Journal of Arid Environments 71 (2007) 250–258

Journal of Arid Environments

www.elsevier.com/locate/jaridenv

Short communication

Causes of individual mortality in the endangered star cactus *Astrophytum asterias* (Cactaceae): The effect of herbivores and disease in Mexican populations

J.G. Martínez-Ávalos[a,d,*], J. Golubov[b], M.C. Mandujano[c], E. Jurado[d]

[a]*Instituto de Ecología y Alimentos, Universidad Autónoma de Tamaulipas, 13 Blvd. López Mateos 928 C. P. 87040, Cd. Victoria Tamaulipas, Mexico*

[b]*Departamento El Hombre y Su Ambiente, Lab. Ecología Sistemática y Fisiología Vegetal, Universidad Autónoma Metropolitana Xochimilco, Sistemática y Fisiología Vegetal, Calzada del Hueso 1100, Col. Villa Quietud, Coyoacán, México D. F. 04960, Mexico*

[c]*Instituto de Ecología, Universidad Nacional Autónoma de México, Aptdo. Postal 70-275, Ciudad Universitaria, México D. F. 04510, Mexico*

[d]*Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León, Km. 145 Carretera Cd. Victoria-Linares, C. P. 67000 A. P. 41, Linares Nuevo León, Mexico*

Received 26 November 2006; received in revised form 2 March 2007; accepted 14 March 2007
Available online 15 June 2007

Abstract

Little is known about the causes of mortality in natural populations of threatened cactus species. In particular we focus on the endangered *Astrophytum asterias* in four populations where most individuals of the species are found. At two sites one of each vegetation type (Tamaulipan thornscrub [TS] and Piedmont thornscrub [PT]) we measured individual mortality by three causes: the plant pathogen *Phytophtora infestans*, a cerambicid beetle and the terrestrial squirrel *Spermophilus mexicanus*. We found that damage by the combination of pathogen and herbivore meant a reduction of more than 50% in population size. From these factors, the most important cause of death was *S. mexicanus* followed by the cerambicid beetle in TS and *P. infestans* in PT. Mortality was concentrated in the small size categories, even though large size plants were also affected albeit to a

*Corresponding author. Instituto de Ecología y Alimentos, Universidad Autónoma de Tamaulipas, 13 Blvd. López Mateos 928 C. P. 87040, Cd. Victoria Tamaulipas, Mexico. Tel.:/fax: +52 834 31 627 21.

E-mail addresses: jmartin@uat.edu.mx (J.G. Martínez-Ávalos), gfjordan@correo.xoc.uam.mx (J. Golubov), mcmandu@miranda.ecologia.unam.mx (M.C. Mandujano), ejurado@fcf.uanl.mx (E. Jurado).

0140-1963/$ - see front matter
doi:10.1016/j.jaridenv.2007.03.017

lesser extent. More quantitative studies in field conditions are necessary to establish sound conservation efforts that could improve the recovery plans for this endangered plant species.

Keywords: Cactaceae; Mortality; *Phytophtora infestans*; Plant pathogen; *Spermophilus mexicanus*; Cerambicidae

The cactus family comprises a large list of species (≈1800 species, Anderson, 2001) many of which are enlisted as threatened or at risk of extinction due to diverse factors that diminish populations (Árias et al., 2005). Such factors include removal of individual plants by illegal collectors, loss of populations due to human activities (basically changes in land use) and loss of individuals by mortality. Demographic studies in the Cactaceae have been done on a variety of species with differing life forms including globose (Contreras and Valverde, 2002), columnar (Clark-Tapia et al., 2005; Esparza-Olguín et al., 2005) and others (Mandujano et al., 2001; Rae and Ebert, 2002). Comparative studies between life forms and across the Cactaceae have suggested that the most important demographic process in the Cactaceae is survival of established individuals (Godínez-Álvarez et al., 2003; Rosas Barrera and Mandujano, 2002). However, few studies have observed mortality in juveniles and adults on a yearly basis (Esparza-Olguín et al., 2005; Schmalzel et al., 1995; Steenbergh and Lowe, 1974; Valverde and Zavala-Hurtado, 2006), and while most of the studies aim at estimating mortality, it is predominantly observed and quantified in seedlings and young life stages in natural populations of long-lived cacti species (Godínez-Álvarez et al., 2003 and references there in; Leirana-Alcocer and Parra-Tabla, 1999; Steenbergh and Lowe, 1974). In addition, demographic models do not include the ecological factors that cause increases or decreases in plant survival needed for effective recovery plans (Schemske et al., 1994) and only some studies have partially addressed the factors affecting adult survival (Esparza-Olguín et al., 2005; Mandujano et al., 1998; Valverde et al., 2004).

