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GRANIVORÍA PRE- Y POST-DISPERSIÓN Y BANCO DE SEMILLAS DE *STENOCEREUS*

***STELLATUS* (CACTACEAE) EN EL VALLE DE TEHUACÁN- CUICATLÁN**

TESIS

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P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 25 de enero de 2016, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **ÁLVAREZ ESPINO RICARDO XAVIER**, con número de cuenta **93386906**, con la tesis titulada **"Granivoría pre- y post-dispersión y banco de semillas de *Stenocereus stellatus* (Cactaceae) en el Valle de Tehuacán-Cuicatlán "**, realizada bajo la dirección del **DR. HÉCTOR OCTAVIO GODÍNEZ ÁLVAREZ**:

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
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DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
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c.c.p. Expediente del (la) interesado (a)

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ÍNDICE

Resumen

La depredación de las semillas y el banco de semillas son procesos ecológicos que afectan la dinámica poblacional de las cactáceas. Sin embargo, la información sobre estos procesos es escasa, por lo que este trabajo tuvo como objetivos (1) determinar la importancia relativa de aves, hormigas y roedores en la depredación de semillas de la cactácea columnar *Stenocereus stellatus* en el Valle de Tehuacán-Cuicatlán, Puebla (México), así como (2) analizar si esta cactácea forma bancos de semillas. Se determinó la diversidad de los posibles granívoros en las épocas de fructificación de 2009 y 2010. Además, se evaluó la producción de semillas y se determinaron las tasas de remoción pre- y post-dispersión a través de experimentos de exclusión. Para analizar el banco de semillas, se tomaron muestras de suelo para comprobar si existían semillas viables y se realizaron experimentos de enterramiento para estimar la longevidad ecológica de las semillas. Se observó que las aves removieron una mayor proporción de semillas que las hormigas y los roedores antes de la dispersión. En este caso el ave *Melanerphes hypopolius* (Picidae), especie que no modifica la viabilidad de las semillas, removió la mayor proporción de semillas. Por esta razón se consideró que la depredación pre-dispersión fue baja. Por otra parte, las hormigas removieron una mayor proporción de semillas que las aves y los roedores, después de la dispersión, pues las hormigas granívoras *Pogonomyrmex barbatus* (Hymenoptera: Formicidae) removieron hasta el 90% de las semillas. No se observaron evidencias de dispersión secundaria, por lo que se consideró que la depredación de semillas post-dispersión fue alta. Las semillas recién dispersadas de *S. stellatus* tuvieron latencia fisiológica primaria que se rompe después de 6-8 meses de post-maduración en el suelo. Si escapan a la depredación, tienen una persistencia en el suelo menor a 2 años, por lo que formarían bancos de semillas persistentes de corto plazo. La cantidad y distribución de las semillas en el banco fue altamente variable en el sitio de estudio. En conjunto, los resultados del presente estudio, sugieren que la magnitud en la depredación de las semillas de *S. stellatus* crea fuertes presiones de selección debido a que la perdida de semillas afectaría de manera importante el reclutamiento de plantas individuales. Sin embargo, el efecto final de los depredadores sobre la dinámica poblacional podría ser imperceptible para esta cactácea perenne de larga vida. En este sentido, se conoce que esta especie no depende de la reproducción sexual para mantener sus poblaciones y puede tolerar la ausencia de reproducción por largos periodos de tiempo. Aunado a lo anterior, la formación de bancos de semillas le permitirían disminuir el impacto negativo de la depredación sobre las poblaciones de semillas. Es necesario incrementar los estudios tendientes a conocer las consecuencias demográficas de la depredación de semillas en las poblaciones de *Stenocereus stellatus*, incluyendo estimaciones realistas de la dinámica del banco de semillas en la construcción de modelos demográficos.

Abstract

Seed predation and soil seed bank are ecological processes affecting cactus population dynamics. However, information on these processes is scarce, thus the goals of this study were: (1) to determine the relative importance of ants, birds, and rodents in seed predation of the columnar cactus *Stenocereus stellatus* at the Tehuacán-Cuicatlán Valley, Puebla, México, and (2) to analyze whether this species forms soil seed banks. Granivore diversity were determined in 2009 and 2010 fruiting seasons. Seed production and pre- and post-dispersal seed removal rates were also estimated by using exclosure experiments. On the other hand, soil samples were analyzed to determine seed's presence in soil. Seeds were buried to determine their ecological longevity. Birds removed a higher proportion of seeds than ants and rodents, before seed dispersal. *Melanerpes hypopolius* (Picidae) removed the highest proportion of seeds. This species however disperses seeds without damaged them, thus pre-dispersal seed predation was low. On the other hand, ants removed a higher proportion of seeds than birds and rodents, after seed dispersal. *Pogonomyrmex barbatus* (Hymenoptera: Formicidae) removed up to 90% of seeds. Seeds have primary physiological dormancy, which is broken after a post-maturation period of 6-8 months in the soil. Their ecological viability is < 2 years, therefore they form short-term persistent soil seed banks where abundance and distribution of seeds is highly variable. Altogether, the results of this study suggest that high rates of seed predation in *S. stellatus* creates strong selection pressures due to that seed loss would affect significantly the recruitment of individual plants. However, the final effect of predators on the population dynamics could be negligible for this perennial long-living cactus. In this sense, it is known that *S. stellatus* not depends on sexual reproduction to maintain their populations and can tolerate the absence of reproduction for long periods of time. In addition, the formation of seed banks would allow reducing the negative impact of predation on seed populations. It is necessary to increase studies aimed to know the demographic consequences of seed predation on the populations of *S. stellatus*, including realistic estimates of the dynamics of the seed bank in the construction of demographic models.

CAPÍTULO I

INTRODUCCIÓN GENERAL

La regeneración natural de las poblaciones de plantas depende de una serie de procesos ecológicos como la polinización, la dispersión y depredación de semillas, la formación de bancos de semillas, y la germinación y el establecimiento de las plántulas (Fenner y Thompson, 2005; Long *et al*., 2014). El estudio de cada uno de estos procesos es fundamental para entender las características de la historia de vida de las plantas y las características demográficas de sus poblaciones.

Las plantas han desarrollado adaptaciones en la morfología, defensas químicas y en los patrones de producción de semillas que pueden disminuir el riesgo de depredación (Janzen, 1971; Brown y Venable, 1991; Hulme, 1998; Hulme y Benkman, 2002). A pesar de esto, la depredación de las semillas, también conocida como granivoría, es una interacción planta-animal que disminuye significativamente la distribución y abundancia de las semillas producidas, afectando el tamaño de las poblaciones (Hulme, 1998; Crawley, 2000; Kolb *et al.*, 2007). En general, existen diferencias entre el consumo de las semillas que están en la planta y aún no han sido dispersadas (i. e. depredación pre-dispersión) y el consumo de las semillas que están en la superficie del suelo, después de que fueron dispersadas (i. e. depredación post-dispersión). Los principales granívoros pre-dispersión en muchos ambientes son invertebrados especialistas (*e. g.* brúquidos, gorgojos, polillas) que consumen las semillas producidas por una especie particular de planta (Janzen, 1971; Hulme, 1998;

Crawley, 2000), disminuyendo la cantidad de semillas disponibles para la dispersión. Por otro lado, los granívoros post-dispersión son invertebrados y vertebrados generalistas (*e. g.* hormigas, roedores) que consumen las semillas de una gran variedad de especies de plantas, modificando su distribución y abundancia en el suelo (Hulme, 1998; Crawley, 2000). Pocos estudios han evaluado las tasas de remoción de semillas pre- y post-dispersión para una misma especie de planta (Hulme, 1998; Forget *et al.*, 1999; Figueroa *et al.*, 2002; Fedriani y Manzaneda, 2005). Los resultados de estos estudios sugieren que la intensidad de la remoción de semillas en la fase post-dispersión es frecuentemente mayor. También se ha destacado que la tasa de remoción de semillas varía entre especies y poblaciones (Crawley, 2000; Fenner y Thompson, 2005), así como entre regiones geográficas (Orrock *et al.*, 2014; Peco *et al.*, 2014). En regiones áridas y semiáridas se ha sugerido que las aves, hormigas y roedores son los principales granívoros (Mull y MacMahon, 1996; Marone *et al.*, 1998; Anderson y MacMahon, 2001). Sin embargo, la importancia relativa y la tasa de remoción de cada grupo varían dependiendo de la región desértica. Por ejemplo, los roedores son los principales depredadores de semillas en los desiertos templados de Norteamérica, mientras que las hormigas y las aves son los principales depredadores en los desiertos de Sudamérica (Mares y Rosenzweig, 1978; Morton, 1985; Marone *et al.*, 1998). A pesar de la amplia información generada, los estudios en los desiertos tropicales son escasos (Ibañez y Soriano, 2004; Pérez *et al.*, 2006; García-Chávez *et al.*, 2010), por lo que es necesario continuar realizando estudios para conocer los

principales grupos de depredadores y su tasa de remoción de semillas. Aunado a lo anterior, la mayoría de los estudios de remoción de semillas en regiones desérticas solamente se han utilizado semillas comerciales, por lo que las estimaciones de las tasas de remoción resultan artificiales (Peco *et al*., 2014). Estos aspectos dificultan la determinación de patrones generales y el entendimiento del efecto de la depredación sobre la estructura y dinámica de las poblaciones de plantas.

Las semillas que escapan a la depredación y permanecen viables en el suelo por distintos periodos de tiempo forman bancos de semillas. Los bancos son una estrategia para la regeneración de las plantas contra las condiciones climáticas adversas, que incrementan las oportunidades de reclutamiento y la dispersión espacial y temporal de las semillas (Venable, 2007; Long *et al.*, 2014). Las semillas que forman bancos pueden presentar latencia y fotoblastismo positivo (Thompson, 2000). En particular, la latencia evita que las semillas germinen hasta que ocurran cambios morfológicos, fisiológicos, o ambos, los cuales son controlados por las condiciones ambientales (Baskin y Baskin, 2004, Vleeshouwers *et al.*, 1995). De esta manera, la germinación ocurrirá cuando las condiciones para el desarrollo y el crecimiento de las plántulas sean adecuadas (Vleeshouwers *et al.*, 1995; Baskin y Baskin, 2004; Venable, 2007). Las semillas con fotoblastismo positivo requieren del estímulo de la luz para germinar, por lo que deben ser desenterradas por animales, agua o viento.

De acuerdo con Thompson (2000), los bancos de semillas pueden ser (1) transitorios, cuando las semillas persisten en el suelo menos de un año, (2)

persistentes de corto plazo, cuando las semillas persisten en el suelo más de un año, pero menos de 5 años, o (3) persistentes de largo plazo, cuando las semillas persisten más de 5 años. La formación de los bancos de semillas depende fuertemente de las condiciones del microhábitat, las cuales afectan la distribución y abundancia de las semillas en el suelo (Eldridge y Whitford, 2014). En zonas áridas y semiáridas, los bancos de semillas son agregados y están asociados al dosel de árboles y arbustos (Reichman, 1984; Marone *et al.*, 1998). Estas plantas atrapan las semillas dispersadas por el viento y sirven como sitio de percha para aves frugívoras, incrementando la probabilidad de que las semillas sean depositadas bajo su dosel (Reichman, 1984). Los bancos de semillas han sido ampliamente estudiados en especies de plantas anuales, o de vida corta, debido a que es una estrategia que les permite escapar de condiciones desfavorables para la germinación, crecimiento y/o establecimiento de las plántulas (Thompson, 2000; Venable, 2007); reducir la competencia intra- e inter-específica (Aikio *et al.*, 2002); y disminuir los efectos negativos de la granivoría (Brown y Lawrence Venable, 1991; Hulme, 1998). La información sobre los bancos de semillas en especies perennes de larga vida es escasa (Mandujano *et al.*, 1997; Rojas-Aréchiga y Batis, 2001), por lo que es necesario realizar estudios que permitan conocer si estas plantas forman bancos de semillas y de qué tipo, así como la posible relevancia para la regeneración y dinámica de sus poblaciones.

