UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSITITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD
BIOLOGÍA EVOLUTIVA

VARIACIÓN FUNCIONAL Y GENÉTICA DE *PROSOPIS LAEVIGATA* (HUMB. ET BONPL. EX WILLD) EN MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

GONZALO CONTRERAS NEGRETE

TUTOR PRINCIPAL DE TESIS: DR. ANTONIO GONZÁLEZ RODRÍGUEZ
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM
COMITÉ TUTOR: DRA. ALICIA GAMBOA DE BUEN
INSTITUTO DE ECOLOGÍA UNAM
COMITÉ TUTOR: DR. ERICK DE LA BARRERA MONTPPELLIER
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

MORELIA MICHOACÁN; MÉXICO, DICIEMBRE, 2021

UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSITITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD
BIOLOGÍA EVOLUTIVA

VARIACIÓN FUNCIONAL Y GENÉTICA DE *PROSOPIS LAEVIGATA* (HUMB. ET BONPL. EX WILLD) EN MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

GONZALO CONTRERAS NEGRETE

TUTOR PRINCIPAL DE TESIS: DR. ANTONIO GONZÁLEZ RODRÍGUEZ
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM
COMITÉ TUTOR: DRA. ALICIA GAMBOA DE BUEN
INSTITUTO DE ECOLOGÍA UNAM
COMITÉ TUTOR: DR. ERICK DE LA BARRERA MONTPPELLIER
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

MORELIA MICHOACÁN; MÉXICO 2021

UNAM POSGRADO
POSGRADO CIENCIAS BIOLÓGICAS

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

ENTIDAD IIES-M

OFICIO CPCB/1121/2021

ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **20 de septiembre de 2021,** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS,** del estudiante **CONTRERAS NEGRETE GONZALO,** con número de cuenta **514012685** con la tesis titulada **"VARIACIÓN FUNCIONAL Y GENÉTICA DE *Prosopis laevigata* (HUMB. ET BONPL. EX WILLD) EN MÉXICO",** realizada bajo la dirección del **DR. ANTONIO GONZÁLEZ RODRÍGUEZ**, quedando integrado de la siguiente manera:

Presidente: DR. NOÉ MANUEL MONTAÑO ARIAS
Vocal: DR. ÁNGEL SALVADOR ARIAS MONTES
Vocal: DR. EDUARDO RUIZ SÁNCHEZ
Vocal: DR. MARIANA YÓLOTL ÁLVAREZ AÑORVE
Secretario: DR. ERICK DE LA BARRERA MONTPPELLIER

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

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 22 de noviembre de 2021

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
Unidad de Posgrado, Edificio D, 1° Piso. Circuito de Posgrados, Ciudad Universitaria
Alcaldía Coyoacán. C. P. 04510 CDMX Tel. (+5255)5623 7002 http://pcbiol.posgrado.unam.mx/

Agradecimientos Institucionales

Al programa de Doctorado en Ciencias Biológicas de la Universidad Nacional Autónoma de México por el apoyo proporcionado durante la realización de mis estudios.

Al Consejo Nacional de Ciencias y Tecnología por la beca de Doctorado otorgada para realizar mis estudios de posgrado (CONACyT- CVU 549242).

Al Presupuesto Operativo del Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES), UNAM para A. Gonzalez-Rodríguez y Apoyos a Proyectos de Investigación e Innovación Tecnológica (PAPIIT) (IA203221) a F. Pineda- García

Al Programa de Apoyo a los estudios de Posgrado (PAEP UNAM) por los apoyos recibidos.

Al Dr. Antonio González Rodríguez, director de tesis y tutor principal de mis estudios de posgrado de maestría y doctorado. A la Dra. Alicia Gamboa y al Dr. Erick de la Barrera, integrantes de mi comité tutor, por su asesoría y consejos durante mi formación doctoral.

Agradecimientos a titulo personal

A los compañeros de los laboratorios de Genética de la Conservación del Instituto de Investigaciones en Ecosistemas y Sustentabilidad y Ecología Funcional de la Escuela Nacional de Estudios Superiores UNAM Morelia por todo su apoyo durante estos años.

A mi jurado de tesis, la Dra. Mariana Álvarez, y los Dres. Noé Montaño, Erick de la Barrera, Eduardo Ruíz y Salvador Árias por sus comentarios y observaciones.

Al Dr. Antonio González, tutor de mis estudios desde hace años…

Al Dr. Fernando Pineda por su gran apoyo técnico, metodológico y conceptual.

A mi familia…

Tu nombre está en la libreta, Bob…

Miklo Velka(1979).

ÍNDICE

Resumen

Prosopis laevigata representa un elemento de gran importancia ecológica, económica y cultural en zonas áridas y semiáridas del país. Dada la gran variación morfológica y su amplia distribución, el objetivo de esta tesis fue evaluar la historia evolutiva, patrones de germinación, así como características eco-funcionales de asignación de biomasa y crecimiento durante el establecimiento y bajo el efecto de la disponibilidad hídrica en poblaciones cubriendo el área de distribución de la especie. Los análisis evolutivos se llevaron a cabo a través de seis microsatélites nucleares y una secuencia intergénica de cloroplasto. Asimismo, se evaluó el desempeño de la germinación bajo diferentes niveles de temperatura, sequía y salinidad. Por su parte, a través de la medición de atributos funcionales simples en plántulas, se evaluaron las estrategias de asignacion de biomasa en las primeras fases del establecimiento. Además, se evaluó el efecto de la disponibilidad hídrica en las estrategias funcionales a través de atributos de asignación de biomasa, crecimiento y fisiológicos. A partir de las secuencias del ADN de cloroplasto, se registró evidencia de una expansión poblacional de *P. laevigata* desde el último interglacial que potencialmente continúa hasta la actualidad. Mediante los marcadores nucleares se detectó un gradiente latitudinal de diversidad genética, aumentando al norte de la distribución, así como una moderada estructura genética (F_{ST}=0.15) y un alto número de alelos privados por población, apoyando los resultados de la expansión demográfica.

