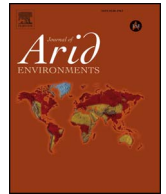




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Effects of nurse plants and the granivore guild in the associational susceptibility of seeds from the columnar cactus *Pilosocereus leucocephalus*

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ABSTRACT

The nurse-protégé interaction involves benefits for the protected species by the reduction in the abiotic stress intensity. Nurse plants, however, could affect other biotic interactions by reducing that natural benefit. Studies about plant-plant-animal interaction assume that plants can recover from and/or avoid granivory when they grow under higher resources availability; nevertheless, in early stages they could be subject to different pressures. Thus, the resistance or susceptibility to granivores could occur because of differential responses of the plants (nurse and protected) to the environment (abiotic factors) or as results of differential responses of the plants to granivores (biotic factors), altering the probability of the resistance or susceptibility of plants to herbivores. We evaluated diurnal and nocturnal granivore activity on *P. leucocephalus* seeds, and we also evaluated if a nurse species could determine the association type (i.e. associational resistance or susceptibility) from the intensity of the granivore in early stage (e.g. seeds) of the *P. leucocephalus* life cycle. We found higher granivory under nurse plants than in open spaces (the control group), indicating associational susceptibility. Furthermore, most of the granivory was performed by nocturnal animals (mice). These results suggest a cost/benefit of the nurse-protégé interaction, which can be modulated by the granivory.

1. Introduction

Studies on plant-environment-animal interactions are indispensable in understanding the factors involved in the susceptibility to herbivores (Hawkes and Sullivan, 2001). Plants have a higher response ability for recovering from and/or avoiding herbivory when they grow under greater resource availability (Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Nykänen and Koricheva, 2004); see the growth rate model from Hilbert et al. (1981) also. Nevertheless, in early stages (i.e. as a seed) plants are subject to more difficult and different pressures than in the adult stage (Janzen, 1970); thus, susceptibility in the seed stage could be more determined by the secure sites for seedling establishment than by the environmental resource's own availability (Crawley, 1983).

Seeds deposited by primary dispersers tend to be found under trees and shrubs, because birds and bats, that are the most important participants in the process use them as roosting, feeding, and nesting sites (Sosa and Fleming, 2002). However, this pattern could be modified by the granivores, thus altering the dynamic of the plant populations (Hawkes and Sullivan, 2001). The combined granivore-environment

effect could change from plant to plant, thereby molding the demography of the plant species (Thies et al., 2003). The plant-plant associations include several interactions such as competition, mutualism, amensalism, and commensalism, based on determining if an interaction is favourable, detrimental or neutral for the interacting species (Callaway and Walker, 1997). These associations could provoke a neighbor plant to have a greater influence on the target plant, by increasing (i.e. associational susceptibility) (see Parker and Root, 1981; Thomas, 1986; White and Whitham, 2000) or by decreasing (i.e. associational resistance) the probability of the detection and/or the vulnerability of the target plant (see Tahvanainen and Root, 1972; Pfister and Hay, 1988; Hambäck et al., 2000; Stiling et al., 2003).

In arid environments or sites having a low availability of some key resources (e.g. water), the plants growing under the shade of nurse plants have some advantage due to the attenuation of light and therefore the subsequent improvement of the microclimatic conditions (by generating low evapotranspiration) that the plants growing in open spaces do not (Flores and Jurado, 2003). Thus, the microenvironment under the nurse plant could also generate a decrease in granivory (see Smith and Huston, 1989; Holmgren et al., 1997).

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The nurse-protégé interaction is a well-recognized association among plant species in arid environments (Shreve, 1931; Flores and Jurado, 2003), in which protected plants can benefit mainly from temperature + buffer and from protection from herbivores (Turner et al., 1966; Callaway, 1995). The nurse-protégé interaction could be described as an associational resistance, if the accumulated benefit is the protection of the target species from the granivores, because some nurse plant can physically protect the seeds from granivores (Sosa and Fleming, 2002). Alternatively, for vertebrate dispersed species, seed accumulation under shrubs or trees could also be greater due to seed discarding from birds perching on branches (Hutto and McAuliffe, 1986; Flores and Jurado, 2003).

The positive interactions among plants, however, could vary in space and time until becoming negative interactions because of the few resources available, which could provoke higher granivory and increase the associational susceptibility in the target plants (Agrawal, 2004; Agrawal et al., 2006; Hambäck and Beckerman, 2003), e.g. Holland and Molina-Freaner (2013) found high granivory for *Pachycereus schottii* under nurse plants in the Sonoran Desert. However, for *Neobuxbaumia tetetzo* and *Pachycereus hollianus* (Flores et al., 2004), for *Stenocereus stellatus* (Álvarez-Espino et al., 2017), and for *Pilosocereus leucocephalus* (Munguía-Rosas and Sosa, 2008), the percentage of seeds removed from the soil surface did not depend on nurse plants. Furthermore, García-Chávez et al. (2010) found that post-dispersal predation under a nurse plant is characterized by marked spatial variability and seed specificity at the scale studied. Thus, the associational resistance or associational susceptibility could occur as a result of differential responses of the target plants and neighbor plants to the key resources from the environments (abiotic factors) or as a result of the differential responses of the target plants and neighbor plants to the granivores (biotic factors), altering thus the probability of the detections and/or vulnerability of the target plant (Barbosa et al., 2009).

