

POPULATION STRUCTURE IN ZAMIA (ZAMIACEAE) IN NORTHERN PUERTO RICO. II. SEED GERMINATION AND STAGE-STRUCTURED POPULATION PROJECTION

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Population biology has been studied in few species of cycads, and these studies have focused on adult demography. We investigated all life-history stages, including seed germination and recruitment, of *Zamia amblyphyllidia* over 3 yr in Cambalache Forest, Puerto Rico, and constructed stage transition matrices from our field data. We found two distinct stages in seed germination: radicle emergence and, 1–7 mo later, leaf emergence. Seeds released from cones early, before the onset of the dry season, germinated faster but suffered greater mortality during the first dry season than seeds released 2 mo later. However, after 3 yr both early and late seed cohorts had similar survivorship (2%–3%). We categorized plants to be seedlings, juveniles, or adults based on the number of leaflets on the longest leaf, as cone production was almost nonexistent among plants with ≤ 10 leaflets. Most “adults” did not cone over the 3 yr of the study. Despite low probability of coning among females, low fecundity of coning females, and low recruitment of seedlings to juveniles, the population was projected to have a finite rate of increase, λ , of nearly 1.0. High annual survivorship of adults, combined with episodic coning, appears to account for the persistence of *Z. amblyphyllidia* populations.

Introduction

The demographic properties of an increasing number of plant species have been investigated using population projection matrices, permitting interspecific comparisons of life histories (Piñero et al. 1984; Pinard and Putz 1992; Silvertown et al. 1993) and enabling conservation research to focus on critical life-history stages (Schemske et al. 1994). However, no such investigations have been made for any cycad species, which are of interest because of their dioecy, longevity, length of cone and seed development, episodic coning, and large seeds (Chamberlain 1935; Jones 1993). Most previous studies have focused on sex ratios and comparative coning patterns of male and female cycads (Clark and Clark 1987; Tang 1990) or on seed dispersal and predation (Ballardie and Whelan 1986; Tang 1989; Negrón-Ortiz and Breckon 1989a). Vovides (1990) constructed a life table for *Dioon edule*, but the age determinations were imprecise. To our knowledge, no stage-based model of population growth has been published for any cycad.

Stages that have received little attention in previous studies are seed germination, seedling survivorship, and recruitment to mature stages. Several authors investigated the germination of cycad seeds in response to different horticultural treatments (Dehgan 1980; Dehgan and Shutzman 1983; Vorster 1988; Kraa 1989; Doughty 1991), but there are few field studies on cycad seed germination and survival. Here we describe the stages of germination of *Zamia amblyphyllidia* seeds in their natural environment and investigate how the timing of seed release and the number of seeds per cone affect germination and seedling survival. We also

identify the criteria that distinguish different life-history stages and quantify the patterns of survivorship and fecundity that characterize each stage. We use demographic data from a 3-yr period to project the growth rate of the population, using stage-transition matrices, and explore the sensitivity of this projection to the various demographic parameters. Finally, we calculate the elasticities of these parameters and compare these with patterns reported for angiosperms and conifers of different life-history categories (Silvertown et al. 1993).

Material and methods

STUDY SITE AND SPECIES DESCRIPTION

The study was conducted in the Cambalache Commonwealth Forest in the municipality of Arecibo on the north coast of Puerto Rico (fig. 1). The forest occurs on limestone hills, which are part of the Aymamón limestone formation, consisting primarily of tower karst (Monroe 1976). Average annual rainfall is between 1400 and 1500 mm and is seasonal in occurrence (Department of Natural Resources 1976). The rainy season begins in May or June and reaches a maximum during September and October. February, March, and April are the dry months (Department of Natural Resources 1976). The forest falls within Holdridge's Subtropical Moist Forest plant formation (Ewel and Whitmore 1973).

Zamia amblyphyllidia has pinnately compound leaves and a fleshy underground stem (fig. 2). Pollination occurs from mid-January through mid-February. Fungus gnats (Mycetophilidae) and beetles are common visitors to the cones, and circumstantial evidence indicates that they are pollen vectors (V. Negrón-Ortiz and G. Breckon, personal observation). The seeds mature 7–13 mo following pollination (Negrón-Ortiz 1987). Seeds are released when spreading of the sporophylls causes disarticulation of the female cone. Seeds are typically deposited in a cluster next to or underneath the maternal plant (fig. 3). The seeds have a fleshy outer layer (sarcotesta) and a hard inner layer (sclerotesta). At the time of seed release, the epidermis of the sarcotesta is bright red.

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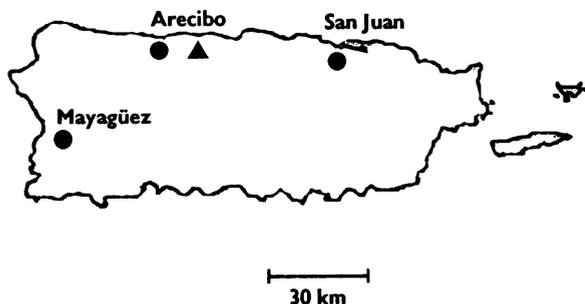


Fig. 1 Map of Puerto Rico showing the location of the study site (triangle), the Cambalache Commonwealth Forest in the municipality of Arecibo.

Introduced rats, *Rattus rattus* Fischer or *Rattus norvegicus* Fischer, are apparently the major contemporary agents for dispersal (Negrón-Ortiz and Breckon 1989a); rodents that were probably important seed dispersers in the past are now extinct.

As discussed in Negrón-Ortiz and Breckon (1989b), there still remain some unresolved nomenclatural and taxonomic problems for the Caribbean zamias. The studied population would be treated as *Zamia latifoliolata* Preneloup in Britton and Wilson (1925) as *Zamia debilis* L.f. in Liogier and Martorell (1982), as *Zamia pumila* L. in Eckenwalder (1980) and as *Z. amblyphyllidia* D. Stevenson in Stevenson (1987). For now we will use the current specific epithet, *Z. amblyphyllidia*. More detailed description of the study site and species are given in Negrón-Ortiz and Breckon (1989b) and Negrón-Ortiz (1987).