Por su parte, las evaluaciones de germinación mostraron que esta especie tiene un alto desempeño en todas las temperaturas evaluadas, patrones diferenciales a nivel poblacional al aumentar la salinidad y una gran susceptibilidad a la sequía, condiciones a las que las poblaciones a lo largo de su distribucion responden a través de un eje funcional de

explotación-tolerancia. Sumado a esto, el desempeño en la germinación está asociado con la variación ambiental local de las poblaciones de origen. Por otra parte, existen patrones diferenciales en la asignación de biomasa y crecimiento de plántulas de la especie, los cuales también están asociados con la temperatura y precipitación local en las poblaciones de origen. Se registraron dos estrategias principales en la asignación de recursos: una estrategia evasiva en la que las plántulas destinan más recursos al desarrollo radicular, mientras que muestran tejidos aéreos menos densos para promover una mayor área fotosintética por unidad de biomasa. Las poblaciones del sur de la distribución de *P. laevigata* mostraron esta estrategia. Por otro lado, se observó una estrategia de explotación, en el que las poblaciones invierten recursos en crecimiento para aprovechar pulsos de condiciones favorables, como se encontró en las poblaciones hacia el norte de la distribución. Finalmente, los resultados del efecto de la disponibilidad hídrica en los atributos funcionales evaluados mostraron una respuesta consistente con el espectro económico de las plantas, ajustándose a estrategias de explotación y tolerancia a través de un continuo rápido-lento en la adquisición de recursos. Adicionalmente, bajo condiciones hídricas adecuadas, las estrategias poblacionales se relacionan con los patrones de temperatura experimentados a lo largo de la distribución. Sin embargo, bajo estrés hídrico, las poblaciones ajustan sus estrategias funcionales en relación con los patrones de precipitación experimentados por las poblaciones locales. En general, la dominancia de *P. laevigata* en zonas áridas y semiáridas del país es congruente con su historia evolutiva reciente, así como con los aspectos funcionales evaluados en el presente estudio

Abstract

Prosopis laevigata is an element of great ecological, economic, and cultural importance in arid and semiarid lands of the country. Given the great morphological variation and its wide distribution, our objective was based on evaluating the evolutionary history, germination patterns, as well as eco-functional characteristics of biomass allocation and growth during establishment and under the effect of water availability in populations covering the whole distribution of the species. Evolutionary analyses were carried out using six nuclear microsatellites and a chloroplast intergenic sequence. We also evaluated germination performance under different levels of temperature, drought, and salinity. By measuring simple functional attributes in seedlings, we evaluated biomass allocation strategies in the early stages of establishment. In addition, we evaluated the effect of water availability on functional strategies through biomass allocation, growth, and physiological attributes. From chloroplast DNA sequences, we found evidence of a population expansion since the Last Interglacial that potentially continues to the present. Using nuclear markers, we found a latitudinal gradient of genetic diversity, increasing north of the distribution, as well as a moderate genetic structure (F_{ST}=0.15) and a high number of private alleles per population, supporting the results of demographic expansion.

Germination evaluations showed high performance at all temperatures evaluated, differential patterns at the population level with increasing salinity and high susceptibility to drought, to which populations respond through a functional axis of exploitation-tolerance. In addition, we found that germination performance is associated with local environmental variation in the populations of origin. On the other hand, we found differential patterns in biomass allocation and seedling growth of the species, which are

also associated with local temperature and precipitation in the source populations. We found two main strategies in resource allocation: an evasive strategy in which seedlings allocate more resources to root development, while displaying less dense aerial tissues to promote greater photosynthetic area per unit biomass. Populations in the southern distribution of *P. laevigata* showed this strategy. On the other hand, an exploitation strategy was observed, in which populations invest resources in growth to take advantage of pulses of favorable conditions, as was found in populations towards the north of the distribution. Finally, the results of the effect of water availability on the functional attributes evaluated showed a consistent response with the plants economic spectrum, adjusting to exploitation and tolerance strategies through a fast-slow continuum in the acquisition of resources. Additionally, we found that, under adequate water conditions, population strategies were related to temperature patterns experienced throughout the distribution. However, under water stress, populations adjust their functional strategies in relation to precipitation patterns experienced by local populations. Overall, the dominance of *P. laevigata* in arid and semiarid lands of the country is consistent with its recent evolutionary history, as well as with the functional aspects evaluated in the present study.

Introducción General

Origen y evolución del género *Prosopis*

El género *Prosopis* (Fabaceae, Mimosoideae) comprende un grupo esencialmente termo-xerófilo compuesto por alrededor de 45 especies, distribuidas principalmente en zonas áridas y semiáridas de Norte y Sur América, Asia y África (Figura 1) (Burkart 1976; Solbrig et al. 1977; Rzedowski 1988; Palacios 2006; Fontana et al. 2018). El género está representando por árboles y arbustos, los cuales muestran adaptaciones a la sequía, altas temperaturas, salinidad, alcalinidad y herbívora. Estas características adaptativas promueven su distribución y dominancia en la vegetación de zonas áridas y semiáridas (Palacios et al. 2001; Felker 2009; Villagra et al. 2010; Carevic 2014). Dada su abundancia y desempeño ecológico, las especies del género *Prosopis* representan elementos de gran importancia ecológica en las zonas áridas y semiáridas del mundo (Golubov et al. 2001; Pasiecznik et al. 2002; Villagra et al. 2010).