Although both biotic and abiotic factors directly alter the conduct of the granivores, by modifying the intensity of the damage and the colonization in the target plant, no studies have researched if these factors together cause + differential responses in the target plants. We selected the columnar cactus *Pilosocereus leucocephalus* (target plant). Seedlings of this plant can establish themselves on rocky soil without vegetation which have low nutrient availability and limited water storage (open habitat) or in places with a little mulch under shrubs or trees (closed habitat). This cactus represents an important food resource for animals because it produces 3000 ± 500 seeds per fruit. Thus, we expected to contribute to the knowledge of plant-plant-animal interaction, as well as to the possible trade-off of the nurse-protégé interaction, in which the abiotic conditions could also affect the biotic conditions, thus reducing the benefits of the nurse-protégé interaction. We also expect to better understand the final consequences of the nurse-protégé interaction, by evaluating the possible indirect cost/benefit product of such an interaction.

In this study, we sought to answer the following questions: (i) can the nurse-protégé interaction determine the association type (e.g. associational resistance or susceptibility) in the early stages (e.g. seeds) of the *P. leucocephalus* life cycle, based on the intensity of granivory?; and (ii) can the intensity of granivory of *P. leucocephalus* in different microsites change in function of the guild of granivores (e.g. nocturnal and diurnal)? In order to answer these questions, we performed an experimental design considering the number of seeds removed from the experimental units placed in eight microenvironments (four replicates per microenvironment). Seven microenvironments were under the canopies of neighbor species (*Casearia corymbosa*, *Cnidoscolus angustidens*, *Lysiloma acapulcense*, *Zanthoxylum fagara*, *Fraxinus schiedeana*, *Pilosocereus leucocephalus*, and *Quercus oleoides*) and one microenvironment in open spaces (control group). We take into account two periods (06:01 to 18:00 h and 18:01 to 06:00 h, for the diurnal and nocturnal guilds, respectively). Diurnal guild of granivores are represented by birds (*Campylorhynchus gularis*, *Columbina passerine*, *Icterus*

gularis, *Passerina cyanea*, and *Passerina versicolor*) and ants (*Pheidole* spp. and *Solenopsis aurea*), and nocturnal ones are represented by bats (*Artibeus jamaicensis*) (Munguía-Rosas et al., 2009). The population abundances and ecological impacts of the seed removers are unknown. In addition, if they are seed dispersers or seed removers remains to be studied for most species, but for ants which remove seeds from fruits on the plant, and consume the fleshy coats and this enhances seed germination and probably seedling survival (Munguía-Rosas et al., 2009).

We hypothesized that if nurse plants increase the favourable environmental conditions for the cactus, the granivory intensity would be high under nurse plants because they are also a favourable site for the granivores (e.g. refuge against predators). In addition, we hypothesized that if during the day the activity of the granivores decreases the nocturnal guild will remove the highest *P. leucocephalus* number of seeds; thus, the seed removal will be determined by the combined effect of the granivore guild and the nurse plant.

2. Materials and methods

2.1. Study species and study site

Pilosocereus leucocephalus is a hermaphrodite, self-incompatible columnar cactus, which is pollinated by bats (Munguía-Rosas et al., 2010); it is distributed from Nicaragua to northeastern Mexico (Guzmán et al., 2003). In the state of Veracruz (México), it is located inside the Dry Forest from 50 to 1200 m.a.s.l. (Bravo-Hollis, 1937), in this region it is the only cactus species surviving over 1100 m.a.s.l., whereas at low elevations it coexists with other columnar cacti such as *Neobuxbaumia scoparia* and *Stenocereus griseus* (Medina Abreo and Castillo-Campos, 1993).

We studied a natural population (about 5 ha) located in San Ignacio, municipality of Xalapa, Veracruz (19°35'26''N, 96°58'38''W). This is the highest site of *P. leucocephalus* (1150 m.a.s.l.). In this region all the plants are located on rocky substrate of lava flux which was deposited during the Holocene, 10, 000 years ago (Negendank et al., 1985). The annual temperature average is 20.4 °C, with averages from the hottest and coldest months, May and January, 29.2 and 11.5 °C). Furthermore, the annual precipitation is 1300.0 mm, with 79.1% of the rainfall during May through October (Fernández-Eguiarte et al., 2012; from 1903 through 2010). The vegetation is tropical deciduous forest, which covers half of the area surface: 50.30% \pm 5.85 (data from five 50 m-long transects). Dominant species are *Dodonaea viscosa*, *Quercus oleoides*, *Cnidoscolus angustidens* and *Tonduzia longifolia* (see Miranda-Jácome et al., 2013). On the other hand, *P. leucocephalus* individuals are distributed with higher frequency under the canopy of woody species such as *Casearia corymbosa* Kunth, *Cnidoscolus angustidens* Torr., *Lysiloma acapulcense* (Kunth) Benth., *Quercus oleoides* Schlcht & Cham., *Fraxinus schiedeana* Schlcht & Cham., and *Zanthoxylum fagara* (L.) Sarg. There are also seedlings and juvenile individuals under adult plants of *P. leucocephalus*, which could come from seeds dispersed by gravity from the mother plant, as well as juvenile adults in open spaces without vegetation.

2.2. *Pilosocereus leucocephalus* seed removal based on the microenvironment and the granivore guild

We placed three plastic cylindrical discs (4 cm in diameter and 1.5 cm high) next to each tree in each of eight microenvironments, seven of them under seven neighbor species (nurse plants) and one in sites without vegetation. Four trees from each of six species were considered replicates in each microenvironment. Seed discs were placed under their crown, separated as much as possible, limited by crown size. The spacing of the discs in sites without vegetation was 2 m.

Discs were placed randomly and replaced each 12 h (at 6:00 and 18:00 h) during nine days of May and June 2015. Thus, we placed 192 discs each day (96 discs each 12 h) to determine the importance of the

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