Las cactáceas son plantas conspicuas en las regiones áridas y semiáridas del continente americano (Godínez-Álvarez, *et al.*, 2003), y en algunas de estas

regiones, como la región semiárida tropical del Valle de Tehuacán-Cuicatlán (Puebla y Oaxaca; México), las cactáceas pueden tener una alta riqueza específica y abundancia, por lo que son elementos dominantes de la vegetación (Dávila *et al.*, 2002). No obstante su importancia, la información sobre los procesos que influyen en la regeneración de las poblaciones de cactáceas es parcial e incompleta. Algunos procesos ecológicos como la polinización, la dispersión, la germinación y el establecimiento han sido relativamente estudiados en distintas especies de cactáceas (Bregman, 1988; Godínez-Álvarez *et al.*, 2003; Mandujano *et al.*, 2010), mientras que otros procesos como la depredación de las semillas y la formación de bancos de semillas han sido escasamente evaluados (Cuadro 1). Con respecto a la depredación, solo existen cuatro trabajos realizados con distintas especies de cactáceas (Ibañez y Soriano, 2004; Pérez *et al.*, 2006; García-Chávez *et al.*, 2010; Contreras y Arizmendi, 2014), en estos trabajos sugieren que esta interacción puede causar una alta mortalidad de semillas. Sin embargo, se desconocen los principales grupos de granívoros que consumen las semillas, su importancia relativa y la tasa de remoción de sus semillas pre- y post-dispersión. Con respecto al banco de semillas, estudios recientes han sugerido que las cactáceas pueden formar bancos (Bowers, 2000; Rojas-Aréchiga y Batis, 2001; Olvera-Carrillo *et al.*, 2009; Cano-Salgado *et al.*, 2012; Cheib y Garcia, 2012). Sin embargo, la mayoría de esta evidencia ha sido obtenida a partir del análisis de la viabilidad de semillas que han sido almacenadas en laboratorio por distintos periodos. Muy pocos trabajos han evaluado la viabilidad de las semillas de cactáceas en los sitios en

donde crecen, por lo que se desconoce qué tipo de banco de semillas tienen y qué factores afectan la dinámica y permanencia de las semillas en el suelo. Esta situación determina que el entendimiento de las consecuencias ecológicas y evolutivas de la depredación de las semillas y los bancos de semillas sobre las poblaciones de cactáceas sea aún limitado.

Considerando lo anterior, los objetivos del presente trabajo fueron (1) determinar las tasas de depredación pre- y post-dispersión de las semillas de la cactácea columnar *Stenocereus stellatus* (Pfeiff.) Riccob*. por aves, hormigas y roedores; y (2) determinar si esta cactácea puede formar bancos de semillas en el suelo, considerando la posible influencia de la variación espacial y temporal. *Stenocereus stellatus* es una especie dominante en la región semiárida del Valle de Tehuacán-Cuicatlán (Casas *et al*., 1999; Arias-Cóyotl *et al*., 2006), en los estados de Puebla y Oaxaca, cuyos frutos son consumidos por una gran variedad de animales vertebrados e invertebrados (Godínez-Alvarez *et al*., 2005). Además, sus semillas tienen latencia primaria y son fotoblásticas positivas (Rojas-Aréchiga *et al*., 2001; Álvarez-Espino *et al*., 2014) y la especie también puede propagarse vegetativamente (Godínez-Alvarez *et al*., 2005), aunque la germinación de las semillas y el establecimiento de las plántulas ocurre solamente debajo de árboles y arbustos (Godínez-Alvarez *et al*., 2005). Para cumplir el primer objetivo, se evaluaron la riqueza y abundancia de aves, hormigas y roedores, en dos años consecutivos (2009 y 2010). Durante este periodo, se estimó la producción de semillas de *S. stellatus* y su disponibilidad en el suelo. Por último, se realizaron experimentos de exclusión para determinar

las tasas de remoción de semillas por aves, hormigas y roedores en las plantas y en el suelo bajo arbustos y espacios sin vegetación. Estos aspectos están incluidos en el capítulo II y fueron enviados para su evaluación a la revista *Plant Biology*. Para cumplir el segundo objetivo, se realizaron muestreos mensuales del suelo para determinar la presencia de las semillas de *S. stellatus*. Además, se realizaron experimentos de enterramiento de semillas para estimar su longevidad ecológica. Los muestreos de suelo y los experimentos de enterramiento se realizaron bajo arbustos y en espacios sin vegetación, a lo largo de un año. Los resultados obtenidos están incluidos en el capítulo III y fueron publicados en la revista *Seed Science Research* en 2014. Por último, en el capítulo 4 se discute el posible impacto de la depredación de semillas y los bancos de semillas en la regeneración de las poblaciones de *Stenocereus stellatus*. Además, se discuten brevemente los patrones de remoción de semillas observados en el Valle de Tehuacán-Cuicatlán, en relación con los patrones reportados para otras regiones áridas y semiáridas americanas.

Cuadro 1. Especies de cactáceas con información sobre la depredación de las semillas y/o longevidad ecológica (E) (en condiciones de campo) o potencial (P) (almacenadas en condiciones de laboratorio). SD = sin datos, (+) pre-dispersión, (-) post-dispersión.

Especie	Persistencia de semillas (meses)	Forma de crecimiento	Banco de semillas	Depredadores de semillas	Referencia
Arthrocereus spp.	≤12 E	Arbustiva	Persistente corto plazo	(-) Hormigas y roedores	(Cheib y Garcia, 2011)
Carnegiea giganteae	<13 E	Columnar	Transitorio	SD	(Bowers, 2005)
Ferocactus wislizeni	≤18 E	Toneliforme	Persistente corto plazo	(-) Aves y roedores	(Bowers, 2000)
Harrisia fragrans	≥18 E	Columnar	Persistente corto plazo	SD	(Goodman *et al.*, 2012)

Mammillaria grahamii	>72 E	Globosa	Persistente largo plazo	SD	(Bowers, 2005)
Neobuxbaumia tetetzo	SD	Columnar	SD	(+) Aves	(Contreras-Gonzalez y Arizmendi, 2014)
Opuntia engelmanii	≥19 E	Arbustiva	Persistente corto plazo	SD	(Bowers, 2005)
Opuntia rastrera	>24 P	Arbustiva	Persistente corto plazo	(-) Roedores, aves, hormigas	(Mandujano *et al.*, 1997; Montiel y Montaña, 2003)
Opuntia tomentosa	7 E, 18 P	Arbustiva	Transitorio	SD	(Olvera-Carrillo *et al.*, 2003; Olvera-Carrillo *et al.*, 2009)

Polaskia chende	>13 E	Columnar	Persistente corto plazo	SD	(Ordoñez, 2008)
Stenocereus stellatus	< 24 E, 41 P	Columnar	Persistente corto plazo	(+) Aves (-) Hormigas	(Rojas-Aréchiga *et al.*, 2001; Álvarez-Espino *et al.*, 2014)
Trichocereus pasacana	<13 E	Columnar	Persistente corto plazo	SD	(De Viana, 1999)

Literatura Citada

Aikio, S., E. Ranta, V. Kaitala y P. Lundberg. 2002. Seed bank in annuals: Competition between banker and non-banker morphs. Journal of Theoretical Biology: 217(3): 341-349

Álvarez-Espino, R., H. Godínez-Álvarez y R. de la Torre-Almaráz. 2014. Seed banking in the columnar cactus *Stenocereus stellatus*: Distribution, density and longevity of seeds. Seed Science Research: 24(4): 315-320

Anderson, C. J. y J. A. MacMahon. 2001. Granivores, exclosures, and seed banks: Harvester ants and rodents in sagebrush-steppe. Journal of Arid Environments: 49(2): 343-355

Arias-Cóyotl, E., K. E. Stoner y A. Casas. 2006. Effectiveness of bats as pollinators of *Stenocereus stellatus* (Cactaceae) in wild, managed in situ, and cultivated populations in la Mixteca Baja, central Mexico. American Journal of Botany: 93(11): 1675-1683

Baskin, J. M. y C. C. Baskin. 2004. A classification system for seed dormancy. Seed Science Research: 14(1):1-16

Bowers, J. E. 2000. Does *Ferocactus wislizeni* (Cactaceae) have a between-year seed bank? Journal of Arid Environments: 45(3): 197-205

Bowers, J. E. 2005. New evidence for persistent or transient seed banks in three sonoran desert cacti. The Southwestern Naturalist: 50(4): 482-487

Bregman, R. 1988. Forms of seed dispersal in Cactaceae. Acta Botanica Neerlandica: 37(1): 395-402

Brown, J. y D. Lawrence Venable. 1991. Life history evolution of seed-bank annuals in response to seed predation. Evolutionary Ecology: 5(1): 12-29

Cano-Salgado, A., J. A. Zavala-Hurtado, A. Orozco-Segovia, M. T. Valverde-Valdés y P. Pérez-Rodríguez. 2012. Composición y abundancia del banco de semillas en una región semiárida del trópico mexicano: Patrones de variación espacial y temporal. Revista Mexicana de Biodiversidad: 83(2): 437-446

Casas, A., Caballero, J., Valiente-Banuet, A., Soriano, J. A., Dávila, P. (1999) Morphological variation and the process of domestication of *Stenocereus stellatus* (Cactaceae) in Central Mexico. American Journal of Botany: 4: 522-533

Cheib, A. L. y Q. S. Garcia. 2012. Longevity and germination ecology of seeds of endemic Cactaceae species from high-altitude sites in South-Eastern Brazil. Seed Science Research: 22(1): 45-53

Contreras-González, A. M. y M. C. Arizmendi. 2014. Pre-dispersal seed predation of the columnar cactus (*Neobuxbaumia tetetzo*, Cactaceae) by birds in Central Mexico. Ornitología Neotropical: 25(4): 373-387

Crawley, M. J. 2000. Seed predators and plant population dynamics. En Seeds: the ecology of regeneration in plant communities, M. Fenner (ed.). Pp.167-182. Wallingford: CAB International.

Dávila, P., M. Arizmendi, A. Valiente-Banuet, J. Villaseñor, A. Casas y R. Lira. 2002. Biological diversity in the Tehuacán-Cuicatlán Valley, Mexico. Biodiversity & Conservation: 11(3): 421-442

De Viana, M. 1999. Seed production and seed bank of *Trichocereus pasacana* (Cactaceae) in Northwestern Argentina. Tropical Ecology: 40(1): 79-84

Eldridge, D. y W. Whitford. 2014. Disturbances by desert rodents are more strongly associated with spatial changes in soil texture than woody encroachment. Plant and Soil: 381(1): 395-404

Fedriani, J. M. y Manzaneda, A. J. 2005. Pre- and postdispersal seed predation by rodents: Balance of food and safety. Behavioral Ecology: 16(6): 1018-1024

Fenner, M. y K. Thompson. 2005. The ecology of seeds. London: Cambridge University Press

Figueroa, J. A., A. A. Muñoz, J. E. Mella y M. T. K. Arroyo. 2002. Pre- and post-dispersal seed predation in a mediterranean-type climate montane sclerophyllous forest in central Chile. Australian Journal of Botany: 50(2): 183-195

Forget, P.-M., K. Kitajima y R. B. Foster. 1999. Pre- and post-dispersal seed predation in *Tachigali versicolor* (Caesalpiniaceae): Effects of timing of fruiting and variation among trees. Journal of Tropical Ecology: 15(1): 61-81

García-Chávez, J., V. J. Sosa y C. Montaña. 2010. Variation in post-dispersal predation of cactus seeds under nurse plant canopies in three plant associations of a semiarid scrubland in central Mexico. Journal of Arid Environments: 74(1): 54-62

Godínez-Alvarez, H., L. Ríos-Casanova y F. Pérez. 2005. Characteristics of seedling establishment of *Stenocereus stellatus* (Cactaceae) in the Tehuacán Valley, Mexico. The Southwestern Naturalist: 50(3): 375-380

Godínez-Álvarez, H., T. Valverde y P. Ortega-Baes. 2003. Demographic trends in the Cactaceae. The Botanical Review: 69(2): 173-201

Goodman, J., D. Walters, K. Bradley, J. Maschinski y A. Salazar. 2012. Seeds of endangered *Harrisia fragrans* form persistent soil seed banks and withstand orthodox storage conditions. Haseltonia: 18: 85-94