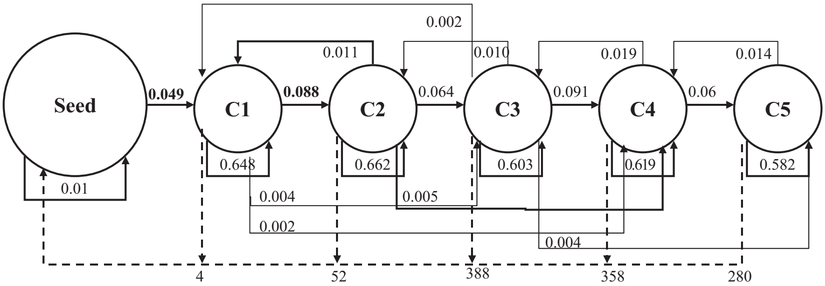
Therefore, little is known of the damage natural herbivores and diseases can have on cacti populations. Only a few cases have been described and the majority are associated with invasive or cultivated cacti such as *Opuntia* and *Hylocereus* (Bashan et al., 1995; Hoffmann et al., 1998; Valencia-Botin et al., 2003). In natural cacti populations, damage by disease or herbivores is not well documented with only a few studies addressing the impact of insects (Blom, 1987; Burger and Louda, 1995), mammals (Hoffman et al.,1993; Kass, 2001) and pathogens (Bashan et al., 1995). There are even fewer studies that have focused on endangered cacti despite the high number of species in national and international threatened species lists (Kass, 2001; Stiling and Moon, 2001; Valverde and Zavala-Hurtado, 2006).

In endangered species, most of which have small populations, the effect of pathogens and herbivores can increase the risk of extinction by lowering population size, limiting genetic variability (which reduces the ability to respond to pathogens or herbivores) and therefore making populations more susceptible to stochastic demographic fluctuations (De Castro and Bolker, 2005). However, surveys have revealed that biotic interactions (competition and predation) play a small part as causal factors in the endangerment of plant species (Foin et al., 1998; Smith et al., 2006). The identification of the causal biological (or other) factors that influence vulnerable or important life stages for rare or endangered plants would help to propose more adequate recovery plans. The importance of biological causal factors could be especially important when the vital rates are affected in either vulnerable life stages (e.g. seedlings) or in adults that decrease survival and reproductive output. The purpose of this manuscript was to (1) document damage by a plant pathogen and herbivores on the endangered cactus *Astrophytum asterias* and (2) relate levels of damage to vegetation type and plant size.

