceremony of the Zoque culture that appears to have been carried out continually since pre-Columbian times (Pérez-Farrera and Vovides, 2006), and that often results in complete defoliation of adult plants. Studies of defoliation of Zamiaceae and their demographic consequences are scarce in Mexico and elsewhere (e.g. Negrón-Ortiz and Gorchoy, 2000; Raimondo and Donaldson, 2003; Contreras-Medina et al., 2003), and therefore, the effects which this tradition could have on survival, growth, and fecundity of *D. merolae* are unknown. This is the only species of Zamiaceae whose fully developed leaves are heavily harvested by humans in Mexico. Herbivory on young leaves of *D. merolae* by caterpillars of the butterfly *Eumaeus debora* (Licaenidae) may occur patchily; no herbivory on adult plants or new germinants is known to occur by native mammals.

Defoliation negatively affects growth and reproduction of some plant species (McNaughton, 1983; Bazzaz et al., 1987; Tuomi et al., 1994; Lovelock et al., 1999), as well as survival of new germinants and adults (Crawley, 1988; Karban and Strauss, 1993). However, photosynthetic efficiency in the remaining tissue may increase as a response to greater light availability, compensating for up to 30% of lost photosynthetic tissue (Hendrix, 1988; Anten and Ackerly, 2001). Effects of defoliation depend on the stage of development and the life cycle of the species (McNaughton, 1983; Bryant et al., 1983; Obeso, 1993), as well as severity and frequency of defoliation (Mendoza et al., 1987; Oyama and Mendoza, 1990; Chazdon, 1991; Trumble et al., 1993; Anten et al., 2003; López-Toledo, 2003; Endress et al., 2004; Parra-Tabla et al., 2004; Martínez-Ballesté et al., 2008).

This study evaluated, over a four-year period, variation in growth, survival, and reproduction of three *D. merolae* populations with different use histories: severe annual harvest, recent sporadic harvest, and the absence of harvest during the past 55 years or more. Research questions were as follows: (1) How do different harvest histories affect current growth, survival, and reproduction of *D. merolae*? (2) Has the population structure of *D. merolae* been differentially modified due to differences in harvest histories over several decades? and (3) Which demographic attributes are most affected due to harvest histories? Answers to these questions provide a basis for recommendations aimed at the sustainable management of *D. merolae*, and may help to define other needed studies.

2. Materials and methods

2.1. Species description

D. merolae De Luca, Sabato, and Vázquez-Torres (Zamiaceae) is an arborescent, tree-like species with a life span encompassing hundreds of years. It is endemic to southeastern Mexico and it has been categorized as endangered (Diario Oficial, 2000; IUCN, 2001). Its populations are distributed in isolated areas of the Central Depression and Sierra Madre of Chiapas (*sensu* Müllerried, 1957), as well as in the Sierra Madre of Oaxaca (De Luca et al., 1981; Sabato and De Luca, 1985). Adult *D. merolae* individuals often have a curved aboveground stem which is barely lignified (Jones, 1993), and may reach >4.5 m long (this measurement is not height; the upwardly arched stem increasingly prostrates with age until lying flat on the ground and dies when it separates from the rootstock). Stems produce basal shoots some of which develop into stems with their own crown of leaves; short branches (<80 cm) are less frequently produced in the distal parts of the main stem. Leaves are positioned in whorls, forming a crown at the stem's apex (Jones, 1993), and are produced in a single annual flush lasting 6–8 weeks. *D. merolae*, like all cycads, is dioecious (De Luca et al., 1981). Male and female strobili are produced on separate plants; male cones can be produced at any time during the year, but female cones are primarily produced in late summer and fall. Male cones (microstrobili) are glabrous and elongated (20–55 cm in length); female cones (megastrobili) are ovoid and tomentose and measure 15–25 cm in diameter (De Luca et al., 1981). Because the seeds are recalcitrant, seed banks are not formed.

2.2. Study sites

Three study sites were selected in the Central Depression of Chiapas (elevation 540 m) (Secretaría de Planeación y Desarrollo Sustentable, 2006). These *D. merolae* populations are located near each other (an average of 1.4 km apart), but at least 48 km from any other population. The landscape consists of: (1) flatlands, where *D. merolae* are not found and currently are used as pastures and rain-fed agriculture, and (2) slopes, gullies and rocky terraces in higher areas of low hills (*inselbergs*) composed of sandstone and metamorphic rocks of the Mesozoic Era (INEGI, 1984, 1999). *D. merolae* stands occupy only shallow soils on a rocky bed (<20 cm deep) in the upland areas. Climate is warm and humid with summer rains (García, 1987). The majority (90%) of annual rainfall (810–950 mm) occurs from May to October, and median annual temperature is 25.3 °C. Soils are sandy lithosols and regosols in the hills and cambisols and rendzinas in the flatlands (INEGI, 1993). Previously, most of the landscape was covered by tropical dry forest (Miranda, 1952); secondary vegetation currently predominates, mostly due to the establishment of rain-fed corn and peanut crops and pasture during the past several decades in flat areas. Light or moderate fires that are set to burn off agricultural residues or old grass in flat

areas surrounding stands of *D. merolae* occasionally reach the slopes and upland rocky areas. No natural fires are known to occur in the region, but the extent of induced fires may be increased by a number of factors during El Niño years (Román-Cuesta et al., 2003). Likewise, occasional damage by livestock trampling may occur sporadically in the three sites.

In this study, sites were selected based on history of *D. merolae* leaf harvest during the last six decades. At El Campanario, EC (16°37'N, 93°34'W) there is no record of any harvest, at least during the past 55 years. Fifteen years ago, annual leaf harvest was stopped at Finca Ocotlán, FO (16°37'N, 93°32'W). At Rancho El Sáuz, RS (16°38'N, 93°33'W) leaves have been harvested in early May for more than 25 years. All leaves on the plant are harvested (not cut but pulled out from their bases) once a year from all adult plants as they produce the preferred large size; short leaves (<100 cm long) from saplings (<100 cm caudex height) are not removed.

2.3. Demographic data

In January 2004, *D. merolae* individuals in each site were marked and mapped: 244 plants at site EC, 250 at site FO, and 240 at site RS. The sample area was 1.7 hectares (ha) for sites EC and FO, and 1.5 ha for site RS. To facilitate sampling, 17 and 15 plots (10 m × 100 m), respectively, were established. For each individual, length of the main and basal stems (provided these latter had a diameter ≥ 10 cm) were measured and summed to assign them to a size class. The number of leaves in each crown was counted. At the beginning of the study, a mark was made below the last row of leaves produced, and the one-year increase in stem length between the two rows of leaves was measured (length at t_1 – length at t_0). The first-year leaves were counted and marked with non-corrosive paint to distinguish them from those produced in subsequent years. Seeds are released from the cones during the dry season, not only mostly between February and May, but also occasionally anytime up to the end of the rainy season (November). All seeds remaining in mature cones from the previous year and all seeds on the ground that could be associated to individual reproductive females were counted at all sites beginning in January 2004 and each subsequent January during the four year study. The seeds were marked and left in the same locations in which they were found in each respective sample plot. One year later, the number of new germinants was tallied within the same area; also counted were the number of marked seeds that did not germinate.

