UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE ESTUDIOS SUPERIORES IZTACALA
BIOLOGIA EXPERIMENTAL

Longevidad y modelo de tiempo térmico en semillas de *Polaskia* (Cactaceae)

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:
CESAR ALEJANDRO ORDOÑEZ SALANUEVA

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FACULTAD DE ESTUDIOS SUPERIORES IZTACALA
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Dra. MARÍA MARGARITA CANALES MARTÍNEZ
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA

MÉXICO, Cd. Mx. Mayo 2016

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UNAM
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COORDINACIÓN

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Subcomité de Biología Experimental y Biomedicina del Posgrado en Ciencias Biológicas, celebrada el día 23 de febrero de 2015, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **ORDOÑEZ SALANUEVA CÉSAR ALEJANDRO,** con número de cuenta **91116572**, con la tesis titulada **"LONGEVIDAD Y MODELO DE TIEMPO TÉRMICO EN SEMILLAS DE POLASKIA (Cactaeae)",** realizada bajo la dirección del **DR. CÉSAR MATEO FLORES ORTÍZ:**

Presidente:	DRA. MARÍA DEL ROCIO CRUZ ORTEGA
Vocal:	DR. JOEL DAVID FLORES RIVAS
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Suplente:	DR. JORDAN KYRIL GOLUBOV FIGUEROA
Suplente:	DRA. MARÍA MARGARITA CANALES MARTÍNEZ

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

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., 16 de marzo de 2016.

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

c.c.p. Expediente del (la) interesado (a)

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Al Posgrado en Ciencias Biológicas, UNAM.

Al CONACYT por la beca recibida (No. 245266)

Al Tutor de la tesis:
Dr. César Mateo Flores Ortiz

A las integrantes del Comité Tutoral:

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AGRADECIMIENTOS

A los integrantes del Jurado:

Dra. María del Rocío Cruz Ortega
Dr. Joel David Flores Rivas
Dr. Jordan Kyril Golubov Figueroa

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RESUMEN

La longevidad ecológica es el tiempo promedio que las semillas permanecen viables en el suelo bajo la influencia del ambiente natural, los principales factores abióticos involucrados en su duración son la temperatura y el potencial hídrico. La persistencia de las semillas en el suelo es importante ya que determina el tipo de banco que estas forman. Los modelos de tiempo térmico predicen la germinación de una población de semillas en función de la temperatura y han sido empleados para estudiar el efecto de los posibles escenarios de cambio climático en la germinación. El conocimiento de bancos de semillas en cactáceas es escaso, estas se encuentran fuertemente amenazadas y se ha propuesto que son uno de los grupos más vulnerables al calentamiento global. En este trabajo se estudió la longevidad ecológica de las semillas de *Poskia chende*, se estableció la asociación de esta especie con plantas nodriza, se generó un modelo de tiempo térmico para *P. chende* y *P. chichipe* y se analizó el efecto del aumento en la temperatura en la germinación bajo diferentes escenarios de cambio climático. Se colectaron frutos maduros de *P. chende* y *P.chichipe* en la reserva de la biosfera de Tehuacán-Cuicatlán. Dos lotes de semillas de *P. chende* fueron enterrados en el área de estudio en condiciones de dosel y sin dosel. Las semillas enterradas fueron exhumadas periódicamente durante 64 meses, se registró la emergencia de las plántulas y la sobrevivencia de estas durante 62 meses. Se realizaron pruebas de germinación en un gradiente de temperaturas de 5 a 40 °C, con los resultados obtenidos se realizó un análisis de regresión para obtener las temperaturas cardinales y posteriormente un análisis probit para obtener el tiempo térmico. Finalmente, se realizaron proyecciones de cambio climático para el área de estudio. Los resultados obtenidos indicaron que las semillas de *P. chende* forman bancos de semillas persistentes de largo plazo y establecen asociación con plantas nodriza. Por otro lado, el aumento en la temperatura producido por los diferentes escenarios de cambio climático acelerara el proceso de germinación pero no tendrá efectos negativos en la germinación de las especies estudiadas.

ABSTRACT

The ecological longevity is the mean time that the seeds remain viable in the soil under the influence of the natural environment; the main abiotic factors involved in this process are the temperature and water potential. Seed persistence in the soil is important because it determines the type of seed bank that they form. Thermal time models predict seed germination in a population as a function of temperature; these models have been employed to study the effect of potential climate change scenarios on germination. Knowledge of seed banks in cacti is scanty, many cacti species are highly threatened and it has been proposed among the most vulnerable groups to global warming. In this dissertation I studied the ecological longevity of *Polaskia chende* seeds, established nurse plant association, generated a thermal time model for *P. chende* and *P. chichipe* and analyzed the effect of temperature increase in germination under different climate change scenarios. Ripe fruits of *P. chende and P.chichipe* were collected in the Biosphere Reserve of Tehuacán-Cuicatlán. Two samples of *P. chende* seeds were buried in the study area in the soil under shrub canopy and in open space. Buried seeds were exhumed periodically during 64 months, seedling emergence and survival was recorded for 62 months. Germination tests were performed in a temperature gradient of 5-40 °C, a regression analysis was performed to obtain cardinal temperatures and a probit analysis was performed to obtain thermal time. Finally, climate change projections were made for the study area. The results showed that *P. chende* seeds form long-term persistent soil seed banks and establish nurse plant facilitation. On the other hand, the increase in temperature produced by the different climate change scenarios may accelerate germination but may not have negative effects on germination in the plant species studied.

INTRODUCCIÓN

El término longevidad en las semillas implica considerar dos aspectos: uno de ellos producto del manejo antropogénico (longevidad potencial) y el otro ligado a la ocurrencia natural de las semillas en el suelo de su hábitat (longevidad ecológica). La longevidad potencial se refiere al tiempo que una población de semillas mantiene su viabilidad bajo condiciones de almacenamiento controladas, su máximo se alcanza durante la fase de maduración regularmente cuando son dispersadas (Probert *et al*., 2009). Por otro lado, el tiempo que las semillas permanecen viables en el suelo bajo la influencia del ambiente natural constituye su longevidad ecológica (Vázquez-Yanes y Orozco-Segovia, 1996). Aunque las condiciones en que se encuentran las semillas en estos fenómenos son completamente diferentes tienen en común que los principales factores que determinan la respuesta fisiológica de las semillas son la humedad y la temperatura, este trabajo está enfocado en el estudio de la longevidad en condiciones naturales.

Las semillas son dispersadas por la planta madre y tarde o temprano se encuentran en la superficie del suelo. La germinación de estas semillas puede ocurrir inmediatamente o puede retrasarse por un periodo indefinido. Durante este tiempo, las semillas viables que se encuentran en o sobre el suelo forman un banco de semillas (Fenner y Thompson, 2005). Los bancos de semillas son esenciales en la dinámica y regeneración de las poblaciones de las plantas (Harper, 1977), estos permiten mantener la variabilidad genética de las especies, persistir en el tiempo, resistir periodos de adversidad y sobrevivir a eventos catastróficos (Harper, 1977; Fenner y Thompson, 2005); también contribuyen a la coexistencia de las especies, la estabilidad de las poblaciones y representan una estrategia de diversificación (bet hedhging) (Baskin y Baskin, 2014; Saatkamp *et al.,* 2014).

Los bancos de semillas en condiciones naturales constituyen una parte dinámica de las poblaciones vegetales, existe un conjunto de factores ambientales que determinan la entrada, permanencia y salida de las semillas en el suelo (Harper, 1977; Saatkamp *et al*., 2014). Estos factores pueden ser bióticos: depredación (Bruun *et al*., 2010; Dalling, 2011; Hulme, 1998), competencia (Saatkamp *et al*., 2014), ataque por micro-organismos

(Dalling, 2011) y simbiosis con micro-organismos (Dalling, 2011; Long *et al*., 2015); o abióticos: temperatura, humedad, precipitación, luz, características físicas y químicas del suelo (Baskin y Baskin, 2014; Long *et al*., 2015), ciclos de hidratación y des-hidratación (Gonzalez-Zertuche *et al*., 2001; Long *et al*., 2015), principalmente.

Para que las semillas formen bancos es necesario que persistan en el suelo, la persistencia se refiere al tiempo que las semillas sobreviven desde que alcanzan su madurez en la planta madre hasta que germinan o mueren; ya sea por envejecimiento, depredación o decaimiento *sensu* Long *et al*. (2015). La persistencia es la expresión de varias características de la semilla que incluyen la latencia, la longevidad y la defensa (contra depredadores o patógenos) y cómo estas características son influenciadas por el ambiente inmediato al que están expuestas las semillas.

La clasificación de bancos de semillas propuesta por Thompson *et al.* (1997) está basada en la longevidad de estos propágulos en el suelo. Así, las semillas que forman bancos transitorios permanecen en el suelo menos de un año, las semillas que forman bancos persistentes de corto plazo permanecen en el suelo por lo menos un año pero no más de cinco años y por último, las semillas que forman bancos persistentes de largo plazo permanecen en el suelo por lo menos cinco años.

La dinámica del banco de semillas de una población está determinado en principio por dos fases: la entrada de semillas en el banco y la pérdida de semillas del banco (Harper, 1977; Parker *et al*., 1989). La entrada de semillas al banco ocurre al momento de la dispersión natural de cada especie y está representada por lo que se conoce como lluvia de semillas (Harper, 1977). De acuerdo con este mismo autor una vez que las semillas se encuentran en o sobre el suelo el banco de semillas se divide en dos: el banco latente y el banco activo. El banco latente lo conforman aquellas semillas que presentan algún tipo de latencia y que por lo tanto no germinan hasta que el estado de latencia se remueve, las semillas que se encuentran en esta condición se pueden perder del banco por depredación, decaimiento o envejecimiento lo cual conduce a la muerte de la semilla. Por otro lado, el banco activo lo conforman las semillas que se encuentran en estado de quiescencia y que al recibir el o los estímulos ambientales adecuados germinan, saliendo de esta manera del banco de semillas. Las semillas pueden transitar del banco activo al banco latente de manera dinámica dependiendo de las condiciones del entorno contiguo en el que se encuentran las semillas.

Existen algunas características de las semillas que favorecen la formación de bancos de semillas persistentes. El tamaño y la forma de las semillas fueron propuestos como indicadores para predecir la persistencia de semillas en el suelo en plantas herbáceas del Reino Unido (Thompson *et al*., 1993), encontrándose que las semillas pequeñas (hasta 3 mg) y con forma esférica son capaces de formar bancos de semillas persistentes. Esta hipótesis ha sido comprobada en diferentes tipos de vegetación en países como el Reino Unido (Hodkinson *et al*., 1998), Argentina (Funes *et al*., 1999), Irán (Thompson *et al*., 2001), Italia (Cerabolini *et al*., 2003) y España (Peco *et al*., 2003).

Por otro lado, Baskin y Baskin (1998), establecieron que la principal razón por la cual las semillas no latentes que se encuentran en el suelo no germinen, es debido a que la mayoría tienen requerimientos de luz para germinar. La existencia de requerimientos de luz para germinar es un atributo que ha sido relacionado con el tamaño pequeño de las semillas (Grime *et al*., 1981; Pons, 2000; Milberg *et al*., 2000) y a su vez ha sido señalado como una de las características que puede favorecer la formación de bancos de semillas en el suelo (Pons, 2000). Milberg *et al*. (2000) mostraron que las semillas pequeñas son más dependientes de la luz para germinar que las semillas grandes y sugirieron que la masa de las semillas y los requerimientos de luz co-evolucionaron. Sin embargo, Fenner y Thompson (2005) encontraron que existe un componente filogenético en la ocurrencia del fotoblastismo ya que algunas familias como Fabaceae y Poaceae tienden a germinar fácilmente en la oscuridad sin importar el tamaño de las semillas.

Otra característica importante de las semillas que favorece su persistencia en el suelo es la latencia. Algunos estudios, en donde se analiza la relación entre varias características de las plantas y la persistencia de las semillas en el suelo, mostraron que las semillas no latentes germinan más rápido y por lo tanto permanecen por menos tiempo en el suelo (Honda, 2008; Saatkamp *et al*., 2011). La presencia de latencia física contribuye a prolongar el tiempo que las semillas permanecen en el suelo, debido a que es necesario romper las estructuras impermeables que se encuentran en la cubierta seminal para que las semillas puedan embeber agua y completar el proceso de germinación (Baskin, 2003). También la latencia fisiológica promueve la persistencia de las semillas ya que se ha observado que muchas especies requieren un periodo de estratificación para poder germinar, en el cual las semillas deben de ser expuestas a temperaturas bajas (< 10 °C) o cálidas (> 10 °C) durante varios meses (Baskin y Baskin, 2014). Finalmente, algunas semillas presentan latencia secundaria a través de ciclos de latencia estacional o no estacional, lo cual contribuye a la formación de bancos de semillas persistentes. Las semillas que entran en latencia secundaria pueden permanecer en este estado por meses o años (Gutterman, 2000; Hill y Kloet, 2005); los ciclos de latencia varían de acuerdo al hábitat y al ciclo de vida de cada especie, pero regularmente duran de una temporada de germinación a la siguiente (Baskin y Baskin, 1998; Probert, 2000). Por lo tanto, las características fisiológicas de la latencia de las semillas son muy importantes para determinar el tipo de banco que estas forman.

La longevidad ecológica está fuertemente asociada con la germinación de las semillas en su hábitat, existen una gran variedad de factores ambientales involucrados en la germinación de las semillas en el suelo como son: la calidad y cantidad de luz que reciben las semillas (Bewley *et al*., 2013; Pons, 2000), la humedad y la temperatura (Bewley *et al*., 2013; Hilhorst y Karssen, 2000), la cantidad y la sincronía de la precipitación (Marone *et al*., 2000), la textura del suelo y la profundidad de enterramiento de la semilla (Wu *et al*., 2007), la densidad aparente del suelo (Leon y Owen, 2004), el potencial de intercambio gaseoso del suelo (Benvenuti, 2003), la presencia de costras biológicas en el suelo (Leblanc *et al*., 2002), el contenido de nitrato en el suelo (Bewley *et al*., 2013; Hilhorst y Karssen, 2000), la disponibilidad de oxígeno en el suelo (Bewley *et al*., 2013), la presencia de humo

(Tang *et al*., 2003), la concentración de CO_2 y etileno en el suelo (Bewley *et al*., 2013; Hilhorst y Karssen, 2000), la concentración de CO y la cantidad de oxígeno disuelto en el agua embebida por la semilla (Dekker *et al*., 2002), la presencia de compuestos alelopáticos (Bewley *et al*., 2013; Hilhorst y Karssen, 2000) y la presencia de compuestos orgánicos promotores de la germinación (Bewley *et al*., 2013; Hilhorst y Karssen, 2000). Varios de estos factores también intervienen en la latencia de las semillas en el campo, por lo cual su respuesta germinativa en el suelo es producto de la interacción de múltiples factores; sin embargo, se ha reconocido que la humedad y la temperatura son los principales reguladores de estos procesos (Allen *et al*., 2007; Bewley *et al*., 2013; Finch-Savage y Leubner-Metzger, 2006).

De manera que se han generado modelos basados en el tiempo térmico (García-Huidobro *et al*., 1982; Ellis *et al*., 1986; Covell *et al*., 1986) y el tiempo hídrico (Bradford, 1995; Gummerson, 1986) los cuales describen los efectos de la temperatura y el potencial hídrico en la germinación. Posteriormente, estos modelos han sido integrados y empleados para describir y predecir la germinación (Batlla *et al*., 2004; Finch-Savage, 2004) y la latencia (Benech-Arnold *et al*., 2000; Alvarado y Bradford, 2005; Allen *et al*., 2007) de las semillas en el campo en respuesta a las condiciones ambientales en el suelo, por lo cual, este trabajo está enfocado en el estudio del tiempo térmico.

La germinación se realiza a diferentes tiempos para cada semilla en una población, lo cual conduce a una curva de germinación acumulada característica para cada lote de semillas. Los modelos poblacionales del umbral base (*population base threshold models*) proveen una herramienta útil para entender y describir la interacción de estas distribuciones en relación a la temperatura y el potencial hídrico (Bradford, 2002). En estos modelos generalmente se asume que las semillas germinan en un orden y que este orden no es afectado por las condiciones de germinación. A cada semilla se le puede asignar un valor de *"g"* el cual determina el tiempo en el cual esa semilla germina en relación a otras semillas en la población (en otras palabras, *g* es la fracción porcentual de la germinación a la cual pertenece la semilla).

