SPATIAL DISTRIBUTION, SURVIVAL, AND FECUNDITY OF DIOON EDULE (ZAMIACEAE) IN A TROPICAL DECIDUOUS FOREST IN VERACRUZ, MEXICO, WITH NOTES ON ITS HABITAT

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A natural habitat of the cycad Dioon edule Lindl. in central Veracruz, Mexico is described. Prolonged drought periods and fire are factors contributing to seedling death resulting in a population structure with a reverse 'J' or Deerey type III survivorship curve. The cycads exhibited a 'clumped' or contagious distribution on shallow soils of the habitat and on rocky outcrops. This distribution was attributed to exclusion by competition from other species for water, soil nutrients, and/or seed dispersal by rodents. Estimated coining frequency varied from 2.8 to 8.8 years in male plants and from 10.0 to 52.0 years in female plants, though shorter intervals are known to occur, especially following exceptionally wet years. Chamberlain’s age estimate for D. edule has been confirmed and a life table is presented.

In view of natural environments in the tropics being under constant threat of destruction as well as the rampant commercial collecting of cycads (Gilbert, 1984; Vovides 1986; Schutzman, Vovides, and Dehgan, 1988) it is felt that ecological and population studies of this ancient group of endangered species are overdue. Work of this type is important for a better understanding of the biology of this interesting group of gymnosperms, and essential to providing adequate guidance for their future in situ conservation in reserves.

Spatial distribution studies and population dynamics of plants have been established for some time now especially on north temperate florals. Gleason (1920) gave an early account on the nonrandom nature of plant distribution within a community, and Kershaw (1962) related the microtopography of a Rhacomitrium heath in Iceland to the distribution patterns of Carex bigelowii and Festuca rubra. Solbrig (1981) showed that competition and physical environment have an effect on plant size and growth rate of Viola sororia. Work of this type on tropical species is less common; Piñero, Sarukhán, and Gonzalez (1977) did a demographic study on a tropical rain forest understory palm Astrocarum mexicanum and found that this species forms a simple structure community within a multi-species complex structure community. Similar work on cycads is sparse, and ecological work on this group has largely been on plant density, phenomenology, and seed dispersal (Eckenwalder, 1980; Dehgan and Yuen, 1983; Newell, 1983; Clark and Clark, 1987; Tang, 1989).

The present investigation is centered on a natural stand of Dioon edule Lindl. in tropical thorn forest in central Veracruz, Mexico where 4 years of data were collected to analyze spatial distribution, survival, growth, and reproduction of the plants.

Geographical distribution of Dioon edule—The early literature concerning D. edule including the original description by John Lindley (1843) is very vague on distribution. In some articles only the country of origin is mentioned (Miquel, 1870). The first authors to mention localities were Wilson (1911) and Chamberlain (1919); Chamberlain reported only Chavarillo as the D. edule locality. Recent work by De Luca, Sabato, and Vazquez Torres (1982) shows the range of D. edule from the southeastern parts of the state of Nuevo León through southern Tamaulipas, San Luis Potosí, Querétaro, Hidalgo, and central Veracruz. Muller (1939) describes extensive scrub-land areas consisting of almost pure stands of Dioon edule in Nuevo León and Tamaulipas, mainly near the town of Linares. This is exceptional, and according to Rzedowski (1978) these stands

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Figs. 1, 2. 1. Map of Mexico showing position of the state of Veracruz (A, black); (B) state of Veracruz enlarged with a projection of the Cerro Papayal-Achichuca area indicating study site just above the 550-m contour. 2. Climatic diagram for nearest meteorological station to study site (based on 17 years of data for precipitation and temperature). Key: dotted = dry period; bars = wet period; black = precipitation > 100 mm.

do not merit being considered independent vegetational communities.

In Veracruz, D. edule is found mainly in tropical deciduous thorn forest and oak woodland, although relict stands can be found in grassland (after removal of the forest). Normally sporadic populations are formed, often locally abundant and very frequently in canyons, steep rocky slopes, and other isolated places with difficult access.