Individuals were assigned the following size classes based on morphological and reproductive criteria: new germinants or individuals with one leaf and no evident stem (Ng); seedlings with a stem height of 2.0–9.9 cm (Se); saplings with a stem length of 10.0–49.9 cm (S1); saplings with a stem length of 50.0–99.9 cm (S2); adult A1 with a sum of stem lengths of 100.0–149.9 cm (A1); adult with a sum of stem lengths of 150.0–299.9 cm (A2); adult with a sum of stem lengths of 300.0–449.9 cm (A3); adult with a sum of stem lengths of >450 cm (A4). Sex was determined by observing reproductive structures; only classes A1–A4 produced cones. The censuses (including new germinants) were carried out in March of each year.

2.4. Analysis

2.4.1. Statistical analyses

Number of individuals within each size class among sites at the start of the study was evaluated with log-likelihood ratio G tests (Zar, 1974), which compare the original population structure with a theoretical distribution obtained from 1000 simulations using a Monte Carlo technique (Martínez Ramos and Hoffman, 2002). Differences between the 2004 and 2008 population structures (non-independent observations) were evaluated with Friedman's

tests for randomized blocks in each site, considering the two years as blocks and size classes as treatment effects (Sokal and Rohlf, 1995). The initial numbers of individuals among sites in each size class were evaluated with pairwise log-likelihood ratio G tests. Stem growth was estimated as the accumulated annual increase (cm) in stem length and was transformed to its natural logarithm to comply with the assumptions of normality and homogeneity of variances. Differences among accumulated stem growth (ln) in new germinants, seedlings, saplings (S1 and S2), and adults (A1–A4) were separately evaluated with a one-way analysis of variance (ANOVA), including sites as a fixed factor and initial stem size as a covariate. Cases with stem loss due to circumstantial damage (88 of 2592) were not included in the analysis of stem growth. A wedge-shaped scatter plot of initial size and average annual growth for each individual from 2004 to 2008 suggested that a quantile regression procedure could help to assess their extreme relationships (Cade et al., 1999; Cade and Noon, 2003). Quantile regression analysis was carried out with the Blossom statistical software version W2008.04.02 (Cade and Richards, 2005). A one-way ANOVA model (with initial number of leaves as a covariate) was used to test for differences in total number of leaves produced during the four years of the study in the three sites (square root transformation; Sokal and Rohlf, 1995). Regression models were fitted to evaluate the relationship between stem size and leaf production.

Survival (l_x) was estimated throughout four years (February 2004–March 2008) as the probability that an individual would remain alive from one year to the next. Kaplan–Meier survival analysis and log-rank Mantel–Cox tests were used to compare survival of plants among sites for the whole period of study (Fisher and van Belle, 1993; SPSS, 1997). Fecundity (m_x) was estimated as the total number of seeds produced in one year divided by number of female plants within each size class, assuming a 1:1 sex ratio (a reasonable assumption for most dioecious species [Rottenberg, 1998, 2000]). This estimate of m_x was weighted by the proportion of seeds that survive to become new germinants. Fecundity was evaluated among sites with one-way ANOVA and Dunnett's post hoc tests due to the heterogeneity of variances detected by Levene's test. The SPSS statistical package, version 11.5 was used to perform statistical analyses.

2.4.2. Matrix analyses

Stasis, growth and fecundity rates were used to construct Lefkovich (1965) matrices for each site in each of the four years of study. Because *D. merolae* is a dioecious species a one-sex (female) model was used. The census of established individuals started in January 2004, after seeds produced the previous year (unknown number) had become new germinants using a post-breeding census model. Each matrix entry a_{ij} represents the probability of transition or mean contribution of an individual in category j to category i in one time step (one year). By multiplying matrix \mathbf{A} by a vector representing the number of individuals in each category at time t (\mathbf{n}_t), a new vector is obtained where each entry represents the number of individuals per category at time $t+1$ (\mathbf{n}_{t+1}): $\mathbf{A}\mathbf{n}_t = \mathbf{n}_{t+1}$ (Caswell, 2001). Stasis values appear in the matrix diagonal and correspond to individuals that survived and remained within the same size class after one year. Values under the diagonal refer to individuals that changed from one size class to the next in the same period. Values above the diagonal correspond to plants that regress in their size classes because of losing parts of stems due to mechanical damage. Fecundity values appear on the top row of the matrix. The dominant eigenvalue (λ) of matrix \mathbf{A} represents the finite rate of population increase; the associated right eigenvector (\mathbf{w}), corresponds to the stable-size distribution; the left eigenvector (\mathbf{v}) expresses the size-specific reproductive value (Caswell, 2001). For each matrix, λ , \mathbf{w} and \mathbf{v} were obtained by iteration until stability was reached (256 iterations). To test the hypothesis that λ

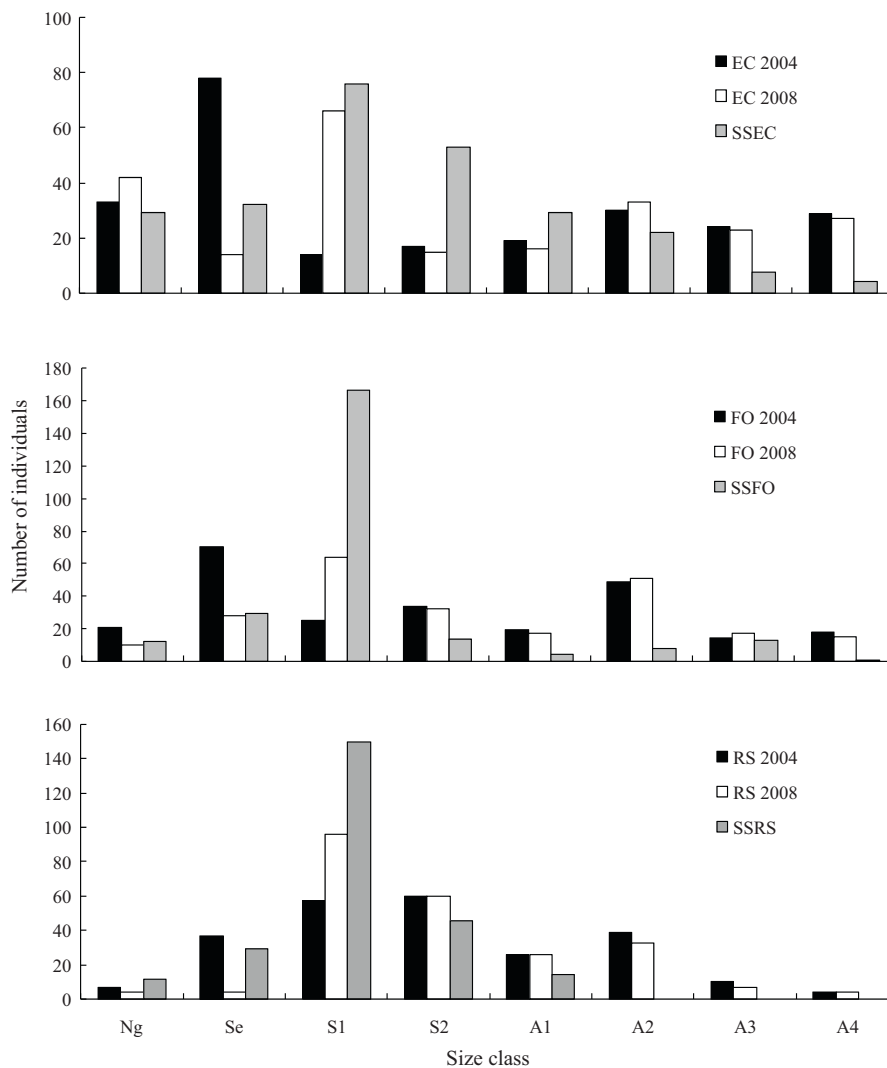


Fig. 1. Population structure (number of individuals in each size class) in three *D. merolae* populations with different leaf harvesting histories at the start (2004) and end of the study (2008). The grey bars show the population stable structure (\mathbf{w}) obtained from Lefkovich matrices. EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years. SSEC = values of population stable structure in site EC, SSFO = values of population stable structure in site FO, SSRS = values of population stable structure in site RS.