Hulme, P. 1998. Post-dispersal seed predation and seed bank persistence. Seed Science Research: 8(4): 513-519

Hulme, P. E. 1998. Post-dispersal seed predation: Consequences for plant demography and evolution. Perspectives in Plant Ecology, Evolution and Systematics: 1(1): 32-46

Ibañez, J. y P. Soriano. 2004. Hormigas, aves y roedores como depredadores de semillas en un ecosistema semiárido andino de Venezuela. Ecotropicos: 17(1-2): 38-51

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics: 2(1): 465-492

Kolb, A., J. Ehrlén y O. Eriksson. 2007. Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation. Perspectives in Plant Ecology, Evolution and Systematics: 9(2): 79-100

Long, R. L., M. J. Gorecki, M. Renton, J. K. Scott, L. Colville, D. E. Goggin, L. E. Commander, D. A. Westcott, H. Cherry y W. E. Finch−Savage. 2014. The

ecophysiology of seed persistence: A mechanistic view of the journey to germination or demise. Biological Reviews: 90(1): 31-59

Mandujano, M. C., I. Carrillo-Ángeles, C. Martínez-Peralta y J. Golubov. 2010, Reproductive biology of Cactaceae. En Desert plants, K. G. Ramawats (ed.). Pp. 197-230. Berlin: Springer-Verlag

Mandujano, M. C., J. Golubov y C. Montaña. 1997. Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert. Journal of Arid Environments: 36(2): 259-266

Mares, M. A. y M. L. Rosenzweig. 1978. Granivory in North and South American Deserts: Rodents, birds, and ants. Ecology: 59(2): 235-241

Marone, L., B. E. Rossi y J. López De Casenave. 1998. Granivore impact on soil-seed reserves in the Central Monte Desert, Argentina. Functional Ecology: 12(4): 640-645

Montiel, S. y C. Montaña. 2003. Seed bank dynamics of the desert cactus *Opuntia rastrera* in two habitats from the Chihuahuan Desert. Plant Ecology: 166(2): 241-248

Morton, S. R. 1985. Granivory in arid regions: Comparison of Australia with North and South America. Ecology: 66: 1859-1866

Mull, J. F. y J. A. MacMahon. 1996. Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: The role of harvester ants. Journal of Arid Environments: 32(2): 181-192

Olvera-Carrillo, Y., J. Márquez-Guzmán, V. L. Barradas, M. E. Sánchez-Coronado y A. Orozco-Segovia. 2003. Germination of the hard seed coated *Opuntia tomentosa* S. D., a cacti from the México valley. Journal of Arid Environments: *55*(1): 29-42.

Olvera-Carrillo, Y., I. Méndez, M. E. Sánchez-Coronado, J. Márquez-Guzmán, V. L. Barradas, P. Huante y A. Orozco-Segovia. 2009. Effect of environmental heterogeneity on field germination of *Opuntia tomentosa* (Cactaceae, Opuntioideae) seeds. Journal of arid Environments: 73(4): 414-420.

Ordóñez, C. 2008. Características ecológicas y fisiológicas del banco de semillas de *Polaskia chende* México. Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México.

Orrock, J. L., E. T. Borer, L. A. Brudvig, J. Firn, A. S. MacDougall, B. A. Melbourne, L. H. Yang, D. V. Baker, A. Bar-Massada, M. J. Crawley, E. I. Damschen, K. F. Davies, D. S. Gruner, A. D. Kay, E. Lind, R. L. McCulley y E. W. Seabloom. 2014. A continent-wide study reveals clear relationships between regional abiotic conditions and post-dispersal seed predation. Journal of Biogeography: 42(4): 662-670

Peco, B., S. W. Laffan y A. T. Moles. 2014. Global patterns in post-dispersal seed removal by invertebrates and vertebrates. PLoS ONE: 9(3): e91256

Pérez, E. M., M. del Mar Weisz, P. Lau y L. Bulla. 2006. Granivory, seed dynamics and suitability of the seed-dish technique for granivory estimations in a Neotropical Savanna. Journal of Tropical Ecology: 22(3): 255-265

Reichman, O. J. 1984. Spatial and temporal variation of seed distributions in Sonoran desert soils. Journal of Biogeography: 11(1): 1-11

Rojas-Aréchiga, M. y A. I. Batis. 2001. Las semillas de cactáceas…¿forman bancos en el suelo? Cactáceas y Suculentas Mexicanas: 46: 76-82

Rojas-Aréchiga, M., A. Casas y C. Vázquez-Yanes. 2001. Seed germination of wild and cultivated *Stenocereus stellatus* (Cactaceae) from the Tehuacán-Cuicatlán valley, Central México. Journal of Arid Environments: 49(2): 279-287

Thompson, K. 2000, The functional ecology of soil seed banks. En Seeds: The ecology of regeneration in plant communities, M. Fenner (ed.) Pp. 215-235. Wallingford: CAB International.

Venable, D. L. 2007. Bet hedging in a guild of desert annuals. Ecology: 88(5): 1086-1090

Vleeshouwers, L., H. Bouwmeester y C. Karssen. 1995. Redefining seed dormancy: An attempt to integrate physiology and ecology. Journal of Ecology: 83(6): 1031-1037

CAPÍTULO II

SEED REMOVAL IN A TROPICAL NORTH AMERICAN DESERT: AN EVALUATION OF PRE- AND POST-DISPERSAL SEED REMOVAL IN *STENOCEREUS STELLATUS*

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Seed removal in a tropical North American desert: an evaluation of pre- and post-dispersal seed removal in *Stenocereus stellatus*

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Pre- and post-dispersal seed removal in *Stenocereus stellatus*

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ABSTRACT

1. To determine seed removal impact on seed populations, we need to quantify pre- and post-dispersal seed removal. Several studies have quantified seed removal in temperate American deserts, but few studies have been performed in tropical deserts. These studies have only quantified pre- or post-dispersal seed removal, thus underestimating seed removal impact. We determined pre- and post-dispersal seed removal impact on seed populations of the columnar cactus *Stenocereus stellatus* in a Mexican tropical desert.

2. We performed selective exclosure experiments to estimate percentage of seeds removed by ants, birds, and rodents during the pre- and post-dispersal phases. We also conducted field samplings to estimate seed remover abundance.

3. Pre-dispersal seed removal varied between 1-28%. Birds such as *Melanerpes hypopolius* removed the highest percentage (10-28%) of seeds from fruits. Post-dispersal seed removal varied between 12-64%. Ants such as *Pogonomyrmex barbatus* removed the highest percentage (20-64%) of seeds from soil.

4. Post-dispersal seed removal by ants is higher than pre-dispersal seed removal by birds in *S. stellatus*. Further studies in other plants with different life forms and fruit types will contribute to determine general patterns of seed removal in tropical American deserts.

INTRODUCTION

Seed removal alters distribution and abundance of seed populations, thus influencing the number of new recruits into plant populations (Janzen 1971; Harper 1977; Crawley 1992; Hulme & Benkman 2002). This influence, however, varies depending on whether seeds are consumed on parent plants (i.e., pre-dispersal seed removal) or in soil surface (i.e, post-dispersal seed removal). Seed removers consuming seeds on parent plants reduce seed crop, decreasing probability of seed dispersal. By contrast, seed removers consuming seeds in soil surface reduce seed rain and seed bank, decreasing probability of germination and establishment (Hulme & Benkman 2002; Ribas-Fernández *et al.* 2009). Hence, to determine the impact of seed removal by animals on seed populations, we need to quantify both types of seed removal.

Several studies have quantified pre- and post-dispersal seed removal in temperate North- and South American deserts (Mares & Rosenzweig 1978; Brown *et al.* 1979; López de Casenave *et al.* 1998; Marone *et al.* 2000; Kelt *et al.* 2004; Sassi *et al.* 2004; Ribas-Fernández *et al.* 2009). In these deserts, bruchids and weevils are the most common pre-dispersal seed removers, while ants, rodents, and birds are the most common post-dispersal seed removers. Post-dispersal seed removers also differ in their importance depending on desert. Rodents are the most important seed removers in North American deserts (Mares & Rosenzweig 1978), while ants and birds are the most important seed removers in South American deserts (López de Casenave *et al.* 1998; Sassi *et al.* 2004). Information on pre- and post-dispersal seed removal in tropical American deserts is limited because only four studies have been performed up to now (Ibañez & Soriano 2004; Pérez *et*

al. 2006; García-Chávez *et al.* 2010; Contreras-González & Arizmendi 2014). All these studies have only quantified one seed removal type, thus underestimating seed removal impact on seed populations. As far as we know, there is no study that has quantified both seed removal types in one plant species either from a North American or South American desert. Therefore, studies aimed at quantifying pre- and post-dispersal seed removal simultaneously in single plant species are necessary to determine seed removal impact on seed populations.

In this study we determined the impact of pre- and post-dispersal seed removal on seed populations of the columnar cactus *Stenocereus stellatus* in a Mexican tropical desert. This columnar cactus can reproduce sexually through seeds and propagate vegetatively through stems (Godínez-Alvarez *et al.* 2005). Seeds are consumed by ants, birds, and rodents. Ants and birds are highly diverse and abundant in this desert (Arizmendi & Espinosa de los Monteros 1996; Ríos-Casanova *et al.* 2004), while rodents are poorly represented (García-Chávez *et al.* 2010). Seeds escaping from predation remain viable in the soil for > 1, but < 5 years forming short-term persistent soil seed banks (Álvarez-Espino *et al.* 2014). These traits suggest that pre- and post-dispersal seed removal may differ in their impact on seed populations depending on seed removers. We quantified pre- and post-dispersal seed removal and determined abundance of the most common seed removers in the region (i.e., ants, birds, and rodents). To this end, we performed selective exclosure experiments to estimate the percentage of seeds removed by pre- and post-dispersal seed removers and field samplings to estimate seed remover abundance. Based on field observations of seed removal and differences in diversity and abundance among seed removers, we predicted that post-dispersal

seed removal would be higher than pre-dispersal seed removal. Also, we predicted that birds and ants would remove the highest percentage of seeds during pre- and post-dispersal removal, respectively.

MATERIAL AND METHODS

Study site and species

This study was performed in Coxcatlán, Puebla, México (18° 14' N, 97° 08' W, 1116 m a. s. l.), within the Tehuacán-Cuicatlán Biosphere Reserve. The mean annual rainfall is 440 mm (80% of which falls from June to September) and mean annual temperature is 24°C (Dávila *et al.* 2002). The vegetation is tropical dry forest in which dominant plant species are *Acacia cochliacantha*, *Conzattia multiflora*, *Escontria chiotilla*, *Opuntia* spp., *Parkinsonia praecox*, *Solanum tridynamum*, and *Stenocereus stellatus* (Valiente-Banuet *et al.* 2009).

Stenocereus stellatus is a columnar cactus that branches at the base and can grow up to 5 m in height. It shows both sexual reproduction and vegetative propagation although their relative contribution to population growth is unknown. Flowering occurs from June to August, while fruiting occurs from August to October (Godínez-Alvarez *et al.* 2005). The long-nosed bat *Leptonycteris curasoae* is the only pollinator of flowers (Arias-Cóyotl *et al.* 2006). Fruits are fleshy, thorny, and indehiscent with red-purple pulp and dull-black seeds (1210 ± 70 mean ± s. e., N = 30). Several birds such as *Melanerpes hypopolius* and *Zenaida asiatica* removed pulp and seeds from fruits in the plant, while ants such as *Pogonomyrmex barbatus* and *Pheidole* spp. (Godínez-Alvarez *et al.* 2005) removed seeds from opened fruits on the ground. Seeds germinate after a ripening period of six months

in the soil and seedling establishment only occur under the canopy of woody plants (Godínez-Alvarez *et al.* 2005; Álvarez-Espino *et al.* 2014). In the Tehuacán-Cuicatlán Valley, there are several *S. stellatus* populations such as wild, managed in situ, and cultivated populations (Casas *et al.* 1999). In this study, however, we only studied wild populations because we were interested in seed removal under natural conditions.

Ant, bird, and rodent abundance

To determine abundance of potential seed removers, we sampled ants, birds, and rodents in September-October 2009 and 2010. Birds were sampled through nine 50-m fixed-radius count points, each separated by 150 m, for a total of 12.5 ha. In each count point, birds were recorded during 15 min periods. Observations were performed from 0730 to 1030-1100 h.

