



NDF Workshop Case Studies
WG 3 - Succulents and Cycads
Case Study 3
Dioon edule
Country – Mexico
Original Language – English

CYCADALES IN MEXICO (*DIOON EDULE*).

AUTHOR:

Andrew Vovides
Instituto de Ecología, Xalapa, Mexico

I. BACKGROUND INFORMATION ON THE TAXA

1. BIOLOGICAL DATA

1.1. Scientific and common names:

Dioon edule Lindl.

Tiotamal, Quiotamal, Chamal, Palma de Teresita

1.2. Distribution

Dioon edule is endemic to the Gulf of Mexico seaboard along the Sierra Madre Oriental and in one coastal habitat (Fig.1). Most populations are fragmented to highly fragmented and relict due to land-use change. Though the annexed map shows the distributional range of the species to be continuous, the populations are discontinuous throughout the range covering an altitudinal range from 10 to 1,500 meters above sea level. Historically populations may have been continuous (Octavio-Aguilar *et al.*, 2008a)

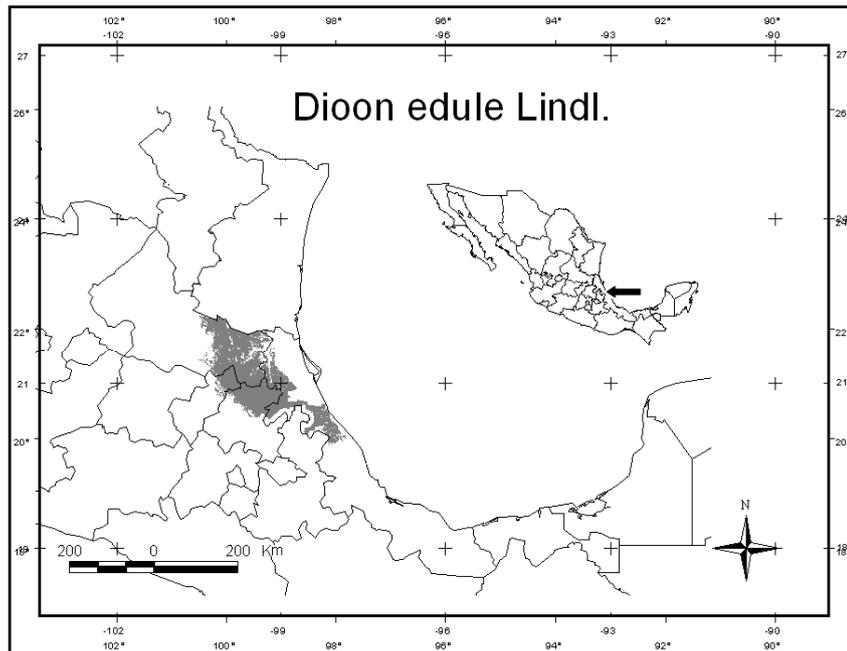


Figura 1. Distribution of *D. edule*

1.3. Biological characteristics

Dioon is an exclusively neotropical (continental) cycad genus with 13 currently known species and 12 are endemic to Mexico with one species known from Honduras and possibly Nicaragua. All species are arborescent with varying trunk lengths and the stems are protected with persistent petiole bases thus protecting the plants from brush fires. *Dioon* spp are entomophilous perennial dioecious long-lived trees (Fig. 2).



Fig. 2. *Dioon edule* in a fire disturbed oak-forest habitat (left). Female cone on plant (right).

1.3.1. Provide a summary of general biological and life history.

Like all cycads, *D. edule* is pachycaulous and dioecious (presenting separate male and female plants). It is arborescent and branching with age, generally from the base, stems can reach up 5 m tall becoming decumbent with age. The cycad behaves like a long-lived tree species and attains great age, exceeding 2000 years (Vovides, 1990). Pollination is entomophilous and the weevil pollinators (possibly *Parallocorynus* or *Rhopalotria* spp) are not yet identified for *D. edule* and are thought to be specific, also Langurid beetles have been seen to be associated with the male cones (Fig. 3). Sex ratio appears to be strongly male biased due to more frequent coning by male plants.