SEEDLING GERMINATION AND DEMOGRAPHY

We selected a site on a very gradual slope having a high density of *Zamia* to monitor seed removal (Negrón-Ortiz and Breckon 1989b), germination, and survivorship of seeds and seedlings. Within the site, 19 female plants with a total of 20 cones having mature (red) seeds were selected on January 6, 1982, (cohort A); these had a total of 529 seeds ($X = 27.8$, $SD = 18.0$, range 7–87). A second group of 20 females (20 cones) with later maturing seeds (cohort B) was selected within the same site on March 9, 1982; these had a total of 604 seeds ($X = 30.2$, $SD = 20.3$, range 6–79). At the time the plants were selected, the cones either were beginning to disarticulate or disarticulated when touched. We mimicked natural cone disarticulation and seed release by breaking apart these mature cones by hand. After breaking up the cones, the location of each fallen seed was marked with wire. A circular “seed plot” was established around the marked seeds of each plant; these ranged from 15 to 45 cm in diameter, depending on the number of included seeds, proximity of other zamias, and the topography resulting from outcrops of the dog-tooth limestone.

Seed plots were censused at irregular intervals (an average of 23 d, with a minimum of 3 d and a maximum of 181 d) until April 1985. The seed plots were censused weekly the first 4 mo of the study because the status of each seed changed continuously. At each census, the number of seeds present in each plot and the status of individual seeds were scored. The following categories were recognized (figs. 4, 5): (1) pregermination stage—sarcotesta present; (2) pregermination stage—sarcotesta removed or desiccated; (3) germination—radicle evident, but first leaf not yet emerged; (4)



Figs. 2–5 *Zamia amblyphyllidia* at Cambalache forest. Fig. 2, Growth habit. Fig. 3, Seed pile from naturally disarticulated cone; seeds with fleshy sarcotesta attached. Fig. 4, Categories of seed germination (left to right): sarcotesta present, sarcotesta removed or desiccated, and germination (radicle evident). Fig. 5, Seedling stage, first leaf emerged.

seedling stage—leaf emerged (fig. 5); (5) dead (with notation whether mortality occurred at pregermination, germination, or seedling stage); and (6) nonviable seeds—no radicle emerged after several months. Once the individual was scored as dead, it was removed from the plot. When a seed was no longer within the plot it was scored “missing” as it may have been dispersed or eaten. These individuals were treated as “right-censored,” i.e., alive at the previous census and date of death unknown (Fox 1993). Seedlings alive at the last census (April 1985) were also treated as right-censored.

For each cohort of seeds, life-table statistics were estimated along with their standard errors by SAS procedure LIFETEST (SAS Institute 1989). We report the cumulative survival function (proportion of individuals alive in each time interval) and the hazard function or conditional mortality rate (the probability an individual will die in an interval given that it was alive at the beginning of the interval [Fox 1993]). For these analyses we used only one census date per month, generally that closest to the middle of the month. In one plot (A-2), 21 of 33 seeds failed to germinate and were apparently inviable; these seeds were excluded from all analyses. In other plots, a few seeds failed to germinate, but these showed signs of fungal or insect attack and were considered viable seeds killed on the date the damage was observed.

We tested whether the survival distribution of cohorts A and B were equal using the χ^2 approximation to the Wilcoxon test (Fox 1993). Two comparisons were made between cohorts: one based on census date and the other on age (where age = 0 was the date of cone break-up). In this latter comparison, 2 mo were subtracted from the census month for cohort B.

To determine whether seed survival (to October 1984) was dependent on cohort of the initial number of seeds in the pile (density dependence), we used logistic regression (SAS procedure LOGISTIC [SAS Institute 1989]).

DEMOGRAPHY ON PERMANENT PLOTS

We marked and censused all *Zamia* individuals on five 1 x 5 m plots on each of four adjacent hillsides, one facing each of the cardinal directions. The long axes of the plots were perpendicular to the slope. The plots were selected so that different microhabitats containing *Zamia* plants were reasonably represented. Plants were censused at irregular intervals (average 32 d, range 9–121 d) between October 1982 and October 1984. Plants were considered seedlings if the sclerotesta was still attached or if leaves were ≤ 12 cm long with only one or two leaflets. For the majority of the seedlings the sclerotesta was still attached or lying next to it at the October 1982 census, indicating they were from the 1981 pollination season. At each census, we scored survival of all plants. For plants other than seedlings, the number of new, mature, and dead leaves, number of leaflets on the longest leaf, and the stage and sex of each cone were scored. These plants were subsequently assigned to stages based on coning history and leaflet number. As only about 7% of the genets in this population were branched (consisted of >1 ramet [Negrón-Ortiz and Breckon 1989b]), we report data at the level of genets.

POPULATION PROJECTION

We recognize five stages in the life cycle of *Z. amblyphyllidia*: seeds, seedlings, juveniles, nonconing adults, and coning adults. Although we could not distinguish males and

Table 1

NUMBER OF NONCONING AND CONING INDIVIDUALS (male and female) STRATIFIED BY THE NUMBER OF LEAFLETS ON THE LONGEST LEAF, BASED ON OCTOBER CENSUS EACH YEAR IN THE PERMANENT PLOTS

Leaflets on longest leaf	1982		1983		1984	
	Coning		Coning		Coning	
	No cone	Fe-male	No cone	Fe-male	No cone	Fe-male
3–6 ...	40	0	37	0	35	0
7–10 ..	46	0	50	0	56	0
11–14 ..	41	6	42	2	34	1
15–20 ..	47	7	57	6	63	1
21–26 ..	46	10	54	4	54	3
27–32 ..	18	9	30	2	34	2
>32 ...	13	11	31	4	28	1

females in the absence of cones, we assumed each individual remains the same sex throughout its life because we never observed sex change in wild or cultivated *Z. amblyphyllidia*; also, sex change was never observed among 114 *Zamia pumila* individuals over 8 yr (Tang 1990). Plants were considered adults if they coned at any point during the study or if they had >10 leaflets on the longest leaf on the census date. This criterion was based on our finding that, with one exception, individuals with 10 or fewer leaflets never bore cones (table 1). Adults were classified as “coning” if they bore a cone produced in the census year.

Based on the life cycle, we modeled population growth using stage transition or Lefkovich matrices. Such stage-based matrices are more appropriate than the age-based Leslie matrices for populations where demographic patterns depend more on an individual's size or stage than its chronological age (Caswell 1989). Each element a_{ij} in such a matrix reflects the probability of an individual in stage j being alive and in stage i 1 yr later or, for reproduction, the average number of offspring produced by an individual presently in stage j that are alive 1 yr later. We modeled reproduction as a “birth-pulse” process with prebreeding census (sensu Caswell 1989). We constructed two transition matrices for this *Zamia* population, one for October 1982–October 1983 and one for October 1983–October 1984. We used data for October because this is a time when developing cones are usually present.

