

Seed banking in the columnar cactus *Stenocereus stellatus*: distribution, density and longevity of seeds

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Abstract

The soil seed bank is the reserve of viable seeds found in the soil. This reserve contributes to plant population persistence in unpredictable environments; thus, determining its presence is basic to understanding recruitment patterns and population dynamics. Studies of soil seed banks in the Cactaceae are scarce, although these plants are ecologically dominant in American arid and semi-arid environments. Most studies have inferred the presence of seed banks by analysing morphological seed traits or germination of seeds stored in the laboratory for different periods of time. Few studies have determined their presence through evaluation of distribution, density and longevity of seeds in the field. To fill this information gap, we determined the existence of, and studied, the soil seed bank of *Stenocereus stellatus*, a columnar cactus endemic to central Mexico. This study reports the evaluation of these characteristics in the field and discusses whether this species forms a soil seed bank. We found a higher number of seeds under shrubs than in areas lacking vegetation. Recently dispersed seeds did not germinate because they have primary dormancy. This dormancy was broken after 6 months of burial in the soil. Seeds buried for 10 months entered secondary dormancy and they were not viable at 24 months, probably because of pathogen attack. Considering dormancy and seed longevity, we suggest that *S. stellatus* has the potential to form a short-term persistent seed bank. However, this should be confirmed by conducting studies on other *S. stellatus* populations throughout their geographical distribution.

Keywords: burial experiment, ecological longevity, *Fusarium oxysporum*, persistent seed bank, *Stenocereus stellatus*, Tehuacán-Cuicatlán Biosphere Reserve

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Introduction

The soil seed bank is the reserve of viable seeds located on the soil surface or buried in the soil or litter. This reserve is essential for plant population persistence in unpredictable environments because it buffers the negative effects of unfavourable climatic conditions (Thompson, 2000; Venable, 2007), high competition intensity (Aikio *et al.*, 2002) and high predation risk (Brown and Venable, 1991; Hulme, 1998). The study of soil seed banks is therefore basic to understanding recruitment patterns and population dynamics of plants. The distribution, density and longevity of seeds are significant characteristics in determining whether plants are able to form soil seed banks. Distribution and density of seeds in the soil can be highly heterogeneous because of spatial and temporal fluctuations in seed production, seed dispersal and seed predation (Mull and MacMahon, 1996; Marone *et al.*, 1998). Thus, seed density can vary by several orders of magnitude among microhabitats (Reichman, 1984; Aguiar *et al.*, 1992). Seed longevity depends on morphological and physiological traits such as seed size and dormancy, but also depends on the mortality caused by predators and pathogens. In fact, soil pathogens such as fungi and bacteria seem to be the main cause of seed mortality (Crist and Friese, 1993; Chambers and MacMahon, 1994; Chee-Sanford *et al.*, 2006). Seeds can form different types of soil seed banks depending on their longevity. Seeds remaining viable in the soil for <1 year form transient seed banks, seeds remaining viable for >1 but <5 years form short-term persistent seed banks, and those remaining viable for >5 years form long-term persistent seed banks (*sensu* Thompson, 1993; but see Walck *et al.*, 2005).

Cacti are conspicuous and dominant plants in American arid and semi-arid environments, especially in Mexico, Argentina, USA and Chile (Ortega-Baes and Godínez-Álvarez, 2006). Despite their ecological dominance, the information about whether cactus plants are able to form soil seed banks is scarce (Bowers, 2000, 2005; Ordoñez, 2008;