La distribución disyunta del género ha sido centro de debate en estudios fitogeográficos, los cuales en sus inicios se enfrentaron a dificultades para definir las características taxonómicas del género y esclarecer sus relaciones filogenéticas, dada la gran variación morfológica en las especies, así como los eventos de introgresión que limitaban las interpretaciones concretas sobre su origen y distribución geográfica (Rzedowski 1988; Catalano et al. 2008). Las primeras aproximaciones taxonómicas y filogenéticas claras sobre el género fueron propuestas por Johnston (1962) y Burkart (1976), siendo la segunda más aceptada, representando el punto de partida en estudios taxonómicos y filogenéticos posteriores.

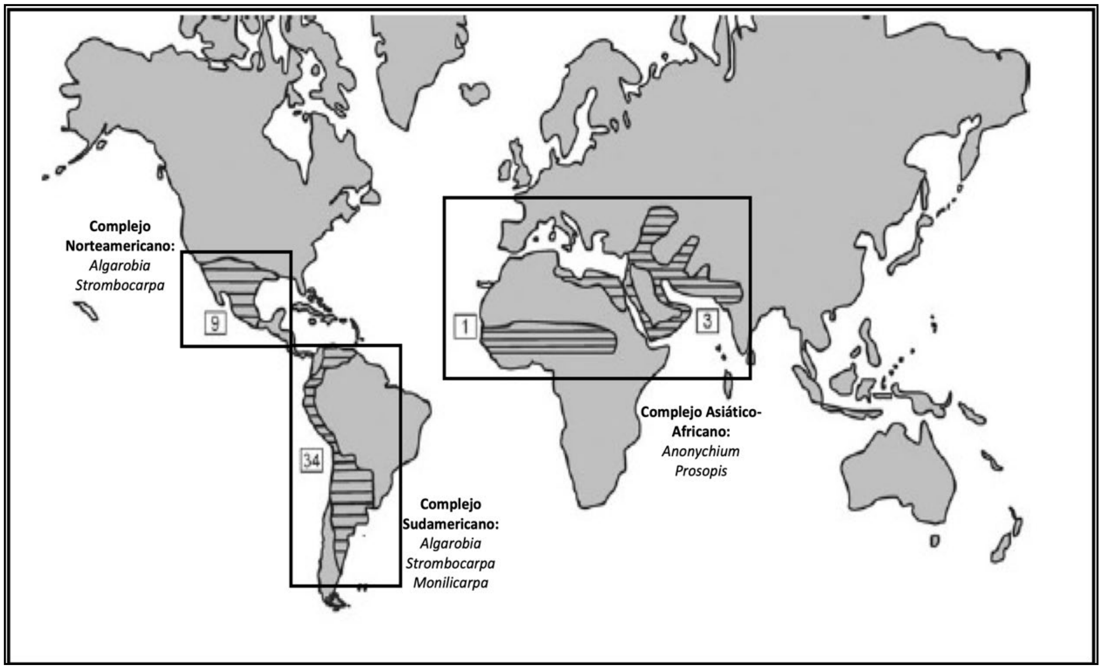


Figura 1. Distribución natural de las especies del género *Prosopis* a través de las zonas áridas del mundo. Se muestra las secciones y el número aproximado de especies reportado para cada complejo de distribución (Modificado de Catalán et al. 2008)

Burkart (1976), definió la circunscripción taxonómica de las especies dividiendo el género en cinco secciones, basándose en caracteres florales y vegetativos, particularmente de las espinas: *Algarobia*, *Strombocarpa*, *Monilocarpa*, *Prosopis* y *Anonychium*. Las secciones *Algarobia* y *Strombocarpa*, representan cerca del 90% de las especies de *Prosopis*, distribuyéndose exclusivamente en el Norte y Sur de América; la sección *Monilocarpa* presenta únicamente una especie restringida en Argentina central; la sección *Prosopis* está representada por tres especies, distribuidas al norte de África y Asia. Por su parte, la sección *Anonychium* únicamente presenta una especie, *Prosopis africana*, distribuida en la zona Sudano-Guineana, siendo la única especie con afinidad mesófila, propuesta como la especie basal del género (Burkart 1976). De acuerdo con el esquema planteado por Burkart (1976), el género *Prosopis* es un grupo primitivo de las mimosoideas. Los ancestros del género *Prosopis* pueden haber estado cercanamente relacionados a géneros como *Adenanthera* y *Pseudoprosopis*, que presentan frutos dehiscentes, los cuales evolucionaron en géneros más especializados con legumbres indehiscentes y frutos carnosos, como los frutos encontrados en *Prosopis* (Burkart 1976).

El carácter primitivo del género *Prosopis* se ha inferido dado que mantiene un número cromosómico basal de n= 14, así como la presencia de granos de polen individuales, caracteres considerados plesiomórficos (Burkart y Simpson 1977). El centro de origen del género *Prosopis* y sus posteriores patrones de dispersión, aun no son claros, postulándose como potenciales centros de origen a África tropical y Sudamérica. Raven y Axelrod (1974), propusieron a Gondwana occidental, la actual Sudamérica, como el centro de origen de las mimosoideas, argumentando que en esta área se originaron los géneros *Prosopis* y *Acacia,* dadas sus afinidades xerófilas, así como por la variación morfológica encontrada en las especies sudamericanas, que incorporan la mayor parte de la diversidad de caracteres encontrados en las demás áreas de distribución de dichos géneros (Burkart 1976; Solbrig et al. 1977; Fontana et al. 2018).