Elements of each matrix were parameterized based on field data. Because we were unable to sex the prereproductive life-history stages, we modeled the survival and transition probabilities of these stages as equivalent between males and females. Because we lacked data on the effects of sex ratio or male cone abundance on seed production, we modeled seed production as a “female-dominant” process (Caswell 1989; Cipollini et al. 1994), where the average fecundity of females was independent of the number of males. Seeds were assumed to be produced at 1:1 sex ratio based on the even sex ratio of 49 wild-collected seeds grown in cultivation (24 male, 21 female, four sterile after 11 yr).

PARAMETER ESTIMATION

Fecundity of coning females was calculated as the product (average cones per coning female) x (proportion of cones producing seeds) x (average number of seeds per seed-bearing cone). Developing cones present in October of 1 yr, if pollinated, would bear seeds 1 yr later, these seeds would

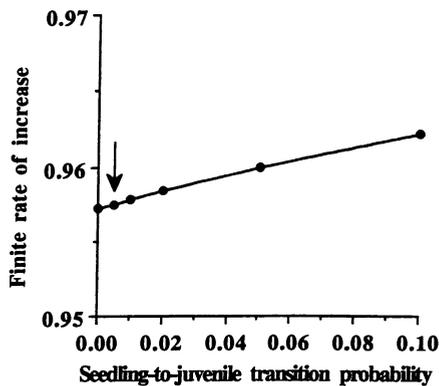


Fig. 6 Finite rate of increase (λ) for the 1983–84 *Zamia* transition matrix, assuming different values for the seedling to juvenile transitions probability. The seedling-to-seedling transition probability was varied in a complementary way, so that the sum of these two probabilities remained = 0.385, the observed survival probability. The arrow indicates the value used in subsequent analyses.

disperse and germinate over the second year. Because the study ended before seed number could be determined for those cones that were developing in October 1983, we used the average seed number for the October 1982 cones for both matrices.

For the transition of seeds to seedlings we averaged the estimates of survival to October 1982 obtained for cohorts A and B from the LIFETEST procedure; this estimate was used in both matrices. Year-to-year survival of seedlings, juveniles, and adults and transitions among these stages were based on the status each October of the individuals marked in the permanent plots, with two exceptions. None of the 96 individuals that were seedlings in 1983 became juveniles in 1984, generating a transition probability of 0. Because this transition is possible, we considered this 0 as an artifact of the small sample size. Therefore, we calculated the seedling to juvenile transition probability as if a doubling of our sample size would have provided one such transition, i.e., $1/192 = 0.005$. We explored the sensitivity of λ to this estimate by substituting values ranging from 0 to 0.1 for this transition probability, with complementary changes in the probability that seedlings survived as seedlings. Over this large range of transition probabilities, λ varied only 0.05 (fig. 6).

Similarly, because none of the five females coning in 1983 coned again in 1984, we set the probability for this transition at the arbitrarily low level of 0.001 rather than 0 and reduced the probability of transition from coning to nonconing females by 0.001. Substituting 0 or 0.005 for this value changed the resulting λ less than 0.0001.

In the calculation of the transition probabilities involving nonconing adults, we divided the adults that failed to cone during the study ($n = 152$) into “nonconing males” and “nonconing females” in a proportion (44.1% male, 55.9% female) that brought the overall adult sex ratio to 1:1. We considered this the most parsimonious way to treat these individuals, given that we have no evidence for differences between sexes in adult mortality. Mortality and stage transition events of these nonconing adults were distributed to nonconing males and nonconing females in the above proportion. In the calculation of each matrix element involving nonconing adults, field data from nonconing adults “assigned” to one sex were pooled with data from the adults known to be of that sex that did not cone that year.

ANALYTICAL PROPERTIES OF THE MATRICES

For each matrix, we analyzed the long-term (or asymptotic) dynamics by eigenvalue and eigenvector analysis (Caswell 1989), using MATLAB (MathWorks, Inc., Natick, Mass.). Ordinarily, in such analyses the largest positive eigenvalue (root), λ_1 , dominates the long-term dynamics and is equal to the population’s finite rate of increase. However, our transition matrix was “reducible,” i.e., there existed some stages that could not contribute to certain other stages: in this case, males could not contribute to the female stages or to male seeds. Because of this reducibility, the projection of the population depends on the initial conditions, e.g., the sex ratio, and each eigenvalue is associated with one of the two submatrices (Caswell 1989). For each of our two matrices, λ_1 was an eigenvalue from the submatrix corresponding to the male portion of the life cycle (the last five rows and columns of the matrix) and, hence, reflected the long-term dynamics of an all male population (gradual decline). Iterative projection of populations by the matrix confirmed that λ_1 equaled the finite rate of increase of an all male population and approximated that of males in a mixed population. Because the matrix was reducible we analyzed the submatrix corresponding to the female portion of the life cycle (the first five rows and columns), which was irreducible. For the matrix of each year, λ_1 of the female submatrix was the second largest eigenvalue of the entire matrix. Iterative projection revealed that this λ_1 described the long-term dynamics of both an all-female population and of females in a mixed population.

We obtained the stable stage structure as the right eigenvector (\mathbf{w}) corresponding to this root, scaled so that the elements summed to 1, and reproductive values of the stages as the corresponding left eigenvector (\mathbf{v}), scaled so that seeds had reproductive value of 1 (Caswell 1989). To determine how sensitive our estimate of λ was to our estimate of each element a_{ij} of the matrix, we calculated the “sensitivity matrix” as the product of these left and right eigenvectors (\mathbf{vw}) (Caswell 1989). Because a change of like magnitude is proportionally smaller for a large element (e.g., fecundity), we also calculated the “elasticity” (proportional sensitivity) of λ with respect to each a_{ij} as the product of a_{ij} and its sensitivity, divided by λ (de Kroon et al. 1986). Elasticities are also interpreted as estimates of the contributions of the a_{ij} ’s to λ (and fitness) and hence in some sense their “importance” (de Kroon et al. 1986). To allow comparison to patterns among species described by Silvertown et al. (1993), we followed their protocol for summing the elasticities of the transitions that corresponded to (1) growth, (2) survival, and (3) fecundity.