Para cada población de semillas existen tres temperaturas cardinales para la germinación: la temperatura máxima (*Tc*) es la temperatura más elevada a la cual las semillas pueden germinar; la temperatura base (*Tb*) es la temperatura más baja en la cual puede ocurrir la germinación y la temperatura óptima (*To*) es aquella en la cual la velocidad de la germinación es mayor (Allen *et al.*, 2007). Estas temperaturas son especificas para cada especie, pero pueden variar de acuerdo a la variedad, el cultivar, el ecotipo, el origen geográfico, el año de colecta, el tiempo de almacenamiento y la presencia de latencia en las semillas (Covell *et al.*, 1986). El rango de temperatura que permite la germinación de las semillas de una especie está relacionado con las condiciones climáticas y ecológicas a las cuales esa especie está adaptada; en el campo las semillas germinan en condiciones de temperatura y otros factores externos (como son el potencial hídrico, la cantidad y calidad de la luz, la estructura física y la composición química del suelo, entre otros) que favorecen el crecimiento posterior de las plántulas, su sobrevivencia y establecimiento (Probert, 2000).

Para cualquier lote de semillas, sin restricciones de agua, la velocidad de la germinación aumenta en función de la temperatura de un umbral mínimo a un óptimo; una vez rebasada esta *To* la germinación disminuye hacia una *Tc* que representa el límite de su tolerancia (Finch-Savage, 2004) (Fig. 1).

A temperaturas sub-óptimas la velocidad de la germinación muestra una relación lineal con la temperatura lo cual se puede describir con la siguiente fórmula:

$$1/t\ (g) = (T\text{-}Tb)/\theta_{T1}\ (\mathrm{g}) \qquad (1)$$

en donde θ_{T1} (g) es el tiempo térmico para la germinación de (g), *T* es la temperatura a la que se están sometiendo las semillas y 1/t (*g*) es el tiempo requerido para la germinación de (*g*) (Bradford, 1995; Finch-Savage, 2004).

En contraste, a temperaturas supra óptimas la velocidad de germinación disminuye en una serie de líneas paralelas (Fig.1). El intercepto por lo tanto difiere para cada (*g*) y por lo tanto:

$$1/t\ (g) = (Tc\ (g) - T) / \theta_{T2} \qquad (2)$$

en donde θ_{T2} es el tiempo térmico arriba de la *To* y se asume que es constante para cada *g*, ya que todas las líneas paralelas tienen la misma pendiente. *Tc* es la temperatura máxima para la germinación de (*g*) (Bradford, 1995; Finch-Savage, 2004).

De esta manera incorporando una distribución apropiada (distribución normal regularmente) para el θ_{T1} y *Tc* en las ecuaciones anteriores, el tiempo para la germinación bajo cualquier régimen de temperatura constante puede ser calculado para cada fracción porcentual de la población (Bradford, 1995; Finch-Savage, 2004).

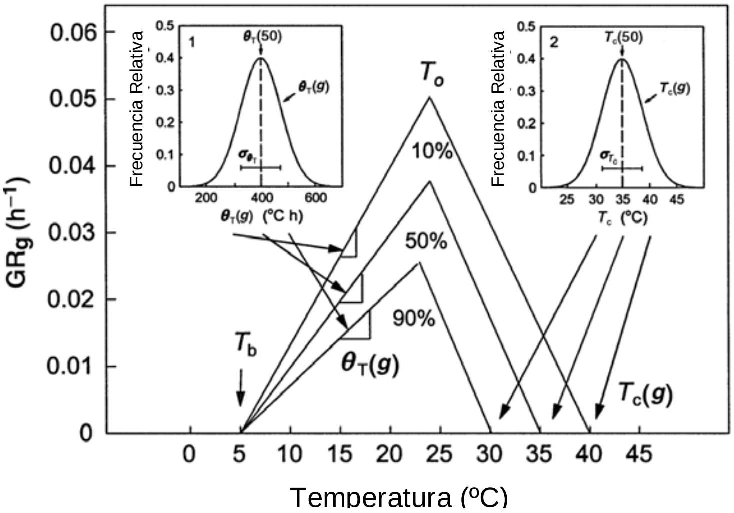

Figura 1. Relación entre la temperatura y la velocidad de germinación (GRg = 1/t*g*). A temperaturas sub-óptimas la velocidad de germinación para diferentes fracciones porcentuales de la población aumenta linealmente a partir de una temperatura base (*Tb*) común para todas las semillas de la población. Las pendientes de las líneas son iguales al inverso del tiempo térmico para la germinación ($1/\theta_T$ (*g*)), las cuales varían entre las semillas de la población en la forma de una distribución normal (recuadro 1). La velocidad de la germinación máxima se presenta en la temperatura óptima (*To*) y rebasando esta temperatura la velocidad de la germinación disminuye linealmente. La temperatura máxima para la germinación (*Tc* (*g*)) varía entre las fracciones porcentuales de la población en una distribución normal (recuadro 2). Modificado de Bradford (2002).

Recientemente se han utilizado los modelos de tiempo térmico para estudiar el efecto que el cambio climático tendría en la respuesta germinativa de algunas especies (Qiu *et al*., 2010; Orrù *et al*., 2012; Porceddu *et al*., 2013). Estos modelos resultan útiles para ayudarnos a entender el rango de distribución de las especies, predecir cambios en la distribución producidas por el calentamiento global y desarrollar estrategias de conservación apropiadas (Qiu *et al*., 2010).

A pesar de su importancia para el reclutamiento de nuevos individuos, producto de la reproducción sexual, el conocimiento de bancos de semillas en zonas áridas es escaso (Kemp, 1989; Kigel, 1995). Los bancos de semillas son importantes en la adaptación de las plantas a los desiertos debido a que algunas condiciones ambientales como la cantidad de precipitación son altamente variables (Archibold, 1995). Ooi (2012) propuso que en las especies de ambientes poco predecibles, como son las zonas áridas, la persistencia de las semillas en el suelo es fundamental y mantener semillas viables entre diferentes episodios de reclutamiento es la principal función de los bancos de semillas. Por otro lado, Thompson *et al*. (1998) encontraron más probable que las semillas de especies anuales y bianuales formen bancos de semillas persistentes que las semillas de especies perennes. Sin embargo, Ehrlen y Lehtila (2002) no encontraron una relación clara entre la presencia de banco de semillas y la esperanza de vida en 71 especies de plantas perennes. En zonas áridas se ha establecido que la formación de bancos de semillas es importante para la permanencia de las plantas anuales y bianuales, mientras que se ha asumido que las especies perennes no necesitan un banco de semillas para permanecer en esos hábitats (Pake y Venable, 1996; Saatkamp *et al*., 2013). La presencia de bancos de semillas representa una estrategia adaptativa de diversificación (bet-hedging) la cual reduce el riesgo del fracaso en la reproducción (Long *et al*., 2015; Saatkamp *et al*., 2013), esta estrategia es el mecanismo evolutivo mejor conocido que conduce al retraso en la germinación y a la evolución en los bancos de semillas en ambientes temporalmente variables e impredecibles (Venable, 2007; Tielbörger *et al*., 2011).

Uno de los grupos más característicos de plantas perennes (de vida larga) en las zonas áridas de América son las cactáceas (Bravo Hollis y Sánchez-Mejorada, 1978). Se han realizado pocos trabajos que estudien sistemáticamente la longevidad ecológica y la presencia de bancos de semillas en cactáceas, aunque se ha propuesto que sus semillas reúnen varias de las características necesarias para formar bancos de semillas persistentes (Rojas–Aréchiga y Batis, 2001). Este grupo es de gran importancia en nuestro país ya que México posee la mayor riqueza de especies y mayor porcentaje de endemismos (Ortega-Baes *et al*., 2010b). Sin embargo, las cactáceas se encuentran fuertemente amenazadas y se ubican dentro de la lista roja de la Unión Internacional para la Conservación de la Naturaleza (IUCN), esta organización sugiere que alrededor de un tercio de las especies de todo el taxón están amenazadas o en peligro de extinción (Hawkins *et al*., 2008). Adicionalmente, se ha reconocido a las cactáceas como uno de los grupos más susceptibles al cambio climático, debido a que estas presentan ciertas características como: rangos restringidos de distribución (tales como las especies raras y endémicas), largos periodos de generación y gran especialización al hábitat/nicho (Gran Canaria Group, 2006). En el caso de México, Téllez-Valdés y Dávila-Aranda (2003) realizaron proyecciones de patrones de distribución utilizando diferentes escenarios de cambio climático y encontraron una drástica contracción en la distribución de varias especies de cactáceas en el Valle de Tehuacán-Cuicatlán. En particular predijeron una reducción del 95 % en la distribución actual de las especies del género *Polaskia*, cuando la temperatura ambiental aumente 2 °C y la precipitación disminuya 15 %.

Estudios demográficos en algunas cactáceas demuestran que el mantenimiento de las poblaciones depende principalmente de la sobrevivencia de las plantas adultas (Esparza-Olguín *et al*., 2002; 2005; Godínez-Alvarez *et al*., 1999; Mendez *et al*., 2004; Valverde *et al*., 2004). Sin embargo, Mandujano *et al*. (2007a) sugieren que el reclutamiento esporádico en *Opuntia macrocentra* puede ser suficiente para mantener la estabilidad de la población y evitar la depresión endogámica. Por lo tanto, la principal función de los bancos de semillas en cactáceas parece estar relacionado al mantenimiento de la diversidad genética, para probar esta hipótesis es necesario saber primero si una fracción de las semillas es capaz de persistir en el suelo durante un periodo largo, producir plántulas en más de una temporada de germinación y para estas plántulas sobrevivir hasta la edad reproductiva. Por otro lado, considerando que la temperatura es un factor fundamental en el proceso de germinación y, por lo tanto, en la longevidad ecológica, es necesario predecir el efecto que el aumento en la temperatura producido por el calentamiento global puede tener en la germinación y en la dinámica del banco de semillas en las cactáceas. Adicionalmente, un elemento que podría influenciar estos procesos es el fenómeno de facilitación, ya que se ha reconocido ampliamente que la presencia de plantas nodriza promueve la germinación de las semillas y el establecimiento de las plántulas de cactáceas, debido a que su dosel disminuye características ambientales adversas tales como la alta temperatura del aire y del suelo, entre otras (Godínez-Alvarez *et al*., 2003; Sosa y Fleming, 2002; Valiente-Banuet y Godínez-Alvarez, 2002), por lo cual la facilitación también podría tener algún efecto en la formación y la dinámica del banco de semillas en cactáceas.

Tomando en cuenta lo anteriormente expuesto en este trabajo se abordaron las siguientes hipótesis:

1) Las semillas de *Polaskia chende* poseen características morfológicas y/o fisiológicas que les permiten formar bancos de semillas persistentes de largo plazo.

2) El aumento en la temperatura producido por el calentamiento global puede modificar la repuesta germinativa en las especies del genero *Polaskia*.

Los objetivos de este trabajo fueron: determinar la longevidad ecológica y generar un modelo de tiempo térmico para la germinación de las semillas del género *Polaskia*. Para presentar la información y los resultados de manera más organizada y sistematizada se estructuró la tesis en dos capítulos. En el primer capítulo se estudió la capacidad de las semillas de *Polaskia chende* para formar un banco de semillas persistentes de largo plazo. Solamente se trabajó con esta especie porque durante el año de colecta no se pudieron obtener suficientes semillas de *P. chichipe* para el estudio de banco de semillas. Se determinó si las semillas de *P. chende* presentan características relacionadas con la persistencia en el suelo y se determinó la longevidad de sus semillas enterradas durante un periodo de un mes a cinco años. Adicionalmente, se evaluó la emergencia y la sobrevivencia de las plántulas en el campo y se estableció si esta especie presenta facilitación por plantas nodriza. En el segundo capítulo se estudió el efecto de la temperatura en la germinación de *P. chende* y *P. chichipe*. Se determinaron las temperaturas cardinales y el tiempo térmico necesarios para la germinación de las semillas de ambas especies. Finalmente, se predijo el efecto del aumento en la temperatura del suelo producido por diferentes escenarios de cambio climático en la germinación, en condiciones de dosel y sin dosel.

CAPÍTULO 1

Soil seed bank, seedling emergence and survival of *Polaskia chende* (Rol-.Goss.) A.C. Gibson & K.E. Horak (Cactaceae).

Soil seed bank, seedling emergence and survivorship of *Polaskia chende* (Cactaceae)

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Abstract

Soil seed banks are essential elements of plant population dynamics, enabling species to maintain genetic variability, withstand periods of adversity and persist over time. However knowledge of the soil seed bank in cactus species is scanty. Early stages of the cactus life cycle such as seedling emergence and survivor are important for the maintenance of cactus populations in the field. In this study, we investigated the ability of *Polaskia chende* seeds to form a long-term persistent seed bank, evaluated seedling emergence and survivorship and established nurse plant facilitation. *P. chende* seeds were found to form long-term persistent soil seed banks. The timing of germination in the field was regulated by the interaction of light, temperature and soil moisture, and seeds entered secondary dormancy at specific times according to the expression of environmental factors, demonstrating an irregular dormancy cycling. *P. chende* established nurse plant facilitation with *Acacia constricta*, which strongly promoted seedling survival.

Key words: Photoblastism, seed persistence, ecological longevity, facilitation, dormancy cycling, cacti.

Introduction

The viable seeds available for potential germination and recruitment of new plants constitute the seed bank (Baskin and Baskin, 1998). This plays a key role maintaining the dynamics and regeneration of plant populations (Harper, 1977). According to Bakker *et al.* (1996) and Thompson *et al*. (1997) seeds form three classes of soil seed banks: transient species persist in the soil for less than one year, short-term persistent species persist in the soil for at least one year but less than five years and long-term persistent species persist in the soil for at least five years. Seed persistence is the survival of seeds in the environment from maturity on the parent plant to the time they germinate, die or are predated (Long *et al*., 2015). This trait is species-specific and promotes the entry and maintenance of seeds in persistent soil seed banks (Fenner and Thompson, 2005). It has been considered that species forming persistent soil seed banks have certain characteristics such as small size (Thompson *et al*., 1993), a light requirement for germination (Baskin and Baskin, 1998; Pons, 1991), primary dormancy and seasonal cycles of dormancy (Baskin and Baskin, 1998; Probert, 2000). In addition, seeds of these species should be able to preserve viability and to avoid predation in the soil (Murdoch, 2006).

Seeds that possess one or more of these characteristics are buried by physical (e.g. rainfall) or biological (e.g. animals) factors and can prevent or delay germination during one or more seasons. To delay the germination of a fraction of seeds after dispersal is a bet-hedging strategy against the risk of reproductive failure (Saatkamp *et al*., 2014; Long, 2015). In this way, seeds can persist in the soil during different periods of time, where the time that seeds remain viable in the soil under the influence of the natural environment represents its ecological longevity (Vázquez-Yanes and Orozco-Segovia, 1996). Thereby, the ecological longevity depends largely on the formation of a persistent seed bank and on the environmental factors that lead to germination.

Unpredictable environments, such as deserts, promote the evolution of persistent seed banks (Saatkamp *et al*., 2014) because of environmental heterogeneity which makes seed banks highly variable in space and time (Kemp, 1989; Thompson, 1987). Knowledge of seed banks in desert environments has focused on annual species (Cohen, 1966; Tielbörger *et al*., 2011; Venable, 2007; Gremer and Venable, 2014), and as a consequence, there is a lack of information about long-lived perennial species (Auld, 1995; Montiel and Montaña, 2003). This may be because perennial species are less reliant on persistent soil seed banks to maintain their populations (Fenner and Thompson, 2005).

One of the most characteristic species of long-lived perennials in American deserts are cacti. There are some studies about cactus soil seed banks (Álvarez-Espino *et al*., 2014; Bowers, 2000 and 2005; Cheib and Garcia, 2012; De Viana, 1999; Goodman *et al*., 2012; Holland and Molina-Freaner 2012; Montiel and Montaña, 2003; Olvera-Carrillo *et al*., 2009), from which there have been several reports that seeds of cacti have the potential to form persistent soil seed banks, but most studies did not test seed longevity in the soil for long periods of time in order to search for long-term persistent seed banks.