1. Materials and methods

Astrophytum asterias (star cactus or *falso peyote*) is a small globose cactus 6–10 cm in diameter, grayish-green, with trichomes, no spines and having 6–9 areoles (Fig. 2A). Flowers are yellow and have a red center. The long red fleshy fruits produce 56–95 brown/black seeds (Rocha, 1995). The species was listed in October 1993 as a priority two species by the US Fish and Wildlife Service (USFWS, 1993), in CITES appendix 1 (Lüthy, 2001) and in the Mexican endangered species list as in danger of extinction (SEMARNAT, 2003). The main threats considered for this species include illegal collection (Sánchez-Mejorada, 1987a, b) because it is a species appreciated in the horticultural industry (Sakato, 1992), and destruction of natural habitat (USFWS, 2003; Martínez-Ávalos et al., 2004). *Astrophytum asterias* is one of the two species of *Astrophytum* outside the Chihuahuan desert and both share the same habitat (Velazco-Macías and Nevárez, 2002), it occurs in a small portion of southern Texas (Star County) and 10 populations (varying widely in number of individuals) have been located in Nuevo León and Tamaulipas in Mexico (Anderson, 2001; Martínez-Ávalos et al., 2004). The species inhabits two vegetation types: Tamaulipan thornscrub (TS) and Piedmont thornscrub (PT). Within these areas it is associated to deep soils (gravelly to clay) having high organic content either with a slight slope or in areas susceptible to flooding (Martínez-Ávalos et al., 2004). The habitats have a homogeneous vegetation structure represented by *Karwinskia humboldtiana*, *Parkinsonia texana*, *Schaefferia cuneifolia*, *Prosopis glandulosa*, *Porlieria angustifolia* and *Ziziphus obtusifolia* (González-Medrano, 1972). The distribution is in areas from 50 to 180 m a.s.l., with a mean annual temperature of 21–24 °C.

In order to assess the damage by the herbivores and disease, we established permanent plots at four populations of *Astrophytum asterias* in Mexico. Two of these populations correspond to TS and the remaining two were located in PT. TS is mainly associated to flat areas, dominated by shrubs 0.5–1.5 m tall (e.g. *Karwinskia humboldtiana*, *Parkinsonia texana*, *Schaefferia cuneifolia*, *Prosopis glandulosa*, *Porlieria angustifolia*, *Z. obtusifolia*) between 55 and 190 m a.s.l. Soils are well drained sands. The Piedmont thornscrub is associated to low lying hills also known as "bajadas", with vegetation dominated by shrubs that can reach 2–4 m (e.g. *Acacia berlandieri*, *Acacia coulteri, Acacia rigidula*, *Acacia greggii*, *Astrocasis neurocarpa*, *Chloroleucon pallens*, *Chloroleucon frutescens*, *Cordia boissieri*, *Castela tortuosa*, *Forastiera angustifolia*, *Fraxinus gregii*, *Gochnatia hypolecuca*, *Helietta parvifolia*, *Lycium berlandieri*, *Mimosa leucaenoides*, *Rhus virens*, *Nepringlea integrifolia*, *Yucca flifera*) between 150 and 2200 m a.s.l. Soils are a mixture of sand-and-clay over limestone. Total monitoring area was approximately 5 ha. These populations were selected because they have the highest density of individuals of the 10 known sites in Mexico. At each location we took an annual population census in which all individuals were measured to the nearest 0.01 cm with a caliper, tagged and mapped for future reference. Individuals were grouped into five size categories (Fig. 1) according to plant diameter and pooled into two size categories after statistical analysis showed that mortality risk only differed between the following sizes: $\leqslant$6 cm and $>$6 cm.



N	41±28.1	41 ± 21.7	39 ±19	27±9.9	11±9.7
mi	16 ±17.2	14 ±13	14 ±9.9	9 ± 4.8	4 ± 1.7

Fig. 1. Mean life cycle diagram of *Astrophytum asterias* from four populations. The vital rates represented correspond to the 2004–2005 and 2005–2006 study period. Circles represent size classes. The figure at the centre of each node indicates the name of the class with the following size intervals: (1) $0<x\leqslant2$ cm; (2) $2<x\leqslant4$ cm; (3) $4<x\leqslant6$ cm; (4) $6<x\leqslant8$ cm; (5) $x>8$ cm; the lower figure is the probability of stasis in the same class; the upper lines (broken) represent individual fecundity (number of seeds × individual^{-1} × year^{-1}). Upper arrows (solid lines) connecting nodes contain the probabilities of retrogression to smaller size classes. Shorter arrows between nodes contain probabilities of growth to the next size category. *N*, mean number of individuals (±SE) and m_i, mean number of deaths in each size class (±SE). For the analysis, size classes C1–C3 and C4–C5 were pooled.