Results

Germination did not occur until a minimum of 17–20 d after the sarcotesta was lost (eaten, decomposed, or desiccated). The temporal pattern of cumulative germination differed between the cohorts, even after adjusting for the 2-mo difference in cone breakage (Kolmogorov-Smirnov test, $D_{\max} = 0.249$ $P < 0.01$). The early cohort A had greater germination in the month immediately following cone break-up. In both cohorts, most germination occurred during a 6–8 wk period at the beginning of the rainy season: in May and June for cohort A and in June and July for cohort B. For the majority of cohort A, the first leaf emerged between June and January, while in cohort B, first leaf

Table 2

NUMBER OF ZAMIA SEEDS AND THEIR FATES IN COHORT A (19 plots, 20 cones) AND COHORT B (20 plots, 20 cones)

	Cohort A		Cohort B	
	<i>n</i>	%	<i>n</i>	%
Initial number of seeds	508		604	
Seeds eaten or dispersed	153	30	228	38
Seeds remaining	355	70	376	62
Not germinating	101	28	69	18
Germinating	254	72	307	82
Germinating and dying	107	42	104	34
Seedlings	147	58	203	66
Seedlings dying	135	92	194	96
Seedlings April 1985	12	8	9	4

Note. Each pair of rows corresponds to death or survival through a portion of the seed-to-seedling transition; number (*n*) of seeds sums to that of the preceding line.

emergence was between August and January. Seedlings would often lose their leaves and remain dormant until the rainy season.

In each cohort about one-third of the seeds were either eaten or dispersed (table 2) and nothing further is known about their fates. Of the 731 remaining seeds (table 2), 21 (2.9%) were alive in April 1985 (cohort A: 3.3%, cohort B: 2.4%); these proportions were not significantly different ($G = 0.62$). The relative frequency of individuals dying at the pregermination, germination, and seedling stages differed significantly between the cohorts ($G = 15.88, P \leq 0.001$). Cohort A had more death at the pregermination stage ($G = 10.43, P \leq 0.005$) and proportionally more germinants dying before the seedling stage (leaf emergence; $G = 4.02, P < 0.05$). The proportion of seedlings dying did not differ between the cohorts ($G = 2.02, P > 0.05$).

The survival distributions of cohorts A and B were significantly different (chi-square approximation of Wilcoxon test $\chi^2 = 43.7, P = 0.0001$; fig. 7), with cohort B maintaining a higher survivorship over the first 3 yr. Even after adjusting for the 2-mo difference in cone breakage, the cohorts still differed ($\chi^2 = 5.04, P = 0.0247$); cohort B had higher survivorship at age 5–9 mo and again at age 18–24 mo. Survivorship was close to linear on a logarithmic scale for both cohorts, as it was for seedlings on the permanent plots, where 79% of the seedlings died over 2 yr (fig. 7).

Most deaths occurred 3–5 mo after cone breakage (May–July for cohort A, July–August for cohort B) and at the end of the following dry season (March–April 1983). The second dry season was a time of peak conditional mortality in both cohorts (fig. 8). Cohort B also had a peak in conditional mortality between June and October 1984. During the first dry season and the months immediately following (February–July 1982), cohort B showed lower conditional mortality than did cohort A.

The proportion of seeds alive as seedlings in October 1984 did not differ between cohorts, nor was it

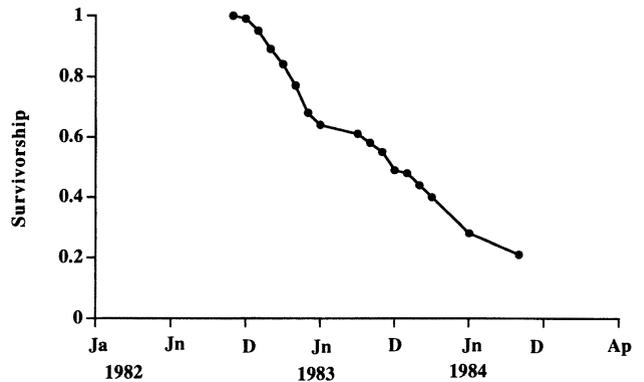
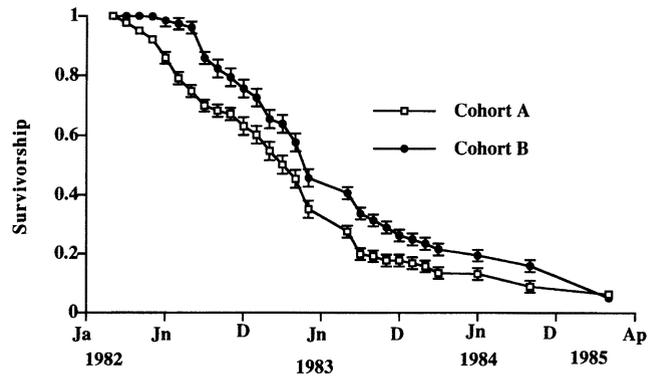


Fig. 7 Survival of seeds and seedlings. Top: Seed cohorts A ($n = 508$) and B ($n = 604$)—estimates and SE from SAS procedure LIFETEST. Bottom: Seedlings censused on permanent plots ($n = 179$).

density dependent (logistic regression score = 4.104, $df = 2, P = 0.1285$).

DEMOGRAPHY

Diagrammatic representation of the survival and stage transition of individuals between years revealed the dynamic patterns in the population (fig. 9). Only

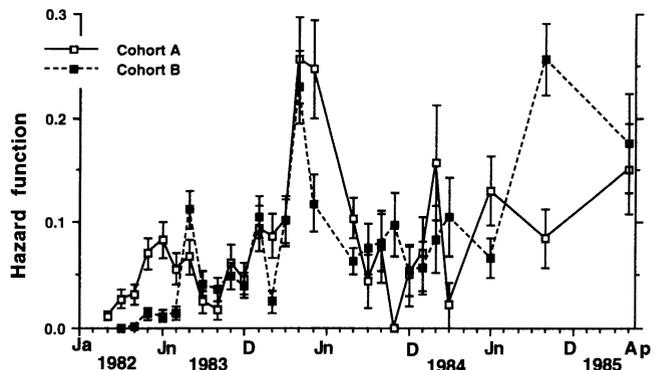


Fig. 8 Hazard function (= conditional mortality: the probability an individual will die in an interval given that it was alive at the beginning of the interval) for seed cohorts A and B—estimates and SE from SAS procedure LIFETEST.