Demographic studies of cactus species showed that their population dynamics depend mainly on adult survival (Esparza-Olguín *et al*., 2002; 2005; Godínez-Alvarez *et al*., 1999; Mendez *et al*., 2004; Valverde *et al*., 2004). In fact, some authors have shown through matrix projection models that increasing the size of the soil seed bank has little effect on the population growth rate (Mandujano *et al*., 2007a; 2007b; 2015). On the other hand, Mandujano *et al.* (2007a) suggested that sporadic sexual recruitment in *Opuntia macrocentra* may be sufficient to maintain a stable population and to avoid the effects of inbreeding depression. Therefore, the main role of soil seed banks in cacti seems to be related to the maintenance of genetic diversity through recruitment of few, but new, individuals. To test this hypothesis, it is necessary to know first if a fraction of seeds is able to persist in the soil long-term, to produce seedlings in more than one germination season and for these seedlings to survive until reproductive age.

Germination and seedling establishment are the highest-risk phases in the life cycle of plants (Harper, 1977). In the case of cactus species the main factors that affect seed germination are water, temperature and light (Godínez-Alvarez *et al*., 2003). Valiente-Banuet and Godínez-Alvarez (2002) have indicated that the early stages of the life cycle of cacti, which include the successful production of seeds, their dispersal and germination, seedling establishment and the survivorship of seedlings and juveniles, are essential for the maintenance of cactus populations in the field. Studies under natural conditions have shown that seedling emergence and survival of cacti improve under the canopy of perennial plants (Godínez-Alvarez *et al*., 2003; Sosa and Fleming, 2002; Valiente-Banuet and Godínez-Alvarez, 2002,) or rocks (Munguía-Rosas and Sosa, 2008; Olvera-Carrillo *et al*., 2009; Peters *et al*., 2008). These perennial nurse plants may facilitate the establishment of other plants by ameliorating harsh environmental characteristics (Callaway, 1995) like soil and air temperature, intensity and composition of solar radiation, evaporation, evapotranspiration and soil moisture (Godínez-Alvarez *et al*., 2003; Sosa and Fleming, 2002; Valiente-Banuet and Godínez-Alvarez, 2002).

In this study we investigated the ability of *Polaskia chende* seeds to form a long-term persistent seed bank, evaluated seedling emergence and survivorship, and established nurse plant facilitation. The objectives of this work were: (1) to establish if *P. chende* present seed characteristics related to persistence in the soil, (2) to determine the persistence of buried *P. chende* seeds during five years, under shrub canopy and in open areas, and (3) to determine seedling emergence and survival during five years, under shrub canopy and in open areas.

Materials and Methods

Plant material and study site

The genus *Polaskia* Backeb is endemic to the Tehuacán-Cuicatlán Biosphere Reserve. According to Valiente-Banuet *et al*. (2000), *P. chende* is a dominant element of the thornscrub forest type called ‘‘chichipera’’ and is restricted to volcanic soils at elevations of 1700–2300 m. A population of *P. chende* was located between San Luis Atolotitlan and Caltepec villages in the municipality of Caltepec state of Puebla, Mexico. Twenty percent of available mature fruits of 15 wild individuals were collected in April 2008 at the time of seed dispersal. Monthly averages of minimum, maximum, mean temperatures and rainfall were obtained for the study site from Caltepec climatic station (SMN) from January 2008 until December 2013 (Fig.1).

Seed cleaning and determination of seed mass

Seeds were manually removed from the pulp, washed with tap water, and air-dried in darkness at room temperature (20 ± 1 ^{o}C). To quantify seed mass, fifteen replicates of a dry seed were weighed on an analytical balance.

Germination tests

Seeds were sown onto 1% agar in 50 mm diameter Petri dishes, twenty five seeds per treatment (n=4), and incubated inside growth chambers at 25 ^{o}C ± 1 and 12 hrs photoperiod under white light (WL), far-red light (FRL) and darkness. To provide WL fluorescent cool white lamps (4100K Sylvania, 32 W) and incandescent lamps (General Electric, 25 W) (R:FR 1.7; 30.63 μmol m-^{2} s-^{1}) were used. To provide darkness Petri dishes were wrapped with five layers of aluminium foil. To provide FRL, the Petri dishes were placed inside boxes (34 x 44 x 10 cm) made with red and blue Plexiglass (Series Nos. 2424 and 2423 respectively; Rohm and Hass, México; R:FR= 0.05, PFD= 9.74 μmol m^{-2}s^{-1}). Germination was recorded every day until 50 days of incubation, where seeds were considered germinated when radicle emergence was ≥ 2 mm length, after which seeds were removed from the Petri dish. A portion of the seeds that did not germinate from each treatment were subjected to a cutting test, all treatments showed a viability above 90%.

Seed storage in the laboratory

Seeds were stored in the laboratory at 10 °C and 30 % RH in darkness. Freshly collected seeds were sown under WL, FRL and darkness. Thereafter, seeds were sown from 1 to 19 months age under WL and FRL. The experimental design was a random factorial arrangement with three light conditions for freshly collected seeds and two light conditions during 19 months.

Seed burial in the soil

Seeds were buried one month after collection, before the start of the rainy season. One hundred seeds were placed inside each of 320 nylon bags (5 x 5 cm). Forty nylon bags were buried 1 cm deep in four open areas and another 40 nylon bags beneath the canopy of four *Acacia constricta* shrubs (which was the most common shrub in the area). Two bags at each burial site, open areas (OA) and shrub canopy (SC), were exhumed every two months during the first 18 months. During the next four years one bag at each burial site was exhumed in the dry season and another at the end of the rainy season. Enough bags were buried to compensate for predation. Exhumed seeds were covered with aluminium foil during exhumation and wrapped, transported to the laboratory and subjected to a germination test within one week after exhumation. Exhumed seeds for the first 18 months were germinated under white light and far-red light. Thereafter, exhumed seeds were germinated just under white light. Stored seeds in the laboratory of the same age as those exhumed from the field were sown to have a control group. The experimental design was a random factorial arrangement with two light and three environmental conditions during the first 18 months, and one light and three environmental conditions during the next years.

Seedling emergence and survival in the field

Under the canopy of the four *A. constricta* shrubs and four open areas, a metal cage (30 x 30 x 15 cm) was placed on the soil surface. Inside the cage was a smaller metal cage (15 cm ø x 10cm) covered with a 100 μm nylon mesh to avoid seed predation and contamination by the seed rain. In July 2008, 100 seeds were sown on the soil surface within the smaller cage and seedling emergence was recorded weakly during the first month, every 15 days during the next two months, monthly until a year was completed and then every four months during the next four years. Once seedlings emerged they were transplanted outside the smaller cage but inside the larger cage. The time when cumulative seedling emergence was higher during the first rainy season was considered the beginning of the survival experiment and the number of seedlings transplanted until this date was the whole population evaluated. Any new seedling emerged thereafter was discarded to avoid affecting monitoring of seedling survival. Seedling survival was recorded every two weeks during the next two months, monthly until complete a year and every four months since then. The number of survivor seedlings was expressed as a percentage. The experimental design was a random factorial arrangement with two environmental conditions.

Statistical Analysis

Cumulative germination percentages were arcsine transformed and fitted to an exponential sigmoid function ($y= a/\{1+b\exp[-cx]\}$), the coefficient of determination R^2 was higher than 0.96 in all fitted curves. The first derivative along the exponential sigmoid curve was fitted to a Gaussian model ($Y= a+b\exp(-0.5[\{x-c\}/d]^2)$) to obtain mean germination time (MGT) using Table Curve 2D, (v. 3 AISN Software, Chicago, IL, USA). Survivorship curves were fitted to a logistic function ($y= a+b/(1+[x/c]^d$) to obtain mean survival time (st_{50}; time in days required to reach 50% mortality of emerged seedlings) using Table Curve 2D. Final germination, emergence and survival percentage and st_{50} were analysed by Multi-factor ANOVA followed by Tukey's HSD test ($p< 0.05$) using

STATGRAPHICS Centurion XV (v. 15. 1. 02. StatPoint Technologies, Inc. U.S.A.). Percentages were arcsine transformed for normality (Sokhal and Rholf, 1995), arcsine transformation fulfilled variance test assumptions in all treatments (Bartlett´s test $p > 0.05$). MGT was analysed with Kruskal–Wallis tests ($p < 0.05$) and visually compared with box-and-whiskers plots using STATGRAPHICS Centurion XV because normality and homoscedasticity were not fulfilled.

Results

Climate data of the study site

The minimum, maximum and mean annual temperatures were (6.2, 31.9 and 18.7 ^{o}C, respectively) and the annual rainfall was 455.4 mm. The rainy season began at the end of April and finished at the beginning of October and the remaining months comprise the dry season (Fig. 1)

Germination of seeds stored in the laboratory

The mean mass of one air-dried seed was 0.78 mg $\underline{+}$ 0.11 mg (SE). Freshly collected seeds show significant difference in final germination ($F_{(2, 11)} = 471.85$, $P < 0.00001$) and MGT ($H = 10.24$, $P = 0.0059$) in response to light condition. Seeds germinated 70 % in white light, 37 % in far-red light and no germination was observed at darkness (Fig. 2A). MGT showed a difference of four days in WL in relation to FRL (8 and 12 days, respectively) (Fig. 2A). Final seed germination of seeds stored in the laboratory during 19 months was significantly different in age and light; interaction between both factors was also significant (Table 1). A positive relationship was found between germination percentage and age during the first seven months of storage, when seeds were exposed to far red light (Fig. 2B). The MGT was affected by age ($H = 73.12$, $P < 0.0001$) but not by light ($H = 0.51$, $P = 0.47$).

Seed longevity in the soil

The germination behaviour of exhumed seeds from OA and SC showed a marked decrease at twelve months of burial, at which the lowest germination percentage was found in both burial conditions, and after this time, germination of seeds buried under SC gradually increased to around 90 % in WL and 40 % in FRL at 18 months (Fig. 3A and 3B). The final percentage of germinated seeds after 18 months of burial was significantly different in age, light and environmental condition; interactions among all factors were also significant (Table 1). In contrast to the percentage of germination, the MGT showed the highest value at twelve months of burial (Fig. 3C). MGT was significantly different in environmental condition ($H = 45.60$, $P < 0.00001$) and time of burial ($H = 40.93$, $P < 0.00001$) but there was no significant difference in light condition ($H = 0.06$, $P = 0.80$).

Over 64 months, the germination of seeds following burial was strongly affected by environmental condition ($F_{(2,119)} = 293.24$, $P < 0.0001$). Tukey's test showed differences from 36 to 48 months among SC and laboratory storage in relation to OA. During the first 28 months of burial seed germination was similar between both environmental conditions, however at 36, 40 and 48 months very low or no germination was found in OA, but seeds germinated again around 40% from 52 to 64 months of burial (Fig. 4). On the contrary seeds buried under SC germinated above 60% from 16 months to the end of the experiment (Fig. 4). The effect of time of burial and the interaction between both factors was significant too ($F_{(9,119)} = 41.98$, $P < 0.0001$; $F_{(18,119)} = 15.9$, $P < 0.0001$ respectively) Tukey's test showed differences in all treatments of seeds buried during 24 months to seeds buried during 64 months.

Seedling emergence and survival

During the first rainy season, cumulative seedling emergence was lower and faster in OA (24 % at 1 month) than under SC (33 % at 1.5 months) (Fig. 5). In OA the maximum emergence (34 %) was reached at 58 months; meanwhile under SC the maximum emergence (61 %) was reached at 50 months (Fig. 5). This represents an increase of 85 %

under SC and 42 % in OA throughout more of four years. The effect of environmental condition and time on seedling emergence was significant ($F_{(1,231)} = 108.74$, $P < 0.0001$; $F_{(1,231)} = 12.66$, $P < 0.0001$ respectively); interaction between both factors was also significant ($F_{(28,231)} = 1.67$, $P = 0.026$).

Seedling survival was strongly affected by the environmental condition ($F_{(1,215)} = 486.12$, $P < 0.0001$). Seedlings which emerged on OA decreased in survivorship from 100 to 47 % in just one month (Fig. 6). By 20.5 months all seedlings which emerged on OA died whereas 28 % of seedlings survived under SC. Seedlings under SC persisted until the end of the experiment, where 6 % survivorship was recorded at 60.5 months (Fig. 6). The seedling mean survival time (st_{50}) was significantly affected by the environmental condition ($F_{(1,6)} = 20.09$, p= 0.006). Seedlings which emerged beneath nurse plants survived longer ($st_{50} = 12.20 \pm 3.8$ months) than seedlings which emerged on open areas ($st_{50} = 0.76 \pm 0.68$ months) (Fig. 7). The logistic regression equations of survivorship curves showed values of $r^2 > 0.96$ and $r^2 > 0.93$ under SC and in OA, respectively.

Discussion

Light is an important germination cue for stimulating germination across time and space (Fenner and Thompson 2005). The lack of germination in darkness showed that seeds of *P. chende* are positively photoblastic (Fig. 2A). Positive photoblastism is a common trait of some cactus seeds (Benítez-Rodríguez *et al.*, 2004; Flores *et al.*, 2006; Flores *et al.*, 2011; Ortega-Baes *et al.*, 2010; Rodríguez-Ortega *et al.*, 2006; Rojas-Aréchiga and Vázquez-Yanes, 2000; Rojas-Aréchiga *et al.*, 1997; Rojas-Aréchiga *et al.*, 2012; Seal *et al.*, 2009; Yang *et al.*, 2003) and has been linked to a low seed mass in cacti (Flores *et al.*, 2006; Flores *et al.*, 2011; Ortega-Baes *et al.*, 2010), but not in the Cacteae tribe (Rojas-Aréchiga *et al.* 2012), and across a wider range of species (Grime *et al.* 1981; Milberg et al. 2000; Pons 2000). Seed photoblastism in cacti has also been linked to plant traits such as taxa, dispersal syndrome and plant height, which agree with this study as *P. chende* belongs to the Pachycereeae tribe, have endozoochory dispersal and the plant height is less than four meters (Flores *et al*., 2011). A light requirement for germination is one characteristic of seeds which form a persistent soil seed bank (Baskin and Baskin, 1989; Pons, 2000).

Seed germination at zero months in white light was significantly lower than older seeds in this light condition (Figure 2B). Some authors have suggested that freshly mature dormant seeds have primary dormancy, which has been induced by ABA during seed maturation on the mother plant (Hilhorst, 1995; Kucera *et al*., 2005). One of the functions of primary dormancy is to allow temporal dispersal of seeds to prevent germination near the mother plant (Murdoch and Ellis, 2000). Although one month is a short period, it can be considered that *P. chende* seeds need an after-ripening period to overcome dormancy and achieve a physiological maturity, a requirement which has been reported in some cactus species (Zimmer, 1967, 1969, 1980, cited by Rojas–Aréchiga and Batis, 2001; Mandujano *et al*., 1997; Bowers, 2000, 2005; Rojas-Aréchiga *et al*., 2001; De la Barrera and Nobel, 2003; Flores *et al*., 2004). Removal of seed dormancy by after-ripening takes place because of a decrease in ABA concentration and sensitivity and an increase in GA sensitivity (Finch-Savage and Leubner-Metzger, 2006).

Although freshly collected seeds of *P. chende* germinated to the highest proportion under WL, seeds also achieved germination under FRL albeit at a lower percentage and increased MGT, similar to that found in *Mammillaria haageana* and *M. carnea* (Benítez-Rodríguez *et al*., 2004); *Pilosocereus arrabidae* (Martins *et al*., 2012); *Opuntia tomentosa* (Olvera-Carrillo *et al*., 2009); *Trichocereus terscheckii* (Ortega-Baes and Rojas-Aréchiga, 2007*);* *Echinocactus platyacanthus* and *Ferocactus flavovirens* (Rojas-Arechiga *et al* 1997). The ability to achieve some germination under FRL extends the germination window to include seeds slightly buried in the soil and under shrub canopies where the availability of water for seed imbibition is high. It was also noted that seeds of *P. chende* became more sensitive to far-red light during the first seven months of storage in the laboratory (Fig. 2B), to our knowledge, this is the first report of this behaviour in cactus species. Delaying germination could be advantageous to seedling establishment in two ways: (1) as seeds are dispersed during the dry season (at the end of March to the end of April), waiting several months would coincide with the peak of the wet season (e.g., precipitation increases by around 300 % in August-September), and (2) the shrub canopy is more developed during the wet season than in the dry season which promotes seedling emergence and survivorship. Seed persistence enables germination to occur over time, avoiding unfavourable conditions for germination and seedling establishment, a so-called bet-hedging strategy (Long *et al.*, 2015). Thus the effects of light in the germination of *P. chende* suggest that this factor regulates the timing of germination in the field under different environmental conditions.