Ants were sampled using 20 pitfall traps consisting of plastic containers (10 cm in diameter, 10 cm in height) filled with 250 ml of 70% ethanol and 30% water solution. Traps were buried at ground level and remained closed for 24 h to avoid digging-in effects. After this time, traps were opened for 24 h. Traps were placed every 5 m within a 10 x 50 m plot during 3 consecutive days, for a total of 60 traps per fruiting season. Pitfall traps were the only sampling method used to capture ants because other studies performed in the region showed that these traps sample not only ants removing seeds from soil (*Crematogaster*, *Pogonomyrmex*), but also ants removing seeds from fruits (*Pheidole*, *Solenopsis*; Ríos-Casanova *et al*. 2004, 2006).

Rodents were sampled using 10 Sherman traps baited with oats and peanut butter. Traps were placed every 10 m within a 10 x 50 m plot during 5 consecutive nights, for a total of 50 traps per fruiting season.

Pre-dispersal seed removal

To quantify pre-dispersal seed removal by ants, birds, and rodents, we performed selective exclosure experiments in September-October 2009 and 2010. We collected fresh ripe fruits, which were randomly assigned to four experimental treatments: (1) Seed removal by ants, in which birds were excluded with wire cages (10-mm mesh opening). No signs of seed predation by other insects such as bruchids or weevils were observed either in the fruits or seeds. (2) Seed removal by birds, in which diurnal ants were excluded with natural resin (Tanglefoot) around the fruit base. (3) Seed removal by rodents, in which frugivorous bats were excluded with wire cages. (4) Control in which diurnal and nocturnal seed removers were excluded with wire cages and natural resin. No ant activity was observed during night, thus we did not evaluate pre-dispersal seed removal by nocturnal ants. Qualitative observations showed that exclosures prevent access by seed removers, except for those in which we were interested on. Furthermore, observations showed that exclosures did not alter seed removers because their foraging behavior was similar in the control and experimental plants. Experiments were performed during 5 consecutive days from 0700 h to 1900 h for seed removal by ants and birds, and control, and from 1900 h to 0700 h for seed removal by rodents. One fruit per treatment was fixed with wire to the tip of one *S. stellatus* branch of 3.5-4 m height, for a total of four branches per plant. Plants with four

treatments were considered complete blocks. Blocks were replicated 25 times in 2009 and 18 in 2010. Fruits were weighed at the beginning and ending of experiment to estimate seed mass removed in each treatment as weight difference. Weight difference in control treatment was attributed only to water evaporation during daytime. Seed mass removed by diurnal seed removers from each fruit was corrected by subtracting fruit weight in control treatment. We did not correct seed mass removed by nocturnal seed removers because observations showed that fruits remained hydrated during the night, thus suggesting that water evaporation was negligible. The fruit weight at the beginning of experiment and seed mass removed in each treatment were transformed to number of seeds by using the *S. stellatus* fruit mass–seed number relationship (i.e., seed number = 20.61 * fruit mass + 0.546; $F = 12.1$, d. f. = 1, 27, $p = 0.002$; $R^2 = 0.31$). After data transformation, we divided the number of seeds removed in each treatment by the number of seeds per fruit at the beginning of experiment and multiplied by 100 to calculate the percentage of seeds removed from each fruit. Data were arcsine transformed and analyzed with linear mixed effects models in which seed removal treatments and year were considered as fixed factors, and day of experiment and plant nested within day as random factors. Differences among treatments were evaluated with LSD multiple comparisons tests. Statistical analyses were performed using SPSS software (SPSS IBM, version 21.0).

Post-dispersal seed removal

To estimate post-dispersal seed removal by ants, birds, and rodents, we performed selective exclosure experiments in October 2009 and November 2010. The

experimental design was a split-plot design in which the whole plot factor was microhabitat treatment with two levels: (1) under shrubs and (2) open areas without vegetation. The subplot factor was seed removal treatment with three levels: (1) Seed removal by ants, in which birds were excluded with wire cages (10 mm opening); (2) Seed removal by birds, in which ants were excluded by placing plastic dishes 7 cm above the ground, with natural resin (Tanglefoot) in its base; and (3) Seed removal by rodents, in which ants were excluded as described above. No ant activity was observed during night, thus we did not evaluate post-dispersal seed removal by nocturnal ants. Experiments were performed during 5 consecutive days from 0700 h to 1900 h for seed removal by ants and birds, and from 1900 h to 0700 h for seed removal by rodents. Seed removal treatments were grouped in blocks, which were replicated 14 times for each microhabitat level in 2009 and 15 in 2010. The experimental unit was one 10-cm diameter plastic Petri dish with 1.5 g of *S. stellatus* seeds, without pulp (ca. 1000 seeds). These seeds represent the seed weight of fruits (ca. 1.8 g) and the way in which animals found seeds on the ground. Petri dishes were weighed after 12 h of the beginning of the experiment to estimate seed mass removed in each treatment. Seeds were no replenished during this time. The seed mass removed in each treatment in turn was divided by the initial seed mass per dish (1.5 g) and multiplied by 100 to calculate the percentage of seeds removed from each dish. This percentage was calculated per day and averaged for each treatment. Data were arcsine transformed and analyzed with linear mixed effects models in which microhabitat, seed removal treatments, year, and their interactions were considered as fixed

factors, and block as random factor. Statistical analyses were performed using SPSS software (SPSS IBM, version 21.0).

RESULTS

Ant, bird, and rodent abundance

We sampled 529 and 413 ants from 9 genera and 13 species in 2009 and 2010, respectively (Table 1). Most ants were granivores (5 species) and generalists (4 species) followed by predators (2 species), leaf-cutters (1 species), and nectarivores (1 species). The granivorous ant *Pogonomyrmex barbatus* was the most abundant species with ca. 50-54% of the total ants sampled in both years. Other granivorous ants such as *Pheidole* spp. were less abundant (ca. 7-9%).

We also sampled 106 and 88 birds from 22 genera and 23 species in both years (Table 1). The most common feeding guilds were insectivore (13 species), granivore (4 species), and frugivore/insectivore (3 species). Other guilds such as carnivore, frugivore/granivore, and nectarivore only had 1 species. The frugivorous/insectivorous bird *Melanerpes hypopolius* was the most abundant species with ca. 22-35% of the total birds sampled in 2009 and 2010. Granivorous birds such as *Aimophila mystacalis*, *Columbina inca*, *Passerina cyanea*, *Pipilo albicolis*, and *Zenaida asiatica* were less abundant with a combined abundance of 10% each year.

We did not capture rodents in none of the years. However, we observed 7-10 kangaroo rats on dirty roads nearby our study plots during night. We found one dead individual of *Dipodomys phillipsii* suggesting that this might be the species observed in the field.

Pre-dispersal seed removal

The percentage of seeds removed from fruits depended on seed removers ($F = 20.49$, d. f. = 2, 91, $p < 0.0001$), but not on plants ($F = 0.91$, d. f. = 26, 91, $p = 0.59$), days ($F = 0.42$, d. f. = 4, 37, $p = 0.79$), or years ($F = 0.98$, d. f. = 1, 91, $p = 0.32$). Birds removed higher percentage of seeds (28% in 2009 and 10% in 2010) than ants (2% in 2009 and 2010; $t = 5.68$, d. f. = 91, $p < 0.001$) and rodents (1% in 2009 and 4% in 2010; $t = 5.50$, d. f. = 91, $p < 0.001$). Ants and rodents, on the other hand, removed similar percentage of seeds ($t = 0.25$, d. f. = 91, $p = 0.80$; Fig. 1). Based on seed remover abundance, the frugivore/insectivore *Melanerpes hypopolius* was probably the main bird species removing seeds from fruits followed by other less abundant species such as the granivores *Haemorhous mexicanus*, *Columbina inca*, and *Zenaida asiatica*. *Pogonomyrmex barbatus* and *Dipodomys phillipsii* were probably the main ant and rodent species removing seeds from fruits, respectively (Table 1).

Post-dispersal seed removal

The percentage of seeds removed from soil surface depended on seed removers ($F = 57.36$, d. f. = 2, 165, $p = 0.017$), year ($F = 97.57$, d. f. = 1, 165, $p < 0.0001$), and seed remover by year interaction ($F = 11.17$, d. f. = 2, 165, $p < 0.0001$), but not on microhabitat ($F = 3.5$, d. f. = 1, 165, $p = 0.202$) or microhabitat by seed remover interaction ($F = 0.49$, d. f. = 2, 165, $p = 0.612$). Ants removed higher percentage of seeds (62-64% in 2009 and 20% in 2010) than birds (34-38% in 2009 and 12% in 2010; $t = 6.05$, d. f. = 165, $p < 0.001$ in 2009 and $t = 1.98$, d. f. = 165, $p = 0.049$ in

2010) and rodents (16-30% in 2009 and 12% in 2010; t = 8.96, d. f. = 165, p < 0.001 in 2009 and t = 1.98, d. f. = 165, p = 0.049 in 2010). Birds removed higher percentage of seeds than rodents in 2009 (t = 2.91, d. f. = 165, p = 0.004) and similar percentages in 2010 (t = 0.0001, d. f. = 165, p >0.05). This pattern was similar in both years, although the percentage of removed seeds was significantly higher in 2009 than 2010 (t = 10.79, d. f. = 165, p < 0.001; Fig. 2). Based on seed remover abundance, *Pogonomyrmex barbatus* was probably the main ant species removing seeds from soil. *Columbina inca* and *Zenaida asiatica* as well as *Dipodomys phillipsii* were probably the main bird and rodent species removing seeds from soil, respectively.

DISCUSSION

Studies on pre- and post-dispersal seed removal in tropical American deserts are limited. Thus, there are no studies in which both types of seed removal had been simultaneously estimated in the same plant species. According to our predictions, we have shown that post-dispersal seed removal is higher than pre-dispersal seed removal in the columnar cactus *Stenocereus stellatus*. We have also shown that birds and ants removed the highest percentage of seeds during pre- and post-dispersal seed removal, respectively.

Pre-dispersal seed removal varied between 1-28% in 2009 and 2010. During both years, birds removed higher percentage of seeds than ants and rodents. These results agree with findings reported for the fleshy-fruited columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán-Cuicatlán Valley, in which birds also removed high percentage of seeds (Contreras-González & Arizmendi 2014).

However, they differ from findings reported for the dry-fruited plants *Mimosa* spp. in the Tehuacán-Cuicatlán Valley, *Astragalus nutallianus* in the Chihuahuan Desert, *Prosopis velutina* in the Sonoran Desert, *Prosopis caldenia* in the Dry Chaco, and *Bulnesia retama*, *Prosopis chilensis*, and *Prosopis flexuosa* in the Monte desert, in which bruchids, weevils, chewing insects, and lepidopteron larvae were the most significant pre-dispersal seed removers (Kingsolver *et al*. 1977; Fowler & Whitford 1983; Camargo-Ricalde *et al.* 2004; Ribas-Fernández *et al.* 2009; Aguilar *et al.* 2012). This indicates that significance of pre-dispersal seed removers in tropical and temperate American deserts might vary depending on fruit type. Vertebrates such as birds might be the main seed removers from fleshy fruits while invertebrates such as insects might be the main seed removers from dry fruits. However, further studies on pre-dispersal seed removal on plants with different fruit types, particularly fleshy fruits, are needed to test these ideas. Based on seed remover abundance, *Melanerpes hypopolius* was the main bird species removing seeds from *S. stellatus* fruits. The seeds removed by this bird might be transported intact to sites away from plants because preliminary observations showed that seeds defecated by this species germinated similarly to seeds from fruits (R. Álvarez-Espino, unpublished data). Other studies have also found that this bird transports intact seeds of other columnar cactus such as *Myrtillocactus geometrizans* (Pérez-Villafaña & Valiente-Banuet 2009) and *Neobuxbaumia tetetzo* (Godínez-Alvarez *et al.* 2002). Seed removal by *M. hypopolius* contrasts with seed removal by other much less abundant birds such as *Columbina inca*, *Haemorhous mexicanus*, and *Zenaida asiatica* which are well-recognized as seed predators. This suggests that pre-dispersal seed removal in *S. stellatus* is actually much lower

than estimates obtained from our experiments. Besides birds, ants and rodents also removed seeds from *S. stellatus* fruits. The low seed removal by these groups, however, might be related to ant foraging strategies and rodent diversity. *Pogonomyrmex barbatus*, the most abundant ant in our study site, is a ground dwelling species that rarely forages on plants (MacMahon *et al.* 2000). So, it is unlikely that it removes *S. stellatus* seeds from fruits on branches. These findings contrast with results reported for other ants such as *Solenopsis aurea* and *Pheidole* spp., which can remove pulp and seeds from fruits on *Pilosocereus leucocephalus* branches (Munguía-Rosas *et al.* 2009). Rodent diversity, on the other hand, is low in the Tehuacán-Cuicatlán Valley. García-Chávez *et al.* (2010) studying predation of cactus seeds in this same region suggested that rodents removed few seeds due to rodent fauna is depauperated. This idea might explain the absence of rodent captures in our study site, although it is necessary to conduct studies on diversity and population dynamics of rodents.