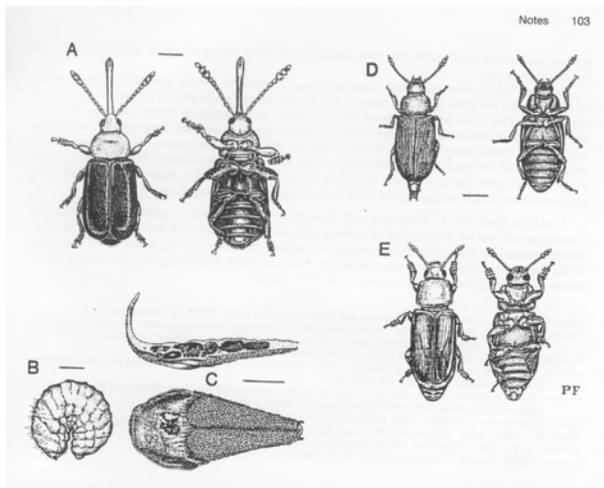
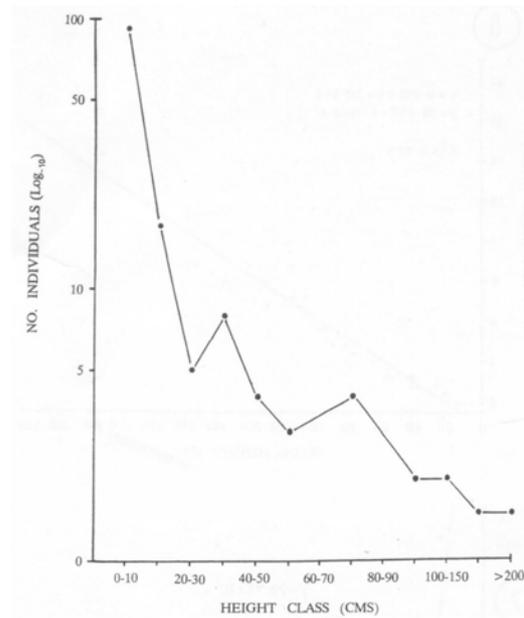


Fig. 3. Weevils and Langurid beetle pollinators (From Vovides, 1991).

The female cone cycle is approximately two years from initiation, pollination to dehiscence. In relatively undisturbed populations of *D. edule* the population structure is a reverse "J" or Deevey type III curve, where there are more seedlings and juveniles than adults (Fig. 4).

Fig. 4. Population structure of *D. edule* (from Vovides, 1990).



Seed production and recruitment is relatively good and between 78% to over 90% germination of seeds. The spatial distribution is non-random and contagious with a preference to shallow rocky soils. Mortality is high during the seed and seedling stages of the life history due to the prolonged droughts in its tropical dry forest habitats as well as seed predation by the field mouse *Peromyscus mexicanus* that is apparently resistant to the cycad toxins (Vovides 1990). The sex ratio is approximately 3:1 male/female respectively but this can be deceiving since male plants cone more frequently than females, hence a greater presence of coning males at any given time. Matrix projection modelling has shown that λ (lambda) is most sensitive to abundance of reproductive adult plants in three populations studied (Octavio-Aguilar *et al.*, 2008a). In spite of its relatively small populations, genetic variation and percentage of polymorphic loci are high, and there is a negative relationship between genetic diversity and latitude. On average, the gene flow between population pairs was found to be relatively high ($Nm = 2.98$); furthermore, gene flow between population pairs was significantly correlated with geographical distances ($r = -0.38$, $P = 0.025$) throughout its range. Patterns of genetic diversity in *D. edule* appear to be associated with the post-Pleistocene spread of the species, from its southerly (origin) to its northerly range (derived populations, including its central distribution) (González-Astorga *et al.*, 2003). *Dioon edule* is also the first cycad where a CAM-cycling photosynthesis pathway has been reported (Vovides *et al.*, 2002a) which is in keeping with its water-stressed environment. Little is known about dispersal and dispersal agents, though gravity plays a great part and the field mouse that often forgets harvested seed in nooks and crannies of its rocky habitat. Dispersal by other small mammals over short distances is likely owing to the sweet sarcotesta of the seed; long-distance dispersal by birds has not been observed and is unlikely owing to the seed size. Natural predators are few with the cycad butterfly larvae (*Eumaeus* spp.) and a chrysomelid beetle that grazes leaves, as well as the field mouse *Peromyscus mexicanus* that predaes seeds. The greatest threat is from humans and is mainly habitat destruction, but since the species also occurs in very steep canyons and cliff faces, at least some small and scattered populations have a good chance of long-term survival. Another threat is crown-decapitation that is practised by illegal traffickers to satisfy a domestic demand for ornamental plants, and has a negative impact on reproductive efficiency (Vovides, 1990; Octavio-Aguilar *et al.*, 2008a) (Figs 5 and 6).