values were different from unity, confidence intervals 95% for each λ were calculated with a Monte Carlo technique (Álvarez-Buylla and Slatkin, 1993), using the program provided by Martínez Ramos and Hoffman (2002). Elasticity analysis decomposes λ into contributions made by the life cycle transitions (de Kroon et al., 1986). Elasticity (e_{ij}) quantifies the proportional change in λ resulting from an infinitesimal proportional change in each element of the matrix transition (a_{ij}) and is calculated as $e_{ij} = (a_{ij}/\lambda)(\partial\lambda/\partial a_{ij})$ (for details see Caswell, 2001).

3. Results

3.1. Population structure and density

All three sites were different in their population structures (log-likelihood ratio G tests): EC vs. FO, $G = 21.85$, d.f. = 7, $P = 0.003$; EC vs. RS, $G = 116.22$, d.f. = 7, $P < 0.001$; FO vs. RS, $G = 50.12$, d.f. = 7, $P < 0.001$ (Fig. 1). The population structures observed in the sites differed from the stable population structures (EC: log-likelihood ratio G test = 119.41, d.f. = 7, $P < 0.001$; FO: $G = 214.60$, d.f. = 7, $P < 0.001$; RS: $G = 123.98$, d.f. = 7, $P < 0.001$; Fig. 1). These differences are mostly accounted for by larger values of saplings (S1, S2) and small adults

(A1) at site EC and by size class S1 at sites FO and RS in the stable structure when compared with the observed 2004 populations (Fig. 1). Individuals of the Se and A2 classes were most abundant at the start of the study at all three sites; at the end of the study, S1 were the most abundant at EC and FO (Fig. 1). However, no differences between the original and final distribution of size classes were found within sites (at all sites Friedman's tests, $\chi^2 < 1.8$, d.f. = 1, $P > 0.17$). Initial density of *D. merolae* was similar among the three populations: EC (unharvested) and FO (not harvested for the past ten years) included 147 ind ha⁻¹, and RS (harvested annually) showed 167 ind ha⁻¹.

3.2. Stem growth

Annual stem growth accumulated during the four years of study was analyzed separately for different size classes. Stem growth of new germinants (ln) was similar among the three sites (Table 1). A site effect on accumulated stem growth was found for seedlings and saplings ($F_{2,203} = 6.11$, $P = 0.003$) and adults ($F_{2,277} = 10.95$, $P = 0.0001$; Table 1). Post hoc pairwise comparisons among sites indicated that accumulated stem growth (ln) of seedlings and saplings in the non-harvested site (1.64 ± 0.12 cm) was higher

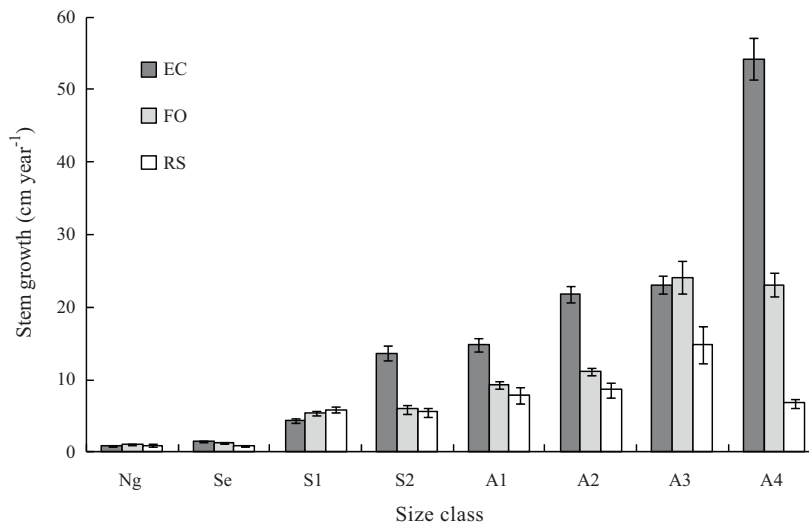


Fig. 2. Annual stem growth (mean \pm 1 s. e.) between 2004 and 2008 in three *D. merolae* populations with different leaf harvesting histories. EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years. See Section 2 for definitions of size classes.

Table 1
Analysis of variance of the effect of one fixed factor (site) on the accumulated stem increment of *D. merolae* individuals between 2005 and 2008 (ln transformed). For all size classes, except new germinants, initial length was used as a covariate.

Source of variation	d.f.	SS	F	P
(a) New germinants				
Site	2	0.182	0.892	0.411
Error	182	18.56		
Total	185	93.14		
(b) Seedlings and saplings (S1, S2)				
ln initial length	1	73.02	164.01	0.001
Site	2	5.44	6.11	0.003
Error	203	90.38		
Total	207	502.52		
(c) Adults (A1–A4)				
ln initial length	1	24.46	27.59	0.001
Site	2	19.41	10.49	0.001
Error	277	245.58		
Total	281	2039.82		

site FO = 2.45 ± 0.09 ; site RS = 2.11 ± 0.11 ; (all pairwise comparisons with $P < 0.018$). (Figure SM1 in 'Supplementary material for online publication' shows mean stem growth data by each size class and site in the four years of study.) At all three sites, average growth (ln) estimated with annual measurements between 2004 and 2008 increased as a function of initial stem length (Fig. 3). The wedge-shaped data clouds suggested using a quantile regression analysis to explore maximum rates of change (Cade et al., 1999; Cade and Noon, 2003). The quantile regression estimated that rates of change between initial stem size and average annual stem growth (ln growth) were greater than those obtained through the ordinary least squares (OLS) procedure (Table 2). The model corresponding to quantile $Q = 0.75$ showed an increase in the slope of the regression of 26% for EC, 16% for FO, and 12% for RS, compared to the value of $Q = 0.50$. The increase in the regression coefficient for $Q = 0.95$ was 22% and 24% at sites FO and RS, respectively.