Study site—The study site lies about 30 km southeast of Xalapa, off the mountain road that runs between Xalapa and Huatusco 600 m above sea level. The site forms part of Cerro Papayal-Achichuca near the Rio de Los Pescados canyon, municipality of Coatepec, Veracruz (Fig. 1). It is a calcareous hill that forms part of the Cretaceous formation of Chavarillo. It consists of metamorphic limestone with steep slopes and rocky outcrops. The soil is a black, shallow tropical rendzina with loose calcareous stones. The slope where the transect was laid out faces south and has an inclination of 43° (93%).

Climatic records over the past 17 years exist for Jalcomulco, the nearest village to the study site. According to García’s (1981) modification of the Köppen classification, the climate corresponds to the following cryptogram: Aw*1 (i’i)g. This translates as: hot (A), dry season during winter months with a short dry spell during the summer rainy period (w*), sub-humid (I), annual temperature oscillation within 5 to 7 °C (i’i), with a Ganges type summer (g, hottest month before June). A mean annual temperature of 24.5 °C with a mean annual rainfall of 1,106.4 mm being distributed principally throughout the summer months leaves a well-defined dry season early in the year. From these data a climate diagram has been constructed (Fig. 2).

The vegetation is mainly ‘selva baja caducifolia’ (tropical deciduous thorn-forest) of Rzedowski (1978), with secondary succession stages in the more disturbed parts. The vegetation at the site was sampled in order to identify the more common species. Some of the more common trees and shrub species found are: Brahea dulcis (HBK) Mart., Bursera simaruba (L.) Sarg., Casearia corymbosa HBK, Comocladia engleriana Loes., Diospyros veracruzensis Standl., D. oaxacana Standl., Lysiloma demostachya Benth., Pistacia mexicana HBK, Plumeria rubra L., Pseudobombax ellipticum (Kunth) Dagd., Quercus laurina Humb. et Bonpl., Q. oleoides Schlechtendal et Cham. and Q. peduncularis Nee. The more common herbaceous and succulent plants are: Agave lophantha Schiede, Callisia fragrans (Lindl.) R. F. Woodson, Hechta sp. nov. and Opuntia sp. The more common epiphytes are: Aechmea bracteata (Swartz) Griseb., Brassavola cucullata (L.) R. Br., Hylocereus undatus (Haw.) Br. R., Tillandsia balbisiana Schultes, and T. schiedeana Steudel. Another cycad reported for
the habitat is *Zamia loddigesii* Miq. This species, however, is less common than *Dioon*.

The site was chosen primarily because it presents the least human disturbance. The site forms part of the Mexican agrarian reform system ‘Tierras Ejidales’ and is known locally as ‘Ejido Tuzamapan.’ On the steeper slopes subsistence farming is practiced resulting in encroachment into the native forest and initiation of soil erosion. The forest itself is exploited for firewood, ornamental plants including the cycads, and the fibrous leaf sheaths of the fan palm *Brahea dulcis* for making suavero or tlapopxtle, a quilted blanket for use under mule and donkey saddles (G. Castillo, personal communication). The exploitation of *Dioon edule* is less intensive here than at other sites owing to its difficult access. The leaf crown is decapitated and sold as an ornamental plant (Vovides and Peters, 1987). The beheaded trunk later off-shoots up to four buds, each producing a separate crown of leaves. Repeated decapitation of the buds long before they reach coning size has resulted in no regeneration from seed at other easily accessible sites, thus rendering these sites useless for any ecological studies since only relict stands remain. The seeds have been used in the past and to a much lesser extent in the present as a source of laundry and edible starch (tiotamal).