Fig. 5. Decapitated *D. edule* in habitat.

Fig. 6. Street vendors selling *D. edule* leaf crowns (Photo Glafiro Alanis).

1.3.2. Habitat types: Specify the types of habitats occupied by the species and, when relevant, the degree of habitat specificity.

Dioon edule is known from bosque tropical caducifolio (tropical dry forests) or bosque de *Quercus* (oak forests) and bosque de pino y bosque de coníferas y *Quercus* (pine-oak forests) according to the Rzedowski (1978) classification. An exception to this is a small population on stable sand dunes in tropical coastal vegetation. Well-drained rocky soils appear to be a habitat requirement.

1.3.3. Role of the species in its ecosystem

It can be considered to occupy the herbaceous to mid strata levels of the forests. Like all cycads, *D. edule* fixes atmospheric nitrogen by means of cyanobacteria in apogeotropic roots forming coralloid masses at soil level. Upon death of the coralloid roots nitrates are released into the soil, but this has not been quantified for this species, see Grove et al. (1980) for N fixation in *Macrozamia*. Like most vascular plants *D. edule* forms symbiosis with arbuscular mycorrhizal fungi (Vovides, 1991). It is host to the cycad butterfly (*Eumaeus* spp) which is apparently specific to cycad leaves during the larval stages (Castillo-Guevara, 2007). The weevil pollinators, though still not yet identified are thought to be specific.

1.4. Population:

1.4.1. Global Population size:

Population trends and genetic variation for *D. edule* is known only for three populations and has been done using standard population dynamic techniques (Octavio-Aguilar *et al.*, 2008a,b). Stevenson *et al.* (2003) estimate over 10,000 plants and consider it near threatened. Disturbance influences the population dynamics of *D. edule* as a function of adult plant persistence. In these long-lived species, the extremely slow capacity for recovery following disturbances renders habitat preservation essential.

1.4.2. Current global population trends:

increasing decreasing stable unknown

Almost all populations of *D. edule* have declined over the past 30 years. No figure exists for this on a global scale, but demographic data for three populations show that there is a decline in one of these populations where decapitation is practiced (Octavio-Aguilar *et al.*, 2008a).

The widespread use of herbicides over the last 20 years or so for land clearing that has replaced traditional slash/burn clearing apparently has had a negative effect on relict populations of the cycad.

1.5. Conservation status

1.5.1. Global conservation status (according to IUCN Red List):

Critically endangered
 Endangered
 Vulnerable
 Near Threatened
 Least concern
 Data deficient

According to IUCN Red List, global conservation status of *Dioon edule* is regarded as Near Threatened. This should be revised since our recommendation for the Mexican Norm is P (endangered).

1.5.2. National conservation status for the case study country.

We recommend endangered status after a subjective assessment using the Method for Risk Evaluation MER (Spanish acronym) for the Mexican Norm because: i) historically the species was once very abundant but now populations have been reduced drastically to less than 5% of the national territory; ii) many populations are relict with poor or nil regeneration and the species is apparently sensitive to herbicides

nowadays in common use; iii) estimated number of adult plants in known populations ca 10,000 (Stevenson *et al.*, 2003); iv) decapitation of reproductive adults lessens seed production in the habitats and the species is protected by only one biosphere reserve. Exact figure of the extent of habitat reduction is not available.