(least significance difference test, $P < 0.008$) than in the harvested sites (1.24 ± 0.09 , and 1.17 ± 0.06 ; $P = 0.48$ between them; Fig. 2). In the case of adult sizes classes (A1–A4), accumulated mean stem growth (ln) was different among all three sites: site EC = 2.80 ± 0.10 ;

3.3. Leaf production

Total number of leaves produced by adults (A1–A4), the only size classes that are harvested, differed among the three sites ($F_{2,270} = 12.74$, $P < 0.001$; Fig. 4). Average (± 1 s.e.) number of leaves

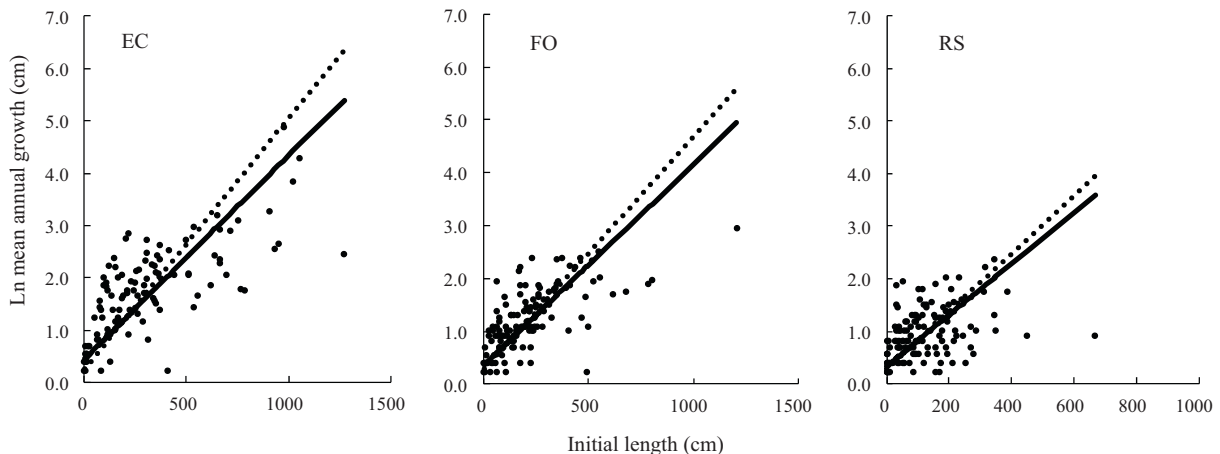


Fig. 3. (a) Scatter graph of mean annual growth (cm) as a function of initial stem length (cm) in 2004 in three *D. merolae* populations with different leaf harvesting histories. EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years. The continuous line represents the $Q = 0.50$ quantile, which is equivalent to the ordinary mean squares regression (OLS). The dotted line corresponds to the $Q = 0.75$ quantile (see Table 2).

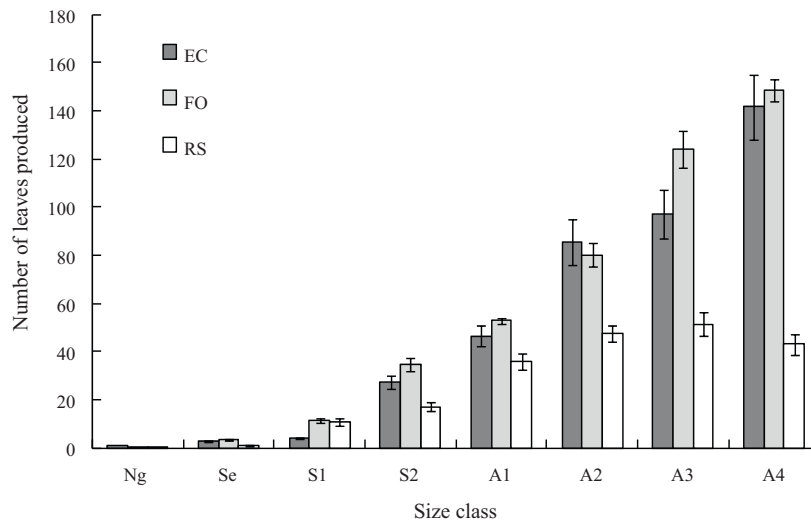


Fig. 4. Annual leaf production (mean \pm 1 s.e.) between 2004 and 2008 by individuals of different size classes in three *D. merolae* populations with different leaf harvesting histories. EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years.

Table 2

Estimates of regression coefficients (*b*) for the model $Y = a + bX$, where *Y* is natural logarithm of stem growth (cm) and *X* is stem length in 2004 ($n = 196$), and *P* values for null hypothesis tests $b = 0$ for four selected quantiles (*Q*) in three sites subjected to different leaf harvest histories. EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years. The slope estimate for $Q = 0.50$ is equivalent to ordinary least squares (OLS).

<i>Q</i>	<i>b</i>		
	EC	FO	RS
0.50	0.0038***	0.0037***	0.0049***
0.75	0.0048**	0.0043**	0.0055***
0.90	0.0042***	0.0039***	0.0055***
0.95	0.0036**	0.0045***	0.0061**

** $P < 0.01$.

*** $P < 0.001$.

produced by adults (stem length ≥ 100 cm) were 23.18 ± 4.89 leaves per plant in EC, 25.35 ± 5.36 leaves in FO, and 11.15 ± 0.83 leaves in RS. (Figure SM2 in ‘Supplementary material for online publication’ shows mean number of leaves produced by each size class and site in the four years of study). At all three sites leaf production increased in direct proportion to stem length (Fig. 5). At sites EC and FO, a linear model with stem length as the predic-

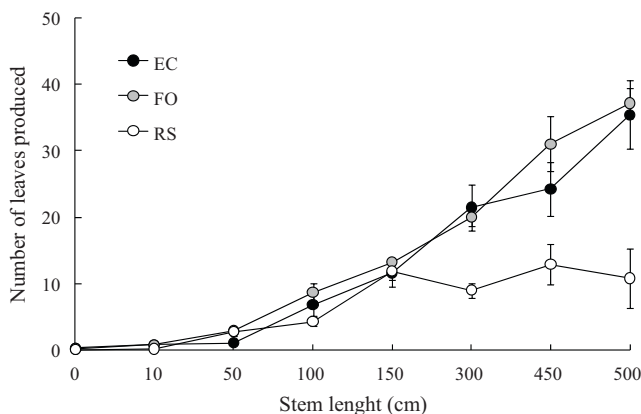


Fig. 5. Mean individual number of leaves produced as a function of initial stem length (2004) and leaf harvest regime in three *D. merolae* populations with different leaf harvesting histories. EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years.

tive variable explained $>95\%$ of observed variation ($Y = 5.88X - 9.05$, $R^2 = 0.96$ and $Y = 6.30X - 8.95$, $R^2 = 0.97$, respectively). In the site with annual harvest (RS) the best fitting between these two variables was obtained with a power model ($Y = 0.38X^{2.03}$, $R^2 = 0.88$).

Total number of leaves produced during the study was not different between female and male individuals in any site: site EC (mean \pm 1 s.d.): females 37.51 ± 35.63 , males 52.65 ± 50.01 (Mann–Whitney’s *U* test, $U = 641.0$, $P = 0.11$); site FO: females, 51.28 ± 43.80 , males, 30.57 ± 26.95 ($U = 98.00$, $P = 0.09$); site RS: females, 31.66 ± 14.98 , males, 28.50 ± 8.58 ($U = 4.50$, $P = 0.59$). Seedlings and saplings (S1 and S2) differed in the number of leaves (non-harvestable because of their small size) produced among sites ($F_{2,359} = 3.67$, $P = 0.027$; Fig. 4).