Cano-Salgado *et al.*, 2012; Cheib and Garcia, 2012; Holland and Molina-Freaner, 2013). Most studies conducted on this topic have analysed morphological and physiological traits such as seed size and dormancy, or germination of seeds stored for different periods of time in laboratory conditions (Rojas-Aréchiga *et al.*, 2001; De la Barrera and Nobel, 2003; Flores-Martínez *et al.*, 2008; for a review see Rojas-Aréchiga and Batis, 2001 and references therein). Based on this evidence, these studies infer the potential of cactus species to form particular types of soil seed banks in the field. Up to now, very few studies have determined the presence of soil seed banks through evaluation of distribution, density and longevity of seeds in the field (Bowers, 2000; Olvera-Carrillo *et al.*, 2009; Cheib and Garcia, 2012). These studies are necessary to determine whether cacti have functional soil seed banks, as well as to record the existing types of seed banks. To fill this information gap, we determined the existence and studied the soil seed bank of *Stenocereus stellatus*, a columnar cactus endemic to central Mexico. Fruiting in this species occurs at the end of the rainy season and dispersal of seeds at the beginning of the dry season; therefore, presence of a soil seed bank would allow seeds to avoid unfavourable climatic conditions for germination and establishment. Currently, there are only a few studies on soil seed banks in columnar cacti, which found contrasting results. One study found that *Carnegiea gigantea* has a transient seed bank, based on incidental observations in the Sonoran Desert (Bowers, 2005). Other studies found that *Arthrocerus glaziovii* and *A. melanurus* (Cheib and Garcia, 2012) as well as *Polaskia chende* (Ordoñez, 2008) have persistent seed banks, based on the evaluation of seed longevity in the field.

This study reports the distribution, density and longevity of seeds of the columnar cactus *S. stellatus* in the field and discusses whether this species has a functional soil seed bank. This information contributes to understanding of the role of soil seed banks in the population persistence of columnar cacti, and increases the information on seed banks in the cactus family.

Materials and methods

Study site and plant species

This research took place in Coxcatlán, Puebla, México (18°14'N, 97°08'W, 1116 m above sea level), within the Tehuacán-Cuicatlán Biosphere Reserve. The mean annual rainfall is 440 mm (80% falling between June and September) and the mean annual temperature is 24°C. The main plant community is a columnar cactus forest mixed with plants from seasonally deciduous forest and secondary vegetation. Dominant species are *Acacia cochliacantha*, *Conzattia multiflora*, *Escontria*

chiotilla, *Opuntia* spp., *Parkinsonia praecox*, *Solanum tridynamum* and *S. stellatus* (Valiente-Banuet *et al.*, 2009).

S. stellatus (Pfeiff.) Riccob. is a columnar cactus that grows up to 5 m, with stems branching from the base. It shows vegetative propagation and sexual reproduction (Godínez-Alvarez *et al.*, 2005). Flowering and fruiting occur during summer (Godínez-Alvarez *et al.*, 2005; García-Suárez *et al.*, 2007). Flowers are pollinated by the lesser long-nosed bat (*Leptonycteris curasoae*; Arias-Cóyotl *et al.*, 2006). Fruits are thorny and indehiscent, with red-purple pulp and dull-black seeds. Seeds are dispersed by the grey-breasted woodpecker (*Melanerpes hypopolius*; R. Álvarez-Espino *et al.* unpublished data) and are predated by the ants *Pogonomyrmex barbatus* and *Pheidole* sp. (Godínez-Alvarez *et al.*, 2005). Germination occurs in open sites and under canopies of trees and shrubs, although seedling survival and establishment are better under plants because they decrease solar radiation and increase soil water availability (Godínez-Alvarez *et al.*, 2005). It occurs in wild, managed *in situ*, and cultivated populations (Casas *et al.*, 1999). However, our study only focused on wild populations because we were interested in determining the ecological significance of the soil seed bank in natural conditions.

Distribution and density of seeds

Distribution and density of seeds were determined by taking soil samples in two microhabitats: (1) under *A. cochliacantha*, the dominant shrub in the study site; and (2) from areas lacking vegetation, throughout 12 months. The number of samples was proportional to the fraction occupied by each microhabitat in five 50-m line transects (i.e. *A. cochliacantha* 0.416, areas lacking vegetation 0.584). Twenty-five samples were collected under shrubs and 35 samples from areas with no vegetation. Soil sampling began in autumn, the time of seed dispersal, and was conducted every 2 months from October 2009 to October 2010. Samples were collected using a cylindrical metal core (5 cm diameter, 3 cm depth), placed in paper bags, and stored in darkness until processing. Samples were sieved with USA Standard Testing Sieves No. 10 (1.73 mm opening) and No. 20 (0.84 mm opening), to separate the soil fraction containing *S. stellatus* seeds. This fraction was placed under running tap water to separate seeds.