**MATERIALS AND METHODS**

Population study and pattern analysis of *D. edule*—Three consecutive 10 × 10-m blocks were laid out forming a 10 × 30-m transect. A total of 139 individuals of *Dioon edule* were mapped and labeled, using two surveyors' tapes and a prismatic compass to obtain coordinates. Older plants, branching at the base, were counted as single individuals though leaf production data of the branches were considered separately. Plant height, diameter, number of leaves per plant (Branch), and reproductive condition were noted. A soil sample was taken from the transect for laboratory analysis and description; color, texture, pH, and major element assays were done according to Black et al. (1965). The site was revisited approximately three times per year to note deaths, leaf production, and fruiting. A total of 4 years of data were collected. Survivorship curves, a life table according to Krebs (1978), and growth rate were calculated. Three additional 10 × 10-m plots were laid out at random at the site but away from the original 10 × 30-m transect, and the plant density data were used to confirm the similarity of the study transect (unpublished data). The plants within the study transect were divided into eight height classes, and observations of leaf production for each height class over the 4-year period enabled an age of *Dioon edule* to be estimated for each height class (Vovides and Peters, 1987).

**Fecundity of wild *Dioon edule*—**Coning events in *Dioon* are marked in the pith where the vascular bundles collect together to enter the peduncle of the cone. The apical meristem is terminated and a new one is initiated after coning, which continues growth until the next cone is produced. Thus, a ladder-like series of ‘cone domes’ can be observed in the pith of a transverse longitudinal section of the trunk, each dome marking a coning event (Chamberlain, 1911). One large *D. edule* specimen was dissected in order to calculate the time interval between cone domes by counting the number of leaf bases on the trunk between the domes and dividing by the average leaf production of the plant (Vovides and Peters, 1987). A quicker and less destructive method was developed to determine the coning frequency of a further two known male and two known female specimens of *D. edule* outside the transect. This consisted of boring vertically from the crown and down into the pith of a plant using a long tree-ring increment borer. This way, a core of the pith was obtained and the vascular traces of the cone dome were seen in the core at intervals along its length. The core was stained with aniline sulphate or chlorogluco-lin-HCl to contrast the lignin of the vascular bundles in the cone domes.

**Distribution pattern of *Dioon edule* plants—**
The method for detecting nonrandomness was that of Svedberg (1922) described by Kershaw (1973), where the Poisson series was used as the basis of random expectation. During this investigation the number of observed plants in 100 randomly distributed 1-m-square quadrats was related to the number expected derived from the Poisson series. The departure of the expected from the observed number for this quadrat size was subjected to the chi-square (X²) test for goodness of fit. To detect the scale at which the nonrandomness occurs, the analysis of a contiguous grid of quadrats technique for the detection of pattern as described by Kershaw (1960, 1973) was used.

**Soil depth in relation to plant distribution—**Forty-nine soil depth soundings were taken at randomly determined coordinates over each of the three 10 × 10-m plots (*n* = 147 total). At each coordinate a metal rod was driven into the soil until it hit a stone or the bedrock and
the depth of penetration and position were recorded. Soil depths were divided into eight depth classes, and pattern analysis was conducted on each depth class using the method described for the plants. For a comparison of plant distribution and soil depth, a frequency histogram for the soil depth classes was superimposed over a bar diagram of the total number of plants found per depth class.

**Growth of Dioon edule seedlings in darkness**—In order to assess the reserves of *D. edule* seeds and survival of seedlings under stress conditions, 20 seeds were sown in thoroughly washed volcanic gravel and germinated and grown under virtually no light and nutrient conditions. They were kept in a dark cupboard and watered only with distilled water. Deaths during a 2-year period were recorded and watering withheld after this period. The total number of leaves produced at the end of this period was recorded. Five 4-year-old seedlings grown under normal conditions in the botanic garden were used as controls.

**RESULTS**

**Population structure and seedling establishment**—The population structure, a survivorship curve based on plant height (Fig. 3), is a reverse 'J' curve or a Deevey type III (Deevey, 1947). This shows a high mortality at the seedling and young stage of the life cycle (plants up to 20 cm tall), that comprise 78% of the total number of individuals in the transect. The remaining 22% are mature and juvenile plants.