3.4. Survival

Survival of individuals could be analyzed only for new germinants, seedlings, and adult classes A1, A2, and A4, as no mortality was recorded in the remaining classes in any site. New germinants showed the lowest survival value (0.64) at site EC: EC vs. FO; log-rank (Mantel–Cox’s test), $\chi^2 = 14.15$, d.f. = 1, $P < 0.001$, and EC vs. RS, $\chi^2 = 14.26$, d.f. = 1, $P < 0.001$; survival of new germinants was not different at sites FO and RS ($P = 0.34$). Survival of seedlings was different only between sites FO and RS: $\chi^2 = 5.23$, d.f. = 1, $P = 0.022$. There were no differences in survival of A1 and A2 size classes for any pair of site comparisons (all $\chi^2 < 2.95$, d.f. = 1, $P = 0.085$). Finally, survival of the largest adults (A4) was higher at site EC vs. RS: $\chi^2 = 5.52$, d.f. = 1, $P = 0.019$, and at site FO vs. RS: $\chi^2 = 9.00$, d.f. = 1, $P = 0.003$. In general, survival of *D. merolae* individuals was >0.7 , with Ng and Se showing the lowest values of all size classes (Fig. 6).

3.5. Reproduction and fecundity

Sex could be determined for 113 of the total 338 reproductive individuals: 69 males (61%) and 44 females (39%). Proportion between sexes was significantly different from 1:1 ($\chi^2 = 5.53$, d.f. = 1, $P = 0.019$). Sex of the remaining adult individuals was not determined as they did not produce cones during the study. Female cones emerged from August to December, and they reached complete development in an average of 13 months (7–27 months, $n = 7$). Male cones were produced throughout the year, and the average length of development was seven months (3–9 months, $n = 10$). In all sites, both males and females only rarely reproduced

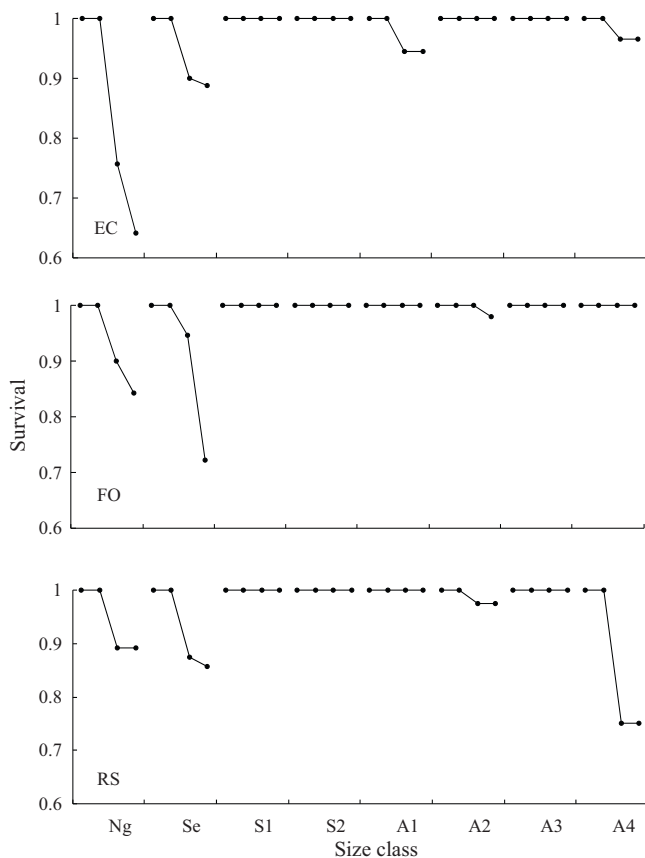


Fig. 6. Survival of *D. merolae* individuals in each size class. Each point represents survival through annual intervals between 2004 and 2008. Values inside circles in the upper panel indicate survival in site EC in the year period after a moderate fire (2006–2007). EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years. See Section 2 for definitions of size classes.

more than twice during the study period (Fig. 7a). Individuals of classes A2–A4 at site EC produced more cones per year than any other individuals at the other two sites (Fig. 7b). Adult females in the A3 and A4 size classes at the site with annual leaf harvest (RS) did not produce cones in any of the four years of study (Fig. 7b). Average annual fecundity (number of seeds produced by an individual within a given year) varied among sites ($F_{2,57} = 7.68$; $P = 0.001$); individuals in the non-harvested site (EC) had higher average annual fecundity when compared with those of sites FO (Dunnett's test, $P = 0.033$) and RS ($P = 0.026$), where they had similar fecundity ($P = 0.99$; Fig. 7c). Size-specific reproductive value obtained as the left eigenvectors of the projection matrices did not differ among sites (Kruskal–Wallis's test, $\chi^2 = 0.245$, d.f. = 2, $P = 0.89$).

3.6. Population growth

The mean annual finite rate of population growth (λ) was $\lambda > 1.00$ at the RS site and did not differ from unity at sites EC and FO (Fig. 8). The non-harvested site (EC) had λ values non-significantly different from unity in the four years of study, even after the fire event in 2006 ($\lambda = 0.9631$); FO had $\lambda > 1.00$ in the first period of study (2004–2005), and RS had $\lambda > 1.00$ in 2005–2006 and 2007–2008 (Fig. 8). (Table SM1 in supplementary material for online publication shows mean λ values and their 95% confidence intervals for each year.) The elasticity analysis indicated that entries corresponding to survival or stasis (L) of individuals in size class S2 was the component that most contributed (19–38%) to the value

of λ in the four study periods, followed by growth (G) (1.2–2.9%) and fecundity (F) (0.2–1.1%; see projection and elasticity matrices of the three populations in supplementary material for online publication', Tables SM2 and SM3, respectively).

4. Discussion

4.1. Population structure and density

Projections of Lefkovich matrices may be helpful to infer equilibrium conditions of populations when λ values are not different from unity such as in the three populations of *D. merolae* in this study. Equilibrium conditions may also be suggested by a convergence between the observed size structure and the predicted stable size distribution. In this study, the observed size class structures at all sites differed from their predicted stable structures, and λ values derived from the transition matrices were, with a few exceptions, different from unity. Small sample sizes in some of the size classes available in rare species such as *D. merolae* may affect model predictions and may help to explain this discrepancy. Raimondo and Donaldson (2003) found a similar difference between the stable and the observed size structures in the African cycad *Encephalartos villosus*, and suggested that the small sample size of adult plants used to estimate survival parameters probably introduced an artifact resulting in overestimation of the number of *E. villosus* plants in the largest size class. In our study system major discrepancies between the stable and the observed structures involve size classes S1, S2, and A1, which had some of the smallest sample sizes in the three sites (Fig. 1); this coincides with large permanence values, particularly in S1 and S2, and may account for the observed lack of fit between the predicted and observed size structures. Alternatively, and not mutually exclusively, this pattern can be accounted for by scarcity or high mortality of new germinants and seedlings caused by such factors as an occasional fire (even a ground level fire may kill new germinants), interspecific competition with shrubs and grasses in lower slope areas where soils might be deeper, or density-dependent drought effects in areas with shallow soils on the slopes limiting transition to the S1, S2 and A1 classes in two of the sites. In the site that has been continuously harvested, S1 and S2 have the highest numbers of individuals, suggesting high recruitment in the past and (or) low mortality of seedlings that does not longer prevails (Fig. 1).