Sin embargo, aunque existe evidencia de intercambios de leguminosas de los géneros *Prosopis* y *Acacia* en las primeras fases de separación entre África y Sudamérica, la persistencia de *P. africana* en África sugiere que el continente africano representa el centro de origen del género y otras especies de legumbres tropicales (Raven y Polhill, 1981). En este contexto, la propuesta del origen sudamericano del género *Prosopis* pierde sustento. Así, aunque Sudamérica muestra una gran diversidad de leguminosas, no presenta grupos tribales endémicos, ni representantes primitivos de los géneros de la familia Leguminosae (Raven y Polhill, 1981). Se especula que la aparición del género *Prosopis* se remonta a alrededor de 70 Ma, cuando el supercontinente de Gondwana ya se encontraba separado y los puentes terrestres entre las porciones occidental y oriental se encontraban cubiertos por vastas extensiones de agua (Raven y Polhill 1981; Pasiecznik et al. 2002). Sin embargo, la distancia entre dichas porciones era sustancialmente menor a la actual, no representando una barrera infranqueable para la dispersión de las leguminosas, para las cuales se ha reportado dispersión por hidrocoria, ya que frecuentemente presentan semillas con una cubierta semipermeable, y son potencialmente capaces de dispersarse largas distancias a través del agua (Raven y Polhill 1981; Rzedowski 1988; Pasiecznik et al. 2002).

Asimismo, el proceso de deriva continental tuvo un fuerte efecto en los patrones de distribución y procesos evolutivos que experimentaron las especies de *Prosopis* a través de su historia evolutiva. Los representantes primitivos del género, se ha propuesto, mostraron adaptaciones a zonas húmedas ecuatoriales de África, los cuales al dispersarse hacia latitudes más áridas pudieron haber promovido adaptaciones a dichas zonas (Pasiecznik et al. 2002). Las características morfofisiológicas de las especies troncales pudieron haber sido la fuente de variación que promovieron la exitosa adaptación de las especies de *Prosopis* en su distribución hacia zonas áridas y semiáridas, lo que posiblemente incrementó su potencial de colonización (Burkart 1976; Pasiecznik et al. 2002).

Las especies del género *Prosopis* evolucionaron adaptándose a ambientes áridos y semiáridos, desarrollando estrategias funcionales para evadir la sequía, incluyendo raíces profundas y adaptaciones fisiológicas para maximizar la captación hídrica y minimizar la pérdida de agua bajo escenarios de aridez (Pasiecznik et al. 2002; Felker 2009; Villagra et al. 2010; Carevic 2014). Sin embargo, *P. africana*, propuesta como la especie basal del grupo, muestra una distribución asociada a bosques húmedos en la zona ecuatorial de África, manteniendo las adaptaciones consideradas plesiomórficas dentro del género *Prosopis* (Burkart 1976; Pasiecznik et al. 2002).

Las poblaciones de África, de la península Arábiga y la India, así como las poblaciones que se diseminaron a través del continente americano, representan los tres principales linajes que divergieron en las primeras fases de la historia evolutiva del género *Prosopis* (Pasiecznik et al. 2002). Es posible que la existencia de pocas especies del género en Asia se deba a la amplia barrera acuática representada por el Mar de Tetis que las separó de África después del Paleoceno (63 Ma), limitando el intercambio y la abundancia de grupos ecológicamente competitivos, restringiendo los procesos de especiación en dicha zona (Raven y Polhill 1981). Así mismo, el número de especies del género en Norte América es menor en comparación a la riqueza encontrada en Sudamérica, lo cual no representa necesariamente un origen más reciente. Las especies norteamericanas se enfrentaron a escenarios fuertemente competitivos frente a la flora boreal en el norte, así como a un gran número de grandes herbívoros que pudieron haber limitado su proceso de diversificación (Burkart 1976; Mooney et al. 1977).

La distribución disyunta, así como la diversidad de especies del género *Prosopis* observada en el continente americano ha despertado interés sobre la secuencia de colonización del género en el continente. Rzedowski (1988), propone que a pesar del origen Gondwandiano del género, es posible que dichas plantas hayan llegado durante el Eoceno a Norteamérica por Laurasia meridional, con una posterior migración a Sudamérica al igual que géneros como *Bursera*, esto, basado en los registros fósiles de *Prosopis* del Eoceno-Oligoceno en Colorado EU y Puebla México (MacGinitie 1953; Magallón-Puebla y

Cevallos-Ferriz 1994). Por otra parte, se ha propuesto que las primeras incursiones se desarrollaron en Sudamérica, con una posterior migración al norte, vía zonas áridas de la costa del Pacífico. De la misma manera, Rzedowski (1988), propone que es poco probable que un ancestro adaptado a climas mesófilos haya promovido una evolución convergente de especies con adaptaciones xerófilas en Norte y Sur América. Especies como *P. palmeri* en México han sido consideradas relicto de las primeras invasiones de *Prosopis* en Norte América (Pasiecznik et al. 2002), mientras *P. argentina*, endémica a Argentina central (Burkart 1976), muestra caracteres considerados primitivos en el grupo, presentando rizomas y sin megablastos/braquiblastos, ubicándolo como un remanente evolutivo de las especies basales del género *Prosopis* en América (Burkart 1976; Pasiecznik et al. 2002).

Por otra parte, las dinámicas climáticas experimentadas en el área de distribución del género, por ejemplo, los periodos glaciales, promovieron la migración de especies y sus respectivos ecosistemas hacia latitudes cercanas al ecuador. Esto pudo provocar contraciones en las poblaciones alternadas de procesos de expansión en zonas templadas, patrón demográfico que continua hasta la actualidad (Holland 1987). Así mismo, el descenso del nivel del mar durante los periodos glaciales pudo haber facilitado la dispersión mediante la formación de puentes terrestres, sumado a la formación de cadenas montañosas y el consecuente cambio de la configuración del paisaje, pudieron alterar patrones climáticos locales afectando directamente el proceso evolutivo y la dispersión de las especies de *Prosopis* (Johnston 1962).