Seeds were tested for germinability at each sampling period by using Petri dishes containing filter paper soaked in distilled water, and sown with 50 seeds each. Five dishes were used for each microhabitat. Germination experiments were conducted under laboratory conditions (20–30°C, 12 h photoperiod) and dishes were watered every 2 d. Germination was recorded every 48 h, for 45 d, and seeds were considered germinated when the radicle

emerged from the testa. Viability of ungerminated seeds was assessed with a cutting test at the end of the experiment. We used this test because it is simple and has been used widely in several studies (Moreira *et al.*, 2010; Jayasuriya *et al.*, 2013). Seeds with firm, yellowish-white, healthy looking embryos were considered viable (Gosling, 2003).

Seed longevity

Seed longevity was evaluated by burying seeds under *A. cochliacantha* shrubs and in areas lacking vegetation, exhuming them at regular intervals, and examining their germinability. Seeds were obtained from 5–10 mature fruits of 30 *S. stellatus* plants at the end of the fruiting season, in October 2009. Germination of these recently collected seeds was lower than 0.1%, but they were viable according to cutting tests. The experimental design used to determine the effect of microhabitat and burial time on germination was a split-plot design. The block was an area within which one *A. cochliacantha* shrub was located with an adjacent area lacking vegetation. The whole plot was microhabitat (i.e. under shrubs and areas lacking vegetation) and the subplot was burial time (i.e. 2, 4, 6, 8, 10 and 12 months). Ten nylon mesh bags (0.5 mm opening) containing 50 seeds each were buried randomly at 3–5 cm depth under shrubs and in areas lacking vegetation at the end of the fruiting season. We used five blocks separated by at least 10 m, for a total of 60 bags under shrubs and in areas lacking vegetation. Five bags from each microhabitat and burial time were randomly exhumed every 2 months. This experiment was originally planned to continue for 12 months, but we were unable to exhume the last bags because local conflicts impeded access to our study region. These bags were exhumed after 24 months of burial.

Exhumed seeds were stored in dark conditions for 5 d until their germinability was determined through germination experiments and cutting tests, as described above. Ungerminated seeds consistently showed mouldy embryos and mycelium in the outer and inner sections of the seed coat. Therefore, fungi were isolated from 100 seeds exhumed from soil under shrubs after 24 months, and from seeds stored in dry and dark conditions in the laboratory for 24 months. Seeds from areas lacking vegetation could not be used because bags were lost. Seeds were cultured on potato-dextrose-agar (PDA). Isolated fungi were identified with taxonomic keys and their identity was confirmed by sequencing polymerase chain reaction (PCR) products (Raeder and Broda, 1985). Details of these methods are available in the accompanying supplementary material. The sequences were deposited in GenBank to obtain the accession numbers and were compared with the database.

Statistical analysis

The number of seeds in the soil was analysed with generalized linear models (GLM) considering the effects of microhabitat, time and their interaction. The link function was logarithmic and the error distribution was quasi-Poisson because of data overdispersion. Germination percentages were arcsine transformed and analysed with linear mixed effects models (LME). Microhabitat and burial time were considered as fixed factors and block as a random factor. The link function was identity and the error distribution was normal. In both cases – number of seeds and germination percentage – the minimum adequate models (i.e. the models that only include significant terms) were fitted through step elimination using R statistical environment, version 2.8.1 (<http://www.r-project.org/>).

Results

Distribution and density of seeds

Distribution and density of seeds varied depending on microhabitat (deviance = 29.79, $df = 1$, $P < 0.00001$) and time (deviance = 33.20, $df = 1$, $P < 0.00001$). The number of seeds was significantly higher under *A. cochliacantha* shrubs (391 seeds m^{-2}) than in areas lacking vegetation (120 seeds m^{-2} ; $t = 3.2$, $df = 405$, $P = 0.0015$). The number of seeds was relatively similar in all months (100–250 seeds m^{-2}), except February. This month had the highest number of seeds (720 seeds m^{-2} ; $t = 3.7$, $df = 405$, $P = 0.0002$), but this was because one of the 60 soil samples collected this month had 20 seeds while the rest of the samples had fewer than 4 seeds (Fig. 1). Seeds found in soil from under shrubs did not germinate, nor seeds found in soil from areas lacking vegetation, although seeds from both microhabitats were viable.

Seed longevity

Germination was similar between microhabitats, but varied depending on burial time ($F = 45.61$, $df = 2,35$; $P < 0.0001$). Germination varied between 0 and 90% throughout 24 months of burial (Fig. 2). The highest germination (60–90%) occurred at 6 months followed by germination at 2, 4 and 8 months (5–45%). The lowest germination occurred in recently collected seeds (0.1%), and at 10 (0.3%) and 24 months (0%).