In the sites studied, highest density of *D. merolae* was relatively low (167 ind ha^{-1}) in comparison to other *Dioon* species, such as *D. mejiae* from Honduras, with 833 ind ha^{-1} (Bonta et al., 2006), and *D. edule* from central Veracruz, with 2100 ind ha^{-1} (Octavio-Aguilar et al., 2008); yet it was similar to that of *D. merolae* in Loma Colorado, Oaxaca (116 ind ha^{-1} ; Flores-Vázquez et al., in press), and much greater than that of *D. purpusii* (37 ind ha^{-1} ; Yáñez-Espinosa and Sosa-Sosa, 2007) in the southern part of the Sierra Madre de Oaxaca. The rarity of *D. merolae* populations in our study sites is related to the spatial extent of the particular type of landscape to which individuals of all size classes are confined: high areas of hills with little human disturbance, lack of soil and fuel, and where interspecific competition is low due to scarce vegetation cover (these same factors are mentioned for *D. spinulosum* in northern Oaxaca (Salomé-Castañeda, 2009). In four *D. merolae* populations studied in the Central Valley of Oaxaca (Flores-Vázquez et al., in press), short-stemmed and non-reproductive individuals were less abundant than adults in comparison to the three populations included in this study.

4.2. Defoliation and stem growth

The growth pattern in small *D. merolae* individuals is similar to that observed for *D. edule* (Vovides, 1990) and some palms (Lugo

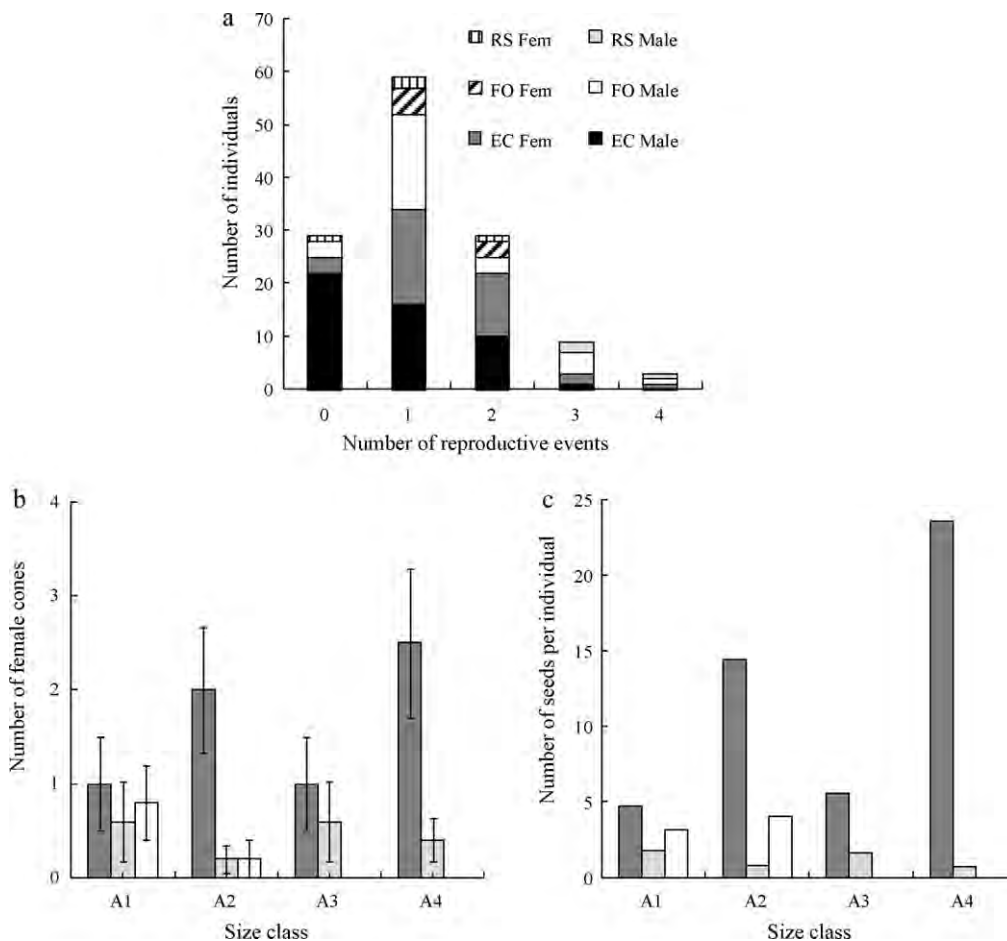


Fig. 7. (a) Number of individuals reproducing 0, 1, 2, 3, or 4 times during a four year period (2004–2008); individuals that did not produce cones during the study were sexed at the start based on remains of cones (the presence of bracts in female cones, and the central axis in male ones). (b) Mean number of cones produced by female plants between 2004 and 2008 as a function of size class in each site. (c) Mean individual number of seeds produced between 2004 and 2008 as a function of size class in each site. In panels b and c black bars = site EC; grey bars = site FO; white bars = site RS.

and Rivera, 1987), where small-stemmed individuals increase mostly in stem thickness. Longitudinal stem growth becomes evident in individuals of the sapling class (S2). Stem growth in *D. merolae* is not as slow as it has been suggested for *D. edule* ($<0.5 \text{ cm year}^{-1}$; Vovides, 1990), but appeared to be drastically reduced by the annual leaf harvest (Fig. 2). Besides being affected

by recent human disturbance events such as uncontrolled fire, leaf harvest, cattle trampling, removal of small plants, and habitat fragmentation, Zamiaceae species may have been exposed over long periods to defoliation on recently produced leaves by caterpillars such as *E. debora* and *E. childrenae* (Licaenidae) on *D. merolae*, *D. mejiae* (M. Bonta and J. Haynes, pers. comm.), *Zamia fischeri*, and

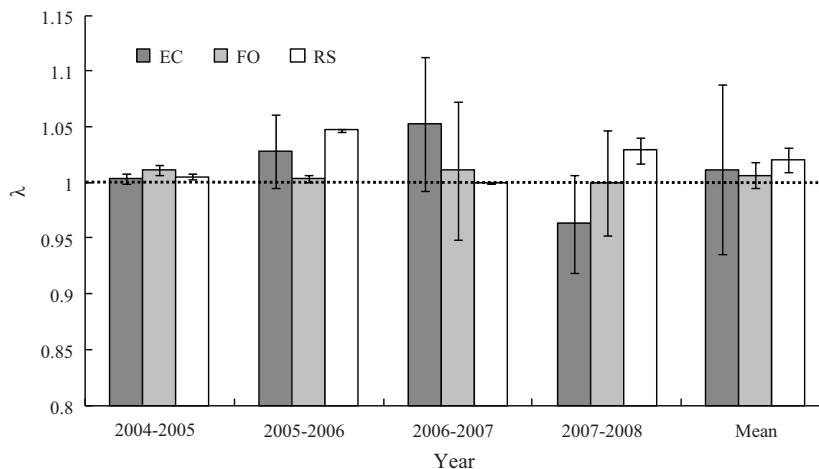


Fig. 8. Annual finite population growth rates (λ) as predicted by Lefkovich matrix models and the mean for the period 2004–2008 in each site (with 95% confidence intervals). The horizontal dashed line indicates $\lambda = 1.0000$. EC = non-harvested site, FO = site harvested until 15 years ago, and RS = site annually harvested for more than 25 years.