**Growth patterns**—Figure 4 shows the relationship of number of leaves to trunk diameter. When the plant is young its leaf production is low. The number of leaves produced is correlated with diameter in a curvilinear fashion reaching a maximum number of leaves in the crown when a maximum diameter of 25–30 cm is attained. The curve that best fits the data follows a cubic polynomial regression. Figure 5 shows the relationship between height and diameter. Maximum diameter is reached when the plant reaches 40–50 cm tall which also corresponds to the minimum height of plants observed with cones in this habitat. Within this range the data reach an asymptote where further increase in diameter stops and height growth continues, giving rise to a sigmoid curve whose best fit is a cubic polynomial regression. Figure 6 shows the relationship between the mean total number of leaf bases accumulated with height (*n* = 3 or 5). In heights below 50 cm the leaf base increment is geometric while the plant is still increasing in diameter, and as a consequence, there is an increase in leaf production during diameter increment. After approximately 50 cm height has been reached the number of leaves produced per flush tends towards a constant number (mean = 8.6, SD = 2.4), and the mean total number of leaf bases shows a linear relationship with height. To obtain an estimated rate of height growth in centimeters per year per height class, the height class increment (Table 1) was divided by the residence time for that height class. The estimated growth rate is given in Table 2.

**Table 1.** Age calculation of *D. edule* based on leaf productivity rate per size class and the mean total number of leaf bases counted from three to five trunks per height class in the field. Leaf production data obtained from 139 individuals in the transect over a period of 4 years at Cerro Papayaal-Achicuaha, Veracruz (from Vovides and Peters, 1987)

<table>
<thead>
<tr>
<th>Height class</th>
<th>Mean total bases</th>
<th>Increment</th>
<th>Mean leaves/year</th>
<th>Residence</th>
<th>Age yr</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–5</td>
<td>12</td>
<td>—</td>
<td>1.0</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>6–10</td>
<td>119</td>
<td>107</td>
<td>1.0</td>
<td>107</td>
<td>119</td>
</tr>
<tr>
<td>11–20</td>
<td>301</td>
<td>182</td>
<td>1.4</td>
<td>126</td>
<td>245</td>
</tr>
<tr>
<td>21–30</td>
<td>1,060</td>
<td>759</td>
<td>2.6</td>
<td>289</td>
<td>534</td>
</tr>
<tr>
<td>31–40</td>
<td>1,498</td>
<td>438</td>
<td>5.7</td>
<td>77</td>
<td>611</td>
</tr>
<tr>
<td>41–70</td>
<td>2,041</td>
<td>543</td>
<td>5.8</td>
<td>94</td>
<td>705</td>
</tr>
<tr>
<td>71–100</td>
<td>3,585</td>
<td>1,544</td>
<td>7.6</td>
<td>203</td>
<td>908</td>
</tr>
<tr>
<td>101–200</td>
<td>7,713</td>
<td>4,128</td>
<td>10.0</td>
<td>413</td>
<td>1,321</td>
</tr>
<tr>
<td>201–300</td>
<td>21,521</td>
<td>13,809</td>
<td>11.0</td>
<td>1,255</td>
<td>2,577</td>
</tr>
</tbody>
</table>
Figs. 4–7. 4. Relationship between number of leaves per plant and trunk diameter of *Dioon edule*. 5. Relationship between trunk diameter and plant height of *D. edule*. 6. Relationship between trunk height and total number of persistent leaf bases in *D. edule*. 7. Relationship between number of surviving plants and age of *D. edule*.

**Age of *Dioon edule***—The estimate of 970 years obtained by Chamberlain (1919) was based on one plant 5 feet tall growing under garden conditions. Chamberlain mentioned that the age estimated was a conservative one as the calculation did not take into account the resting periods the plants undergo after coning, and also that seedlings and juvenile plants do not produce the same number of leaves per flush as adult plants. In an attempt to improve on Chamberlain’s method, Vovides and Peters (1987) based age estimates on 3 to 5 plants per height class in the field (Table 1). In general, these estimates corroborate the age estimate found by Chamberlain (1919). An attempt was made to confirm this aging by using radiocarbon-14 dating on cellulose extracted from xylem tissue from the base of a 2.7-m-tall plant (Vovides, 1988). The results did not match that based on leaf-base counts owing to the presence of “bomb-carbon” (C¹⁴ released during nuclear bomb tests during the 1950s and early 1960s). This was probably due to cellulose contamination from the live parenchymatous rays that
are common throughout cycad xylem and are difficult to remove. C\textsuperscript{14} aging on chemically extracted lignin may give better results.