1.5.3. Main threats within the case study country

No Threats

Habitat Loss/Degradation (human induced)

Invasive alien species (directly affecting the species)

Harvesting [hunting/gathering]

Accidental mortality (e.g. Bycatch)

Persecution (e.g. Pest control) toxic to cattle

Pollution (affecting habitat and/or species)

Other. The use of herbicides in some habitat-clearing for pastureland

Unknown

The main threats are largely due to human induced habitat loss through deforestation and land use change, illegal collecting especially decapitation of leaf crowns. Purposeful elimination of the plants owing to the cycads toxicity to cattle (no precise data other than anecdotal). The species is on several "Toxic Plants to Cattle" lists. The exact figure of number of plants destroyed by cattlemen is not available since this has been an on-going process over a very long period of time. Also the recent use of herbicides over the last 20 years to induce pastureland is believed to have seriously affected the cycad populations (amount not quantified).

2. SPECIES MANAGEMENT WITHIN THE COUNTRY FOR WHICH CASE STUDY IS BEING PRESENTED.

2.1. Management measures

Conservation through propagation with aims toward sustainable utilization coupled with habitat conservation. This is being done with the collaboration of peasant farmers at Monte Oscuro, Veracruz. Other similar projects with a *D. edule* populations that fall within a Biosphere Reserve (Sierra Gorda, San Luis Potosí and Querétaro) in the municipality of Tamasopo (Community Cuesta Blanca, Ejido la Palma) where the cycad *Ceratozamia microstrobila* among three orchid species are being managed, and in the municipality of Jalpan Querétaro at San Antonio Tancoyol where *D. edule* is also managed in this way by 13 farmers. Some of these farmers were given a three-day workshop at the JBC during 2004. Unfortunately figures on plants cultivated or other data are unavailable.

2.1.1. *Management history*

Based on demographic studies on *D. edule* by Vovides (1990), a group of campesinos (peasant farmers) were invited to collaborate in a pilot project that forms part of the Jardín Botánico Fco J. Clavijero (JBC) botanic garden's outreach to communities' policy for the conservation of endangered and useful native plants. The project began in 1990 to establish a small rustic nursery by the farmers on their ejido lands (allotments for agricultural production) at Monte Oscuro (MO) in central Veracruz near Xalapa. The nursery received its official permit in 1991 in order to operate as a non-forest products nursery that became the forerunner to the concept of UMAS for plants (Unidades de Manejo y Aprovechamiento de la vida Silvestre) or wildlife management units. These are overseen and authorized by the environmental authority of Mexico that monitors and administers permits. MO had a history of exploitation of the cycad by outsiders who decapitate adult plant crowns to be sold by peddlers in the main cities of the country. These crowns rarely root and demographically do affect the seed input into the ecosystem. The farmers, concerned about this practice were willing to take part in our project and received basic horticultural training at the JBC and talks given to them at their nursery with continuous assessment. The process of seed harvest from the wild, sowing and cultivating plants to provide an additional alternative income for the farmers is aimed to create an incentive to reforest and to protect the habitat from poachers and loggers (Vovides & Iglesias, 1994; Vovides *et al.*, 2002b).

2.1.2. *Purpose of the management plan in place*

The main objective of this management is to encourage incentive for conservation through propagation and plant sales by a system of harvesting seed, sowing and cultivation and eventual sales. In return they pledge to conserve the habitat and reintroduce back into the wild a small percentage of their production in order to compensate for seed removal. The farmers along with the ejido collective have declared 80 hectares of forest habitat as an ejido reserve.

2.1.3. *General elements of the management plan*

The farmers organized themselves as a small cooperative group. A plot of land (approx. one ha) is borrowed from one of the members and each member donates a number of man/hours per week for its maintenance, though this system has recently been modified. Seed collecting is done on an individual or group basis and there are no set rules. The authorities require a management plan where nursery area is specified, availability of water and other infrastructure, the species to be

managed, the approximate number of seeds to be harvested per year, number of plants to be cultivated and a yearly inventory of plants under cultivation, sold, deaths etc. Permits are issued once the management plan is approved and a stipulated percentage of seedling production to be reintroduced, usually 10% but is never done in reality. Annual reports are required for permit renewal.