Ceratozamia mexicana (Contreras-Medina et al., 2003). Larvae of *E. debora* cause more severe herbivory on new leaves of *D. merolae* in the site without leaf harvesting (up to >50%) than in the other two sites, sometimes as frequently as every two years. Nevertheless, these plants may withstand this defoliation and usually grow twice as much compared to similarly sized individuals that have been severely defoliated by humans during the past 25 years (Fig. 2). As in other Zamiaceae (Negrón-Ortiz and Breckon, 1989; Negrón-Ortiz and Gorchoy, 2000), it appears that the defoliated *D. merolae* plants may translocate resources from remaining parts (old leaves, stem and (or) roots) to support a new pulse of leaves; in this study, individuals that have been annually defoliated by humans greatly decreased their stem growth (Fig. 2), produced less leaves (Fig. 4), or ceased reproduction (Fig. 7b and c).

Stimulation of basal meristems and subsequent stem branching may occur in response to a variety of types of stress (Schwartz and Hermann, 1999; Negrón-Ortiz and Gorchoy, 2000) or in response to plant age when the stems become prostrate (Norstog and Nicholls, 1997). In time, a few basal shoots may develop into stems, produce their own crown of leaves and cones, and may affect individual growth and reproduction, with effects on fitness of elder individuals (Pérez-Farrera et al., 2006). As in *E. villosus* (Raimondo and Donaldson, 2003) and *Ceratozamia mirandae* (Pérez-Farrera et al., 2006), the production of basal stems in *D. merolae* from a common rootstock favors the permanence of the genet after the main tilted stem separates from the rootstock and eventually dies.

Quantile regression analysis estimated rates of change between individual annual stem growth as a function of initial stem length. Yet stem growth can hardly be explained only by its length at the beginning of the evaluation period, and other potentially limiting factors can be envisaged (even if not measured) such as leaf harvest, predation by caterpillars, limited availability of soil nutrients, and annual variations in temperature or precipitation. Although quantile regression analysis does not pinpoint hidden causal factors, it does allow an estimation of their combined effect (Cade et al., 1999; Cade and Noon, 2003). In this study, the slope of the regression between annual stem growth as a function of initial stem size increased (12–26%), with a data subset representing more extreme values ($Q \geq 0.75$), as if the effect of hidden factors had been controlled (Huston, 2002).

4.3. Defoliation and survival

The initial stages of the life cycle are considered to be the most risky for plants (Harper, 1977), and for *D. merolae* mortality risks are higher and survival lower when the stem has not exceeded 10 cm in length. After four years, mortality of established new germinants was higher (17%) than that of saplings and adults (S1, S2, and A3; 0%), yet new germinant survival in areas not completely open was considerably higher than in populations of *D. spinulosum* ($\geq 30\%$; Salomé-Castañeda, 2009) and *D. edule* (60%; Octavio-Aguilar et al., 2008). New germinant death caused by occasional trampling and ground level fires is possible; however, the low accumulation of fuel due to cattle grazing and cutting of woody stems for firewood in flat areas, does not foster intense fires and high mortality in the slopes and rocky upland areas to which the distribution of *D. merolae* is mostly restricted. As *D. merolae* individuals grow, their chances of survival increase, similar to *E. villosus* and *E. cycadifolius* (Raimondo and Donaldson, 2003). Ninety percent of adults (A1–A4) remained alive during the four years of study, with the exception of A4 individuals at site RS (75% in 2007). Despite their large size, these latter individuals are almost completely defoliated every year, and in the process they may suffer incidental mechanical damage that eventually increases their probability of dying (as reported for *Zamia pumila* by Negrón-Ortiz and Gorchoy, 2000).

4.4. Defoliation and reproduction

No data are available on age at which the first cone is produced in the wild by female plants of *D. merolae*, whose age from germination is known, and no cones have been observed on individuals aged 13–15 years-old maintained in nurseries. This contrasts with observations of male cones produced by 15 years-old plants of *D. edule*, and 18-year-old females of the same species reported from a botanical garden at the tropical humid locality of Xalapa, Veracruz (A. P. Vovides, Instituto de Ecología, A.C., pers. comm.). According to leaf production rates during the four years of study and the number of leaf scars on the stem, monopodic individuals observed at their supposed first reproduction event and with 80–100 cm stem length may be expected to have at least ca. 80 years at site EC, ca. 110 years at site FO, and ca. 180 years at site RS. Reproductive plants of *D. merolae* have a supranual but irregular pattern of cone and seed production. This could be due to (1) insufficient pollen production to fertilize all ovules within a cone (Ehrlén and Eriksson, 1995; Brookes et al., 2008), (2) the absence of pollinators to carry out fertilization that is not mediated by wind (Norstog, 1987; Ornduff, 1989; Terry et al., 2004), or (3) low number of ovules produced (Haig and Westoby, 1988; Niesenbaum, 1996). On the one hand, in *Cycas* and *Zamia* species that have a close relationship to fire regimes, seed viability may be negatively affected by fires that may partially or completely destroy cones and damage embryos (Watkinson and Powell, 1997; Negrón-Ortiz and Gorchoy, 2000); on the other hand, Vovides (1990) and Ornduff (1991) have reported that fires may stimulate production of female cones in *D. edule* and male cones in *C. media*, respectively, and production of female cones of *Z. pumila* (Negrón-Ortiz and Gorchoy, 2000). In *D. merolae*, occasional fires seems to decrease the capability of producing cones in both sexes only in the years following an event: only six female cones were produced two years after the fire, which is one-half the number of cones produced the year before the fire. Fires may also result in abortive cones through the removal of pollinating insects (Tang, 1990).

4.5. Germination and seed predation

Dehgan (1983) reported that seeds of Zamiaceae show physiological dormancy. For *Dioon edule* in Veracruz, a germination rate of 76.1% was reported (Pavón-Suárez, 1999). In this study, *in situ* germination was higher (only 4% out of 149 seeds did not germinate after 50 days at site EC (Lázaro-Zermeño and Gómez-Vázquez, unpubl. data; no data are available from the harvested sites). In addition to availability of viable seeds, another factor that may influence recruitment is the presence of seed predators, including Coleptera of the Chrysomelidae (*Aulacoscelis melanocereus*), Nitidulidae (*Carpophilus* spp.), and Bituridae (unidentified species) families, and the rodent *Lyomis pictus* (Heteromyidae), that is capable of breaking the sclerotesta. In the unharvested site, up to 70% of seeds produced per individual per year may be damaged by these predators. Seeds also germinate in the dens of rodents after being transported and lost by them; >50% of the new germinants emerging in dens have been observed to survive up to two years after germination.