El género *Prosopis* como fuente de recursos y elemento cultural de las poblaciones nativas en América

Existen vastos registros acerca del uso de las especies de *Prosopis* a través de su área de distribución por parte de las poblaciones nativas, principalmente a lo largo de su distribución en zonas áridas del continente americano. La utilización de especies de *Prosopis* por los pueblos americanos está registrada en la evidencia arqueológica, las crónicas de los conquistadores europeos, así como en la cultura popular de las poblaciones nativas (Galindo-Almanza y Garcia-Moya, 1986;Pasiecznik et al. 2002). La historia de aprovechamiento y explotación del género *Prosopis* en América consta de al menos tres etapas, en función de la intensidad de su explotación: la prehistoria, la colonia y la época moderna (Pasiecznik et al. 2002). Las especies de *Prosopis* representaron recursos de gran importancia para las primeras poblaciones que habitaron las zonas áridas del continente americano, llegando a existir una gran identidad cultural al hacer referencia a dichas plantas (Berlin 1973). El registro arqueológico muestra evidencia del consumo de frutos de *Prosopis* en el valle de Tehuacán en México hace alrededor de 6500 AP (Smith 1967), pudiendo haberse consumido desde al menos 1000 años antes (Towle 1961). Por otra parte, se han encontrado registros de madera de *Prosopis* en tumbas en varios sitios arqueológicos de Perú que datan de al menos 2500 AP (D'antoni 1977). Dichos registros muestran que el consumo de los frutos y la utilización de madera de las especies del género fue amplio entre los primeros colonizadores del continente americano.

En un segundo periodo de explotación, las culturas americanas utilizaron la madera de *Prosopis* como recursos naturales para la construcción y fabricación de herramientas, mientras que los frutos se utilizaban en la preparación de alimentos más elaborados como bebidas fermentadas y harinas, práctica encontrada en las poblaciones africanas que utilizan

Prosopis africana (Achi 1992). Después de proceso colonial el uso de las especies de *Prosopis* por parte de las poblaciones americanas continuó por varios siglos, conservándose algunas prácticas hasta la actualidad (Pasiecznik et al. 2002). Sin embargo, el uso de herramientas fabricadas con la madera de *Prosopis* fue sustituido por nuevas tecnologías traídas durante el periodo de colonización (Díaz Celis 1995). El gran potencial de aprovechamiento de las especies de *Prosopis* no pasó desapercibido por parte de los colonizadores europeos, que identificaron en las especies un alto potencial de aprovechamiento, principalmente en zonas áridas y con suelos pobres, promoviendo su introducción a lo largo de zonas áridas, principalmente en el hemisferio sur (Pasiecznik et al. 2002).

Las especies de *Prosopis* como plantas invasoras a través de las zonas áridas

La invasión de malezas leñosas, principalmente en tierras agrícolas, se ha convertido en un problema de gran importancia en muchas regiones del mundo (Pasiecznik et al. 2002). Las especies de *Prosopis* muestran un papel polémico en este problema, al representar recursos aprovechables en sus áreas nativas de distribución y a la vez convertirse en especies invasoras altamente competitivas como plantas introducidas (Zimmermann 1991; Golubov et al. 2001; Pasiecznik et al. 2002; Alvarez et al. 2017). Las especies de *Prosopis* han sido introducidas deliberadamente en zonas áridas del mundo, algunas convirtiéndose en amenazas a la flora nativa (Golubov et al. 2001; Pasiecznik et al. 2002; El-Keblawy and Al-Rawai 2005; Miranda et al. 2014; Alvarez et al. 2017; Usman et al. 2019). La atención sobre estas especies se centra en los múltiples productos obtenidos, altos rendimientos en suelos pobres, tolerancia a la sequía, y su valor en sistemas agroforestales dada su capacidad de regeneración vegetativa. Las características maderables, así como la palatabilidad de los frutos representaron los principales caracteres seleccionados en las especies del género *Prosopis* al utilizarse como plantas introducidas (Von Maydell 1986; Pasiecznik et al. 2002). Las primeras invasiones de especies de *Prosopis* en su área natural de distribución se remontan a inicios de siglo XIX y aún continúan en una etapa de expansión, mientras sus primeras introducciones a zonas áridas del hemisferio sur se registraron principios del siglo XX (Figura 2) (Pasiecznik et al. 2002).

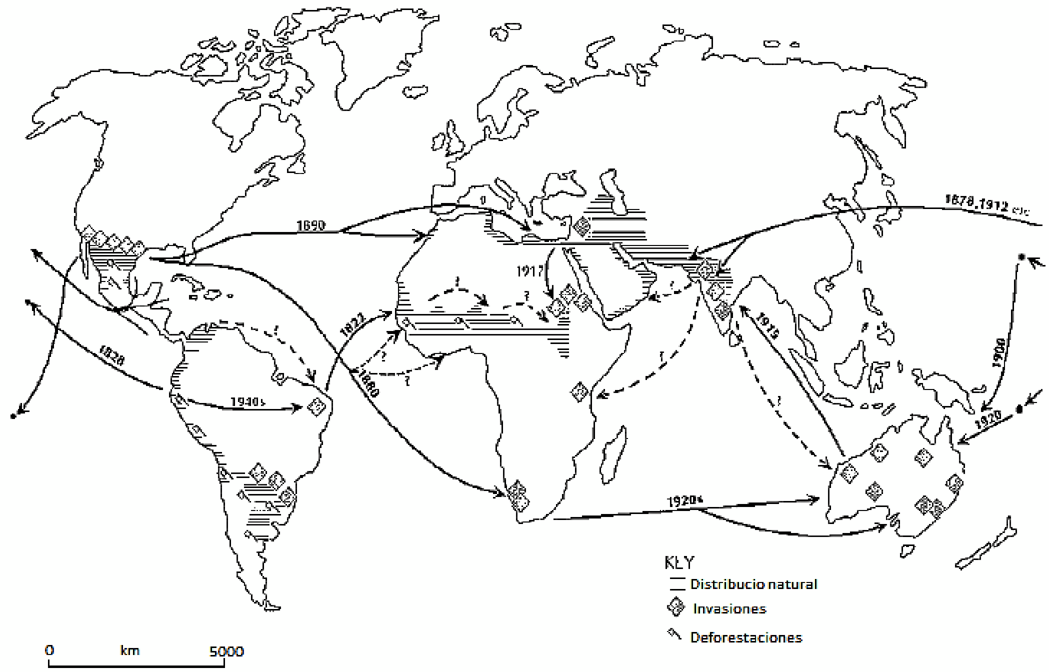


Figura 2.- Distribución aproximada del género *Prosopis* en la actualidad. Se muestra el área de deforestación, invasión natural y por introducción, así como las fechas aproximadas de sus introducciones (Pasiecznik et al. 2002)