The proportion of viable seeds varied among recently collected seeds and seeds buried for 10 and 24 months. All recently collected seeds were viable. However, this proportion decreased at 10 months, being 38% under *A. cochliacantha* shrubs and 65% in areas lacking vegetation. At 24 months,

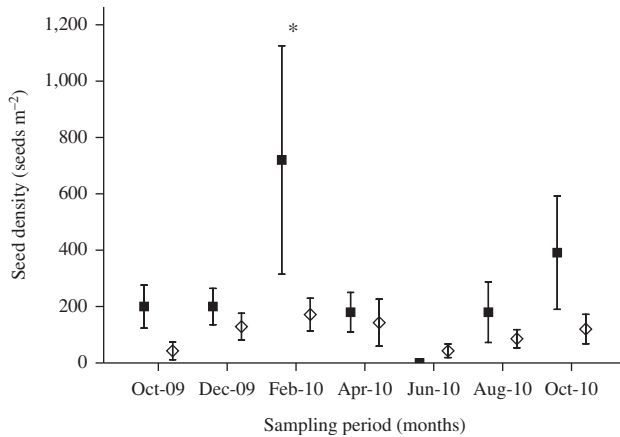


Figure 1. Number of seeds of *Stenocereus stellatus* (mean \pm 1 standard error) found under *Acacia cochliacantha* shrubs (solid squares) and in areas lacking vegetation (open diamonds). The * indicates statistically significant differences ($P < 0.001$).

the proportion of viable seeds decreased to 0% under *A. cochliacantha* shrubs. The proportion of viable seeds in areas lacking vegetation could not be evaluated because bags were lost.

Fungi found in exhumed seeds (*Fusarium oxysporum* – GenBank accession number KC734517, similarity 99%; *F. solani* – KC764912, 99%; *F. nivale* – KC764913, 99%; and *Curvularia inaequalis* – KC764914, 98%) differed from those found in stored seeds (*Pleiochaeta ghindensis* – KC764915, 98%; *Cladosporium* sp. – KC764916, 97%; and *Eurotium* sp. – KC764917, 98%).

Discussion

Field studies on soil seed banks of the Cactaceae are limited, particularly for columnar cactus species. In this study, we have shown that distribution, density and longevity of *S. stellatus* seeds indicate that this columnar cactus is able to form a soil seed bank. Seed distribution and density varied spatially because we found a higher number of seeds under dominant shrubs than in areas lacking vegetation. This pattern agrees with those reported for other species of the Cactaceae (de Viana *et al.*, 2000; Montiel and Montaña, 2003; Ordoñez, 2008). The higher number of seeds found under shrubs could be due to the fact that trees and shrubs in desert landscapes trap seeds dispersed by the wind and serve as perches for frugivorous birds, increasing the probability that seeds will be deposited under their canopies (Whitford, 2002; Li, 2008). Trees and shrubs also play an outstanding role in cactus establishment because they decrease soil surface temperatures and evapotranspiration, increase nutrient and soil water availability and provide protection against predators, enhancing seed germination and seedling survival of many species (for a review, see

Godínez-Alvarez *et al.*, 2003 and references therein). In our study, germination of *S. stellatus* seeds was seemingly higher under *A. cochliacantha* shrubs than in areas lacking vegetation, although we did not find significant differences between these microhabitats.

Seeds collected just at the beginning of the dry season did not germinate, although most of them were viable. This indicates that *S. stellatus* seeds have primary dormancy when dispersal occurs (*sensu* Baskin and Baskin, 2004). Seeds reached their maximum germination after 6 months of burial under shrubs and in areas lacking vegetation, showing that primary dormancy is broken by an afterripening period. This finding agrees with Rojas-Aréchiga *et al.* (2001), who found that wild and cultivated seeds of *S. stellatus* increased their germination percentage with an increase in storage time under laboratory conditions. Seeds from other cactus species, such as *Ferocactus wislizeni* (Bowers, 2000), *Opuntia tomentosa* (Olvera-Carrillo *et al.*, 2009), *P. chende* (Ordoñez, 2008) and *Stenocereus griseus* (Silvius, 1995), also require an afterripening period before they can germinate. Seed germination decreased to almost 0% after 10 months of burial, although 38–65% of seeds were viable, suggesting that they enter secondary dormancy and remain viable in the soil for at least 1 year. This idea is reinforced by the relatively similar densities of seeds found in soil samples taken from under shrubs and in areas lacking vegetation throughout the year, as well as by their lack of germination. Seeds found in soil samples from both microhabitats did not germinate, probably because they had already entered secondary dormancy. Seeds buried for 24 months did not germinate, nor were viable, because they were probably attacked by *Fusarium* fungi. This negative effect does not agree with the results reported for other cactus species, such as *Opuntia streptacantha* (Delgado-Sánchez *et al.*, 2011) and *O. tomentosa*