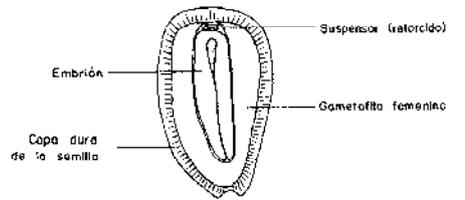
2.1.4. Restoration or alleviation measures

In order to address this point an experiment was set up in the wild during 1997 where 300 seedlings of varying age (2, 4 and 7 years) were reintroduced and monitored on a yearly basis to record growth, deaths or losses due to environmental factors. The objective of this exercise was to verify the minimum age class that can be reintroduced with an acceptable mortality after a period of several years. So far, after ten years we found that all age classes survived with a mortality rate of not exceeding 20% (unpubl. data). Seedling growth rate was practically un-measurable compared to their sisters grown at the nursery that gave five times more leaf production and caudex growth over the 10-year period. Male plants coned after 15 years and females after 17 years of age from seed under rustic nursery conditions. We came to the conclusion that seedlings of 2 years can be safely reintroduced.

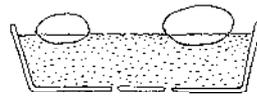
2.2. Monitoring system

2.2.1. Methods used to monitor harvest

No formal method has been established, other than to examine seed by incision before harvesting the cone to verify embryo presence and maturity. Seeds are excised from a cone then cut lengthwise in order to examine the embryo (Fig.7). This should be developed to over 3/4 of the overall length of the seed. If embryo development is less, seed the cone is left to mature for a further few months (3-4) on the mother plant, if it is approximately 3/4 of the seed length or more the cone may be harvested. Each cone may bear between 100 to 400 seeds with generally over 90% germination.



CORTE LONGITUDINAL DE SEMILLA MADURA DE *CICADAPITA*



METODO DE SEMBRAR SEMILLAS ACOSTADAS A UN 1/3-1/2 EN EL SUSTRATO

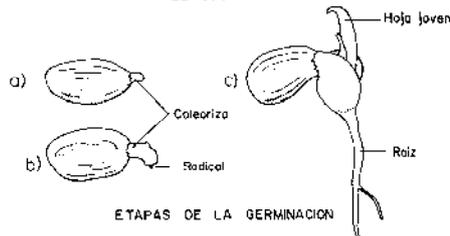


Fig. 7. Illustration of long section of seed showing mature embryo, seed sowing and germination.

2.2.2. Confidence in the use of monitoring

Embryo monitoring ensures that pre-fertilization cones are not cut, nor cones that require further maturation in situ on the mother plant. The female cone cycle is two years and cones look apparently ripe in less than one year. Collecting immature seeds leads to poor germination and death through desiccation and or fungal infections. Long term population monitoring other than the demographic studies mentioned have not yet began.

2.3. Legal framework and law enforcement:

All native cycads are covered by the national Norma Oficial Mexicana and international CITES legislation. The national legislation protects all species listed and it is unlawful to collect, transport and trade with listed species within Mexico without an appropriate collecting permit or UMAS permit that allows the collection of seed for cultivation and subsequent sale as is being carried out at MO (Fig. 8). Each plant to be sold must have a label with the nursery and permit number displayed. Breaching of these laws is considered federal crime with heavy fines and/or imprisonment.

Cycads in Mexico are of conservation priority (INE-SEMARNAP, 2000) and national funding agencies for research and conservation of cycads regard them as priority funding. There are also priority areas (biodiverse hot-spots) that are considered by many Mexican and international funding agencies.



Fig. 8. *D. edule* plants cultivated from seed at the Monte Oscuro Nursery and label.

3. UTILIZATION AND TRADE FOR RANGE STATE FOR WHICH CASE STUDY IS BEING PRESENTED.

3.1. Type of use and destinations:

Historically *D. edule* has been and is still being used as a source of starch by indigenous and mestizo (mixed blood) peoples. Seeds are harvested from wild populations, soaked or boiled to remove toxins and ground to obtain flour for tortillas in times of maize harvest failure. Also in central Veracruz the seeds were used in the past as a source of laundry starch. Cattlemen in the northern limits of the cycad's distribution purposely cut the plants down since the freshly emerging leaves attract cattle and are eaten resulting in hind-leg paralysis syndrome and death. Unfortunately figures on the number of plants destroyed are not available.