At all sites, we recorded mortality by one of three main factors during a two year period (2005 and 2006): a Cerambicid beetle (Coleoptera: Insecta), *Phytophtora infestans* (plant pathogen, Oomycete) or by the terrestrial squirrel *Spermophilus mexicanus* (Mammalia, Rodentia). In all cases, damage resulted in death of the individual. The cause of mortality was easily identified in field conditions: damage by the Cerambicid beetle leaves a characteristic bore hole at the center of the plant (Fig. 2B) damage by *Phytophtora* leaves the external tissue of the plant intact (Fig. 2C) and damage by *Spermophilus mexicanus* was identified by the damage of aerial sections of the plant and markings left of the two squirrel's incisors on the plant tissue (Fig. 2D).

2. Statistical analysis

We used generalized linear models assuming a Poisson error distribution on a three way contingency table to assess the proportion of plants damaged by each type of mortality (Cerambicid beetle, *Phytophtora infestans* and *Spermophilus mexicanus*) for each vegetation type (TS and PT), and to determine if mortality was associated to small or large plants. The response variable was the number of individuals for each factor. Once the saturated model was adjusted, we deleted terms until we got a minimum adequate model (Crawley, 2002) and *t*-tests were done to determine differences between levels of each factor. All analyses were done using GLIM 4 (Royal Statistical Society).

3. Results

A total of 210 in TS and 317 in PT individuals were found to be affected by all three types of damage (Table 1). The total number of individuals in the plots of each vegetation type was 318 (TS) and 541 (PT) so mortality in each population was very high (66% and