Seed mass has been a good predictor of seed persistence in the soil for British (Hodkinson *et al.*, 1998), Argentinean (Funes *et al.*, 1999), Iranian (Thompson *et al.*, 2001), Italian (Cerabolini *et al.*, 2003) and Spanish (Peco *et al.*, 2003) vegetation. Seeds of less than 3 mg are predicted to persist for a long-term in the soil (Thompson *et al*. 1993). Here, the seed mass of *P. chende* was well within this threshold (0.78 mg ± 0.11 mg) and germinated well after more than five years (Fig.4), thus forming a long-term persistent soil seed bank. There is only one previous report for long-term persistent soil seed bank in cacti with seedlings of *Mammillaria grahamii*, however the author did not rule out the possibility that seeds could have been introduced accidentally to the plots (Bowers, 2005). In this study, care was taken to exclude accidental introductions of seeds with the addition of a nylon mesh to a cage set up. Short-term persistent soil seed banks have been found for some cacti, including *Stenocereus stellatus* (Álvarez-Espino *et al.*, 2014); *Ferocactus wislizeni* (Bowers, 2000; 2005); *Arthrocereus glaziovii*, *A. melanurus* subsp. *magnus* and *A. melanurus* subsp. *odorus* (Cheib and Garcia, 2012); *Trichocereus pasacana* (De Viana, 1999); *Harrisia fragrans* (Goodman *et al.*, 2012); *Opuntia rastrera* (Montiel and Montaña, 2003) and *O. tomentosa* (Olvera-Carrillo *et al.*, 2009), and a transient seed bank has been found in *Carnegiea gigantea* (Bowers, 2005) and *Pachycereus schottii* (Holland and Molina-Freaner 2012).

Low germination of seeds buried under SC and in OA at 12 months (Fig. 3) and in OA from 36 to 48 months (Fig. 4) suggested that seeds entered secondary dormancy. Some environmental factors like anaerobic atmospheres, soil moisture, water potential, temperature and light have been shown to induce secondary dormancy of seeds in the soil (Benech-Arnold *et al*. 2000; Bewley *et al*., 2013; Murdoch and Ellis, 2000; Probert, 2000). The decrease in germination during these months was unrelated to a seasonal dormancy cycle based on the climate data, thus *P. chende* seeds follow an irregular dormancy cycling that seems to be a product of various environmental factors acting simultaneously or sequentially. For instance, the soil temperature of unshaded areas during the hot and dry season of 2012 oscillated between 13 ^{o}C to 60 ^{o}C and remained above 43 ^{o}C for around 5 hours each day (data not shown). During the hot and rainy season of 2012, the soil temperature of unshaded areas showed daily oscillations of around 33 ^{o}C (a minimum of 17 ^{o}C and maximum of 50 ^{o}C) and remained above 43 ^{o}C for 5 hours each day (data not show) which might induce thermodormancy (Corbineau *et al*., 1993; Small and Gutterman, 1991). This is consistent with Kigel (1995) who suggested that large daily soil temperature oscillations (30-40 ^{o}C) may affect seed dormancy in warm deserts. In addition, the low soil water potential, as a consequence of the high temperatures and the absence of precipitation, in combination with the very-low-fluence response (VLFR) occurring under few mm of the soil may induce dark dormancy (Khan and Karssen, 1980; Pons, 1991). According to Pons (1991) dark dormancy is a mechanism for avoidance of germination in the soil and hence, for the formation of a persistent seed bank. It is likely that more than one kind and or state of dormancy may be present in *P. chende* seeds at specific times of the year according to the expression of environmental factors, demonstrating seed dormancy cycling in cactus species for the first time.

Seedling emergence in the field is regulated by two environmental factors, water and temperature (Bewley *et al*., 2013; Finch-Savage, 2004). For the first month, rainfall promoted the emergence of *P. chende* seedlings which was initially highest in OA than under SC. The higher germination rate in OA than under SC was due to the higher temperatures presented in OA, where Ordoñez-Salanueva *et al*., (2015) reported a difference of 1.65 days in the time required to reach 50 % germination. However, in the long term, seedling emergence was twice as high under SC than in OA. The promoting effect of nurse plants in seedling emergence was reported in some cacti species including *Stenocereus thurberi* (Nolasco *et al*., 1997), *Opuntia tomentosa* (Olvera-Carrillo *et al*., 2009) and *Neobuxbaumia tetetzo* (Valiente-Banuet and Ezcurra, 1991). The last emergence event of the study took place at 50 months beneath SC and at 58 months in OA, showing that seeds of *P. chende* have a long ecological longevity and form a persistent seed bank. In addition, seedling emergence in this study showed that seeds are able to germinate in more than one germination season and therefore a cohort of seeds are able to produce more than one cohort of seedlings (Baskin and Basking, 2014). Moreover, seedlings that emerged after the first germination season were more vigorous and survive longer than seedlings that emerged in the first germination season (personal observation), thus persist in the seed bank for some time seems to enhance competitiveness of seedlings in this species.

Survivorship curves of *P. chende* seedlings growing in OA and beneath SC showed a type III shape, like most cactus species (Godínez-Alvarez *et al*., 2003). Seedling survival was strongly affected by SC; st_{50} was sixteen times slower under SC than in OA (Fig. 7). In this study st_{50} in OA was faster than that reported by Flores *et al* (2004) in two columnar succulents, but it was slower beneath SC than st_{50} reported by the same authors. These results support the findings that cactus species survive better beneath nurse plants than in the open areas (Esparza-Olguín *et al*., 2002; Godínez-Alvarez *et al*., 1999; Holland and Molina-Freaner, 2012; Mandujano *et al*., 1998; McAuliffe, 1984; Munguía-Rosas and Sosa, 2008; Nobel, 1988; Nolasco *et al*., 1997; Turner *et al*., 1966; Valiente-Banuet and Ezcurra, 1991). Although, some authors did not find differences between both environmental conditions in *N. tetetzo* and *P. hollianus* (Flores *et al*., 2004); *N. mezcalaensis* and *N. macrocephala* (Miquelajauregui and Valverde, 2010) and *Cylindropuntia leptocaulis* (Flores-Torres and Montaña, 2012). It has been suggested that the shade provided by nurse plants ameliorate abiotic conditions (Sosa and Fleming, 2002), specifically reduce evapotranspiration and buffer extreme temperatures (Godínez-Alvarez *et al*., 2003). Meanwhile, Holland and Molina-Freaner (2012) suggested that nurse plant facilitation of germination and initial seedling recruitment in *Pachycereus schottii* depended on rainfall. According to Callaway (1995) facilitation is a positive interaction where one species enhances the survival, growth or fitness of another; in this work the results obtained about seedling emergence and survival support the association between *A. constricta* and *P. chende*.

5. Conclusion

In summary, this study provides evidence that *P. chende* seeds are able to form long-term persistent soil seed banks. A fraction of seeds persist in the soil for long-term showing a long ecological longevity, which allows that seeds to produce seedlings in more than one germination season. Seeds in the soil seed bank enter secondary dormancy and show an irregular dormancy cycling. Seedling emergence and survival are enhanced by shrub canopy and therefore *P. chende* establish nurse plant facilitation with *A. constricta*.

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Tables and Figures

Table 1. Analyses of variance

Effects of age and light on final germination percentage of seeds stored in the laboratory

Source of variation	ss	df	*F*- value	*P*-value
Age (A)	7910.85	10	17.39	**<0.0001**
Light (L)	1206.82	1	26.52	**<0.0001**
A x L	2865.57	10	6.3	**<0.0001**
Error	3003.2	66		

Effects of age, light and environmental condition on final germination percentage of exhumed seeds

Source of variation	ss	df	*F*-value	*P*-Value
Age (A)	21606.6	8	82.3	**<0.0001**
Light (L)	15644.5	1	476.71	**<0.0001**
Environmental condition (EC)	42053.2	2	640.71	**<0.0001**
A x L	1515.5	8	5.77	**<0.0001**
A X EC	8033.81	16	15.3	**<0.0001**
L x EC	6684.66	2	101.85	**<0.0001**
A x L x EC	3144.66	16	5.99	**<0.0001**
Error	5316.47	162		

Significant P values less than 0.05 are in boldface

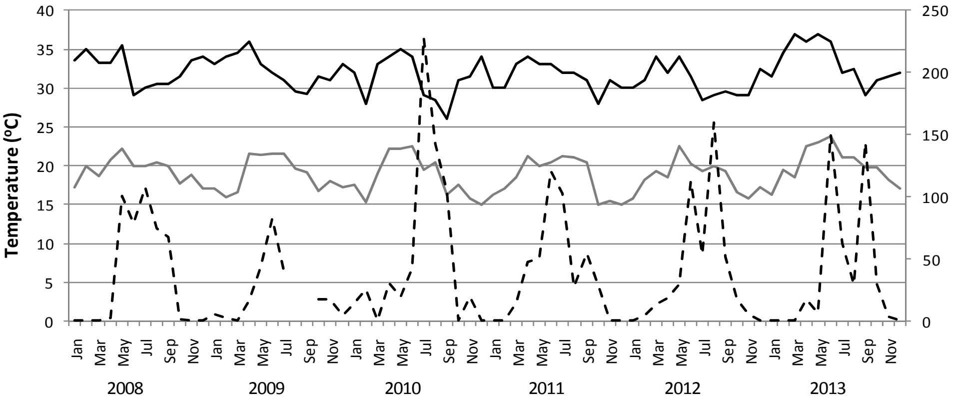

Figure 1. Climatic data from the study site. Monthly average for maximum temperature (black line), mean temperature (grey line) and rainfall (dashed line).

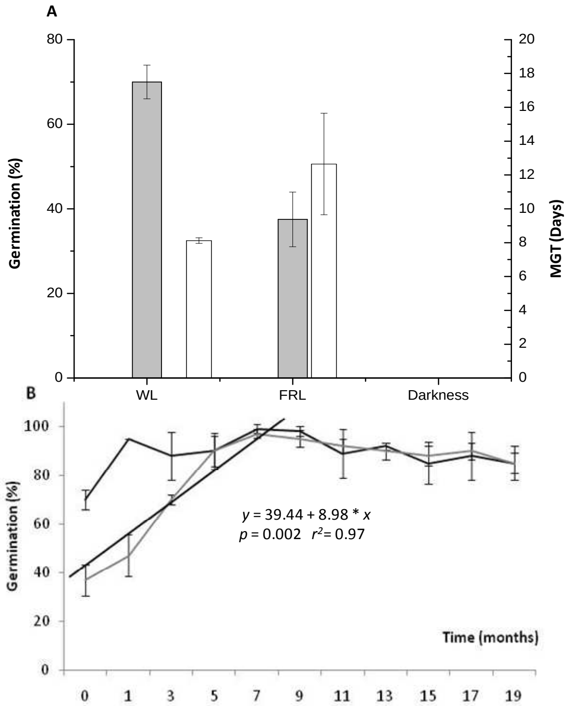

Figure 2. (A) Effect of light on final germination percentages (grey bars) and mean germination time (MGT) (white bars) of freshly collected seeds, germinated under white light (WL), far-red light (FRL) and darkness. (B) Effect of age and light condition on final germination percentages of seeds stored in the laboratory, germinated under white light (black line) and far red light (grey line). Line regression indicates the correlation between time of storage in the laboratory and germination during the first seven months. Data are means ± s.e. for 4 x 25 seeds per treatment.

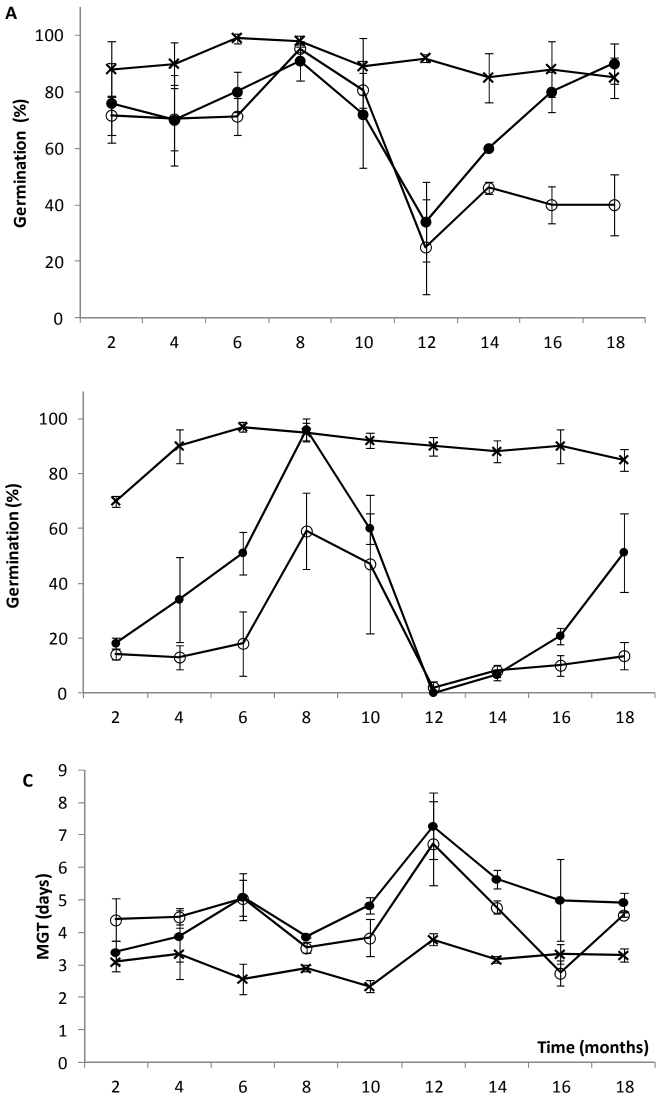

Figure 3. Percentages of final germination in white light (A), far-red light (B) and mean germination time in white light (C) during the first 18 months of burial. Symbols are: seeds buried under shrub canopy (closed circles), seeds buried in open areas (open circles) and seed stored at laboratory (cross). Data are means ± s.e. for 4 x 100 seeds per treatment.

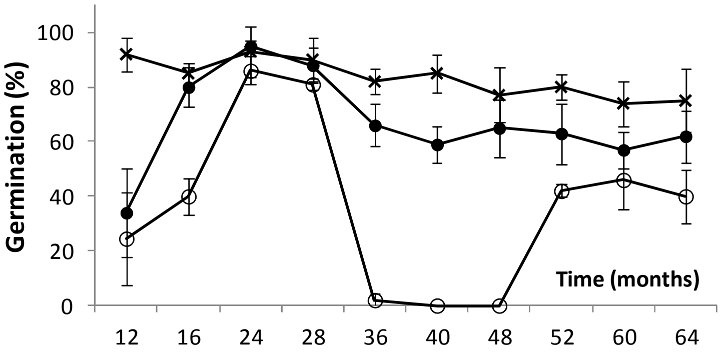

Figure 4. Percentages of final germination of seeds buried during 64 months for seeds buried under shrub canopy (closed circle), seeds buried in open areas (open circle) and seeds stored at laboratory (cross). Data are means ± s.e. for 4 x 100 seeds per treatment.

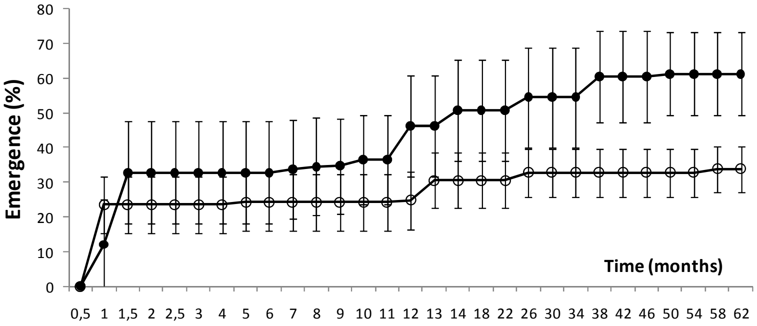

Figure 5. Seedling emergence of seeds during 62 months under shrub canopy (closed circles) and in open areas (open circles). Data are means ± s.e. for 4 x 100 seeds per treatment.

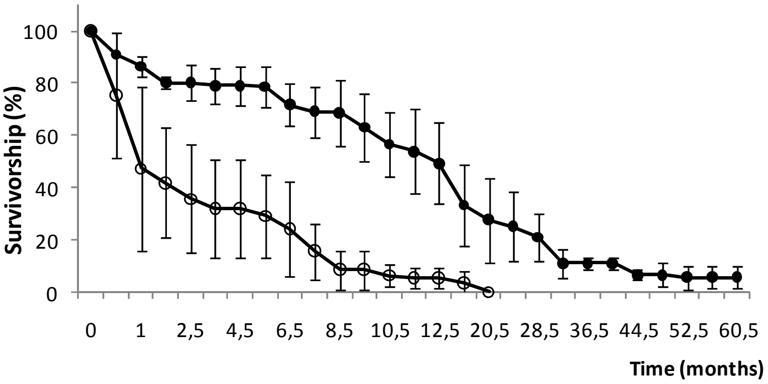

Figure 6. Seedling survival during 60.5 months under shrub canopy (closed circles) and in open areas (open circles). Data are means ± s.e. for 4 x 100 seeds per treatment.