4.6. Population dynamics

In this study, all λ values were at or above unity, indicating that all three populations are either stable or increasing. The elasticity analysis indicated that the reproductive component contributed in only a tiny proportion to λ values. As in other studies, stasis or permanence was the demographic variable that most contributed to the value of λ (Negrón-Ortiz et al., 1996; Raimondo and Donaldson, 2003; Aguirre-Fey, 2004; Octavio-Aguilar et al.,

2008; Cabrera-Toledo, 2009), and its influence tended to increase with size class (see elasticity matrices in supplementary material, Table SM3). Yet these results should be viewed with caution vis-à-vis practical recommendations for the conservation of *D. merolae* and of other species with similar life history attributes. Demographic studies of long-lived and rare plants that grow slowly are complicated by a relatively small number of size classes with limited sample size (Enright et al., 1995). In this study, size classes were defined using clear-cut morphological criteria and a balance of sample sizes. Probability of transition from the new germinants to the seedlings size class within a year is relatively high in our study system. Yet transitions between size classes after the seedling class are rather low because of low growth rates recorded either annually or over the four years of study, accounting for the high value of stasis of λ . Survival was high among saplings and adults during the same period, but this may be too short a time span to account for occasional severe disturbances that could result in significant demographic changes in such a long-lived species. Therefore, it is not surprising that values of $\lambda \geq 1$ are observed at all sites, even if almost no reproduction occurred during the four years of study, in particular in the annually harvested site (RS). This seemingly contradictory result does not guarantee that subsequent harvests as currently performed (i.e. with almost complete defoliation) will not cause long-term population decrease (a similar case with the more dynamic populations of the palm *Chamaedorea elegans* is reported by Valverde et al., 2006). Further monitoring of our study populations is needed to include a wider variation of environmental conditions and the incidence of more extreme disturbance factors to obtain more reliable estimates of their λ values and to support the ensuing conservation recommendations. The studied populations include individuals aged from only a few months to at least 500 years old (estimated upon number of leaf scars and rate of leaf production). In contrast, the four years of study (2004–2008) did not include extreme environmental conditions that may affect survival, growth and fecundity, as caused by severe El Niño years like the one recorded in southern Mexico in 1998 (Román-Cuesta et al., 2003; Martínez Ramos et al., 2009). A considerable extension of the observation time in this sort of study using projection matrices may be the only way to include significant effects of fecundity on population growth, in addition to survival, for very long-lived species studied within a small sample of the environmental conditions experienced by the whole population (Floyd and Ranker, 1998; Bierzychudek, 1999; Caswell, 2000; Raimondo and Donaldson, 2003; García, 2003; Miller et al., 2007). Meanwhile, conclusions on population dynamics should be regarded as preliminary and the ensuing conservation recommendations for *D. merolae* should thus mostly guided by precautionary principles.

At site EC, a fire occurred in 2006 before the onset of the rainy season, but it did not cause λ to drop below 1.0 in subsequent years, suggesting adaptation to occasional fires by size classes S1, S2 and adults. Yet the relatively lower survival of new germinants observed after the fire in this site might not be traceable within the set of individuals that will eventually become saplings (S1 and S2) after the considerable number of years needed to attain such size classes (at least 30 years). This study incorporates the occurrence of a fire in the analysis of population growth using projection matrices (see Raimondo and Donaldson, 2003). This demographic approach has been used to analyze the evolutionary history of plants assumed to be driven by exposure to recurrent fires (e.g. the grass *Zea diploperennis* by Sánchez-Velásquez et al., 2002, and the palm *Borassus aethiopicum* by Barot et al., 2000). In our study system, however, the influence of fire (occasional and mostly at ground level only) is restricted mostly to new germinants and seedlings and based on available information cannot be considered a recurrent and severe disturbance factor influencing population structure and dynamics.

4.7. Practical recommendations

This study provides evidence of mid- or long-term effects of annual severe defoliation on population and individual performance attributes of *D. merolae*. Results of vital rates (survival, growth and fecundity) and population projection matrices focused recommendations aimed towards sustainable leaf harvest and conservation of this endangered species. Population growth or equilibrium conditions at all sites are suggested by λ values exceeding unity, which could lead to allowing the continued current practice of complete defoliation; yet long-term negative effects on population parameters suggested by poor reproductive performance of continuously harvested individuals cannot be discarded considering the short time span of this study (four years) given the age that adult plants are estimated to reach (centuries). Therefore, a precautionary approach is warranted in proposing recommendations. Demographic fluctuations of an order not yet observed within the time-frame of this study may occur under particularly stressful annual climatic conditions, and could accentuate the negative effects imposed by severe defoliation in those years (García, 2003; Esparza-Olguín, 2004; Hernández-Apolinar et al., 2006; Gaoue and Ticktin, 2010).

A general possible recommendation aimed to increase the local abundance of the studied species includes the protection of the sites through fencing in the lower parts of slopes that occur near pastures. *D. merolae* populations could be increased by natural establishment or transplant into these areas but will probably require fencing to maintain them free of livestock or human damage by trampling or removal. Additionally, herbaceous cover on both sides of the fence should be removed to avoid the escape of fire from nearby pastures. The most vulnerable individuals identified in this study (A3 and A4 sizes classes) should be removed from annual complete defoliation, or at least be subjected to such practices as deferred harvests (one or two years), or the setting of limits on the number of leaves that could be removed annually (30%, Lázaro-Zermeño, unpubl. data). Considering the deeply entrenched ceremonial tradition of removing leaves by neighboring communities of pilgrims (though they may even arrive from localities at 150–200 km away), and mindful of the need to avoid animosity towards the conservation project, possible deferral of harvests should be negotiated with them. Likewise, it can be recommended to negotiate changes in harvest regimes either regarding the proportion of leaves removed or concentrating leaf removal to the most vigorous individuals (classes A1 and A2; an experimental study on levels of defoliation over a number of years is currently being conducted and it is expected that it will provide additional input to define this practice).

The results of this study indicate that long-term severe defoliation may have deleterious consequences on the ability of plants to recover their photosynthetic tissues, with eventual effects on their reproductive capacity and population recruitment. It should be noted that reproduction of large adults in the annually harvested site was nil, and the number of new germinants over the period of study was very low compared with the non-harvested site (Fig. 1). At this time, we consider that λ values equal to or above unity may mislead recommendations that require a longer period of field studies. During a more advanced stage of conservation action, intensive education efforts should focus on convincing people to stop collecting or to collect fewer leaves for ceremonial purposes. The collaboration of both conservation and Catholic religious authorities with academic groups would be particularly helpful in this regard. Germination was not found to be a problem in the production of new germinants in nurseries, and this can be put in work for conservation. Seeds could be carefully collected in the field before they are attacked by predators, and taken to

local nurseries to produce new germinants, which could then be transplanted into the sites at the start of the rainy season when they have become seedlings five to ten years-old. Youth from the communities where the leaves are used should be involved in collecting the seeds and maintaining school nurseries, even possibly creating a stewardship program with class activities tied to the ceremonial offerings maintained by their parents. The results of this study provide basic guidelines aimed towards the conservation and (or) sustainable management of *D. merolae*. Yet it is acknowledged that to attain success, further long-term physiological and ecological research should be conducted on the population and individual effects of leaf harvesting in addition to relevant social outreach with multiple stakeholders.

5. Conclusions

This four-year study shows that frequent long-term defoliation of *D. merolae* individuals has consequences on population structure, stem growth, leaf production, reproductive performance, and recruitment; yet no differences in population growth were evident among sites. Lack of recruitment by the largest adult classes in the annually harvested population is particularly worrisome, and indicates that urgent measures should be implemented to favor their reproduction and survival. Due to the very long life span of *D. merolae*, values of $\lambda \geq 1$ observed over a period of four years in defoliated and non-defoliated populations do not necessarily reflect long-term trends and should be taken with caution when defining harvesting regimes. Occasional fires, as the one that occurred in the non-harvested site in 2006, may have effects on reproduction and recruitment within one or two years following the fire; yet their sporadic occurrence does not seem to cause detrimental trends in reproductive variables such as those observed in the annually defoliated population. The analysis of individual and demographic responses to defoliation pinpoints certain practices that could be implemented to foster the sustainable management of *D. merolae*; yet any recommendations in the change of practices can only be implemented in full agreement with all stakeholders (landowners, pilgrims, conservation organizations, and authorities).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.10.028.

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