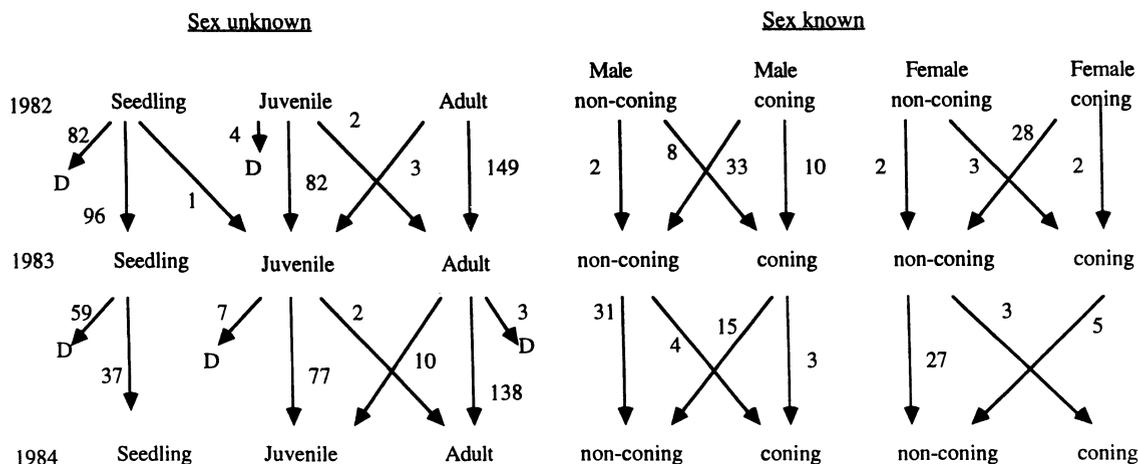


Fig. 9 Stage transitions of *Zamia amblyphyllidia* individuals in permanent plots. Data are from October of each year.

one of the 179 seedlings in the plots recruited to the juvenile class; this was during the first year. Each year a small proportion of juveniles recruited to the adult class, although none coned. However, a similar proportion of nonconing adults “regressed” to the juvenile class. Mortality of juveniles was low, and mortality of adults occurred only between 1983 and 1984 and was then limited only to nonconing adults.

The major change in the stage structure of the population over the 3 yr was in the proportion of adults coning (fig. 9). Of the 240 adults, 53 (22%) bore male cones and 35 (15%) bore female cones during the study. For both sexes, the number coning was greatest in 1982 and lowest in 1984. In each year, the number of coning males exceeded the number of coning females; coning sex ratios (sensu Clark and Clark 1987) ranged from 1.4 to 2.3. Ten of the 53 males coned in two or more consecutive years (seven in 1982 and in 1983, and three in all 3 yr). Only two of the 35 females coned in two consecutive years (1982 and 1983; fig. 9). The relative proportions of adults and juveniles changed little over the years.

Fecundity was higher for females initiating cones in 1983 than the previous year because of more cones per female and a threefold increase in the proportion of cones producing seeds (table 3).

Table 3

NUMBER OF FEMALE PLANTS INITIATING CONES AND COMPONENTS OF FECUNDITY IN THE PERMANENT PLOTS DURING EACH YEAR OF THE STUDY

Year of cone initiation	Females coning	Cones per female	Proportion of cones setting seed	Seeds per cone
1982	30	1.13	0.18	15.2
1983	5	1.60	0.50	...
1984	3	1.00

Note. Ellipsis dots reflect data that could not be obtained by October 1984.

PROJECTED LONG-TERM DYNAMICS OF THE POPULATIONS

For both years, the finite rate of increase (λ) was <1 , indicating negative population growth. Despite the greater fecundity in the second year of the study, λ was lower for the transition matrix of that year (0.9575) than for 1982–83 (0.9898). This resulted from the lower survivorship of all age classes in the latter matrix (tables 4, 5). At the higher rate the population would halve every 68 yr, whereas at the lower rate the population would halve every 16 yr. We did not test whether these λ 's differed significantly from each other or from 1.0.

ANALYTICAL PROPERTIES OF THE FEMALE SUBMATRICES

The stable stage distributions derived for both matrices had a predominance of adults and a low frequency of coning (table 6). In comparison, the actual stage structure observed in 1983 had proportionately more seeds and seedlings and fewer adults. Seeds and seedlings were particularly infrequent in the stable stage distribution derived for the 1982–83 matrix because of the low fecundity value in that matrix.

Reproductive values were much higher (>2 orders of magnitude) for adult females than for younger stages (table 6). This reflects the low probability of recruitment to the adult stage combined with the very high likelihood that an adult will continue to survive and occasionally reproduce. Interestingly, the reproductive value of coning females was only slightly higher than that of nonconing females; this is attributable to the very low probability of a female remaining in the coning class in consecutive years.

Sensitivity analysis revealed that our estimates of λ were most sensitive to variation (or errors) in the probabilities of a nonconing female becoming a coning female or remaining as nonconing (table 7). Estimation of λ was also sensitive to variation in the probability of juveniles recruiting to adult stages but was relatively insensitive to variation in fecundity, seed and seedling survival, juvenile recruitment (fig. 6), and the dy-

Table 4

STAGE TRANSITION MATRIX FOR OCTOBER 1982–OCTOBER 1983 FOR ZAMIA AT CAMBALACHE FOREST

	Females					Males				
	Seed	Seed-ling	Juvenile	Noncon- ing adult	Coning adult	Seed	Seed-ling	Juvenile	Noncon- ing adult	Coning adult
Females:										
Seed	0	0	0	0	1.516	0	0	0	0	0
Seedling	0.752	0.536	0	0	0	0	0	0	0	0
Juvenile	0	0.006	0.932	0.018	0	0	0	0	0	0
Nonconing adult ..	0	0	0.023	0.949	0.933	0	0	0	0	0
Coning adult	0	0	0	0.033	0.067	0	0	0	0	0
Males:										
Seed	0	0	0	0	1.516	0	0	0	0	0
Seedling	0	0	0	0	0	0.752	0.536	0	0	0
Juvenile	0	0	0	0	0	0	0.006	0.932	0.018	0
Nonconing adult ..	0	0	0	0	0	0	0	0.023	0.878	0.767
Coning adult	0	0	0	0	0	0	0	0	0.104	0.233

namics of coning females. For instance, increasing the seedling to juvenile recruitment probability to 0.1 or increasing the proportion of both coning and nonconing females that coned the next year to 0.5 failed to bring λ above 1.0 for either matrix. However, increasing both parameters simultaneously did result in $\lambda > 1.0$ (1982–83: 1.02; 1983–84: 1.03).

The elasticity matrix for each year revealed that λ was more sensitive to proportional changes in the stasis (survival without stage transition) of nonconing adult females and, secondarily, to stasis of juveniles (table 8). The sum of all stasis terms (main diagonal of the elasticity matrix) was 0.9277 for 1982–83 and 0.9279 for 1983–84. Following the criteria of Silvertown et al. (1993), the sum of all elasticities associated with survival (stasis and retrogression) equaled 0.9628 and 0.9631, respectively. Elasticities associated with growth equaled 0.0359 and 0.0365, whereas those associated with fecundity were only 0.0002 and 0.0003.