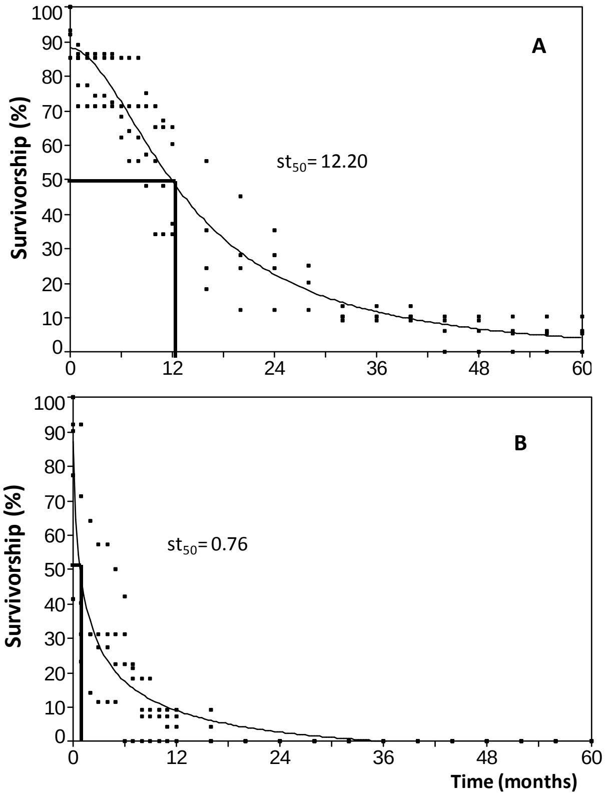

Figure 7. Survivorship curves fitted to a logistic function (y= a+b/(1+[x/c]^d) to obtain mean survival time (st$_{50}$) under shrub canopy (A) and in open areas (B). Points are observed values and line are estimated values.

CAPÍTULO 2

Cardinal temperatures and thermal time in *Polaskia* Backeb (Cactaceae) species: Effect of projected soil temperature increase and nurse interaction on germination timing.

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Cardinal temperatures and thermal time in *Polaskia* Backeb (Cactaceae) species: effect of projected soil temperature increase and nurse interaction on germination timing.

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Abstract

Cardinal temperatures and thermal time are useful tools to quantify the impact of climate change on plant developmental processes such as seed germination. In this study, we quantified the thermal germination behavior of two cactus species and predicted the effect of increased soil temperature (under a shrub canopy and in unshaded areas) on germination timing under projected climate change scenarios. To achieve these aims, seeds of both species were germinated across a range of temperatures from 5 to 40 °C, and a probit cardinal temperature model was employed to obtain the thermal coefficients. Projected temperature increase by 2090-2099 according to IPCC scenarios B1, A1B and A2 were estimated and environmental and soil heat sum were calculated. We conclude that an increase in soil temperature is predicted to alter the timing of germination but this will not be detrimental to the proportion of seeds which germinate. Thus mitigation of extreme temperatures, such as achieved under a shrub canopy, is not a crucial factor for germination success in these *Polaskia* species during the 21st century.

Key words: abiotic stress, climate change, facilitation, seed germination, cacti.

1. Introduction

In seasonal climates temperature is an indicator of the time of year (Fenner and Thompson, 2005) and is therefore implicated in determining physiological and phenological processes, such as the timing of germination. In the field, seeds germinate at temperatures that are favourable to subsequent seedling growth and establishment. The temperatures over which germination can occur determine the number of germinating seeds and the time taken to complete the germination process within the seed population (Probert, 2000).

The germination response to temperature can be characterized through the germination rate and is defined by three cardinal or threshold temperatures: a base temperature (T_b) below which germination does not proceed; an optimal temperature (T_o) at which the rate of germination is highest; and a maximum or ceiling temperature (T_c) above which germination ceases (Garcia-Huidobro et al., 1982). The T_b for germination of any fraction of the seed population is considered to be a constant, whereas T_c varies among each percentile fraction in a normal distribution (Covell et al., 1986; Ellis et al., 1986,). In addition, the sub-optimal and supra-optimal thermal time (θ_1 and θ_2 respectively) describe the relationship between the germination rate and temperature (Covell et al., 1986; Ellis et al., 1986; Garcia-Huidobro et al., 1982). An advantage in the use of these thermal models is the generation of coefficients for comparing seed lots for vigour, screening germplasm for quality (Covell et al., 1986; Ellis et al., 1986) and characterizing seedling emergence (Bradford, 2002), particularly under changing environmental conditions.

The predicted changes in global temperature will also be reflected in the soil temperature; in a recent study, Ooi et al. (2012) found that for every 1°C increase in air temperature the associated soil temperature increased by 1.5°C. Any change in soil temperature under predicted global warming may impact upon the regulation of seed phenological and physiological process. For example, some studies have reported an increase in the percentage of germination, decreased seed viability and changes to the dynamics of soil seed banks (Ooi et al., 2009); accelerated germination (Milbau et al., 2009); shift in the timing of seed germination (Mondoni et al., 2012); and increased dormancy loss (Ooi et al., 2012), when the soil temperature increased between 1 to 4 ^{o}C. The identification of spatial patterns in germination thresholds can help to understand a species distribution range, predict possible changes in their distribution as a result of global warming, and to develop suitable conservation strategies (Qiu et al., 2010). Although population-based threshold models have been widely employed for agricultural proposes (Finch-Savage, 2004), their application to wild species to estimate the impact of predicted climate change scenarios on seed germination is less common (Orrù et al., 2012; Porceddu et al., 2013).

In 2003, Téllez-Valdés and Dávila-Aranda examined the effect of climate change on the distribution of plants in the Tehuacán-Cuicatlán Valley, México. The biodiversity of the Tehuacán-Cuicatlán Valley is highly remarkable and contains 10–11.4 % of the Mexican flora of which 13.9 % is endemic (Davila et al., 2002). Focusing on the Cactaceae, Téllez-Valdés and Dávila-Aranda (2003) used a floristic database and a bioclimatic modeling approach and predicted a drastic distribution contraction of 20 species and the extinction of three species. In particular, species of the genera *Polaskia* reduced their range by about 95 % with a temperature increase of 2 ^{o}C and a decrease in rainfall of 15 % over an 80 year period. *Polaskia* is endemic to the Tehuacán-Cuicatlán Valley (Dávila et al., 1993) and is considered one of the most economically important columnar cacti in the region; people consume their fruits and seeds, and use part of or the whole plant for fodder and living fences (Casas et al., 2002).

In cacti, a “nurse plant syndrome” has been reported where the canopy of adult plants create favorable conditions for seed germination and seedling establishment (Niering et al., 1963), and is considered to be a type of facilitation (Callaway and Walker, 1997). In some deserts this interaction between seedlings and adult plants has played a central role in the preservation of the global biodiversity, the conservation of ecological traits and stabilizing selection over evolutionary time scales, and may be crucial for seedlings of species that cannot survive in full sunlight (Valiente–Banuet et al., 2006). One of the effects of facilitation is the mitigation of extreme soil temperature (Godínez-Alvarez et al., 2003; Sosa and Fleming, 2002; Valiente-Banuet and Godínez-Álvarez, 2002) as surface temperatures in open spaces between nurse plants can be up to 65 ^{o}C, whereas in the shaded microsites under nurse plants, the soil surface temperatures can be 10 to 20 ^{o}C lower (Valiente-Banuet and Godínez-Álvarez, 2002). Valiente-Banuet and Verdú (2007) suggest that facilitation may be increasingly important when the climate becomes more extreme and therefore could be an important factor in the survival of cactus seeds and seedlings during climate change. According to the predicted scenarios proposed by The Intergovernmental Panel on Climate Change (IPCC, 2007), Mexico will be exposed to drier summers and long periods of high temperatures. In this study, we investigated the effect of temperature on the seed germination of *Polaskia chende* (Rol-.Goss.) A.C.Gibson & K.E.Horak (Cactaceae) and *Polaskia chichipe* (Rol.-Goss.) Backeb (Cactaceae). The objectives were to estimate cardinal temperatures and thermal time of *P. chende* and P. *chichipe* seeds, to predict the effect of increased soil temperature on germination timing and to examine if the shrub canopy can maintain a favorable temperature for germination under predicted climate change scenarios.

2. Material and methods

2.1. Study area and seed collections

Populations of both species were located between San Luis Atolotitlan and Caltepec villages in the municipality of Caltepec state of Puebla, Mexico, belonging to the Tehuacán-Cuicatlán Biosphere Reserve. The mean annual rainfall in Caltepec is 394.6 mm and the average temperature is 18.4 °C (Caltepec climatic station, SMN). According to Valiente-Banuet et al., (2000) *P. chende* and *P. chichipe* are dominant elements of the thornscrub forest type called ''chichipera'' and are restricted to volcanic soils at elevations of 1700–2300 m. Mature fruits of wild individuals were collected in 2009 at the time of seed dispersal for each species: April for *P. chende* and May for *P. chichipe*. Seeds were manually removed from the pulp, washed with tap water, and air-dried in darkness at room temperature (20 ± 1 °C). Seeds were stored in glass bottles containing a small envelop of silica gel under laboratory conditions (20 ± 1 °C and 30 ± 5 % relative humidity).

2.2. Germination tests

Four replicates of 25 seeds were sown onto one layer of filter paper (Whatman # 1) imbibed with distilled water in 50-mm-diameter plastic Petri dishes. Seeds were incubated at constant temperatures from 5 °C to 40 °C (with intervals of 5 °C), with a 12 h photoperiod (50-100 W/m^2). Seeds were considered germinated when radicle emergence was ≥1 mm in length, after which seeds were removed from the Petri dish. Germination was recorded twice daily for 65 days, when no more germination was observed during the final two weeks. At the end of the germination tests, a cut-test was carried out to determine the viability of the remaining seeds.

2.3. Thermal model coefficients

Germination percentages were scaled by dividing the daily germination percentage by the maximum germination percentage for each species (Covell et al., 1986). Days required to achieve 10 – 80 % germination were calculated for each species by linear interpolation from the cumulative germination curves (Covell et al., 1986). Germination rate as a function of temperature was plotted for each species and fraction (10 – 80 %) (Covell et al., 1986). The data for each fraction were separated into a sub-optimal and supra-optimal temperature range and regressed to estimate the T_b and T_c. A simple linear regression was used to estimate the x-intercept and the slope of each regression line. An average of the x-intercept among fractions in the sub-optimal and supra-optimal temperature range was calculated to establish the T_b and T_c for each population (Ellis et al., 1986). Linear regression equations were then recalculated for each fraction, but constrained to pass through T_b for the sub-optimal temperature data and T_c for the supra-optimal temperature data (Hardegree, 2006). In the case of T_b, R^2 values were highest and residual variances were smallest when it was assumed that T_b was constant among fractions in both species. On the other hand, R^2 values were highest and residual variances were smallest when it was assumed that T_c varied normally among fraction, Optimum temperature was calculated for each fraction as the intercept of sub and supra-optimal temperature-response functions (Hardegree, 2006).

The inverse slope of the regression lines for each fraction of each species were calculated separately to estimate the thermal time (θ, ^{o}Cd) in the sub-optimal (θ_1) and supra-optimal (θ_2) temperature range (Covell et al., 1986). Percentage data were transformed using Probit Analysis in Genstat (version 11.1.0.1504, International Ltd, UK). Linear regression for the sub- and supra-optimal temperature range for each species was used to express probit (G) as a function of θ and log θ (Covell et al., 1986). For the sub-optimal temperature range, R^2 values were highest and residual variances were smallest when probit values were expressed as a function of log θ_1. Thus the following equation was used to describe the form of cumulative germination response of seeds:

$$\text{probit (G)} = K + \log \theta_1 / \sigma \tag{1}$$

where K is an intercept constant when thermal time is zero and σ is the standard deviation of the response to log θ_1 (Covell et al., 1986). Thermal time required for germination of 50% of the population (θ_1(50)) was determined from equation 1.

For the supra-optimal temperature range, R^2 values were highest and residual variances were smallest when probit values were expressed as a function of θ_2. Thus the following equation was used to describe the form of cumulative germination response of seeds:

$$\text{probit (G)} = Ks + (T + \theta_2 / t\,(\text{G}))/\sigma \tag{2}$$

where the dose ($T + \theta_2 / t$ (G)) is the T_c, K_s is an intercept constant at 0 °C and σ is the standard deviation of T_c (Covell et al., 1986). Thermal time required for germination of 50% of the population (θ_2(50)) was determined from equation 2.

2.4. Simulated soil temperatures and heat sum

The soil temperature was recorded in the study area under the shrub canopy and in unshaded areas; measurements were taken at 30 minute intervals using UA-002-08 HOBO Pendant data loggers (ONSET, Cape Cod, MA. U.S.A) buried in the soil at 1 cm depths (n=3) between January 2007 and January 2008. The average monthly soil temperature of both environmental conditions was compared with the average monthly environmental temperature registered by the Caltepec climatic station. The projected temperature increase by 2090-2099, using the best estimate model, according to IPCC scenarios B1 (low emissions scenario; + 1.8 °C), A1B (a medium-high emissions scenario; + 2.8 °C) and A2 (high emissions scenario; + 3.4 °C) were estimated for the study area and for each month, based on regionalized projections for México of the General Circulation Models used in the 4th Assessment Report of the IPCC (Magaña and Caetano, 2007). According to Ooi et al. (2012), for every 1 °C increase in air temperature the associated soil temperature in unshaded areas increases by 1.5 °C; thereby this adjustment was made in order to have a more accurate projection of the increase in soil temperature in open areas.

The environmental heat sum was calculated according to Orrù et al. (2012) as follows:

$$\text{Heat sum } (^{\circ}\text{Cd}) = (EnvT_m - T_b)\, t_m \tag{3}$$

where T_b is the base temperature for germination, $EnvT_m$ is the average monthly temperature of the month (m) and t_m is the number of days of the month (m), until reaching the thermal time $\theta_1(50)$ value.

The soil heat sum was calculated according to Bierhuizen and Wagenvoort (1974) with some modifications:

$$\text{Soil heat sum } (^{\circ}\text{Cd}) = (ST_m - T_b)\, t_m \tag{4}$$

where T_b is the base temperature for germination, ST_m is the average monthly soil temperature of the month (m) and t_m is the number of days of the month (m), until reaching the thermal time $\theta_1(50)$ value. The months used to calculate the environmental and soil heat sum were April for *P. chende* and May for *P. chichipe* (i.e. the time of natural seed dispersal).

2.5 Statistical Analysis

Final germination percentages of each replicate were arcsine transformed (Zar, 1999). Subsequently, final germination percentages, T_b, T_o, T_c and time to reach θ_1 (50) were compared using analysis of variance (ANOVA) followed by a post-hoc Fisher least significance difference (LSD) test at p<0.05, using STATGRAPHICS Centurion XV (v. 15. 1. 02. StatPoint Technologies, Inc. U.S.A.).

3. Results

3.1. Cardinal temperatures and thermal time

Seed germination was significantly different among species ($F_{1,\,63} = 74.65$, $P < 0.0001$) and temperature treatments ($F_{7,63} = 243.69$, $P < 0.0001$). The interaction of species and temperature was also significant ($F_{7,63} = 4.34$, $P = 0.0009$). Both species did not germinate at 5 and 10 ^{o}C. *P. chende* germinated more than 60 % from 15 to 35 ^{o}C and reached the maximum germination of 86 % at 20 ^{o}C, but LSD analysis did not indicate significant differences between 15, 20 and 25 ^{o}C. *P. chichipe* germinated more than 80 % from 15 to 35 ^{o}C and reached the maximum germination of 97 % at 20 ^{o}C. At the highest temperature (40 ^{o}C), both species germinated (54 % for *P. chende* and 74 % for *P. chichipe*). At all temperatures where germination was present, *P. chichipe* showed higher germination than *P. chende* (Fig.1).