Post-dispersal seed removal varied between 12-64% during 2009 and 2010. During both years, ants removed higher percentage of seeds than birds and rodents. These results agree with findings reported for *Myrtillocactus geometrizans* and *Opuntia pilifera* in the Tehuacán-Cuicatlán Valley (García-Chávez *et al.* 2010), and for *Stenocereus griseus* and *Sesamum indicum* in the semiarid regions of Venezuelan Andes (Ibañez & Soriano 2004), in which ants were the most significant seed removers. Ants were also the main post-dispersal seed removers of native and exotic seeds in temperate South American deserts such as the Monte desert and Chilean matorral (Vázquez *et al.* 1995; López de Casenave *et al.* 1998). Our results, however, differ from findings reported for temperate North and South

American deserts, in which rodents and birds were the main seed removers compared to ants (Mares & Rosenzweig 1978; Kelt *et al.* 2004; Pérez *et al.* 2006). This indicates that ants might be the most important post-dispersal seed removers in tropical deserts, suggesting that these deserts are more similar to temperate South American deserts than to temperate North American ones. However, further studies on post-dispersal seed removal in plant species with different life forms and regeneration strategies are needed to determine patterns of post-dispersal seed removal in tropical deserts. Based on seed remover abundance, *Pogonomyrmex barbatus*, was the main ant species removing *S. stellatus* seeds from soil. This harvester ant is a generalist species that removes high numbers of seeds from different plant species. For instance, in the Tehuacán-Cuicatlán Valley it removes seeds from 48 plant species (Ríos-Casanova *et al.* 2004, 2006; Ramírez-Lucas & Ríos-Casanova 2015). Similarly, *Pogonomyrmex rastratus* and *Pogonomyrmex pronatalis* remove seeds from 18 plant species in the Monte desert (Pirk & López de Casenave 2006). This indicates that ants of the genus *Pogonomyrmex* might influence the distribution and abundance of plant populations in tropical and temperate American deserts (MacMahon *et al.* 2000). In addition to ants, birds and rodents also removed *S. stellatus* seeds from soil, although they removed low percentages of seeds. The low seed removal by birds might be related to their relative abundance and foraging strategies. Granivores such as *Columbina inca* (0.9-4.4%) and *Zenaida asiatica* (3.8-5.9%) had low relative abundances throughout the study period. These species further spend little time foraging on ground, thus decreasing the probability of finding *S. stellatus* seeds. Birds depend on predictable seed patches and spend few time locating new ones (Mares &

Rosenzweig 1978; Marone *et al.* 1998; Pérez *et al.* 2006). In the case of rodents, the low seed removal might be due to the depauperated rodent fauna of the Tehuacán-Cuicatlán Valley (García-Chávez *et al.* 2010), as previously described.

In conclusion, this is the first study that simultaneously quantifies pre- and post-dispersal seed removal in a single plant species from a tropical American desert. Our results show that post-dispersal seed removal is higher than pre-dispersal seed removal in *S. stellatus*. They also show that birds and ants are the main pre- and post-dispersal seed removers, respectively. While further studies in other *S. stellatus* populations and plants with different life forms and fruit types will be necessary to determine seed removal patterns in tropical American deserts, this study provides evidence that only by evaluating pre- and post-dispersal seed removal is possible to determine seed removal impact on seed populations.

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REFERENCES

Aguilar, R., Ashworth, L., Calviño, A., Quesada, M. (2012) What is left after sex in fragmented forests: assessing the quantity and quality of progeny of

Prosopis caldenia (Fabaceae) an endemic tree from central Argentina. *Biological Conservation*, **152**, 81-89.

Álvarez-Espino, R., Godínez-Alvarez, H., De la Torre-Almaráz, R. (2014) Seed banking in the columnar cactus *Stenocereus stellatus*: distribution, density, and longevity of seeds. *Seed Science Research*, **24**, 315-320.

Arias-Cóyotl, E., Stoner, K. E., Casas, A. (2006) Effectiveness of bats as pollinators of *Stenocereus stellatus* (Cactaceae) in wild, managed in situ, and cultivated populations in La Mixteca Baja, central Mexico. *American Journal of Botany*, **93**, 1675-1683.

Arizmendi, M. C., Espinosa de los Monteros, A. (1996) Avifauna de los bosques de cactáceas columnares del valle de Tehuacán, Puebla. *Acta Zoológica Mexicana*, **67**, 25-46.

Brown, J. H., Reichman, O. J., Davidson, W. (1979) Granivory in desert ecosystems. *Annual Review of Ecology and Systematics*, **10**, 201-227.

Casas, A., Caballero, J., Valiente-Banuet, A., Soriano, J. A., Dávila, P. (1999) Morphological variation and the process of domestication of *Stenocereus stellatus* (Cactaceae) in Central Mexico. *American Journal of Botany*, **4**, 522-533.

Camargo-Ricalde, S. L., Dhillion, S. S., García-García, V. (2004) Phenology, and seed production and germination of seven endemic *Mimosa* species (Fabaceae-Mimosoideae) of the Tehuacán-Cuicatlán Valley, México. *Journal of Arid Environments*, **58**, 423-437.

Contreras-González, A. M., Arizmendi, M. C. (2014) Pre-dispersal seed predation of the columnar cactus (*Neobuxbaumia tetetzo*, Cactaceae) by birds in central Mexico. *Ornitología Neotropical*, **25**, 373-387.

Crawley, M. J. (1992) Seed predators and plant population dynamics. In: Fenner, M. (Ed), *Seeds: the ecology of regeneration in plant communities*. CAB International, Wallingford, UK: 157-191.

Dávila, P., Arizmendi, M. C., Valiente-Banuet, A., Villaseñor, J. L., Casas, A., Lira, R. (2002) Biological diversity in the Tehuacán-Cuicatlán Valley, México. *Biodiversity and Conservation*, **11**, 421-442.

Figueroa, J. A., Muñoz, A. A., Mella, J. E., Arroyo, M. K. (2002) Pre- and post-dispersal seed predation in a Mediterranean-type climate montane sclerophyllous forest in central Chile. *Australian Journal of Botany*, **50**, 183-195.

Fowler, H. G., Whitford, W. G. 1983. Pre-dispersal seed feeding insects of a desert legume, *Astragalus nutallianus*. *The Southwestern Naturalist*, **28**, 466-469.

García-Chávez, J., Sosa, V. J., Montaña C. (2010) Variation in post-dispersal predation of cactus seeds under nurse plant canopies in three plant associations of a semiarid scrubland in central Mexico. *Journal of Arid Environments*, **74**, 54-62.

Godínez-Alvarez, H., Valiente-Banuet, A., Rojas-Martínez, A. (2002) The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology*, **83**, 2617-2629.

Godínez-Álvarez, H., Ríos-Casanova, L., Pérez, F. (2005) Characteristics of seedling establishment of *Stenocereus stellatus* (Cactaceae) in the Tehuacán Valley, México. *The Southwestern Naturalist*, **50**, 375-407.

Harper, J. L. (1977) *Population biology of plants*. Academic Press, London, UK: 892 pp.

Hulme, P., Benkman, C. W. (2002) Granivory. In: Herrera, C. M., Pellmyr, O. (Eds), *Plant-animal interactions*. Oxford University Press, Oxford, UK: 132-156.

Ibáñez, J., Soriano, P. (2004) Hormigas, aves y roedores como depredadores de semillas en un ecosistema semiárido andino de Venezuela. *Ecotrópicos*, **17**, 38-51.

Janzen, D. H. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics*, **2**, 465-492.

Kelt, D. A., Meserve, P. L., Gutiérrez, J. R. (2004) Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. *Journal of Biogeography*, **31**, 931-942.

Kingsolver, J. M., Johnson, C. D., Swier S. R., Teran, A. L. (1977) *Prosopis* fruits as a resource for invertebrates. In: Simpson, B. B. (Ed), *Mesquite. Its Biology in Two Desert Scrub Ecosystems*. US/IBP Synthesis Series 4. Dowden, Hutchinson & Ross, Stroudsberg, Pa. USA: 108-122.

López de Casenave, J., Cueto, V., Marone, L. (1998) Granivory in Monte desert: is it less intense than in other arid zones of the world? *Global Ecology and Biogeography Letters*, **7**, 197-204.

MacMahon, J. A., Mull, J. M., Crist, T. O. (2000) Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics*, **31**, 265-291.

Mares, M. A., Rosenzweig, M. L. (1978) Granivory in north and South American deserts: rodents, birds and ants. *Ecology*, **2**, 235-241.

Marone, L., Rossi, B. E., López de Casenave, J. (1998) Granivore impact on soil-seed reserves in the central Monte desert, Argentina. *Functional Ecology*, **12**, 640-645.

Marone, L., López de Casenave, J., Cueto, V. R. (2000) Granivory in southern South American deserts: conceptual issues and current evidence. *Bioscience*, **50**, 123-132.

Munguía-Rosas, M. A., Jácome-Flores, M. E., Sosa, V. J., Quiroz-Cerón, L. M. (2009) Removal of *Pilosocereus leucocephalus* (Cactaceae, tribe Cereeae) seeds by ants and their potential role as primary seed dispersers. *Journal of Arid Environments*, **73**, 578-581.

Pérez, M. E., Weisz, M., Lau, P., Bulla, L. (2006) Granivory, seed dynamics and suitability of the seed-dish technique for granivory estimations in a Neotropical savanna. *Journal of Tropical Ecology*, **22**, 255-265.

Pérez-Villafaña, M., Valiente-Banuet, A. (2009) Effectiveness of dispersal of an ornitochorous cactus *Myrtillocactus geometrizans* (Cactaceae) in a patchy environment. *The Open Biology Journal*, **2**, 101-113.

Pirk, G. L., López de Casenave, J. (2006) Diet and removal rates by the harvester ants *Pogonomyrmex rastratus* and *Pogonomyrmex pronatalis* in the central Monte desert, Argentina. *Insect Sociaux*, **53**, 119-125.

Ramírez-Lucas, I. L., Ríos-Casanova, L. (2015) Semillas removidas por la hormiga *Pogonomyrmex barbatus* (Smith): Especies, familias y formas de vida. In: Castaño-Meneses, G., Vásquez-Bolaños, M., Navarrete-Heredia, J. L., Quiroz-Rocha, G., Alcalá-Martínez, I. (Eds), *Avances de Formicidae de México*. Universidad Nacional Autónoma de México, México: 211 pp.

Ribas-Fernández, Y., Quevedo-Robledo, L., Pucheta, E. (2009) Pre- and post-dispersal seed loss and soil seed dynamics of the dominant *Bulnesia retama* (Zygophyllaceae) shrub in a sandy Monte desert of western Argentina. *Journal of Arid Environments*, **73**, 14-21.

Ríos-Casanova, L., Valiente-Banuet, A., Rico-Gray, V. (2004) Las hormigas del Valle de Tehuacán (Hymenoptera: Formicidae): una comparación con otras zonas áridas de México. *Acta Zoológica Mexicana,* **20**, 37-54.