Discussion

Dormancy factors (immature embryo, fleshy sarco-testa, hard sclerotesta, plant growth regulators) delaying seed germination have been reported for several cycads (Smith 1978; Dehgan and Johnson 1983; Dehgan and Yuen 1983; Dehgan and Shutzman 1989; Landry 1990). In *Zamia amblyphyllidia*, germination occurred only after the fleshy outer layer was removed or rotted away, which is true for cycads in general (Smith 1978). Both germination and first leaf production coincided with wet periods. The greater risk of mortality of the early cohort (A) during and immediately after the first dry season resulted from being on the ground and beginning to germinate during an unusually wet period in late January and February of 1982. Although February is generally a dry month in Puerto Rico, in 1982 the dry season did not begin until March and continued through April, subjecting the

Table 5

STAGE TRANSITION MATRIX FOR OCTOBER 1983–OCTOBER 1984 FOR ZAMIA AT CAMBALACHE FOREST

	Females					Males				
	Seed	Seed-ling	Juvenile	Noncon- ing adult	Coning adult	Seed	Seed-ling	Juvenile	Noncon- ing adult	Coning adult
Females:										
Seed	0	0	0	0	6.080	0	0	0	0	0
Seedling	0.752	0.380	0	0	0	0	0	0	0	0
Juvenile	0	0.005	0.895	0.046	0	0	0	0	0	0
Nonconing adult ...	0	0	0.023	0.913	0.999	0	0	0	0	0
Coning adult	0	0	0	0.026	0.001	0	0	0	0	0
Males:										
Seed	0	0	0	0	6.080	0	0	0	0	0
Seedling	0	0	0	0	0	0.752	0.380	0	0	0
Juvenile	0	0	0	0	0	0	0.005	0.895	0.046	0
Nonconing adult ...	0	0	0	0	0	0	0	0.023	0.902	0.833
Coning adult	0	0	0	0	0	0	0	0	0.039	0.167

Table 6

STABLE STAGE DISTRIBUTIONS AND REPRODUCTIVE VALUES
FOR FEMALE *ZAMIA* DERIVED FROM THE TRANSITION
MATRICES FOR 1982-83 AND 1983-84

Life-history stage	Stable stage distribution		Reproductive value	
	1982-83	1983-84	1982-83	1983-84
Seed	0.036	0.079	1.00	1.00
Seedling	0.060	0.103	1.32	1.27
Juvenile	0.214	0.346	99.54	147.06
Nonconing adult ..	0.666	0.459	249.93	399.61
Coning adult	0.024	0.012	254.35	423.72

Note. For each matrix, the reproductive values were scaled so that of seeds = 1.0.

germinated seeds to water stress. During this period the seeds of cohort B were released; they remained dormant until the rains began in May and were not subjected to a prolonged dry period until the following February. Cohort B's better survival through the first dry season appears to explain the difference between the cohorts in the cumulative survival function. Water stress may also have resulted in the peak in both cohorts' conditional mortality that occurred during the second dry season. In addition, mortality could have been associated with exhaustion of the stored food supply (gametophytic tissue) of the seedling and subsequent dependence solely on photosynthesis. Vovides (1990) experiments suggest that dehydration, rather than herbivory or depletion of reserves, was the main source of seedling mortality in *Dioon edule*.

Other workers have found differences in seed survivorship depending on the time of release (Baskin and Baskin 1972; Kalisz 1986; Willson 1983). The lack of replication makes it difficult to determine whether the difference in survival between the two groups (3.3% vs. 2.4%) is of importance.

The "nonviable" seeds were not noticeably different in morphology from the viable seeds, although some appeared to be at the small end of the size range. The complete failure to germinate of one cone's seeds may have been due to intrinsic inviability. Full-size seeds containing no embryos have been reported for the cycads *Encephalartos transvenosus* (Grobelaar et al. 1989), *Dioon edule*, and some species of *Zamia* (Landry 1990). Fungal attack and predation by insect larvae in a few of the nonviable seeds in the piles were observed, but no attempt was made to determine if disease, predation, or lack of embryo were a cause or a result of germination failure.

The stage structure and coning ratios recorded in our permanent plots were representative of the larger Cambalache *Zamia* population. Censuses of *Zamia* in 10 random transects, 1 m wide by 24-92 m (average 46 m) long in January 1983 on two hillsides adjacent to those with the plots revealed no significant differences from those in the permanent plot in proportion fertile or coning sex ratio (Negrón-Ortiz 1987). The propor-

Table 7

SENSITIVITY MATRICES FOR 1982-83 AND FOR 1983-84 STAGE
TRANSITION FOR FEMALE *ZAMIA* AT CAMBALACHE FOREST

	Seed	Seed-ling	Noncon-		Coning adult
			Juvenile	adult	
1982-83:					
Seed	0.0002	0.0003	0.0011	0.0034	0.0001
Seedling	0.0002	0.0004	0.0015	0.0045	0.0002
Juvenile	0.0187	0.0310	0.1098	0.3419	0.0122
Nonconing adult ..	0.0470	0.0779	0.2757	0.8584	0.0307
Coning adult	0.0479	0.0793	0.2805	0.8736	0.0312
1983-84:					
Seed	0.0003	0.0004	0.0014	0.0019	0.0001
Seedling	0.0004	0.0006	0.0018	0.0024	0.0001
Juvenile	0.0486	0.0633	0.2122	0.2815	0.0077
Nonconing adult ..	0.1320	0.1719	0.5767	0.7648	0.0208
Coning adult	0.1400	0.1823	0.6115	0.8110	0.0220

Note: Each entry is the relative sensitivity of λ to changes in the probability of transition from the stage represented by the column to the stage represented by the row.

tion of "adults" coning each year (30%, 10%, and 4%) compares with 14% reported for a population further east in Puerto Rico in 1981-82 (Newell 1983), although that included a 2-yr production of female cones. Over the 3 yr of our study, 37% of the adults coned at least once. In an 8-yr study of south Florida *Zamia pumila*, 87% of nonseedlings coned at least once (Tang 1990). For *Zamia skinneri*, 26% of adults in primary forest-produced cones during a 6-yr study, compared with 73% in secondary forest where light levels were higher (Clark and Clark 1987). Within any 1 yr, the proportion of individuals coning ranged from 0% to 19% (primary forest) or 61% (secondary forest). Similarly, for three Australian cycad species, Ornduff (1989, 1990, 1991) reported low proportions of putative mature plants coning in a given year.