The effect of temperature on the rate of germination was similar in both species (Fig. 2). Linear regressions of the relationship between temperature and germination rate generally accounted for >90% of the variation in both species (data not shown). In the sub-optimal temperature range, each 10th percentile of the population (from 10% to 70% and 10% to 80% in *P. chende* and *P. chichipe*, respectively) was regressed and a mean T_b estimated. The linear regressions equations were then recalculated for each fraction constraining them to pass through the mean T_b which gave the highest R^2 values (>91% in *P. chende* and >95% in *P. chichipe*) and the smallest residual variances (< 0.002 in both species) than when T_b was varied for each fraction. The mean T_b was statistically different between the two species ($F_{1,14} = 6.70$, $P = 0.0225$; Table 1).

In the supra-optimal temperature range, each 10th percentile was also regressed (10% to 50% in *P. chende* and 10% to 70% in *P.chichipe.*). The T_c for each percentile showed a normal distribution (R^2 > 99.48 % and > 97.70 % in *P. chende* and *P. chichipe*, respectively; Fig. 2). The highest R^2 values (>95% in both species) and the smallest residual variances (<0.001 in *P. chende* and < 0.002 in *P. chichipe*) were reached when T_c was allowed to vary for each fraction rather than constraining to a common value. The mean T_c was 54.5 and 51.3 °C for *P. chende* and *P. chichipe* respectively and was not statistically different ($F_{1,11}$ = 2.53, P = 0.1431). The range of T_c was from 51.3 to 57.8 °C and from 45.7 to 57.6 °C in *P. chende* and *P. chichipe*, respectively (Table 1). T_o , calculated for each fraction as the intercept of sub- and supra-optimal temperature response functions, was constant across percentiles and was not statistically different ($F_{1,9}$ = 0.34, P = 0.5781) between species (Table 1).

The relationship between log-thermal time (log θ_1) and probit germination for both species according to equation (1) is show in Figure 3. The regression accounted for 91 and 98 % of the variation of the germination response to θ_1 in *P. chende* and *P. chichipe*, respectively (Table 2). Seeds of *P. chichipe* had a lower K constant than seeds of *P. chende*, however the sensitivity of *P. chichipe* seeds to thermal time was higher (σ= 3.9) than *P. chende* seeds (σ= 2.9) (Table 2). As a result, θ_1 (50) was lower in *P. chichipe* (53.65 °C d) than in *P. chende* (64.77 °C d (Fig. 3, Table 2). In the supra-optimal range, θ_2 was constant between the seed fractions of the population of both species (Figure 2), and the θ_2 was lower in *P. chichipe* (55.36 °C d) than in *P. chende* (61.19 °C d) seeds (Table 2).

3.2. Projected temperature increase

The projected increase in the environmental and soil temperatures by 2090-2099 according to IPCC scenarios B1, A1B and A2 was estimated for each month for the study area (Figure 4). The environmental temperature increased from January until April when it reached the highest value under the current and all projected scenarios, thereafter gradually decreasing. Similarly, soil temperature under shrub canopy increased during the first months of the year but reached the highest value in June under the current and all projected scenarios, thereafter gradually decreasing. Meanwhile, the soil temperature on unshaded areas showed a different behavior in that the temperature increased during the first four months but remained constant until August, and decreased after this period under all climate change scenarios.

The environmental and soil heat sum were calculated for both species taking the mean temperature of April for *P. chende* and May for *P. chichipe*. From these data, the time to reach θ_1 (50) was estimated for each projected scenario and environmental condition (Table 3). The time to reach θ_1 (50) was significantly affected by species, scenario, environmental condition, species x scenario interaction and species x environmental condition interaction. The factor that accounted for the highest percentage of the total variance was environmental condition (59.29%) followed by scenario (39.21%) and finally species (1.5%) (Table 4). Multiple Range Tests showed differences between the species, among all scenarios and between unshaded areas with respect to the environmental temperature and the shrub canopy, but these two conditions did not show differences between them.

4. Discussion

The estimation of cardinal temperatures and thermal time, based on the germination rate, is scarce in cactus species and limited to a few species such as *Hylocereus setaceus* (Salm-Dyck ex DC.) Ralf Bauer (Cactaceae) (Simão et al., 2010) and *Echinopsis schickendantzii* F.A.C.Weber (Cactaceae) (Ortega-Baes et al., 2011). In this study, we extended this approach for characterizing the thermal germination behavior to seeds of *P. chende* and *P. chichipe*. Both species germinated across a range of temperatures from 15 to 40 ^{o}C, with no germination at ≤ 10 ^{o}C which is consistent with a study by Zimmer (1982 cited by Seal et al., 2009) on *P. chende* seeds. Values of T_b were similar in *P. chende* and *P. chichipe* (11.2 and 12.0 ^{o}C respectively), and more sensitive to low temperatures than reported for *H. setaceus* and *E. schickendantzii* (T_b of 7 ^{o}C in both species). At low temperatures (< 10 ^{o}C), germination of tropical species is generally poor (Simon et al., 1976) due to damage sustained from membrane changes and impartment of respiratory activity (Bedi and Basra, 1993), free radical accumulation (Sun et al., 2011) and lipid peroxidation (Roskruge and Smith, 1997).

Values of T_o were very similar between *P. chende* (31.5 ^{o}C) and *P. chichipe* (31.4 ^{o}C), and much higher than reported for the cacti *H. setaceus* (20 ^{o}C; Simão et al., 2010) and *E. schickendantzii* (26.8 ^{o}C; Ortega-Baes, et al., 2011). The higher values of T_b and T_o for *Polaskia* species in comparison to *E. schickendantzii* could be due to differences in the annual mean temperature in each study area. Ortega-Baes et al. (2011) reported an annual mean temperature of 10.2 ^{o}C at El Sunchal (Salta, Argentina) compared to 18.4 ^{o}C at Caltepec (Puebla, Mexico). According to Labouriau (1983 cited by Simão et al., 2010), the cardinal temperatures reflect the geographical distribution of species, consistent with Trudgill et al. (2000) who found that T_b is higher for tropical than temperate species.

At 35 ^{o}C, both species of *Polaskia* germinated above 50 %, similar to other species from the study area (Rojas-Aréchiga et al., 1998). At 40 ^{o}C, *P. chende* and *P. chichipe* reached 54 and 74 % of germination respectively, meaning these species could be considered as thermophilous (Orozco-Segovia et al., 1996). However, it may be necessary to test the germination at temperatures beyond 40 ^{o}C to have a more realistic estimation of T_c in *Polaskia*. Based on the data values generated in this study, estimated T_c (50) values for *P. chende* (54.5 ^{o}C) and *P. chichipe* (51.3 ^{o}C) were higher than values in *E. schickendantzii* (49 ^{o}C; Ortega-Baes, et al., 2011) and *H. setaceus* (49.8 ^{o}C; Simão et al., 2010). A decrease in germination at supra-optimal temperatures could be due to changes in membrane composition affecting lipid transition temperatures or molecular mobility of membrane components (Hilhorst, 1998).

The thermal time model for both species can be summarized by: (1) a positive linear relationship between the germination rate and sub-optimal temperatures (Covell et al., 1986; Dahal et al., 1990; Ellis et al., 1986; Garcia-Huidobro et al., 1982; Orrù et al., 2012; Pritchard and Manger, 1990; Pritchard et al., 1999); (2) T_b was constant among each seed fraction and hence within the population (Covell et al., 1986; Dahal et al., 1990; Ellis et al., 1986; Orrù et al., 2012; Pritchard and Manger, 1990); (3) a negative linear relationship between the germination rate and supra-optimal temperatures (Covell et al., 1986; Ellis et al., 1986; Garcia-Huidobro et al., 1982; Pritchard and Manger, 1990); (4) seed fractions were sensitive to different ceiling temperatures; (Covell et al., 1986; Ellis and Butcher, 1988; Ellis et al., 1986); (5) θ_1 was log-normally distributed among seed fractions (Covell et al., 1986; Ellis and Butcher, 1988 Pritchard and Manger, 1990) and (6) θ_2 was constant for all seed fractions (Ellis and Butcher, 1988; Ellis et al., 1986).

It has been shown that plant life-cycle transition stages that link one generation to the next, such as the germination-emergence transition stage, are likely to be highly vulnerable to environmental change (Cochrane et al., 2011). Here, we considered how the germination of *Polaskia* would be affected by the projected climate change scenarios B1, A1B and A2 (IPCC, 2007) and the influence that facilitation may have on germination success.

The difference between the environmental and soil temperature was much less under the shrub canopy, with data logger records showing that the daily temperature oscillation in the soil was around 30 ^{o}C in the shrub canopy and 45 ^{o}C in unshaded areas (data not shown). This is consistent with other studies which have found that facilitation decreases both the soil temperature (Godínez-Alvarez et al., 2003; Sosa and Fleming, 2002; Valiente-Banuet and Godínez-Álvarez, 2002) and the contrast between the maximum and minimum soil temperatures (Arriaga et al., 1993; Hutto et al., 1986; Jordan and Nobel, 1981; Shreve, 1931; Suzán et al., 1996; Valiente-Banuet et al., 1991, cited by Godínez-Alvarez et al 2003). Although it has been reported that an oscillation range of between 30-40 ^{o}C may affect seed dormancy and germinability in some desert species (Kigel, 1995), a recent study has shown that short-term exposure to high temperature does not prevent germination for tree cactus species (Pérez-Sánchez et al., 2011). The shrub stratum of the study area is composed predominantly by deciduous species such as *Acacia constricta* A.Gray (Fabaceae), *Eysenhardtia polisthachya* (Ortega) Sarg. (Fabaceae), *Ipomoea arborescens* (Humb. & Bonpl. ex Willd.) G. Don (Convolvulaceae), *I. murucoides* Roem. & Schult. (Convolvulacea), *Leucaena pueblana* Britton & Rose (Leguminosae), *Lippia* spp. L. (Verbenaceae) and *Mimosa luisana* Brandegee (Leguminosae). These species produce leaves at the end of May when the first rains fall, until September and October, and as a consequence, the soil temperature under shrub canopy markedly decreases from June onwards compared to unshaded areas (Fig. 4). The leaves which fall during the autumn form a litter layer over the soil surface which may decrease incident solar radiation on the ground and prevent the rapid soil temperature increase early in the year which occurs in the unshaded areas.

Under projected climate change scenarios, the environmental and soil temperature during the time of natural seed dispersal of *P. chende* and *P. chichipe* will remain above T_b and well below the T_c for germination (Fig. 4), and even the average minimum temperature will not exceed T_b (data not shown). Thus germination will occur regardless of facilitation (Fig.4). Rather, facilitation will impact on the germination timing with the estimated time to reach θ_1 (50) significantly shorter in unshaded areas compared to under shrub canopy. Assuming necessary moisture is available, seeds of both *Polaskia* species will readily germinate within a few days following dispersal. Fast germination is an adaptive feature of species from arid lands where water availability is limited (Guterman, 1993; Kigel, 1995).

It is widely accepted that microclimatic stress amelioration, e.g. shade canopy, is the most common mechanism underlying plant–plant facilitation in cacti (reviewed by, Godínez-Alvarez et al., 2003; Sosa and Fleming, 2002; Valiente-Banuet and Godínez-Álvarez, 2002) and several other factors such as solar radiation, temperature, evaporation, evapotranspiration and moisture have been proposed to stimulate germination and establishment of cacti under shrub canopies (Godínez-Alvarez et al., 2003; Sosa and Fleming, 2002; Valiente-Banuet and Godínez-Alvarez, 2002). However, the effect of amelioration of each individual factor has not been shown or requires investigation. Our results suggest that environmental and soil temperatures (both unshaded and under facilitation) are not limiting factors for the germination of *P. chende* and *P. chichipe*, under present and future climate change scenarios. By defining the thermal coefficients for germination, these can be used in bioclimatic models to predict changes in population distribution under predicted climate change scenarios and to develop suitable conservation strategies for *Polaskia* species.

5. Conclusions

The thermal time for seed germination of *P. chende* and *P. chichipe* is affected by shrub canopy. Plant facilitation in desert lands is an important process for seedling recruitment; however mitigation of extreme temperatures by nurse plants is not a determining factor for germination in these species. Projected climate change scenarios may alter plant distribution, but it is important to know which stages of the life cycle are more sensitive to global warming. Our results showed that soil temperature increase in the semi-arid Tehuacan-Cuicatlan Valley alter the germination timing but may not have detrimental effects on germinability for the remainder of this century.

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Tables and Figures.

Table 1. Cardinal temperature coefficients (^{o}C) obtained from the linear regressions of germination rate and temperature (mean ± s.d.)

	T_b	T_o	T_c
P. chende	11.23 ± 0.80 ^{a}	31.46 ± 0.18 ^{a}	54.5 ± 2.9 ^{a}
P. chichipe	12.00 ± 0.56 ^{b}	31.38 ± 0.28 ^{a}	51.3 ± 3.9 ^{a}

^{a,b} Values followed by a different letter within a species are significantly different $P < 0.05$

Table 2. Estimated thermal time (^{o}Cd) in seeds of *P. chende* (T_b = 11.2 ^{o}C) and *P. chichipe* (T_b = 12^{o}C) from probit regressions in the sub-optimal temperature range . θ_1 is shown in log and normal scale. θ_2 was constant between seed fractions of the population in both species.

	P. chende (mean ± s.d.)	***P. chichipe*** (mean ± s.d.)
R^2 =	91.89	98.47
K =	-5.39 ± 0.36	-6.83 ± 0.40
σ =	2.98 ± 0.20	3.95 ± 0.23
log θ_1 (50)	1.81 ± 0.01	1.73 ± 0.006
θ_1 (50)	64.77 ± 3.60	53.65 ± 2.04
θ_2	61.19 ± 1	55.36 ± 2.74

Table 3.Estimated time (days) to reach θ_1 (50) in *P. chende* (T_b= 11.2 ^{o}C; θ_1 (50)= 64.7 ^{o}C d) and *P. chichipe* (T_b= 12 ^{o}C; θ_1 (50)= 53.6 ^{o}C d) seeds under different projected climate change scenarios and environmental conditions.

	Polaskia chende			***Polaskia chichipe***		
	Environmental temperature $^{1\ a}$	**Shrub canopy** $^{2\ a}$	**Unshaded areas** $^{2\ b}$	**Environmental temperature** $^{1\ c}$	**Shurb canopy** $^{2\ c}$	**Unshaded areas** $^{2\ d}$
Current	6.7	6.65	5	5.83	5.43	4.53
B1	5.5	5.39	3.97	4.9	4.6	3.7
A1B	5.02	4.96	3.62	4.56	4.31	3.42
A2	4.65	4.59	3.33	4.28	4.06	3.2

[1] Data were calculated according to the equation: Heat sum (^{o}Cd) = $(EnvT_m - T_b)\ t_m$

[2] Data were calculated according to the equation: Soil heat sum (^{o}Cd) = $(ST_m - T_b)\ t_m$

[a,b,c ,d] Values followed by a different letter are significantly different $P < 0.05$

Table 4. Analyses of variance for the time to reach θ_1 (50) in *P. chende* and *P. chichipe* (see Table 3)

Source of variation	**ss**	**df**	***F*-value**	***P*-value**
Species (S)	1.793	1	587.09	**< 0.0001**
Scenario (Sc)	9.546	3	1041.88	**< 0.0001**
Env Condition (EC)	8.373	2	1370.8	**< 0.0001**
S x Sc	0.221	3	24.15	**0.0009**
S x EC	0.283	2	46.38	**0.0002**
Sc x EC	0.053	6	2.93	0.1085
Residual	0.018	6		