Dentro de las invasiones registradas en el área de distribución nativa de *Prosopis*, se encuentran los casos de *P.glandulosa* var. *torreyana* en Texas*,* *P. ruscifolia* en el norte de

Argentina y en el Chaco Paraguayo, *P. velutina* en México y *P. campestris, P. hassleri*, *P. humilis*, *P. kuntzei*, *P. nigra* al norte de Argentina y Paraguay, así como *P. affinis* y *P. caldenia* en Argentina y Uruguay (Figura 2) (Burkart 1976; Felger 1977; Pires et al. 1990; Lima y Silva 1990; Lima et al. 1996; Pasiecznik et al. 2002). Dichas invasiones se han presentado bajo diferentes condiciones ambientales, sin embargo, el trasfondo es similar, las invasiones se han desarrollado después de eventos de aclaramiento con fines productivos, principalmente para fines agrícolas y ganaderos, práctica que aumenta en intensidad durante la época colonial y se acentúa durante las etapas industriales en Norte y Sur América (Pasiecznik et al. 2002). A nivel mundial, las principales cuatro especies invasoras son *P. glandulosa* var. *torreyana* y *P. velutina* en la mayor parte de zonas subtropicales, mientras que *P. juliflora* y *P. pallida* se encuentran como invasoras de zonas tropicales. Otras especies como *P. alba* y *P. chilensis* han sido introducidas de forma menos exitosa, las cuales no presentan el estatus de maleza (Pasiecznik et al. 2002). En Sudáfrica y Australia la propagación de *P. glandulosa* var. *torreyana* y *P. velutina*, así como sus híbridos, fue rápida y extensiva, continuando hasta la actualidad, convirtiéndose en malezas nocivas capaces de desplazar a la vegetación nativa. De la misma manera, *P. juliflora* y *P. pallida* son clasificadas como especies invasoras nocivas en Australia. Además, *P. juliflora* muestra un gran avance en Pakistán y Sudán y está clasificada bajo el estatus de maleza en partes de otros países de África Saheliana, Brasil y el sur de Asia (Burkart 1976; Csurhes 1996; Perry 1998; Panetta and Carstairs 1989; Dubey 1988; Reddy 1978; Muthana y Arora 1983; Oliveira et al. 2017). Otras especies como *P. cineraria*, *P. pubescens* y *P. tamarugo* también se han introducido ampliamente, pero rara vez han proliferado (Pasiecznik et al. 2002). Sin embargo, la identificación incorrecta de las especies del género *Prosopis* ha llevado a confusión taxonómica y, por lo tanto, los registros de introducción no son claros (Pasiecznik et al. 2002).

La capacidad de estas especies para colonizar amplias extensiones a partir de una simple introducción o pocos árboles/arbustos dispersos se ha observado en las dinámicas de expansión registradas en Oceanía, África y Asia (Pasiecznik et al. 2002). Al parecer algunas especies de *Prosopis* muestran una naturaleza más competitiva que otras, presentando un intervalo ecológico mayor con adaptaciones a una amplia gama de condiciones (Golubov et al. 2001; Pasiecznik et al. 2002). El género *Prosopis* es actualmente considerado como maleza a lo largo de millones de kilómetros cuadrados de regiones áridas y semiáridas, donde reducen drásticamente la producción de plantas forrajeras, amenazando los sistemas productivos locales (Pasiecznik et al. 2002), haciendo de las especies del género objetivos prioritarios en la evaluación de sus dinámicas poblacionales y ecológicas a través de su distribución natural y como planta invasora.

Evaluaciones genéticas en especies del género ***Prosopis***

La mayor parte de los estudios genéticos en el género *Prosopis* se han realizado en especies americanas, dado que representan el principal centro de diversidad del género a nivel mundial. Las primeras aproximaciones se centraron en evaluar las relaciones entre las especies de la sección *Algarobia* y *Strombocarpa* mediante el uso de isoenzimas y RAPDs (Hunziker et al 1986; Saidman y Vilardi 1987 1993; Saidman et al. 1996; Burghardt et al. 2004; Ferreyra et al. 2004, 2007; Hamza et al. 2010). Para la sección *Algarobia*, se han reportado altos valores de diversidad genética dentro de las especies, atribuidos a su sistema de polinización cruzada, así como bajos niveles de diferenciación genética entre las distintas especies analizadas, patrones atribuidos a las altas tasas de hibridación (Bessega et al. 2016, 2019; Fontana et al. 2018, Moncada et al. 2019; Castillo et al. 2021). Para la sección *Strombocarpa*, al contrario, se han reportado relaciones filogenéticas bien definidas y bajos niveles de diversidad genética, asociados a la capacidad de dichas especies a reproducirse vegetativamente y a sistemas reproductivos autogámicos (Ferreyra et al. 2004). Por su parte, para las especies menos diversas como *P. argentina* (*Monilocarpa*), especie de distribución restringida, se ha propuesto que la baja variación genética es debida a la autogamia, la reproducción vegetativa y una alta especialización (Bessega et al. 2006).