For both males and females, the proportion of in-

Table 8

ELASTICITY MATRICES FOR 1982-83 AND FOR 1983-84 STAGE
TRANSITION MATRICES FOR FEMALE *ZAMIA* AT CAMBALACHE FOREST

	Seed	Seed-ling	Noncon-		Coning adult
			Juvenile	adult	
1982-83:					
Seed	0	0	0	0	0.0002
Seedling	0.0002	0.0002	0	0	0
Juvenile	0	0.0002	0.1034	0.0062	0
Nonconing adult ...	0	0	0.0064	0.8230	0.0289
Coning adult	0	0	0	0.0291	0.0021
1983-84:					
Seed	0	0	0	0	0.0003
Seedling	0.0003	0.0002	0	0	0
Juvenile	0	0.0003	0.1984	0.0135	0
Nonconing adult ...	0	0	0.0139	0.7293	0.0217
Coning adult	0	0	0	0.0220	0

Note. Each entry gives the proportional change in λ resulting from a change in the matrix element. By definition, elasticities sum to 1.

dividuals coning was greatest in 1982 and least in 1984. Similarly, the years of high coning were synchronized between males and females of *Z. skinneri* (Clark and Clark 1987).

Several findings indicate that conditions for this population declined during this study. Not only did the proportions of males and females coning decline, but also, during 1983–84, there was greater seedling, juvenile, and adult mortality than the previous year and no recruitment of juveniles from seedlings. In addition, in the latter year 4% of the total adults “regressed” to the juvenile class, based on our criterion of leaflet number.

Since a transition from adult to juvenile conflicts with the general use of the latter term to designate individuals that have not yet reached reproductive age, we realize our criterion to distinguish these stages is not perfect. We believe that the achievement of reproductive status does not always coincide with the production of a leaf with >10 leaflets but that leaflet number is a good indicator of life-history stage. Similarly, in *Z. skinneri* reproduction was associated with number of leaflets on the longest leaf; very few of the plants with fewer than 12 leaflets coned (Clark and Clark 1987). We found that new leaves produced on a plant usually have the same or nearly the same number of leaflets as those on the longest of the leaves present. Even for those adults that regressed to juveniles, most (11 of 13) declined only from a maximum of 11–14 leaflets on the longest leaf to a minimum of eight to 10 during the study. Another line of evidence that leaflet number is an indicator of stage is its correlation with number of leaves on the plant (Negrón-Ortiz 1987). In two Australian cycads, the number of leaves was greater for coning than nonconing individuals and was used as the criterion for distinguishing mature from immature plants (Ornduff 1990, 1991).

We hypothesize that the stress that caused the reduction in leaflet number on many plants over the 2 yr of the study, as well as the increases in mortality and reductions in coning, was related to drought. In both 1982 and 1983, rainfall throughout Puerto Rico, including that recorded at the station closest to Camalache Forest (Dos Bocas), was below normal, with January–March 1983 extremely dry (<8 cm total; National Oceanic and Atmospheric Administration 1983, 1984). Alternatively, the low proportion of individuals coning in 1983 and 1984 may be due to “mast” coning in 1982, when a large proportion of adults coned, associated with a depletion of stored reserves due to cone production in these individuals.

It would be desirable to test our assumption that survival and stage transition probabilities of prereproductive stages are equal for males and females. It is most critical to test this for the transition from juvenile to adult, as our estimates of λ are more sensitive to this than to transitions among the prereproductive stages. Our finding that males greatly outnumber females among adults with few leaflets (table 1) indicates that males first cone at a younger age and smaller

size than females. If true, females would be expected to have a greater accumulated risk of mortality before they first reproduce. The male-biased sex ratio among adults with fewer leaflets has also been reported in *Z. skinneri* and interpreted as indicative of earlier reproduction in males (Clark and Clark 1987). Tang (1990) found disproportionately more reproductively active *Z. pumila* males than females in lower leaf-number classes but no significant difference in leaf number between males and females. Ornduff (1989, 1990, 1991) reported that coning males and females generally did not differ in leaf number in three Australian cycads. In our random transects (but not permanent plots), males averaged fewer leaves than did females (Negrón-Ortiz 1987).

Although about half of the individuals in the population were adults, the proportion of these producing cones varied greatly from year to year. If the proportion of females coning remained as low as it was in 1983 or 1984, the population would decline, even if recruitment of juveniles was increased by more than one order of magnitude. During its decline, a population in which such low rates of coning were maintained would also reach a stable stage distribution with fewer seeds and seedlings than we observed. Populations are probably able to persist because of periodic increases in the proportion of adults coning, i.e., mast coning. Sensitivity analysis revealed that λ was much more sensitive to changes in the proportion of females coning than it was to fecundity or demographic parameters of prereproductive stages. However, even an increase in the proportion of females coning to 50% was insufficient to bring λ above 1.0, unless accompanied by an increase in another parameter.

Our finding that λ was most sensitive to the proportion of adult females coning was markedly different than the pattern found for the palm *Astrocaryum mexicanum* (Piñero et al. 1984), where λ was most sensitive to estimates of growth and survivorship of prereproductive individuals, or for the perennial tropical herb, *Calathea ovoidensis*, where λ was most sensitive to rapid growth of seeds and seedlings (Horvitz and Schemske 1995). The sensitivity of λ to the coning behavior of adult females results from their very high reproductive values, which in turn is attributable in large part to their very high year-to-year survival rate, making numerous reproductive seasons probable.

The very high sum of elasticities associated with survival (stasis and retrogression), and very low sums of elasticities associated with growth and fecundity, matches the pattern found for many woody plants, particularly those of forests, and contrast with those of most herbs (Silvertown et al. 1993). This indicates that *Zamia* is similar to many trees in that its population growth rate depends more on survival than on growth or fecundity. We predict that this pattern will hold for other cycads as well.

These analyses highlight the importance of the high annual survival rates of adults to the persistence of *Zamia* populations. With such high adult survival, popu-

lations decline very slowly even when coning, fecundity, dry-season seedling survival, and juvenile recruitment are all low, as they were 1982 to 1984. Occasional episodes of mast coning would provide sufficient recruitment to allow such populations to persist.