The leaves of the cycad are sometimes harvested from wild populations and used for decorating altars during religious festivities and is non-destructive to the plants. However, plants are illegally collected and adult plants decapitated and both the crowns and plants are sold as ornamentals. The implementation of UMAS are slowly giving a positive solution to this, but has happened to a limited extent but nevertheless encouraging. The municipality of Xalapa has on two occasions bought from the MO nursery several hundred *D. edule* plants for municipal landscaping (Fig. 9), also private sales at the JBC garden shop and town fairs as well as garden centres has also been encouraging to the producers.

3.2. Harvest:

3.2.1. Harvesting regime:

Legally, seed harvesting by UMAS is extractive and usually on a 'what is available' policy, there are no pre set quotas other than they should be reported in the annual reports by the UMAS. Crown decapitation is illegal but it still occurs but we have no detailed data on this, nor the quantity of plants illegally trafficked.

3.2.2. Harvest management/:

The UMAS permit covers harvesting of seed, there are no set quotas nor seasons stipulated. Management will probably be refined in the future taking into account information generated by the population studies of Octavio-Aguilar *et al.* (2008a,b) such as taking 20% of seeds per ripe cone and sampling as many cones as possible in order to represent genetic variation in the nursery and subsequent reintroduction.

3.3. Legal and illegal trade levels:

The nursery at MO has the capacity to produce around 2,000 plants per year, this considering the input of seeds from the habitat which may vary between about 500 seeds during bad years and up to 10,000 seeds or more during good (flush) years. However, the farmers do not always harvest seeds every year owing to seedling saturation in the nursery. They will harvest seed following a period of good sales that free up space in the nursery.

Legal trade – In terms of income the MO nursery between the years 1991 to 1995 earned approximately \$1,500 US total. For the years 1996 to 1998 a total of \$2,700 US; and for the years 1999 to 2006 a total of \$4,600 US and from 2007 to date approx. \$10,000 US. All this is through domestic sales (Fig. 9).

Export experience of cultivated plants has been bad. During 1998, 500 plants were exported to Germany through a GTZ-Germany/ ProTrade/Mexico funded project in order to explore international markets. An exhibition stand was presented at the international horticultural trade exhibition at Essen, Germany on two occasions but no significant sales occurred. This owing to fierce competition from professional nursery produced *Cycas revoluta* plants, and we feel a non-specialist ornamental plants market was being explored.

No exports have occurred recently, nor do we have details on illegal trade.



Fig. 9. Municipal Landscaping with *D. edule* and sales at the Monte Oscuro nursery

II. NON-DETRIMENTAL FINDING PROCEDURE (NDFs)

1. IS THE METHODOLOGY USED BASED ON THE IUCN CHECKLIST FOR NDFS?

The methodology based on the IUCN checklist for NDFs was not used. The findings were based on a previous demographic study on the population being managed (Vovides, 1990) based largely on the natural mortality in the seed and seedling stage. Further population dynamic studies that include elasticity matrixes (Octavio-Aguilar *et al.*, 2008a) may enable the fine-tuning of seed harvesting and plant reintroductions.

2. CRITERIA, PARAMETERS AND/OR INDICATORS USED FOR THE MONTE OSCURO (MO) NURSERY:

The population harvested is in ca 80 ha of relatively well-preserved tropical dry forest. We estimate at least 3,000 reproductive adult plants and only seeds are harvested. There is no set criterion or any specific indicators used. However, since the female cone cycle for *D. edule* is two years from emergence to dehiscence and there is no visible external difference to distinguish immature and ripe cones the producers have been trained to monitor embryo development of the seed without removing the cone. This is easily done by excising a sporophyll (seed scale) from the cone, removing a seed and cutting it longitudinally with a sharp pen-knife, the embryo is easily seen and the criterion for cone removal is that the embryo should be at least 3/4 of the seed length and if less, the cone is left to ripen for a further 3 to 4 months. A practical manual has been published that covers these instructions for the cycad species managed in Mexico (Pérez-Farrera & Vovides, 1997).