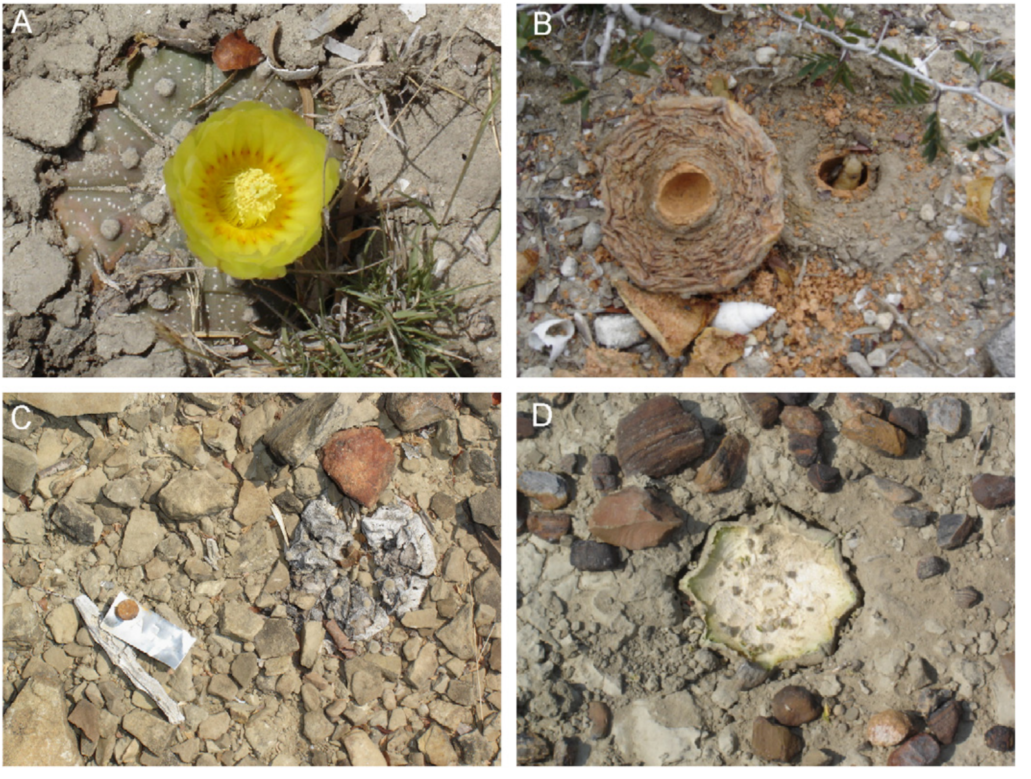


Fig. 2. (A) Healthy individual of *Astrophytum asterias* in flower; (B) damage by the cerambicid beetle, leaving the characteristic bore hole where larvae develop; (C) damage by the plant pathogen *Phytophtora infestans*, leaving the outside walls intact with yellowing of tissue commonly found and (D) damage caused by the terrestrial squirrel *Spermophilus mexicanus* that consume the aerial portions of the plant.

59%, respectively). The minimum adequate model included significant effects of the main factors (vegetation type, VT; damage, D; and size, S) and the significant interactions VT $\times$ D and VT $\times$ S (Table 2). The damage by size interaction was not significant and was therefore dropped from further analysis (Table 2). The only significant differences we found were between mortality caused by rodent *Spermophilus mexicanus* and by the Cerambicid beetle at PT ($t = 7.57$, $P = 0.017$; Table 1) and mortality by *Phytophtora infestans* between habitats ($t = 6.156$, $P = 0.02$; Table 1). Death by *Phytophtora infestans* and *Spermophilus mexicanus* accounted for 24.1% of total mortality in TS and 56% in PT. However, mortality by *Phytophtora infestans* was more than twice in PT than at TS. Clearly the most important cause of mortality for both populations was by *Spermophilus mexicanus*, which dramatically reduced population sizes, followed by the Cerambicid beetle in TS and *Phytophtora infestans* in PT.

We found significant differences in mortality between small size categories and vegetation type ($t = 5.27$, $P = 0.006$), and between small and large size classes in TS ($t = 6.95$, $P = 0.002$) and PT ($t = 3.94$, $P = 0.016$). We found no significant differences in mortality between vegetation types for the large size category ($t = 2.64$, $P = 0.057$) in which mortality was the lowest at both vegetation types.

Table 1
Mortality by size category of *Astrophytum asterias* damaged by *Phytophtora infestans*, *Spermophilus mexicanus* and the cerambicid beetle at two vegetation types in northern Mexico

Size category	Tamaulipan thornscrub (TS)			Piedmont Thornscrub (PT)		
	P. infestans	*S. mexicanus*	Cerambicidae	*P. infestans*	*S. mexicanus*	Cerambicidae
Small (⩽6 cm)	36	61	61	104	148	16
Large (>6 cm)	3	27	22	17	26	6
Total	39 (7.4%)	88 (16.7%)	83 (15.7%)	121 (23%)	174 (33%)	22 (4.2%)

Numbers in parenthesis indicate the percentage of total number of individuals damaged by each species for each site.

Table 2
Analysis of deviance considering the minimum adequate model on damage and size of *Astrophytum asterias* in two vegetation types in northern Mexico

Terms	Deviance	df	*P* value
S	215.58	1	0.001
D	71.51	2	0.001
VT	21.88	1	0.001
VT × D	88.74	2	0.001
VT × S	6.94	1	0.008
D × S	5.01	2	NS
VT × D × S	6.63	2	NS

S, size (small and large plants); D, damage (*Phytophtora infestans*, *Spermophilus mexicanus* and the Cerambicidae beetle); VT, vegetation type (Tamaulipan thornscrub and Piedmont thornscrub).