**Life table**—Table 3 shows a life table constructed from data obtained from the age calculation table and the number of individuals observed within each height class along the transect. The age interval used was 250 years (column X), and the number of individuals in each age interval was obtained by referring to the height classes contained within that age interval. The calculation of the columns of the life table is according to Krebs (1978). In the age class 0–250 years there are 109 individuals (nx column). In other words, from the seed input over 250 years only 109 have survived in the area of the transect. The ‘ex’ column shows the average life expectancy of that size class. For the age class 750–1,000 years, the average expected life is 625 years (2.5 × 250). The heaviest death rate (qx column) occurs during the early part of the plant’s life cycle, i.e., 88% of individuals aged between 0 and 250 years die. This is in general agreement with the survivorship curve.

**Fecundity of Dioon edule**—Only two known female plants were reported in the transect during the 4-year study. One coned before the study (remains of cone on the plant), and the other was in production during the first year of the study. Two exceptionally dry years were followed by an unusually wet summer in 1984, and by the end of this wet season (November) a cone production flush occurred at the site, within the transect and outside it. Three plants within the transect coned for the first time during the study. A large female plant that was in production during the first year of the study coned again giving a 4-year interval between cones for this plant. Mature female cones on the site were found to be variable in their weight and number of seeds contained. Cone weights ranged from 2.5 to 5.0 kg (n = 4) and seed content from 86 to 230. The percentage of germination is remarkably high; trials in the botanic garden showed over 98%. A fecundity schedule calculated by measuring the cone dome intervals from the pith cores obtained from four adult *D. edule* plants of known sex, two males and two females (Fig. 8), and dividing by the height growth rate for the height class of plant the core, was taken (Table 4). This gave an estimate of the interval in years between coning; for the males from 2.8 to 8.8 years and for the females a much longer interval of 10 to 52 years was observed. During exceptionally favorable years this interval can be considerably shorter as observed. Coning events could not clearly be seen as constrictions on the surface of the trunk as in *D. spinulosum* reported by Chamberlain (1911).

**Spatial distribution and pattern analysis of Dioon edule**—Plants are subject to a multitude of factors affecting their distribution. These factors include those intrinsic to the plant, such as seed dispersal distance, predation, and its relation to other organisms as well as environmental factors like temperature and rainfall. Field experience shows that most environmental factors do not have a random distri-

<table>
<thead>
<tr>
<th>X Age years</th>
<th>Nx Observed No. plants/age class</th>
<th>lx Proportion surviving Nx/No</th>
<th>dx No. dying age class interval Nx/Nx + 1</th>
<th>qx Death rate/age class interval dx/Nx</th>
<th>ex Mean life expectancy/age class</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–250</td>
<td>109</td>
<td>1.000</td>
<td>96</td>
<td>0.881</td>
<td>0.78</td>
</tr>
<tr>
<td>251–500</td>
<td>13</td>
<td>0.119</td>
<td>2</td>
<td>0.154</td>
<td>0.81</td>
</tr>
<tr>
<td>501–750</td>
<td>11</td>
<td>0.101</td>
<td>9</td>
<td>0.818</td>
<td>1.05</td>
</tr>
<tr>
<td>751–1,000</td>
<td>2</td>
<td>0.018</td>
<td>0</td>
<td>—</td>
<td>2.50</td>
</tr>
<tr>
<td>1,001–1,250</td>
<td>2</td>
<td>0.018</td>
<td>1</td>
<td>0.500</td>
<td>1.50</td>
</tr>
<tr>
<td>1,251–1,500</td>
<td>1</td>
<td>0.009</td>
<td>1</td>
<td>1.000</td>
<td>1.50</td>
</tr>
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<td>1,501–1,750</td>
<td>0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>1,751–2,000</td>
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<td>—</td>
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</tr>
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<td>2,001–2,250</td>
<td>1</td>
<td>0.009</td>
<td>0</td>
<td>—</td>
<td>0.05</td>
</tr>
</tbody>
</table>
Fig. 8. Longitudinal section through trunk of *Dioon edule* showing cone-domes (arrows) in pith (A). Bar = 1 cm. Increment borer cores of pith showing distantly spaced vascular bundles (arrows) of cone-domes from a female plant (B) and closely spaced vascular bundles of cone-domes from pith of male plant (C).