Los altos valores de diversidad y baja estructura genética a través de las especies de la sección *Algarobia*, atribuidas a la hibridación, así como a la plasticidad fenotípica de genotipos multipropósito en respuesta a las limitantes ecológicas, han generado diferentes hipótesis en relación a las tendencias evolutivas y adaptativas de las especies de la sección a través de su distribución (Catalano et al. 2008; Bessega et al. 2016, 2019; Fontana et al. 2018 Moncada et al. 2019; Castillo et al. 2021). Por una parte, se han propuesto la existencia de mecanismos evolutivos diferenciales entre genes asociados a caracteres vegetativos y metabólicos, que potencialmente mostrarían diferentes tasas de mutación en función de las presiones selectivas, de esta manera incrementaría la variabilidad morfológica y se conservarían las estrategias metabólicas (O'rourke et al. 2014; Bessega et al. 2006). Por otra parte, las altas tasas de hibridación entre las especies de *Algarobia*, podrían deberse a que dicho proceso contribuyó de manera importante en la evolución temprana de la sección, promoviendo un proceso de evolución reticulada, impulsando su capacidad invasora al retener diversidad genética asociada con adaptaciones a ambientes áridos (Bessega et al. 2016, 2019; Fontana et al. 2018). Dicho planteamiento, es congruente con los resultados encontrados para *P. laevigata, P. glandulosa* var. *torreyana* y *P. juliflora* en México, las cuales fueron analizadas utilizando microsatélites nucleares y secuencias de cloroplasto, encontrando una alta similitud genética entre las tres especies a nivel de núcleo, así como haplotipos compartidos a nivel de cloroplasto (Contreras-Negrete et al. datos no publicados). Por otra parte, los resultados para *P. laevigata* evidencian una expansión poblacional reciente , lo que posiblemente promovió la ampliación de su rango de distribución (Contreras-Negrete et al. 2021). Previamente, Galindo-Almanza et al. (1992), reportaron hibridaciones entre poblaciones naturales de *P. laevigata y P. glandulosa* var. *torreyana* en San Luis Potosi, México, encontrando mayores proporciones de parentales puros en la zona, evidenciando que aunque es posible la hibridación, los patrones autogámicos de polinización mantienen la coexistencia de los dos taxa.

Asimismo, cabe destacar que las especies que representan problemas como invasoras pertenecen a la sección *Algarobia* (*P. juliflora, P. pallida, P. glandulosa* y *P. velutina*) (Pasiecznik et al. 2002) las cuales aún en sus áreas de invasión muestran altos valores de diversidad genética (Torales et al. 2013). A la fecha, las aproximaciones en la exploración genética del género *Prosopis* se han llevado a cabo utilizando marcadores moleculares como isoenzimas, RAPDs y microsatélites, existiendo unicamente pocas aproximaciones filogenéticas mediante el uso de secuencias (e.g. Catalano et al. 2008) así como secuenciación completa del genoma de cloroplasto (*P. juliflora* y *P. cineraria*; Asaf et al. 2020) . Por lo tanto, se han dilucidado las principales limitantes en la caracterización filogenética de las especies y se han podido evidenciar aspectos evolutivos relacionados con las dinámicas ecológicas del género.

Patrones de germinación en el género *Prosopis*

La sequía, temperaturas extremas y la salinidad son factores altamente variables que afectan directamente la germinación y desarrollo de las plántulas en las zonas áridas (Flores et al. 2006; Hassanein 2015; Solarik et al. 2018). Las especies vegetales se han adaptado para tolerar, evadir y escapar de los escenarios con baja disponibilidad hídrica y salinidad variable, generando estrategias de germinación y establecimiento que permiten la continuidad de las especies bajo dichos escenarios (Salisbury 1992; Westphal et al. 2015). Para el género *Prosopis*, se ha evaluado el efecto de los distintos factores durante la germinación, así como en las primeras fases del desarrollo de las plántulas.

Con relación a lo anterior, se ha reportado un amplio intervalo en la temperatura de germinación, en algunas especies situado entre los 15 y 40 °C (Contreras-Negrete et al. *in litt*.). La mayor parte de las especies evaluadas muestran la temperatura óptima de germinación entre los 25 y 35°C (Tabla 1), intervalo asociado directamente a las condiciones climáticas a través de su área de distribución. Por otra parte, las evaluaciones encaminadas al efecto de la salinidad y el déficit hídrico muestran, de la misma manera, un amplio intervalo de tolerancia. Tal es el caso de *P. chilensis*, especie para la cual se reporta germinación bajo concentraciones salinas de hasta 600 mM de NaCl (Catalán et al. 1994) (Tabla 1), mientras que *P. flexuosa* muestra una concentración cardinal de hasta 800mM NaCl (Seeman et al. 1984). Por otra parte, al evaluar el efecto del déficit hídrico en los patrones de germinación, se ha reportado germinación aún bajo potenciales hídricos de -3MPa (*P. alba*; Tabla 1), mientras algunas otras especies detienen su proceso germinativo bajo potenciales hídricos de alrededor de -2MPa (Tabla 1).

Tabla 1.- Patrones de germinación y porcentajes de supervivencia en especies del género *Prosopis* bajo diferentes escenarios de temperatura, salinidad y déficit hídrico.