Ríos-Casanova, L., Valiente-Banuet, A., Rico-Gray, V. (2006) Ant diversity and its relationship with vegetation and soil factors in an alluvial fan of the Tehuacán Valley, Mexico. *Acta Oecologica*, **29**, 316-323.

Sassi, P. L., Tort, J., Borghi, C. E. (2004) Effect of spatial and temporal heterogeneity on granivory in the Monte Desert, Argentina. *Austral Ecology*, **29**, 661-666.

Valiente-Banuet, A., Solís, L., Dávila, P., Arizmendi, M. C., Silva P. C., Ortega-Ramírez, J., Treviño C. J., Rangel-Landa, S., Casas, A. (2009) *Guía de la vegetación del Valle de Tehuacán-Cuicatlán*. UNAM, México: 206 pp.

Vázquez, R. A., Bustamante, R. O., Simonetti, J. A. (1995) Granivory in the Chilean matorral: extending the information on arid zones of South America. *Ecography*, **18**, 403-409.

Table 1. Relative abundance and feeding guilds of ant and bird species recorded during the *Stenocereus stellatus* fruiting season in 2009 and 2010. Feeding guilds: C - carnivores, F - frugivores, G - granivores, Gf - generalist foraging, I - insectivorous, Lc - leaf-cutting, N - nectarivore, P - predator.

Species	Number of individuals (%)		Feeding guild
	2009	2010	
Ants			
Atta Mexicana	32 (6.0)	66 (16.0)	Lc
Camponotus rubrithorax	13 (2.5)	18 (4.4)	Gf
Dorymyrmex sp. 1	24 (4.5)	15 (3.6)	Gf
Dorymyrmex sp. 2	19 (3.6)	11 (2.7)	Gf
Forelius sp.	108 (20.4)	54 (13.1)	Gf
Myrmecocystus sp.	7 (1.3)	7 (1.7)	N
Odontomachus sp.	1 (0.2)	-	P
Pheidole sp. 1	29 (5.5)	16 (3.9)	G
Pheidole sp. 2	50 (0.9)	12 (2.9)	G
Pheidole sp. 3	3 (0.6)	4 (1.0)	G
Pheidole sp. 4	1 (0.2)	3 (0.7)	G
Pogonomyrmex barbatus	285 (53.9)	206 (49.9)	G
Pseudomyrmex sp.	2 (0.4)	1 (0.2)	P
Total	529	413	
Birds			
Aimophila mystacalis	4 (3.8)	-	G
Buteo jamaicensis	1 (0.9)	-	C
Columbina inca	1 (0.9)	3 (4.4)	G
Dendroica virens	1 (0.9)	-	I
Empidonax sp.	-	3 (4.4)	I
Haemorhous mexicanus	-	2 (2.9)	FG
Icterus sp.	11 (10.4)	-	FI
Melanerpes hypopolius	37 (34.9)	15 (22.1)	FI
Mimus polyglottos	1 (0.9)	-	I
Myiarchus sp.	3 (2.8)	21 (30.9)	I
Myiozetetes similis	2 (1.9)	-	I
Passerina cyanea	1 (0.9)	-	G
Picoides escalaris	-	1 (1.5)	FI

|			
Pipilo albicollis	1 (0.9)	-	G
Polioptila caerulea	4 (3.8)	11 (16.2)	I
Pyrocephalus rubinus	1 (0.9)	-	I
Pheugopedius maculipectus	3 (2.8)	-	I
Toxostoma curvirostre	3 (2.8)	-	I
Troglodytes aedon	1 (0.9)	-	I
Tyrannus verticalis	-	2 (2.9)	I
Tyrannus crassirostris	1 (0.9)	-	I
Vermivora virginae	-	3 (4.4)	I
Zenaida asiatica	4 (3.8)	4 (5.9)	GF
Trochilidae	26 (24.5)	3 (4.4)	N
Total	106	68	
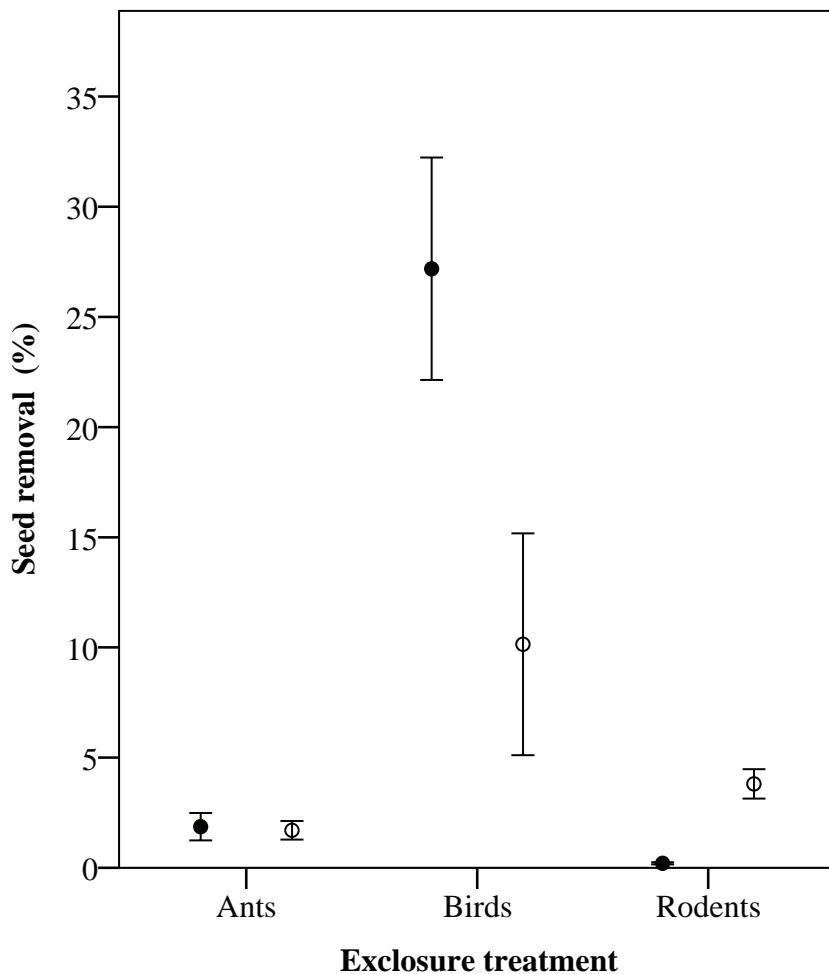
Fig. 1. Pre-dispersal seed removal (mean ± 1 standard error) of *Stenocereus stellatus* in 2009 (•) and 2010 (○). The percentage of seeds removed was significantly affected only by seed removal treatment (p < 0.001, see Results section).
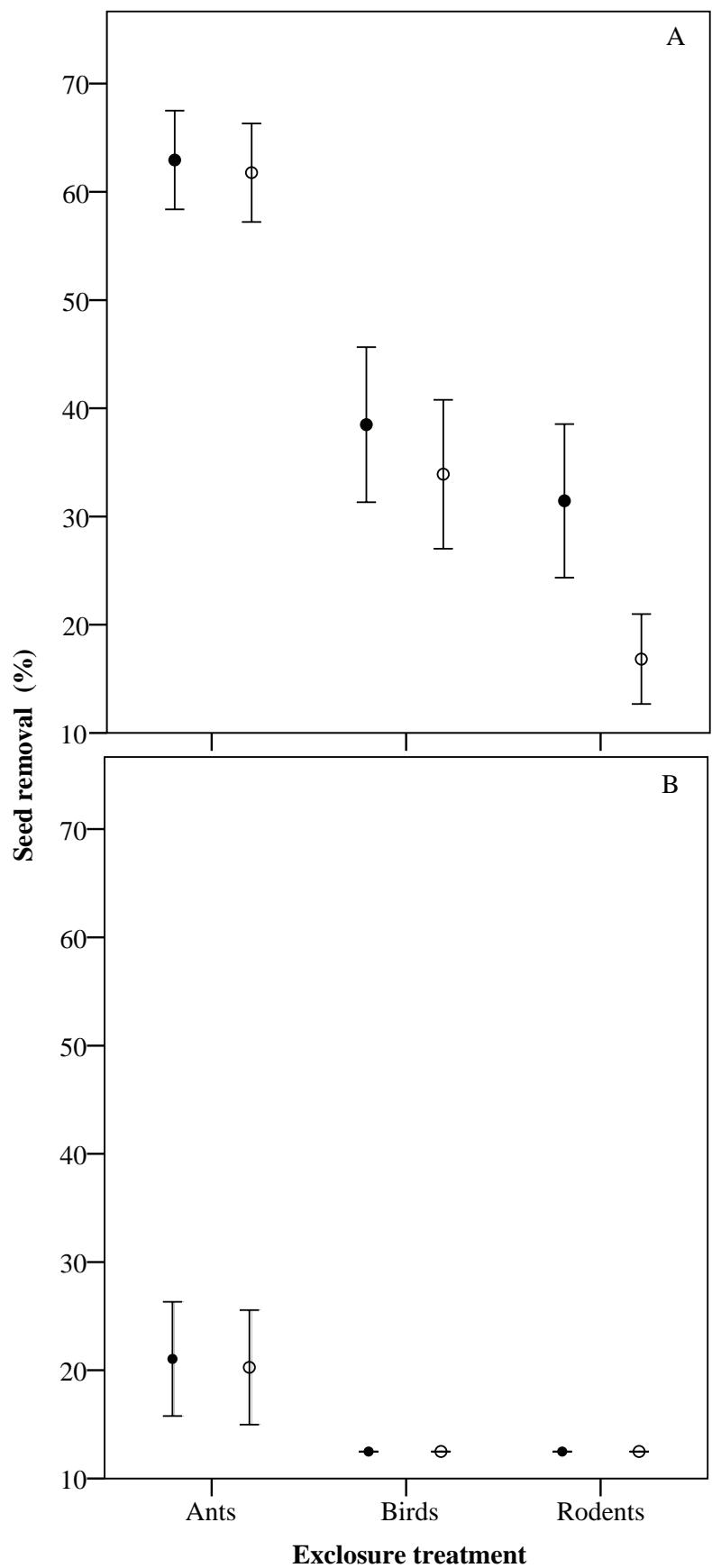
Fig. 2. Post-dispersal seed removal (mean ± 1 standard error) of *Stenocereus stellatus* seeds in open areas (○) and under shrubs (●) during 2009 (A) and 2010 (B). The percentage of seeds removed was significantly affected by seed removal treatment, year, and their interaction ($p < 0.001$, see Results section).

CAPÍTULO III

SEED BANKING IN THE COLUMNAR CACTUS *STENOCEREUS* *STELLATUS*: DISTRIBUTION, DENSITY AND LONGEVITY OF SEEDS

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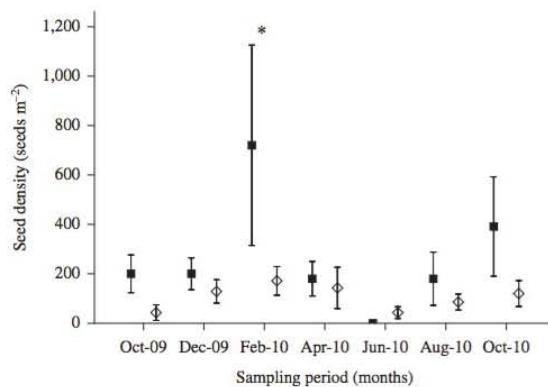
Figure 1. Number of seeds of *Stenocereus stellatus* (mean ± 1 standard error) found under *Acacia cochliacantha* shrubs (solid squares) and in areas lacking vegetation (open diamonds). The * indicates statistically significant differences ($P < 0.001$).

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*
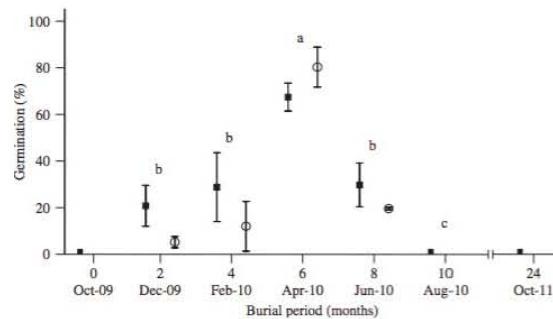

Figure 2. Germination percentage (mean ± 1 standard error) of *Stenocereus stellatus* seeds buried under *Acacia cochliacantha* shrubs (solid squares) and in areas lacking vegetation (open circles). Months marked with different letters are significantly different ($P < 0.001$). Germination percentages 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 (Ordóñez, 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

Conflicts of interest

None.