Distribution of different values, and therefore, rarely do plants have a random distribution (Greig-Smith, 1983).

The plants were found to exhibit a nonrandom distribution, $\chi^2 = 10.73$, df = 1, $P = < 0.005$. The pattern analysis (Fig. 9) showed a contagious or clumped distribution at block size 16 for total plants and block size 8 for plants 0–10 cm tall; this corresponded to approximately 8 and 4 m$^2$, respectively. The pattern for soil depth class 0–5 cm shows a small peak at block size 2, the highest peak at block size 8, and an intermediate peak at block size 16. Pattern was also detected for the other soil depth classes, showing a somewhat similar trend with a major peak at block size 8 and a lesser one at block size 16; for example the patterns for soil depth class 6–10 cm, 26–30 cm, and intermediate depth classes were found to be similar but with a lower variance than depth class 0–5 cm. Although replicate transects would have provided results for a more
TABLE 4. Fecundity schedule for Dioon edule. Estimated coning interval established by measuring distance between cone domes of two male and two female adult plants of D. edule at Cerro Papayal-Achichua, Veracruz

<table>
<thead>
<tr>
<th>Male 70 cm tall</th>
<th>Male 68 cm tall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cone dome interval cm</td>
<td>Coning interval yr</td>
</tr>
<tr>
<td>0.09</td>
<td>2.8</td>
</tr>
<tr>
<td>1.1</td>
<td>3.4</td>
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<tr>
<td>1.9</td>
<td>5.9</td>
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<tr>
<td>1.6</td>
<td>5.0</td>
</tr>
<tr>
<td>2.4</td>
<td>7.5</td>
</tr>
<tr>
<td>2.8</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Female 96 cm tall</th>
<th>Female 122 cm tall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cone dome interval cm</td>
<td>Coning interval yr</td>
</tr>
<tr>
<td>4.3</td>
<td>28.7</td>
</tr>
<tr>
<td>6.8</td>
<td>45.3</td>
</tr>
<tr>
<td>7.8</td>
<td>52.0</td>
</tr>
<tr>
<td>6.4</td>
<td>42.3</td>
</tr>
<tr>
<td></td>
<td>7.8</td>
</tr>
</tbody>
</table>

Young tender leaves are eaten by the butterfly larva *Eurnaeus debora*. The insect lays its eggs on the petioles and abaxial surfaces of the leaflets. On hatching, the young larvae feed voraciously on the leaflets leaving a denuded and even partly eaten rachis, thus lowering the plant’s photosynthetic potential. This infestation, although not quantified, appears variable from year to year. Only plants upon which eggs have been deposited are affected. Once the young leaves have become sclerified they are generally more resistant to predation. The continual production of etiolated leaves over a 2-year period during the continuous darkness experiment (Fig. 13; 5.7 ± 0.3 leaves, n = 17), however, showed that this predation is unlikely to have been solely responsible for the high seedling mortality, if it is assumed that the etiolated nonfunctional leaves are equivalent to leaves removed by the larvae. The control seedlings produced 0.4 ± 0.2 (n = 5) leaves/plant over this 2-year period.

Abiotic factors—Dehydration of seedlings during the hot dry season is a more likely factor causing high seedling mortality since these shallow rendzina soils are subject to extreme drying out. During the 1983 dry season the majority of 1–2-year-old seedlings were observed to have died. Dehydration appears to be the main cause of seedling mortality and this was supported by the continuous darkness experiment when water was withheld for 2 weeks after a 2-year period of regular watering. All the surviving 18 seedlings out of 20 seeds that were originally sown had died during this 2-week “no water” period.