The bold P-value mean significance difference

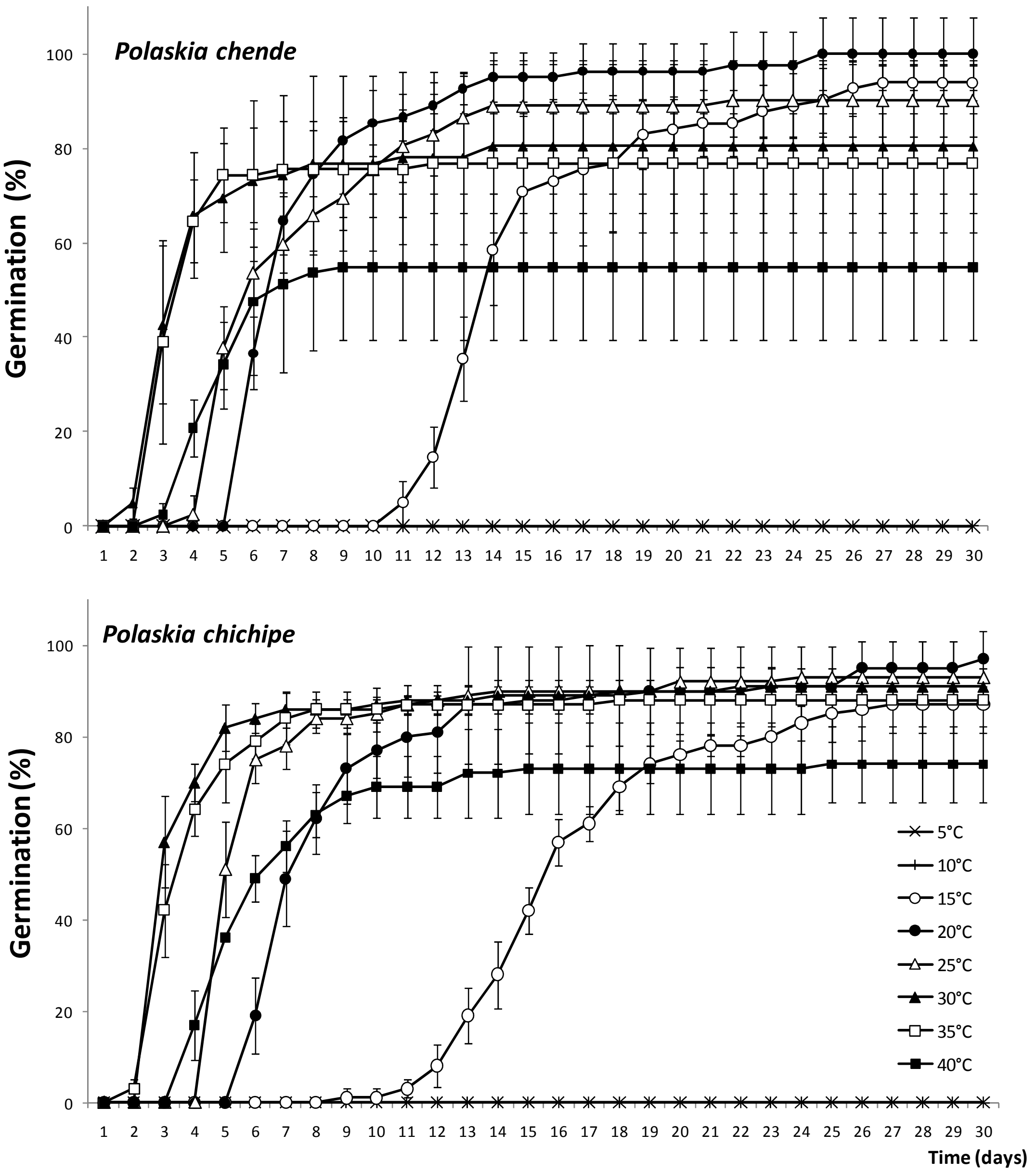

Figure 1. Germination time courses of each species at different temperatures. Seeds were germinated on filter paper (Whatman # 1) imbibed with distilled water. The photoperiod was 12 h light/12 h dark. Data are means ± s.d. for 4 x 25 seeds per treatment. Germination percentages were scaled by dividing the daily germination percentage by the maximum germination percentage for each species, 86 and 97 % for *P. chende* and *P.chichipe* respectively.

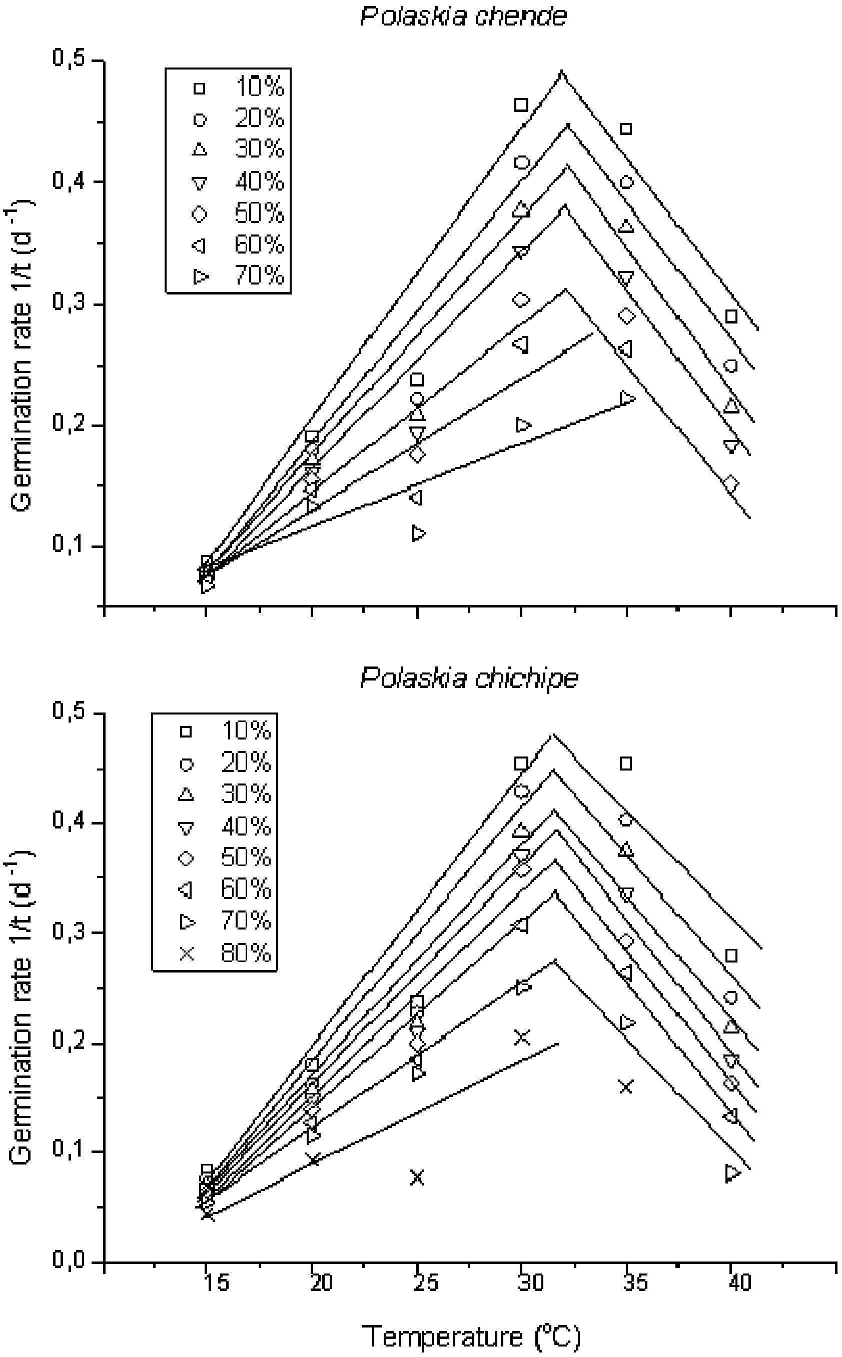

Figure 2. Relationship between the reciprocal of time for germination and temperature (15 °C - 40 °C) for different percentile fractions of the seed population.

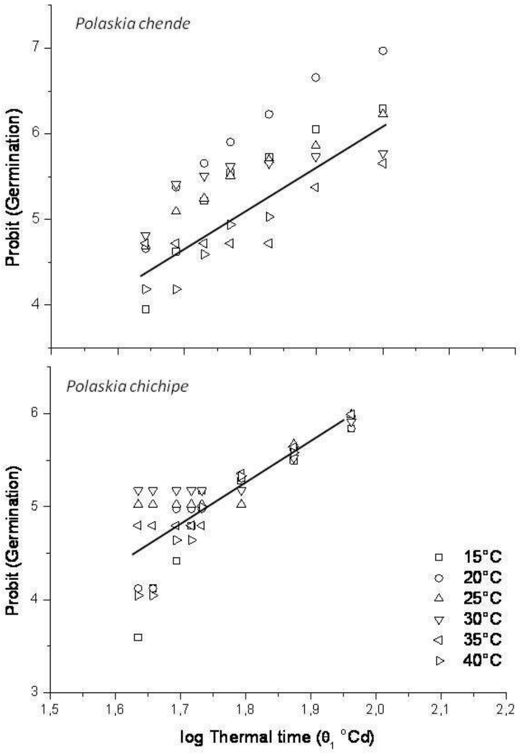

Figure 3. Seed germination (Probits) as a function of log-thermal time (θ_1 °C d) in *P. chende* (T_b = 11.2 °C) and *P. chichipe* (T_b = 12.0°C) according to the equation: probit (G) = $K + \log \theta_1 / \sigma$. Symbols are observed values and line are predicted values.

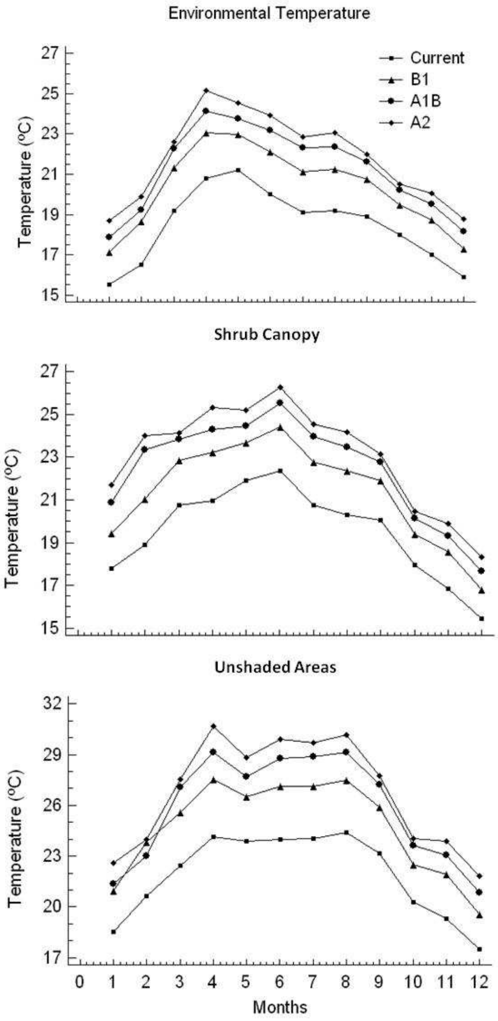

Figure 4. Monthly increase of environmental and soil mean temperature under projected IPCC climate change scenarios in the study area: current temperature (square), and projected scenarios B1 (+ 1.8 °C; triangles), A1B (+ 2.8 °C; circles) and A2 (+ 3.4 °C; diamonds). Soil temperature is shown in two conditions: shrub canopy and unshaded areas.

DISCUSIÓN Y CONCLUSIONES

La familia Cactaceae es una de las más importantes en nuestro país, el estudio de cada una de las fases de su ciclo de vida es importante para contribuir al conocimiento de las adaptaciones de estas plantas a su hábitat. Una de las etapas en la dinámica poblacional de las cactáceas que ha recibido poca atención es su capacidad para formar bancos de semillas, probablemente debido a que no es la etapa crítica en el ciclo de vida de estas plantas. Por lo tanto, no se conoce específicamente el tipo de banco que estas forman y si los posee cuál es su función y la dinámica del mismo. En este trabajo se determinó la persistencia de las semillas de *P. chende* en un estudio de largo plazo (> 5 años) para aportar conocimiento acerca de la longevidad ecológica de esta especie.

La información acerca de los bancos de semillas y las estrategias de germinación en zonas áridas se ha desarrollado básicamente con el estudio de las plantas anuales pero existen pocos trabajos que analicen sistemáticamente estos procesos en plantas perennes. Esta información es fundamental para entender las estrategias adaptativas de estas plantas en las zonas áridas, ya que estas características pueden estar estrechamente relacionadas al ambiente en el cual se desarrollan las poblaciones vegetales (Long *et al*., 2015) y por lo tanto ser influenciadas por diferentes fuerzas de selección (Saatkamp *et al*., 2011).

Las semillas de *P. chende* mostraron varias características asociadas con la formación de bancos de semillas persistentes. En primer lugar tuvieron un peso (0.78 mg ± 0.11 mg) menor a 3 mg e inclusive menor a 1 mg, los cuales representan los rangos establecidos por Thompson *et al*. (1993) y Peco *et al*. (2003) que favorecen la persistencia de las semillas en el suelo. Además, las semillas de *P. chende* mostraron fotoblastismo positivo. Estas dos características se encuentran estrechamente relacionadas propiciando la formación de bancos de semillas de largo plazo. En el caso de las cactáceas el fotoblastismo es un carácter común en varias especies que ha mostrado una buena relación respecto a la masa de las semillas (Flores *et al*., 2006; Flores *et al*., 2011; Ortega-Baes *et al*., 2010a); aunque en un estudio de 54 especies de la Tribu Cacteae no se observa este comportamiento, pero si se encuentra un relación filogenética en la respuesta fotoblastica de estas especies (Rojas-Aréchiga *et al*. 2013).

Por otro lado, las semillas de *P. chende* presentaron latencia secundaria después de estar enterradas por diferentes periodos. Inclusive, los resultados obtenidos en este estudio permitieron establecer la existencia de ciclos de latencia no estacionales lo cual es una característica que ha sido relacionada con la formación de bancos de semillas de largo plazo (Thompson *et al*., 1993; Pons, 2000; Baskin y Baskin, 1998), este trabajo representa el primer reporte de ciclos de latencia en cactáceas. Los ciclos de latencia son un mecanismo endógeno que ayuda a regular el tiempo en que las semillas germinan y por lo tanto influye en la emergencia y establecimiento de las plántulas (Cao *et al*., 2014)

Basados en la presencia de latencia las plantas de zonas áridas son susceptibles de formar bancos de semillas persistentes, sobre todo si tomamos en cuenta que los principales tipos de latencia en estas especies son la física y la fisiológica. Baskin y Baskin (2014) reportan que el 70 % de los arboles estudiados en los desiertos presentan latencia física; en el caso de los arbustos 51% presentan latencia fisiológica y 38% presentan latencia física; en las plantas suculentas 72% presentan latencia fisiológica y 13 % latencia física; en cuanto a las herbáceas perenes se refiere 61 % presentan latencia fisiológica y finalmente el 70 % de las plantas anuales también presentan latencia fisiológica. Una de las consecuencias de la latencia física es que las semillas pueden ser capaces de persistir por mucho tiempo en el suelo, por su parte también la latencia fisiológica promueve la persistencia de las semillas. Estos resultados sugieren que la formación de bancos de semillas persistentes puede ser un fenómeno común en las especies perennes de zonas áridas, sin embargo es necesario realizar estudios de largo término (> 5 años) con un mayor número de especies y formas de vida para determinar la importancia y función que estos tienen.

Como se puede observar, las características de las semillas tienen una gran influencia en la formación y dinámica del banco de semillas; desde una perspectiva ecológica un ambiente temporalmente variable, como lo es el valle de Tehuacn-Cuicatlan, puede favorecer los caracteres en la estrategia del ciclo de vida que reducen la heterogeneidad ambiental y el riesgo del fracaso reproductivo (bet- hedging) (Long *et al*., 2015; Saatkamp *et al*., 2014). Pake y Venable (1996) estudiaron el banco de semillas en plantas anuales en el desierto de Sonora y proponen que el tamaño de la semilla y la latencia estacional deben disminuir la variación temporal en la adecuación biológica. También Fenner y Thompson (2005) establecen que la perennidad (ciclos de vida largos), el tamaño de las semillas, la latencia y los bancos de semillas persistentes, permiten la sobrevivencia a través de periodos no favorables para la reproducción. Por otro lado, un análisis que divide a las especies en efectivamente dispersadas y no efectivamente dispersadas, utilizando criterios morfológicos, sostiene la existencia de un balance o intercambio (trade-off) entre la dispersión y la persistencia de las semillas en la flora británica (Rees, 1993).

Consecuentemente estas estrategias están negativamente relacionadas (Rees, 1994). En otras palabras los balances entre dos caracteres no se derivan de conexiones mecanicistas entre ellos sino por su función evolutiva (Venable y Brown, 1988). Por ejemplo, si la dispersión y la persistencia de las semillas ambas reducen la percepción de la variabilidad ambiental, entonces la existencia de un carácter reduce el valor adaptativo del otro. Esto sugiere que las características de las plantas que protegen contra la variabilidad espacial o temporal en el hábitat pueden tener impacto en la evolución de los bancos de semillas persistentes (Saatkamp *et al*., 2014).