3. MAIN SOURCES OF DATA, INCLUDING FIELD EVALUATION OR SAMPLING METHODOLOGIES AND ANALYSIS USED:

Demographic information from the literature and especially the population study by Vovides (1990) was used based on a 30 x 10 m transect through the cycad population and observations over a four year period as well as empirical data from the MO nursery and personal data. No set sampling or seed harvesting methodology was used save the reintroduction experiment of planting 300 seedlings between 50 and 100 cm distance and annual monitoring and measuring of growth done by a vernier calliper gage and counting leaves produced.

4. EVALUATION OF DATA QUANTITY AND QUALITY FOR THE ASSESSMENT:

No particular prescribed method was used. High germination percentage with small losses through deaths was observed but not quantified. Seed harvest is not done on a yearly basis and can vary between 500 and 10,000 seeds collected. Comparison between growth in the nursery and growth of reintroduced plants has found to be about five times faster in the nursery under rustic conditions.

The reintroduction experiment indicated that seedlings from 2 years old and more can be reintroduced without any heavy losses during establishment. Though the demographic and population genetic study by Octavio-Aguilar *et al.* (2008a,b) indicated finite population growth to be sensitive to changes in adult plant density and the population is less diverse genetically when compared with two other populations, that is likely due to habitat fragmentation and adult plant crown decapitation. Population elasticity is greater than 80% due to permanence of the adult class, but the seed and seedling classes were found to be a reservoir for genetic diversity of the species (Octavio-Aguilar *et al.*, 2008b). This is an important factor to consider for management of the species and we sustain that it is best to conserve reproductive adult plants and stop crown decapitation, which will in turn result in greater seed production giving rise to positive repercussions in genetic composition, such as avoiding bottlenecking effects and decrease in effective population size. With this in mind we are reconsidering the reintroduction techniques. Nursery grown plants take 17 years for female and 15 years for male plants to enter reproductive age (Fig. 10). We are contemplating in reintroducing a much lower number of nursery produced adult reproductive plants, perhaps one for every 10,000 seeds collected rather than hundreds of seedlings which will take very much longer to mature under natural condition. The collection of small proportions of seed over a wide range of ripe cones available, rather than the total seed of just a few cones will conserve genetic diversity.



Fig. 10. 17 year old female coning *D. edule* (left); 15 year old male coning *D. edule* plant (right).

The success of the nursery has been through outcome from plant sales and the long-term organization of the nursery. There are currently three sales points for the nursery; i) a local garden centre ii) botanic garden shop and iii) attendance to town fairs and local horticultural events.



Plant sales at botanic garden shop (left); and local garden centre (right).

5. MAIN PROBLEMS, CHALLENGES OR DIFFICULTIES FOUND ON THE ELABORATION OF NDF:

The initial stages were found to be the most difficult since not all members of the farming community were convinced in growing 'a weed' for profit and there were many dropouts among the convinced members (25 members at onset in 1990 reducing to three at present).

Other important challenges to the project were; i) absence of consistent funding during the early stages of the project; ii) a need to

constantly provide continuous assessment to the growers and to consider their idiosyncrasies that debilitates work force and budget.

Marketing was specifically a problem for lack of expertise and looking into this factor at a late stage of the project had caused frustration among the growers by having a nursery full of plants but few sales. Important aspects of marketing are just beginning to be addressed. Marketing assessment is a must before or during the early stages of such a project (Vovides *et al.*, 2002).

6. RECOMMENDATIONS:

- i) Marketing assessment is crucial during the early stages of innovative sustainable management projects.
- ii) More long-term funding is required to get projects such as this one working.
- iii) A multidisciplinary team is required for these projects especially in the fields of conservation biology, horticulture, anthropology and sociology as well as marketing expertise.
- iv) Projects involving sustainable management of threatened species should be encouraged nationally and internationally, especially within buffer zones of biosphere reserves.
- v) It is highly recommended to start first with small medium-term pilot project and grow on from this rather than to inject mega-scale funding on a short-term basis.
- vi) The species to be managed should be on the farmers' collective (ejido) or individual private property and the habitat must be an integral part of the management system in which the habitat is managed for seed thus creating incentive to conserve. Establishing mother seed plants at the nursery is contrary to this since independence from the habitat is not recommended.
- vii) There should be a mechanism for assisting the growers during their permit renewal applications and other paperwork, since on a local basis in Mexico the farming communities are in remote communities on Reserves. This is being addressed in Chiapas since 2006 where the authorities were willing to assist the growers on these matters. In the absence of this aid, then projects should contemplate an administrative section, possibly a part to the marketing officer's duties.