DISCUSSION

This habitat is subject to bushfires during the dry season, and although this does not affect established plants owing to their armor of persistent leaf bases, it can kill the less protected seedlings. Fire in the preceding year may induce females to cone during the following season (Grobbleaar, Meyer, and Burchmore, 1989), probably due to the temporary release of minerals and nutrients. Grove, O’Connell, and Malajczuk (1980) have shown that the Australian cycad *Macrozamia riedlei* contributes significantly to the nitrogen balance of its forest ecosystem as a result of forest burning. The high points of the survival curve (Fig. 3) in the 30- to 40-cm and 70- to 80-cm classes could probably be a reflection of a high input of seeds in the distant past when various female plants coned simultaneously. This was observed during late 1984 when a number of...
female plants coned. The years 1984 and 1985 were unusually wet and were probably responsible for these cone flushes in the population as well as better seedling survival. Grobbelaar, Meyer, and Burchmore (1989) found increased cone production of wild *Encephalartos transvenosus* in areas of the Modjadi Nature Reserve where watering was practiced.

The height growth rate is high at the seedling stage where the plant is tapping seed store reserves; this rate falls off and is low during the juvenile stages where leaf production is low and growth in diameter is high. The height growth rate increases after the plants reach 40 cm as by this time they have approached near the maximum number of leaves per flush and have also stopped increasing in girth. The lower height growth rate after the plants have reached 100 cm in height is probably influenced by compression of the stem tissues due to the increased weight of the stem.

The cone dome interval seen on the cores can be used to determine the sex of the plants because in females the interval between domes
appears much longer than in males. There has always been a difficulty in sexing cycads that are not in cone, and it is felt that this method would probably work on other species of cycads.

The spatial distribution of these cycads on the shallower soils is probably due to competition for the deeper soils by the faster growing angiosperm species, thus leaving the more inhospitable niches like these other rocky outcrops and shallow soils open for the cycads and other xeric species that can colonize them (Fig. 11). The dispersal of the cycad seeds by the rodent *Peromyscus mexicanus* that hoards seeds in small caverns and crevices in and around the rocky outcrops would also contribute to this distribution pattern. This rodent appears to be tolerant to the cycad toxins. In controlled experiments, *Peromyscus* ate ground-up *Dioon* seeds with impunity, whereas the *Rattus rattus* controls died within 24 hours after being fed the same diet (Gonzalez, 1988).

Endomycorrhiza has been detected in this population of *D. edule* (Vovides, 1988), and it has been widely reported that this kind of mycorrhizal association in angiosperms enhances the ability of the host plant to absorb nutrients and water (Sanders and Tinker, 1971; Safir, Boyer, and Gerdemann, 1972; Clarkson, 1974; Barrow, Malajczuk, and Shaw, 1977; Cox et al., 1980). It is also known that cycads have symbiotic blue-green algae in coralloid roots that fix atmospheric nitrogen (Schneider, 1894; Bergrersen, Kennedy, and Whittman, 1965; Halliday and Pate, 1976), and Grove, O'Connell, and Malajczuk (1980) have shown this to be significant to the nitrogen budget of their ecosystem. These factors along with its xerophytic morphology may well give *Dioon edule* a selective advantage to survive on the poor soils of these exposed and harsh microhabitats.

Both biotic and abiotic factors would necessarily have profound effects on the establishment of the cycads. Seedlings would be quickly eliminated during the dry season by fires and from areas where the soil is subject to drying and where quick anchoring by the seedling's vigorous taproot was not possible. The shallower soils and rocky outcrops are favorable to plant establishment by the presence of fissures where the taproots can obtain good anchorage and moisture from condensation, and also by seeds being 'forgotten' by rodents in shady crannies around the limestone rocks, thus contributing to the spatial distribution observed.

The banning of repeated decapitation of adult plants and human encroachment in this habitat would result in higher seed production. Owing to the high natural seedling mortality in the field it is thought that seeds could be harvested on a regular basis for propagation provided a minimum number of seedlings are artificially established in the field. Further work is needed to evaluate a management of this nature.

**LITERATURE CITED**