References

Aguiar, M., Soriano, A. and Sala, O. (1992) Competition and facilitation in the recruitment of seedlings in Patagonian steppe. *Functional Ecology* **6**, 66–70.

Aikio, S., Ranta, E., Kaitala, V. and Lundberg, P. (2002) Seed bank in annuals: competition between banker and non-banker morphs. *Journal of Theoretical Biology* **217**, 341–349.

Arias-Cóyotl, E., Stoner, K.E. and Casas, A. (2006) Effectiveness of bats as pollinators of *Stenocereus stellatus* (Cactaceae) in wild, managed *in situ*, and cultivated populations in La Mixteca Baja, central Mexico. *American Journal of Botany* **93**, 1675–1683.

Baskin, J.M. and Baskin, C.C. (2004) A classification system for seed dormancy. *Seed Science Research* **14**, 1–16.

Bowers, J.E. (2000) Does *Ferocactus wislizeni* (Cactaceae) have a between-year seed bank? *Journal of Arid Environments* **45**, 197–205.

Bowers, J.E. (2005) New evidence for persistent or transient seed banks in three Sonoran Desert cacti. *The Southwestern Naturalist* **50**, 482–487.

Brown, J.S. and Venable, D.L. (1991) Life history evolution of seed-bank annuals in response to seed predation. *Evolutionary Ecology* **5**, 12–29.

Cano-Salgado, A., Zavala-Hurtado, J.A., Orozco-Segovia, A., Valverde-Valdés, M.T. and Pérez-Rodríguez, P. (2012) Composición y abundancia del banco de semillas en una región semiárida del tropico mexicano: patrones de variación espacial y temporal. *Revista Mexicana de Biodiversidad* **83**, 437–446.

Casas, A., Caballero, J., Valiente-Banuet, A., Soriano, J.A. and Dávila, P. (1999) Morphological variation and the process of domestication of *Stenocereus stellatus*

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(Cactaceae) in Central Mexico. *American Journal of Botany* **86**, 522–533.

Chambers, J.C. and MacMahon, J.A. (1994) A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* **25**, 263–292.

Chee-Sanford, J.C., Williams, M.M., Davis, A.S. and Sims, G.K. (2006) Do microorganisms influence seed-bank dynamics? *Weed Science* **54**, 575–587.

Cheib, A.L. and Garcia, Q.S. (2012) Longevity and germination ecology of seeds of endemic Cactaceae species from high-altitude sites in south-eastern Brazil. *Seed Science Research* **22**, 45–53.

Crist, T.O. and Friese, C.F. (1993) The impact of fungi on soil seeds: implications for plants and granivores in a semiarid shrub-steppe. *Ecology* **74**, 2231–2239.

De la Barrera, E. and Nobel, P.S. (2003) Physiological ecology of seed germination for the columnar cactus *Stenocereus queretaroensis*. *Journal of Arid Environments* **53**, 297–306.

Delgado-Sánchez, P., Ortega-Amaro, M.A., Jiménez-Bremont, J.F. and Flores, J. (2011) Are fungi important for breaking seed dormancy in desert species? Experimental evidence in *Opuntia streptacantha* (Cactaceae). *Plant Biology* **13**, 154–159.

de Viana, M.L., Sühring, S. and Manly, B.F.J. (2000) Application of randomization methods to study the association of *Thrichocereus pasacana* (Cactaceae) with potential nurse plants. *Plant Ecology* **156**, 193–197.

Flores-Martínez, A., Manzanero, G.I., Rojas-Aréchiga, M., Mandujano, M.C. and Golubov, J. (2008) Seed age germination responses and seedling survival of an endangered cactus that inhabits cliffs. *Natural Areas Journal* **28**, 51–57.

García-Suárez, F., Carreto-Montoya, L., Cárdenas-Navarro, R., Díaz-Pérez, J. and López-Gómez, R. (2007) Pitaya (*Stenocereus stellatus*) fruit growth is associated to wet season in Mexican dry tropic. *Phyton* **76**, 19–26.

Godínez-Alvarez, H., Valverde, T. and Ortega-Baes, P. (2003) Demographic trends in the Cactaceae. *The Botanical Review* **69**, 173–203.

Godínez-Alvarez, H., Ríos-Casanova, L. and Pérez, F. (2005) Characteristics of seedling establishment of *Stenocereus stellatus* (Cactaceae) in the Tehuacán Valley, Mexico. *The Southwestern Naturalist* **50**, 375–380.

Gosling, P.G. (2003) Viability testing. pp. 445–481 *in* Smith, R.D.; Dickie, J.B.; Linington, S.H.; Pritchard, H.W.; Probert, R.J. (Eds) *Seed conservation: Turning science into practice*. Kew, UK, Royal Botanic Gardens.

Holland, J.N. and Molina-Freaner, F. (2013) Hierarchical effects of rainfall, nurse plants, granivory and seed banks on cactus recruitment. *Journal of Vegetation Science* **24**, 1053–1061.

Hulme, P.E. (1998) Post-dispersal seed predation: consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics* **1**, 32–46.

Jayasuriya, K.G., Qijetunga, A.S., Baskin, J.M. and Baskin, C.C. (2013) Seed dormancy and storage behaviour in tropical Fabaceae: a study of 100 species from Sri Lanka. *Seed Science Research* **23**, 257–269.

Li, F.-R. (2008) Presence of shrubs influences the spatial pattern of soil seed banks in desert herbaceous vegetation. *Journal of Vegetation Science* **19**, 537–548.

Marone, L., Rossi, B.E. and Lopez De Casenave, J. (1998) Granivore impact on soil-seed reserves in the central Monte desert, Argentina. *Functional Ecology* **12**, 640–645.

Montiel, S. and Montaña, C. (2003) Seed bank dynamics of the desert cactus *Opuntia rastrera* in two habitats from the Chihuahuan Desert. *Plant Ecology* **166**, 241–248.

Moreira, B., Tormo, J., Estrelles, E. and Pausas, J.G. (2010) Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. *Annals of Botany* **105**, 627–635.

Mull, J.F. and MacMahon, J.A. (1996) Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: the role of harvester ants. *Journal of Arid Environments* **32**, 181–192.

Olvera-Carrillo, Y., Márquez-Guzmán, J., Sánchez-Coronado, M.E., Barradas, V.L., Rincón, E. and Orozco-Segovia, A. (2009) Effect of burial on the germination of *Opuntia tomentosa's* (Cactaceae, Opuntioideae) seeds. *Journal of Arid Environments* **73**, 421–427.

Ordoñez, C. (2008) Características ecológicas y fisiológicas del banco de semillas de *Polaskia chende*. Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México.

Ortega-Baes, P. and Godínez-Alvarez, H. (2006) Global diversity and conservation priorities in the Cactaceae. *Biodiversity and Conservation* **15**, 817–827.

Raeder, U. and Broda, P. (1985) Rapid preparation of DNA from filamentous fungi. *Letters in Applied Microbiology* **1**, 17–20.

Reichman, O.J. (1984) Spatial and temporal variation of seed distributions in Sonoran desert soils. *Journal of Biogeography* **11**, 1–11.

Rojas-Aréchiga, M. and Batis, A. (2001) Las semillas de cactáceas... ¿forman bancos en el suelo? *Cactáceas y Suculentas Mexicanas* **46**, 76–82.

Rojas-Aréchiga, M., Casas, A. and Vázquez-Yanes, C. (2001) Seed germination of wild and cultivated *Stenocereus stellatus* (Cactaceae) from the Tehuacán-Cuicatlán Valley, Central México. *Journal of Arid Environments* **49**, 279–287.

Sánchez-Coronado, M.E., Márquez-Guzmán, J., Rosas-Moreno, J., Vidal-Gaona, G., Villegas, M., Espinosa-Matías, S., Olvera-Carrillo, Y. and Orozco-Segovia, A. (2011) Mycoflora in exhumed seeds of *Opuntia tomentosa* and its possible role in seed germination. *Applied and Environmental Soil Science* **2011**, 1–8.

Silvius, K.M. (1995) Avian consumers of Cardon fruits (*Stenocereus griseus*: Cactaceae) on Margarita Island, Venezuela. *Biotropica* **27**, 96–105.

Thompson, K. (1993) Persistence in soil. pp. 199–202 *in* Hendry, G.A.F.; Grime, J.P. (Eds) *Methods in comparative plant ecology: A laboratory manual*. London, Chapman & Hall.

Thompson, K. (2000) The functional ecology of soil seed banks. pp. 215–235 *in* Fenner, M. (Ed.) *Seeds: The ecology of regeneration in plant communities* (2nd edition). Wallingford, UK, CABI Publishing.

Valiente-Banuet, A., Solís, L., Dávila, P., Arizmendi, M.C., Silva, P.C., Ortega-Ramírez, J., Treviño, C.J., Rangel-Landa, S. and Casas, A. (2009) *Guía de la vegetación del Valle de Tehuacán-Cuicatlán*. México, Universidad Nacional Autónoma de México.

Venable, D.L. (2007) Bet hedging in a guild of desert annuals. *Ecology* **88**, 1086–1090.

Walck, J.L., Baskin, J.M., Baskin, C.C. and Hidayati, S.N. (2005) Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. *Seed Science Research* **15**, 189–196.

Whitford, W.G. (2002) *Ecology of desert systems*. London, Academic Press.

CAPÍTULO IV

DISCUSIÓN GENERAL Y CONCLUSIONES

En el presente trabajo encontramos que las semillas de la cactácea columnar *S. stellatus* son depredadas por aves y hormigas. Además, encontramos que las semillas que escapan a la depredación forman bancos de semillas persistentes de corto plazo. Sin embargo, estos procesos ecológicos varían en el impacto que tienen sobre la regeneración de las poblaciones de esta especie de planta.

Con respecto a la depredación, las aves fueron el grupo que removió la mayor proporción de semillas, antes de la dispersión, en comparación con las hormigas y los roedores. No obstante, la depredación de las semillas fue baja debido a que las aves frugívoras visitaron los frutos más frecuentemente que las aves granívoras. La especie de ave frugívora-insectívora *Melanerpes hypopolius* tuvo la mayor frecuencia de vistas, por lo que es posible suponer que consumió la mayor proporción de pulpa y semillas. Sin embargo, esta ave dispersa intactas las semillas de *S. stellatus* debido a que el paso por el tracto digestivo no destruye las semillas y tampoco afecta negativamente su germinación (Álvarez-Espino, datos no publicados). Por el contrario, las especies de aves granívoras como *Haemorhous mexicanus, Columbina passerina* y *Zenaida asiatica* tuvieron menores frecuencias de visitas, por lo que probablemente removieron una baja proporción de semillas. La mayor frecuencia de visitas de las aves frugívoras en comparación con las aves granívoras puede deberse a las características morfológicas de los frutos de *S. stellatus*. Los frutos maduros son indehiscentes y armados con espinas, por lo que el pájaro carpintero es la única especie capaz de

perforar el exocarpo de los frutos para consumir la pulpa y las semillas. El resto de las especies de aves solo pueden visitar los frutos y consumir las semillas, después de que el pájaro carpintero ha abandonado los frutos. La baja depredación pre-dispersión encontrada en *S. stellatus* contrasta con los resultados reportados para la cactácea columnar *Neobuxbaumia tetetzo* en la misma región. Los frutos de esta especie son dehiscentes y tienen exocarpos sin espinas. Sus semillas son depredadas por las aves *Ara militaris*, *Haemorhous mexicanus* y *Zenaida asiatica*, las cuales pueden consumir el 41% de las semillas (Contreras-González y Arizmendi, 2014). En relación con la depredación post-dispersión, las hormigas fueron el grupo que removió la mayor proporción de semillas en el suelo en comparación con las aves y los roedores. La hormiga *Pogonomyrmex barbatus* fue el principal depredador de la semillas, pues removió cerca del 90% de las semillas colocadas en los dispositivos experimentales. La alta abundancia y tasa de remoción de semillas de *P. barbatus* encontradas en este trabajo son consistentes con otros reportes para el Valle de Tehuacán-Cuicatlán (Ríos-Casanova y Rico-Gray, 2004; Ríos-Casanova *et al.*, 2006; García-Chávez *et al.*, 2010; Cano-Salgado *et al.*, 2012). Esta hormiga puede remover las semillas de 48 especies de plantas, incluyendo *S. stellatus* (Ramírez-Lucas y Ríos-Casanova, 2015), por lo que podrían ser un factor relevante en la distribución y abundancia de las poblaciones de plantas en esta región semiárida tropical.