Existen entonces dos conjuntos de características de las plantas en *P. chende* y muchas cactáceas columnares; por un lado son plantas policárpicas, suculentas, perennes y de tamaño grande los cuales por sí mismos son caracteres que favorecen la persistencia de las poblaciones. Las plantas que presentan estos rasgos generalmente invierten menos recursos en la reproducción, ya que estas características permiten disminuir la variabilidad ambiental y disminuir la varianza en el fracaso reproductivo (Saatkamp *et al*., 2014). Por otro lado, *P. chende* produce gran cantidad de semillas de tamaño pequeño, presenta ciclos de latencia y puede formar bancos de semillas persistentes; todos estos caracteres se relacionan más con la estrategia de vida de las plantas anuales. Por lo tanto, *P. chende* muestra una estrategia diversificada la cual en conjunto le ayuda a asegurar su permanencia en los hábitats desérticos del centro de México.

Además de las características de las plantas también los factores ambientales pueden influir en la latencia y la germinación y por lo tanto en la longevidad ecológica, de acuerdo con Hill y Kloet (2005) la longevidad de las semillas es un carácter que también se relaciona con el hábitat. Algunos autores consideran que la latencia de las semillas es una estrategia adaptativa de diversificación en ambientes variables temporal y espacialmente (Snyder, 2006; Venable y Brown, 1988). Es importante señalar que en esta especie la expresión de factores ambientales específicos tales como la luz y la temperatura pueden actuar de forma sucesiva o simultánea para inducir la latencia o inhibir la germinación. En particular las altas temperaturas que se presentan en el área de estudio pueden ocasionar la termo-inhibición de la germinación, por otro lado las fluctuaciones diarias en la temperatura pueden inducir que las semillas entren en estado de latencia (termo-latencia). Por su parte, la alta incidencia de radiación desencadena una respuesta específica para inhibir la germinación denominada respuesta HIR, por sus siglas en ingles. Adicionalmente, la combinación de altas temperaturas y baja irradiación que se presenta cuando las semillas se encuentran enterradas en el suelo puede inducir latencia obscura. Por lo tanto, se pueden presentar diferentes tipos de latencia en las semillas de *P. chende* dependiendo de los factores ambientales prevalecientes a lo largo del año.

Estas diferentes respuestas fisiológicas (plasticidad) en la germinación y la latencia provienen de la adaptación al medio en la historia de vida de estas plantas, sobre todo si tomamos en cuenta que la latencia evolucionó como una estrategia para: asegurar la persistencia de las especies en ambientes riesgosos, evitar la competencia con la planta madre o las plantas hermanas, sobrevivir a las estaciones no favorables para el establecimiento y maximizar la adecuación de las especies a su hábitat (Baskin y Baskin, 2014). En este contexto evolutivo retrasar la germinación es una estrategia de diversificación para reducir el riesgo de fracaso reproductivo, la cual es particularmente importante en ambientes impredecibles. Teóricamente, para que las semillas persistan hasta que las condiciones para el establecimiento sean favorables deben exhibir adaptaciones específicas en su morfología, latencia, germinación y longevidad; las cuales reflejen ciertas características del ambiente (la estacionalidad, los riesgos de depredación y decaimiento) en las que estas especies evolucionaron (Long *et al*., 2015).

Las semillas germinan cuando las condiciones ambientales (humedad, oxígeno, temperatura y luz, principalmente) indican una ventana espacial o temporal para la emergencia y sobrevivencia. La variación genética en características claves como la germinación y la latencia pueden conferir un beneficio en la persistencia de las semillas de una población o una especie. Las poblaciones con mayor diversidad genética en estas características pueden presentar una ventaja en ambientes variables ya que es probable que alguna proporción de sus semillas germinen o persistan a través de una gama más amplia de condiciones ambientales (Saatkamp *et al*., 2011).

En los desiertos las plantas anuales han desarrollado diferentes estrategias de germinación a lo largo del tiempo. Gutterman (1994; 2002) dividió estas estrategias en dos categorías generales: por un lado se encuentra la estrategia oportunista la cual presenta alto porcentaje y rápida velocidad de germinación, las semillas no presentan latencia o es muy baja; por otro lado se encuentra la estrategia cautelosa, la cual está caracterizada por bajo porcentaje y baja velocidad de germinación y alta incidencia de latencia en las semillas. De esta división se puede deducir que cuando las plantas presentan una estrategia de germinación oportunista forman bancos de semillas transitorios mientras que cuando presentan una estrategia cautelosa forman bancos persistentes. En el caso de *P. chende* la mayoría de sus semillas germinan después de las lluvias en verano lo cual coordina con el tipo de estrategia oportunista; sin embargo una proporción de sus semillas es capaz de persistir en el suelo, entrar en estado de latencia y germinar después de una o varias temporadas de germinación, mostrando así una estrategia cautelosa. Cuando los ambientes son menos predecibles, por ejemplo los desiertos, una estrategia de persistencia más plástica puede ser más favorable, de tal manera que las características de la longevidad y la germinación en una población sean menos rígidas (mayor variabilidad entre las semillas individuales) (Saatkamp *et al.*, 2014). Lo cual permite que se presente una estrategia combinada que puede aumentar la sobrevivencia de esta especie en su hábitat.

Por otro lado, las semillas de *P. chende* presentaron una longevidad ecológica larga ya que mantuvieron su potencial germinativo durante 62 meses de permanecer enterradas. Adicionalmente, se observó la emergencia de plántulas durante 50 y 58 meses (dosel y sin dosel, respectivamente) de permanecer en o sobre el suelo. La información disponible acerca de la longevidad ecológica de las plantas perennes en los desiertos muestra que las semillas de estas especies pueden formar bancos transitorios y bancos persistentes. Siendo hasta el momento los bancos de semillas persistentes de corto plazo los más reportados, contrario a lo establecido por Pake y Venable (1996) y Kemp (1989) acerca de la ausencia de bancos de semillas persistentes en especies perennes del desierto.

En el caso de las especies que forman bancos transitorios se observan dos comportamientos: en el primero las semillas de algunos arbustos perennes como *Haloxylon salicornicum* y *Salsola imbricata* germinan rápidamente después de la dispersión y pierden su viabilidad en el suelo al cabo de algunos meses (El-Keblawy, 2013); por otro lado las semillas de *Casuarina pauper*, un árbol australiano, permanecen por unos meses en el suelo formando bancos transitorios y germinan en respuesta a la temporada de lluvia (Auld, 1995). En el caso de las especies que forman bancos persistentes se observa que la latencia es un factor determinante para la persistencia de las semillas, por ejemplo: *Penstemon palmeri*, una planta herbácea perenne de corta vida, mostró un ciclo de latencia estacional similar al de las plantas anuales de invierno (Meyer y Kitchen, 1992); también el arbusto perenne halófito *Kalidium gracile* forma bancos de semillas persistentes de corto termino y muestra ciclos de latencia (Cao *et al.*, 2014); otra especie herbácea perenne *Lesquerella fendleri* mantuvo semillas viables en el suelo hasta por tres años (Evans y Cabin, 1995); finalmente varias especies de Acacia mostraron una longevidad ecológica en el suelo entre 12 y 30 meses (Auld, 1986a; 1986b; 1995).

Específicamente en el caso de las cactáceas también los bancos de semillas persistentes de corto plazo han sido los más reportados encontrándose la longevidad ecológica más corta en tres especies de *Arthocereus* con 14 meses (Cheib y García, 2012) y la longevidad ecológica más larga en *Harrisia fragrans*, ya que sus semillas mantuvieron altos porcentajes de germinación después de haber permanecido enterradas durante 23 meses (Goodman *et al*., 2012). En el caso de *P. chende* sus semillas forman bancos persistentes de largo plazo ya que mantienen su potencial germinativo durante más de cinco años, es importante señalar que este es el primer reporte de banco de semillas persistentes de largo plazo en cactáceas. Es probable que este tipo de bancos se encuentre en muchas especies de cactáceas columnares que presenten características semejantes a las de *P. chende*, sin embargo no se han realizado estudios de largo término para determinar la presencia de este tipo de bancos.

En cuanto al establecimiento de las plántulas de *P. chende* se observó que la emergencia en condición de dosel fue el doble que en zonas sin dosel (después de 5 años) y la sobrevivencia fue dieciséis veces mayor cuando las plántulas se encontraron debajo de los arbustos de *A. constricta.* En un análisis de la estructura poblacional de varias especies de cactáceas Godínez Álvarez *et al*. (2003) observan dos formas principales. En la primera y la más habitual se muestra una distribución desigual de los individuos, lo cual sugiere que el reclutamiento ocurre en pulsos esporádicos aparentemente asociados con condiciones favorables para la germinación y el establecimiento (Mandujano *et al*., 2001, Esparza Olguín *et al*., 2002; citados por Godínez Álvarez *et al*., 2003). En la segunda se muestra un tipo de estructura poblacional en la cual el número de individuos disminuye monotónicamente, este tipo de estructura sugiere poblaciones en crecimiento que se están regenerando constantemente en las cuales la tasa de mortalidad disminuye con el tamaño o la edad de los individuos (Martinez-Ramos y Alvarez-Buylla, 1995; citado por Godínez Álvarez *et al*., 2003).

En la mayoría de los estudios demográficos de cactáceas se observa una gran contribución de los adultos a la tasa de crecimiento poblacional, la sobrevivencia de los individuos más longevos determina la dinámica poblacional y la contribución más importante corresponde a la persistencia de los individuos en su clase actual (stasis) (Contreras y Valverde, 2002; Esparza-Olguín *et al*., 2005; Godínez-Álvarez *et al.,* 2003; Mandujano *et al*., 2007a, 2007b, 2015; Méndez *et al*., 2004;). La reproducción sexual contribuye muy poco a la tasa de crecimiento poblacional inclusive si se aumenta considerablemente el banco de semillas (Mandujano *et al*., 2007a, 2007b, 2015).

Erickson (1997) sugiere que el reclutamiento sexual esporádico (raro) podría, a través del tiempo, resultar en poblaciones con alta variabilidad genética; e inclusive, el reclutamiento accidental de las plántulas puede balancear la tendencia a la baja en la variabilidad genética de las plantas perenes y mantener la diversidad genética. En el caso del cactus *Opuntia macrocentra* Mandujano *et al*. (2007a) sugieren que el reclutamiento esporádico puede ser suficiente para mantener la estabilidad de la población y evitar la depresión endogámica. Por lo tanto, la principal función de un banco de semillas persistente en cactáceas no está relacionada con el mantenimiento de la población, sino con el mantenimiento de la diversidad genética de la población.

Por otro lado, en este estudio la presencia del dosel de plantas nodriza favoreció la emergencia y la sobrevivencia de las plántulas de *P. chende*, como se ha reportado en varias especies de cactáceas (Godínez-Alvarez *et al*., 2003; Sosa y Fleming, 2002; Valiente-Banuet y Godínez-Alvarez, 2002). De a cuerdo con Calaway (1995) la facilitación es una interacción positiva en donde una especie favorece la sobrevivencia, el crecimiento o el vigor de otra. El efecto del dosel en la formación del banco de semillas está relacionado con la distribución de las semillas en el suelo, ya que en un estudio previo Ordoñez (2008) reportó una mayor densidad de semillas de *P. chende* presentes en condición de dosel respecto a las semillas presentes en áreas desprovistas de vegetación. Sin embargo, en la dinámica del banco de semillas de *P. chende* en este trabajo, se observó que las semillas que se encuentran en áreas abiertas (sin dosel) son las que presentan ciclos de latencia, propiciando así su permanencia en el banco. Adicionalmente, si tomamos en cuenta que la emergencia de semillas en condición de dosel fue el doble que en áreas abiertas al cabo de cinco años, se puede concluir que las plantas nodriza promueven la formación del banco pero no su persistencia, ya que las plantas nodriza favorecen la acumulación de las semillas en el suelo pero también favorecen su germinación evitando así que las semillas permanezcan en el suelo.

En relación al efecto de la temperatura en la germinación se generó un modelo de tiempo térmico para *P. chende* y *P. chichipe*. Ambas especies germinaron arriba del 50 % a altas temperaturas, por lo cual pueden ser catalogadas como termófilas (Orozco-Segovia *et al*., 1996). En base a las temperaturas cardinales y el tiempo térmico obtenidos se estableció que las semillas de ambas especies pueden germinar en pocos días después de su dispersión, siempre y cuando las condiciones de luz y disponibilidad de agua no sean limitantes.

Los modelos de cambio climático predicen que las zonas áridas experimentaran aumento en la temperatura y mayor variabilidad en la frecuencia y magnitud de la lluvia (IPCC, 2007), traduciéndose esto en condiciones más cálidas y secas. Específicamente refiriéndose a la temperatura, las consecuencias del cambio climático en los desiertos incluyen el aumento en la temperatura promedio del aire y del suelo, así como el aumento en la frecuencia de temperaturas diarias extremadamente altas (heat waves) (Ooi *et al*., 2012).

Algunas de las características de las semillas que hemos revisado pueden ser alteradas bajo estas condiciones, sobre todo las relacionadas a la germinación y la latencia. Por ejemplo, el aumento en la temperatura del aire cambiará las condiciones ambientales a las que están expuestas las plantas progenitoras, lo cual genera un efecto en la etapa de pre-dispersión en la formación y dinámica del banco de semillas, ya que se producirían semillas en mayor cantidad y menor tiempo pero menos latentes (Fenner, 1991).

Las especies con latencia física podrían ser especialmente susceptibles al aumento en la temperatura del suelo, ya que el mantenimiento de este tipo de latencia depende de la impermeabilidad de la cubierta seminal, y uno de los factores que puede remover este tipo de latencia son las oscilaciones diarias en la temperatura del suelo (Baskin y Baskin, 2014; Ooi *et al*., 2009; Vázquez-Yanes y Orozco-Segovia, 1982). También, muchas especies que presentan latencia fisiológica pueden ser afectadas ya que necesitan estratificación o periodos de post-maduración a temperaturas específicas para remover la latencia. Por lo tanto, la persistencia de los bancos de semillas puede disminuir debido a que el aumento en la temperatura conduce a la remoción de la latencia en una mayor proporción de semillas. Esto no solo puede afectar la longevidad de las semillas en el banco sino también la sobrevivencia de las plántulas, ya que pueden germinar durante eventos de lluvia que no sean suficientes para el establecimiento de las mismas (Ooi *et al*., 2009).

Por otro lado, la longevidad de *Wahlenbergia tumidifructa*, una especie de ambientes semiáridos, disminuyó cuando las plantas progenitoras fueron sometidas a una temperatura ambiental mayor, estos resultados sugieren que la capacidad de la estrategia de diversificación (bet-hedging) puede verse comprometida bajo condiciones ambientales futuras (Kochanek *et al*., 2010). Adicionalmente, Ooi (2012) también concluye que el aumento en la temperatura puede comprometer la estrategia de diversificación debido a la disminución en la latencia y/o el aumento en la germinación de las semillas que se encuentran en el banco, y de esta manera tener impactos severos en la persistencia de las especies.

En este estudio, las proyecciones de la temperatura del suelo producidas por los diferentes escenarios de cambio climático mostraron que el aumento en la temperatura acelerará el proceso de germinación en ambas especies, sobre todo en las zonas desprovistas de dosel. Se ha establecido que uno de los beneficios generados en el proceso de facilitación es mitigar las temperaturas extremas a las que están expuestas las semillas (Godínez-Alvarez *et al*., 2003; Sosa y Fleming, 2002; Valiente-Banuet y Godínez-Alvarez, 2002), sin embargo, los resultados encontrados en este estudio indicaron que la disminución en la temperatura producido por el dosel de plantas nodriza no es un factor determinante en la germinación de *P. chende* y *P. chichipe*. Además, aun en el escenario de cambio climático más drástico el aumento en la temperatura ambiental y del suelo no representara un factor limitante en la germinación de estas especies. No obstante, es necesario evaluar el efecto que este aumento en la temperatura puede tener en la sobrevivencia y el establecimiento de las plántulas para ubicar que etapas del ciclo de vida son más susceptibles al cambio climático.

Por todo lo anteriormente expuesto se muestran evidencias suficientes para concluir que las semillas de *P. chende* forman bancos de semillas persistentes de largo plazo, son capaces de persistir en el suelo y germinar en varias temporadas de germinación, presentan ciclos de latencia no estacional, la facilitación promueve la formación del banco de semillas pero no la persistencia de las semillas en el banco, establecen asociación con plantas nodriza y finalmente, el aumento en la temperatura producido por los diferentes escenarios de cambio climático disminuirá el tiempo requerido para la germinación de las semillas pero no representara un factor limitante para la germinación de estas especies.

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