4. Discussion

Few studies have documented mortality by herbivores or pathogens in natural populations of cacti and from these, a small subset have addressed damage in endangered species (Kass, 2001; Stiling and Moon, 2001; Valverde and Zavala-Hurtado, 2006). In a review by Zimmermann and Granata (2002) they reported approximately 58 species of insects of the Pyralidae and Cerambicidae that feed on different species of cacti. The study emphasizes that the Cerambicidae have the highest impact on populations mainly reported in the Opuntitoid subfamily. The possible effects mortality by herbivores or pathogens can have on natural populations of endangered species of cacti have not been given the necessary importance, or play minor roles compared to other causal factors (habitat reduction or modification and population reduction; Foin et al., 1998). This paper is the first to document effects caused by a pathogen and two herbivores on the endangered *Astrophytum asterias*. In other endangered cacti such as *Sclerocactus wrightiae* mortality by *Moneilema semipunctatum* (Cerambicidae) in certain size classes was relatively high (40%; Kass, 2001) and for *Opuntia corallicola* more than 25% of small individuals close to plants infested with the phytophagous insect *Cactoblastis cactorum* (Lepidoptera: Phycitidae) were attacked (Stiling and Moon, 2001). Valverde and Zavala-Hurtado (2006) also found herbivory by beetle larvae (Cerambicidae; Coleoptera) to be an important cause of death in the threatened *Mammillaria pectinifera*, especially among adult individuals, were they report a death rate of 7.4% and 17.6% within adult reproductive categories. For *Astrophytum asterias*, damage was high for small size classes (probably more vulnerable to all three types of damage) and was significantly higher in small size classes in PT. This vegetation type is dominated by taller plants which may provide fewer defenses and make plants more prone to damage. In other endangered cacti (*Turbinicarpus horripilus* and *Ariocarpus scaphirostris* attacked by a Meloideae beetle), (M. Mandujano personal observation, and *Ariocarpus fissuratus* attacked by a Tenebrionid beetle, Martínez-Peralta, 2007) damage by beetles has been seen only on floral structures which may decrease seed output by 50% (Martínez-Peralta, 2007), further affecting population dynamics. For *Astrophytum asterias* mortality was related to the type of herbivore: *Spermophilus mexicanus* and the cerambicid beetle (species identification is pending), but was low due to the pathogen, however, damage was high overall and differed between habitats. The increase of mortality by *Phytophtora infestans* in PT possibly responds to the habitat which is more prone to flooding than TS due to the higher clay content in soil. The most significant mortality was by *Spermophilus mexicanus* in PT. Even though we present the first quantitative report of mortality by the cerambicid beetle, its damage was not as high as that of *Spermophilus mexicanus*. Still, the cerambicid beetle accounted for 19.9% of total mortality. The recovery plan of *Astrophytum asterias* (USFWS, 1993) stated the necessity for evaluating predation as an important component of the threats (USFWS, 2003) on populations especially as individuals do not recover from extensive damage in field conditions. Here we have quantified the effects of two herbivores and a plant pathogen and have shown that damage by these three factors are an important component that can determine population dynamics for *Astrophytum asterias*. This is especially relevant as no illegal extraction has been recorded at these sites. The most important cause of population declines in the star cactus is still habitat modification, but herbivory and pathogens will add to the increasingly low populations of this species. Sound conservation and improvement of recovery plans should emphasize the need to conserve native habitat and increase population size so as to diminish the effects of other biotic interactions that only add to the risk of extinction in endangered species.

Acknowledgments

We would like to thank Fortunato Garza Ocañas for the identification of *Phytophtora infestans*, and Manuel Lara Villalón for identifying the beetle. This paper is part of the PhD Dissertation of JGMA at the Universidad Autónoma de Nuevo León, Facultad de Ciencias Forestales; under supervision of EJ and MCM. Financial support was provided by PROMeP-UAT to JGMA-COTACYT, CONACyT-SEMARNAT 0350 to MCM and Fundación BBVA (BBVABIOCON 04-084) to JG, CONACYT 44806Q and PAICYT CN1134-05 to EJ.

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