Los resultados de los pocos trabajos que se han realizado en regiones desérticas tropicales (Ibañez y Soriano, 2004; Pérez *et al.*, 2006; García-Chávez *et al.*, 2010; Contreras y Arizmendi, 2014) muestran que las hormigas son los principales granívoros, por lo que estas regiones tienen mayor similitud con

Sudamérica que con Norteamérica. La baja importancia relativa de otros granívoros como los roedores en las regiones desérticas tropicales puede deberse, al menos en el caso del Valle de Tehuacán-Cuicatlán, a una baja riqueza y abundancia de especies asociada con las actividades humanas (García-Chávez *et al.*, 2010). En el caso de las aves, su importancia relativa ha sido subestimada debido a que los métodos usados para evaluar la remoción no consideran aspectos tales como sus patrones de forrajeo (Morton, 1985; Marone *et al.*, 1998; Pérez e*t al.*, 2006).

Las semillas de *S. stellatus* que escapan a la depredación post-dispersión, logran permanecer viables < 2 años en el suelo por lo que forman bancos de semillas persistentes de corto plazo. Esto es debido a que las semillas no germinan inmediatamente después de su dispersión ya que tienen latencia fisiológica primaria, la cual se rompe después de un periodo de post-maduración de 6-8 meses en el suelo bajo plantas perennes (Álvarez-Espino *et al.*, 2014). Después de este periodo las semillas en el suelo alcanzan su mayor capacidad germinativa (*ca*. 80%), coincidiendo con el inicio del periodo de mayor precipitación en su área de distribución. Estos resultados sugieren que la latencia primaria impide que las semillas de *S. stellatus* germinen durante los breves periodos de precipitación que pueden ocurrir a finales del invierno o principios de la primavera, evitando la mortalidad de las plántulas. La existencia de un banco de semillas en *S. stellatus* coincide con lo reportado para otras especies de cactáceas con distintas forma de crecimiento, que habitan en diferentes regiones desérticas (De Viana, 1999; Bowers, 2000; Bowers, 2005; Ordoñez, 2008; Olvera-Carrillo *et al.*, 2009; Cano-Salgado *et al.*, 2012; Cheib y Garcia, 2012; Goodman *et al.*, 2012).

El reclutamiento de plántulas en cactáceas es raro (p. ej. décadas) y está restringido a "ventanas estrechas de oportunidad" que se presentan cuando las semillas escapan a la depredación y existen condiciones ambientales favorables (Jordan y Nobel, 1979; Godínez-Álvarez *et al.*, 2003). No obstante, *Stenocereus stellatus* junto con otras especies del mismo género, como *S. eruca* y *S. pruinosus* también tienen la capacidad de propagarse vegetativamente (Clark-Tapia *et al.*, 2005; Godínez-Alvarez *et al.*, 2005; Cruse-Sanders *et al.*, 2013; Parra *et al.*, 2014). En el caso de *S. stellatus*, este mecanismo contribuye al reclutamiento de nuevos individuos en las poblaciones, manteniendo niveles constantes de diversidad genética, así como bajos valores de endogamia (Cruse-Sanders *et al.*, 2013).

En conjunto, los resultados de este trabajo sugieren que la depredación de las semillas, en particular la depredación post-dispersión, puede afectar negativamente la regeneración de las poblaciones de *S. stellatus*. Sin embargo, estos efectos negativos pueden ser contrarrestados por la formación de bancos de semillas debido a que las semillas se distribuyen espacial y temporalmente, disminuyendo el riesgo de depredación. Además del banco de semillas, se ha sugerido que existen otros factores que pueden contribuir a disminuir el impacto negativo de la depredación como: (1) la propagación vegetativa, (2) la producción de altas cantidades de semillas que sacien a los depredadores, (3) la regeneración no limitada por la disponibilidad de semillas, y (4) la abundancia de granívoros limitada por la depredación y el parasitismo, en lugar de la abundancia de semillas (Hulme y Benkman, 2002). La estrategia de regeneración de *S. stellatus* incluye varios de estos factores, debido a que puede reproducirse sexualmente o propagarse vegetativamente, produce cantidades relativamente altas de semillas y

el establecimiento está limitado a micrositios ubicados bajo el dosel de plantas perennes (Godínez-Álvarez *et al*., 2005; Álvarez-Espino *et al*., 2014). Estos factores sugieren que la depredación post-dispersión tiene un impacto menor sobre la regeneración de las poblaciones de *S. stellatus*, independientemente de la magnitud de las tasas de remoción de las semillas.

Recientemente se ha sugerido que el efecto de distintos factores físicos y biológicos sobre la regeneración de las cactáceas es dependiente del contexto en el que actúan dichos factores (Holland y Molina-Freaner, 2013). En este sentido, es necesario determinar si la depredación y los bancos de semillas observados en este estudio son similares en distintas comunidades vegetales y distintas regiones geográficas, a lo largo de distintos años. La riqueza y abundancia de los granívoros puede variar espacial y temporalmente, afectando de distinta manera las poblaciones de cactáceas. Además, distintas especies de cactáceas pueden formar bancos de semillas debido a que producen semillas pequeñas, con latencia innata y fotoblastismo positivo (Bowers, 2000; Rojas-Aréchiga y Batis, 2001). La evaluación de la depredación y el banco de semillas es imprescindible para entender la regeneración de las poblaciones y las características de historia de vida de las cactáceas. Esta información puede ser útil para proyectos futuros destinados a la conservación y la restauración ecológica.

Se concluye que la magnitud en la remoción de las semillas crea fuertes presiones de selección, debido a que se afecta de manera importante el reclutamiento de plantas individuales de *S. stellatus*, sin embargo, el efecto final de los depredadores sobre la dinámica poblacional pudieran ser imperceptible en esta planta perenne, ya que forma bancos de semillas, no depende de la

reproducción sexual para mantener sus poblaciones, y puede tolerar la ausencia

de reproducción por largos periodos de tiempo.

Literatura Citada

Álvarez-Espino, R., H. Godínez-Álvarez y R. De la Torre-Almaráz. 2014. Seed banking in the columnar cactus *Stenocereus stellatus*: Distribution, density and longevity of seeds. Seed Science Research: 24(4): 315-320

Bowers, J. E. 2000. Does *Ferocactus wislizeni* (Cactaceae) have a between-year seed bank? Journal of Arid Environments: 45(3): 197-205

Bowers, J. E. 2005. New evidence for persistent or transient seed banks in three sonoran desert cacti. The Southwestern Naturalist: 50(4): 482-487

Cano-Salgado, A., J. A. Zavala-Hurtado, A. Orozco-Segovia, M. T. Valverde-Valdés y P. Pérez-Rodríguez. 2012. Composición y abundancia del banco de semillas en una región semiárida del trópico mexicano: Patrones de variación espacial y temporal. Revista Mexicana de Biodiversidad: 83(2): 437-446

Cheib, A. L. y Q. S. Garcia. 2012. Longevity and germination ecology of seeds of endemic Cactaceae species from high-altitude sites in South-Eastern Brazil. Seed Science Research: 22(1): 45-53

Clark-Tapia, R., M. C. Mandujano, T. Valverde, A. Mendoza y F. Molina-Freaner. 2005. How important is clonal recruitment for population maintenance in rare plant species?: The case of the narrow endemic cactus, *Stenocereus eruca*, in Baja California, México. Biological Conservation: 124(1): 123-132

Contreras-González, A. M. y M. C. Arizmendi. 2014. Pre-dispersal seed predation of the columnar cactus (*Neobuxbaumia tetetzo*, Cactaceae) by birds in Central Mexico. Ornitología Neotropical: 25(4): 373-387

De Viana, M. 1999. Seed production and seed bank of *Trichocereus pasacana* (Cactaceae) in northwestern Argentina. Tropical Ecology: 40(1): 79-84

García-Chávez, J., V. J. Sosa y C. Montaña. 2010. Variation in post-dispersal predation of cactus seeds under nurse plant canopies in three plant associations of a semiarid scrubland in central Mexico. Journal of Arid Environments: 74(1): 54-62

Godínez-Alvarez, H., L. Ríos-Casanova y F. Pérez. 2005. Characteristics of seedling establishment of *Stenocereus stellatus* (Cactaceae) in the Tehuacán Valley, Mexico. The Southwestern Naturalist: 50(3): 375-380

Godínez-Álvarez, H., T. Valverde y P. Ortega-Baes. 2003. Demographic trends in the Cactaceae. The Botanical Review: 69(2): 173-201

Goodman, J., D. Walters, K. Bradley, J. Maschinski y A. Salazar. 2012. Seeds of endangered *Harrisia fragrans* form persistent soil seed banks and withstand orthodox storage conditions. Haseltonia: 18: 85-94

Hulme, P. E. y C. W. Benkman. 2002, Granivory. En Plant–animal interactions: An evolutionary approach, C. M. Herrera y O. Pellmyrs (eds.). Pp. 132-156. Oxford: Blackwell Science

Ibañez, J. y P. Soriano. 2004. Hormigas, aves y roedores como depredadores de semillas en un ecosistema semiárido andino de Venezuela. Ecotropicos: 17(1-2): 38-51

Jordan, P. W. y P. S. Nobel. 1979. Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the Northwestern Sonoran Desert. American Journal of Botany: 66(9): 1079-1084

Marone, L., B. E. Rossi y J. Lopez De Casenave. 1998. Granivore impact on soil-seed reserves in the Central Monte Desert, Argentina. Functional Ecology: 12(4): 640-645

Morton, S. R. 1985. Granivory in arid regions: Comparison of Australia with North and South America. Ecology: 66(6): 1859-1866

Olvera-Carrillo, Y., J. Márquez-Guzmán, M. E. Sánchez-Coronado, V. L. Barradas, E. Rincón y A. Orozco-Segovia. 2009. Effect of burial on the germination of *Opuntia tomentosa's* (Cactaceae, Opuntioideae) seeds. Journal of Arid Environments: 73(4-5): 421-427

Ordoñez, C. 2008. Características ecológicas y fisiológicas del banco de semillas de *Polaskia chende* México. Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México

Parra, F., A. Casas, V. Rocha, A. González-Rodríguez, S. Arias-Montes, H. Rodríguez-Correa y J. Tovar. 2014. Spatial distribution of genetic variation of *Stenocereus pruinosus* (otto) buxb. in Mexico: Analysing evidence on the origins of its domestication. Genetic Resources and Crop Evolution: 62(6): 893-912

Pérez, E. M., M. del Mar Weisz, P. Lau y L. Bulla. 2006. Granivory, seed dynamics and suitability of the seed-dish technique for granivory estimations in a Neotropical Savanna. Journal of Tropical Ecology: 22(3): 255-265

Ramírez-Lucas, I. L. y L. Ríos-Casanova. 2015, Semillas removidas por la hormiga *Pogonomyrmex barbatus* (Smith): Especies, familias y formas de vida. En Avances de Formicidae de México, G. Castaño-Meneses, M. Vásquez-Bolaños, J. L. Navarrete-Heredia, G. Quiroz-Rocha y I. Alcalá-Martínez (eds.). p. 129. Universidad Nacional Autónoma de México, Universidad de Guadalajara, México

Ríos-Casanova, L., A. Valiente-Banuet y V. Rico-Gray. 2006. Ant diversity and its relationship with vegetation and soil factors in an alluvial fan of the Tehuacán Valley, Mexico. Acta Oecologica: 29(3): 316-323

Rojas-Aréchiga, M. y A. I. Batis. 2001. Las semillas de cactáceas…¿forman bancos en el suelo? Cactáceas y Suculentas Mexicanas: 46: 76-82