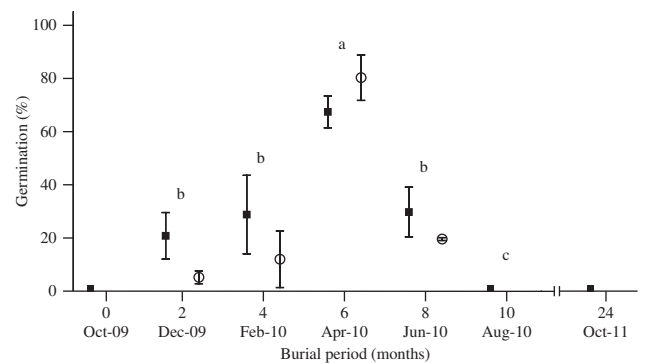


Figure 2. Germination percentage (mean \pm 1 standard error) of *Stenocereus stellatus* seeds buried under *Acacia cochliacantha* shrubs (solid squares) and in areas lacking vegetation (open circles). Months marked with different letters are significantly different ($P < 0.001$). Germination percentages in October 2009 and 2011 were not included in the statistical analysis.

(Sánchez-Coronado *et al.*, 2011), in which *Fusarium* fungi promote seed germination.

Considering that *S. stellatus* seeds enter secondary dormancy and retain their viability for less than 24 months, we suggest that they have the potential to form a short-term persistent seed bank (*sensu* Thompson, 1993). However, this should be confirmed by determining seed viability after 12 months of burial. The potential of *S. stellatus* to form a soil seed bank is related to some traits found in their seeds, such as a light requirement for germination and a post-maturation period (Rojas-Aréchiga and Batis, 2001; Rojas-Aréchiga *et al.*, 2001). Seeds of *S. stellatus* remain viable in the field for less than 24 months (i.e. ecological longevity) whereas those stored in the laboratory remain viable for 41 months (i.e. potential longevity; Rojas-Aréchiga *et al.*, 2001). This difference between ecological and potential longevity highlights the importance of evaluating seed longevity in the field to determine the presence of a functional soil seed bank. Studies on soil seed banks in columnar cacti are still limited and contradictory because some species, such as *A. glaziovii* and *A. melanurus* in south-eastern Brazil (Cheib and Garcia, 2012) and *P. chende* in central Mexico (Ordoñez, 2008), form short-term persistent seed banks. However, other species, such as *C. gigantea* in south-western USA, form transient seed banks (Bowers, 2005) or lack soil seed banks (e.g. *Lophocereus schottii* in north-western Mexico; Holland and Molina-Freaner, 2013). These few studies do not reflect clear patterns among types of soil seed bank, geographic distribution and taxonomy. The potential of *S. stellatus* to form a short-term persistent seed bank would increase the probability of germination, because seeds dispersed at the beginning of the dry season could survive until the rainy season of the following year. This soil seed bank and the ability of *S. stellatus* to propagate vegetatively could be viewed as complementary mechanisms that contribute to population persistence in the field (Godínez-Alvarez *et al.*, 2005).

This study represents one of the few efforts to determine the presence of a soil seed bank through the evaluation of distribution, density and longevity of seeds in the field. Our results suggest that *S. stellatus* has the potential to form a short-term persistent seed bank. However, it is necessary to conduct studies on other *S. stellatus* populations throughout their geographical distribution to confirm our results. Finally, the results of this study and those reported for other columnar cactus species might be used as a basis to determine whether there are general patterns among types of seed banks in certain genera or species.

Supplementary material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0960258514000324>

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Conflicts of interest

None.

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