REFERENCES

- CASTILLO-GUEVARA, C. 2007. Herbivores and chemical defenses in cycads – an ecological and evolutionary approach. In: Vovides, A.P., D.Wm. Stevenson, & R. Osborne (eds), *Proceedings of Cycad 2005 the 7th international conference on cycad biology. Memoirs of the New York Botanical Garden* 97: 87-103. New York. New York Botanical Garden Press.
- FISHER, J. B., & A.P. Vovides. 2004. Mycorrhizae are present in cycad roots. *The Botanical Review* 70: 16-23.
- GONZÁLEZ-ASTORGA, J., A.P. Vovides, M.M. Ferrer, & C. Iglesias. 2003. Population genetics of *Dioon edule* Lindl. (Zamiaceae, Cycadales): biogeographical and evolutionary implications. *Biological Journal of the Linnean Society* 80: 457-467.
- GROVE, T.S., A.M. O'Connell, & N. Malajezuk. 1980. Effects of fire on the growth, nutrient content and rate of nitrogen fixation of the cycad *Macrozamia riedlei*. *Australian Journal of Botany* 28: 271-281.
- INE-SEMARNAP. 2000. *Prep 6: Protección, conservación y recuperación de la familia Zamiaceae (Cycadales) de México*. México D.F., INE-SEMARNAP.
- OCTAVIO-AGUILAR, P., J. González-Astorga, & A.P. Vovides. 2008a. Population dynamics of the Mexican cycad *Dioon edule* Lindl. (Zamiaceae): life history stages and management impact. *Botanical Journal of the Linnean Society* 157: 381-391.
- OCTAVIO-AGUILAR, P., J. González-Astorga, & A.P. Vovides. 2008b. Genetic diversity by life-history of *Dioon edule* Lindl. (Zamiaceae, Cycadales). *Plant Biology* (Accepted).
- RZEDOWSKI, J. 1978. *Vegetación de México*. México, D.F., Limusa.
- STEVENSON, D. W., A. Vovides, & J. Chemnick. 2003. Regional overview: New World. In: Donaldson, J. (ed.) *Cycads Status Survey and Conservation Action Plan*. Pp. 31-38. Gland, IUCN.
- VOVIDES, A.P. 1991. Vesicular-arbuscular mycorrhiza in *Dioon edule* Lindl. (Zamiaceae, Cycadales) in its natural habitat in central Veracruz, Mexico. *Brenesia* 35: 97-103.
- VOVIDES, A.P. 1990. Spatial distribution, survival and fecundity of *Dioon edule* (Zamiaceae) in a tropical deciduous forest in Veracruz, Mexico, with notes on its habitat. *American Journal of Botany* 77: 1532-1543.
- VOVIDES, A. P., & C.G. Iglesias. 1994. An integrated conservation strategy for the cycad *Dioon edule* Lindl. *Biodiversity and Conservation* 3: 137-141.
- VOVIDES, A.P., J.R. Etherington, P. Quentin Dresser, A. Groenhof, C. Iglesias, & J. Flores-Ramirez. 2002a. CAM-cycling in the cycad *Dioon edule* Lindl. in its natural tropical deciduous forest habitat in central Veracruz, Mexico. *Botanical Journal of the Linnean Society* 138: 155-162.
- VOVIDES, A.P., C. Iglesias, M.A. Pérez-Farrera, M. Vázquez Torres & U. Schippmann. 2002b. Peasant nurseries: A concept for an integrated conservation strategy for cycads in Mexico. In: Maunder, M., C. Clubbe, C. Hankamer, & M. Groves (eds), *Plant Conservation in the Tropics: perspectives and practice*. Pp. 421-444. Richmond, Royal Botanic Gardens, Kew.