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Literature cited

- Ballardie RT, RJ Whelan 1986 Mastling, seed dispersal and seed predation in the cycad *Macrozamia communis*. *Oecologia* 70:100–105.
- Baskin JM, CC Baskin 1972 The influence of germination date on survival and seed production in a natural population of *Leavenworthia stylosa*. *Am Midl Nat* 88:318–323.
- Britton NL, P Wilson 1925 Descriptive flora of Porto Rico and the Virgin Islands: Cycadales. Pages 329–330 in *Scientific survey of Porto Rico and the Virgin Islands*. Vol 6. New York Academy of Sciences, New York.
- Caswell H 1989 *Matrix population models*. Sinauer, Sunderland, Mass.
- Chamberlain C 1935 *Gymnosperms: structure and evolution*. University of Chicago Press, Chicago.
- Cipollini ML, DA Wallace-Senf, DF Whigham 1994 A model of patch dynamics, seed dispersal, and sex ratio in the dioecious shrub, *Lindera benzoin* (Lauraceae). *J Ecol* 82:621–633.
- Clark DA, DB Clark 1987 Temporal and environmental patterns of reproduction in *Zamia skinneri*, a tropical rain forest cycad. *J Ecol* 75:135–149.
- Dehgan B 1980 Improving seed germination of Florida coontie. *Woody Ornamentalist* 5:11–12.
- Dehgan B, CR Johnson 1983 Improved seed germination of *Zamia floridana* (sensu lato) with H₂SO₄ and GA₃. *Sci Hortic* 19:357–361.
- Dehgan B, B Shutzman 1983 Effect of H₂SO₄ and GA₃ on seed germination of *Zamia furfuracea*. *HortScience* 18:371–372.
- Dehgan B, CKKH Yuen 1983 Seed morphology in relation to dispersal, evolution and propagation in *Cycas* L. *Bot Gaz* 144:412–418.
- De Kroon H, A Plaisier, J Van Groenendael, H Caswell 1986 Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1477–1431.
- Department of Natural Resources 1976 The master plan for the commonwealth forests of Puerto Rico. Department of Natural Resources, Río Piedras, P.R.
- Doughty S 1991 Cycad seed germination as of 1991. *Cycad Newsl* 14:12–20.
- Eckenwalder J 1980 Taxonomy of the West Indian cycads. *J Arnold Arb Harv Univ* 61:701–722.
- Ewel JJ, JL Whitmore 1973 The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Institute of Tropical Forestry, Río Piedras, P.R.
- Fox GA 1993 Failure-time analysis: emergence, flowering, survivorship, and other waiting times. Pages 253–289 in SM Scheiner, J Gurevitch, eds. *Design and analysis of ecological experiments*. Chapman & Hall, New York.
- Grobbelaar N, JJM Mayer and J Burchmore 1989 Coning and sex ratio of *Encephalartos transvenosus* at the Modjadji Nature Reserve. *S Afr J Bot* 55:79–82.
- Jones DL 1993 *Cycads of the world*. Smithsonian Institution Press, Washington, D.C.
- Horvitz CC, DW Schemske 1995 Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecol Monogr* 65:155–192.
- Kalisz S 1986 Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). *Evolution* 40:479–491.
- Kraa W 1989 Alternative method of germinating cycads seeds. *Cycad Newsl* 12:11–12.
- Landry G 1990 Flotation of cycad seeds as a test for viability. *Cycad Newsl* 13:7–8.
- Liogier HA, LF Martorell 1982 Flora of Puerto Rico and adjacent islands: a systematic synopsis. Editorial de la Universidad de Puerto Rico, Río Piedras.
- Monroe WH 1974 The karst landforms of Puerto Rico. U.S. Department of the Interior Geological Survey Professional Paper 899. Government Printing Office, Washington, D.C.
- Negrón-Ortiz V 1987 Study of natural history and ecology of *Zamia* in Puerto Rico. M.S. thesis. Recinto Universitario de Mayagüez, Mayagüez, P.R.
- Negrón-Ortiz V, GJ Breckon 1989a A note on the dispersal of *Zamia* (Zamiaceae) in Puerto Rico. *Caribb J Sci* 25:86–87.
- 1989b Population structure in *Zamia debilis* (Zamiaceae). I. Size classes, leaf phenology, and leaf turnover. *Am J Bot* 76:891–900.
- Newell SJ 1983 Reproduction in a natural population of cycads (*Zamia pumila* L.) in Puerto Rico. *Bull Torrey Bot Club* 10:464–473.
- National Oceanic and Atmospheric Administration 1983 Climatological data: Puerto Rico and the Virgin Islands, 1982. National Oceanic and Atmospheric Administration, Asheville, N.C.
- 1984 Climatological data: Puerto Rico and the Virgin Islands, 1983. National Oceanic and Atmospheric Administration, Asheville, N.C.
- Ornduff R 1989 Size distribution and coning behavior of the Australian cycad *Lepidozamia peroffskyana*. *Aust J Ecol* 14:241–245.
- 1990 Geographic variation in reproductive behavior and size structure of the Australian cycad *Macrozamia communis* (Zamiaceae). *Am J Bot* 77:92–99.
- 1991 Coning phenology of the cycad *Macrozamia riedlei* (Zamiaceae) over five-year interval. *Bull Torrey Bot Club* 118:6–11.
- Pinard MA, FE Putz 1992 Population matrix models and palm resource management. *Bull Inst Fr Etud Andines* 21:637–649.
- Piñero D, M Martínez-Ramos, J Sarukhan 1984 A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. *J Ecol* 72:977–991.
- SAS Institute 1989 *SAS/STAT user's guide*, version 6. SAS Institute, Cary, N.C.
- Schemske DW, BC Husband, MR Ruckelshaus, C Goodwillie, IM Parker, JG Bishop 1994 Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75:584–606.
- Silvertown J, M Franco, I Pisanty, A Mendoza 1993 Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J Ecol* 81:465–476.
- Smith G 1978 Seed scarification to speed germination of ornamental cycads (*Zamia* spp.). *HortScience* 13:436–428.
- Stevenson D 1987 Again the West Indian zamias. *Fairchild Trop Gard Bull* 42:23–27.
- Tang W 1989 Seed dispersal in the cycad *Zamia pumila* in Florida. *Can J Bot* 67:2066–2070.
- 1990 Reproduction in the cycad *Zamia pumila* in a fire-climax habitat: an eight-year study. *Bull Torrey Bot Club* 117:368–374.
- Vorster P 1988 Growing *Encephalartos* in a Miami-type climate. *Cycad Newsl* 11:3–12.
- Vovides, AP 1990 Spatial distribution, survival, and fecundity of *Dioon edule* (Zamiaceae) in a tropical deciduous forest in Veracruz, Mexico, with notes on its habitat. *Am J Bot* 77:1532–1543.
- Willson MF 1983 *Plant reproductive ecology*. Wiley, New York.