Especie	Sección	Distribución	Atributo	Factor	Tratamiento	Resultado	Cita
				Temperatura			
P. chilensis	Algarobia	Natural	Ger	TO	25-40°C	80%	Cony y Trione, (1998).
P.flexuosa	Algarobia	Natural	Ger	TO	20-25	100%	Cony y Trione, (1998).
P. glandulosa var. *torreyana*	Algarobia	Natural	Ger	TO	30°C	100%	Sosebee y Wan (1987)
P. velutina	Algarobia	Natural	Ger	TO	30°C	90%	Sosebee y Wan (1987)
P.laevigata	Algarobia	Natural	Ger	TO	30-35°C	90%	Contreras- Negrete et al. *in litt*.
P.juliflora	Algarobia	Introducida	Ger	TO	25°C	80%	El-Keblawy y Al-Rawai (2005).
				Salinidad y Pot. Hídrico			
P. chilensis	Algarobia	Natural	Ger	PH	-2MPa	0%	Cony y Trione, 1998
P.flexuosa	Algarobia	Natural	Ger	PH	-2MPa	0%	Cony y Trione, 1998
P. farcta	Prosopis	Natural	Ger	PH	-1.8MPa	20%	Bazzaz, 1973
P. alba	Strombocarpa	Natural	Ger	PH	-3 MPa	80%	Arce et al. 1990
P. strombulifera	Strombocarpa	Natural	Ger	PH	-1.9MPa	20%	Sosa et al. 1995
P. argentina	Monilocarpa	Natural	Ger	Sal	600 mM NaCl	0%	Villagra et al. 1997
P. alpataco	Algarobia	Natural	Ger	Sal	600 mM NaCl	0%	Villagra et al. 1997
P. farcta	Prosopis	Natural	Ger	Sal	200 mM NaCl	70%	Sherif y Ali, 2007
P. chilensis	Algarobia	Natural	Ger	Sal	600 mM NaCl	70%	Westphal et al. 2015
P.juliflora	Algarobia	Introducida	Ger	Sal	600 mM NaCl	0%	El-Keblawy y Al- Rawai, 2005
				Salinidad-supervivencia			
P.flexuosa	Algarobia	Natural	Sup	Sup(%)	800 mM NaCl	96%	Catalan et al. (1994)
Prosopis spp.		Natural	Sup	Sup(%)	4% NaCl	61%	Arce y Balboa (1990)

Ger: Germinación; **Sup**: Supervivencia; **TO**: Temperatura óptima de germinación; **DT**: diferentes temperaturas evaluadas; **PH:** Potencial Hídrico; **Sal:** Salinidad; **Sup (%):** Porcentaje de supervivencia.

Al evaluar el efecto de la salinidad en la supervivencia de plántulas durante las primeras fases del desarrollo, se ha encontrado gran tolerancia, como son los casos de *P. flexuosa* (Arce et al. 1990) y otras especies de algarrobos argentinos (Seeman et al. 1984). Para el primer caso, se registró una supervivencia de hasta 91% en plántulas sometidas a 800mM NaCl, mientras que el segundo grupo mostró una supervivencia de 60% bajo una solución salina a 700 mM de NaCl (Tabla 1).

Estrategias funcionales en especies del género *Prosopis*

A lo largo de su área de distribución, las especies del género *Prosopis* constituyen recursos de gran importancia al proveer una gran variedad de bienes y servicios, además de mostrar una gran capacidad para desarrollarse en suelos con baja disponibilidad de nutrientes (Golubov et al. 2001; Pasiecznik et al. 2002; Felker 2009; Carevic 2014; Flores et al. 2017). A nivel ecosistémico las especies del género *Prosopis* representan una fuente de alimento para un gran número de organismos (Germano y Hungerford 1981; Cates y Rhodes 1977; Golubov et al. 2001; Wisdom 1991; Simpson 1977; Tiedemann y Klemmedson 1973), además de que forman islas de diversidad y fertilidad dada su capacidad de fijar nitrógeno atmosférico (Steenbergh y Lowe 1977; Fulbright et al. 1995; Van den Berg y Zeng 2006). En zonas áridas y semiáridas de México diferentes estudios han reportado la existencia de islas de fertilidad bajo el dosel de *P. laevigata*, encontrando altas concentraciones de carbón orgánico, nitrogeno y fósforo en relacion a otros elementos vegetales con los que coexiste (Perroni-Ventura et al. 2010; García-Sánchez et al. 2012). Sumado a esto, se ha reportado una alta riqueza de especies vegetales debajo del dosel de individuos de *P. laevigata*, pertenencientes principalmente a las familias Asteraceae, Cactaceae y Leguminosae, riqueza que aumenta bajo arboles, pero disminuye de manera significativa debajo de arbustos de dicha especie (Cruz-Rodríguez et al. 1997; Bernal-Ramírez et al. 2019).

Las ventajas adaptativas presentes en el género han promovido que algunas especies hayan ampliado su rango de distribución, de manera natural o al ser introducidas (Zimmermann 1991; Golubov et al. 2001; Pasiecznik et al. 2002; Alvarez et al. 2017). La alta adaptabilidad por parte de las especies de *Prosopis* a diferentes escenarios propios de zonas áridas ha llamado la atención en la exploración de las características ecofisiológicas de sus especies.

La disponibilidad de agua representa la principal limitante en el establecimiento y desarrollo de las comunidades vegetales en relación con cualquier otro factor ambiental (Kozlowski 1964; de la Barrera 1997). Principalmente en ambientes áridos y semiáridos este recurso es limitado, disminuyendo las posibilidades del desarrollo de las plantas (Nobel 1999; Wiegeand et al. 1999; Passera 2000). La distribución del género *Prosopis* ocurre en ambientes áridos y semiáridos, en donde las especies han desarrollado mecanismos morfofisiológicos que promueven su persistencia espacial y temporal (Golubov et al. 2001; Felker 2009; Villagra et al. 2010; Carevic 2014). Las especies de *Prosopis* tienen una amplia variedad de adaptaciones que les permiten una gran competitividad y persistencia, por lo que llegan a caracterizar fisonómicamente zonas en las que el déficit hídrico representa la principal limitante (Golubov et al. 2001; Felker 2009; Villagra et al. 2010; Carevic 2014).

Las fotosíntesis representan uno de los procesos más sensibles al daño causado por altas temperaturas y estrés hídrico (De Soyza et al. 1996; Quero et al. 2008). Las plantas pueden diferir en su tolerancia al calor, pues algunas son capaces fisiológicamente de incrementar su tolerancia y su temperatura óptima para la asimilación de carbono en respuesta al incremento de la temperatura (Berry y Bjorkman 1980). Los metabolismos vegetales se clasifican en función de los mecanismos para fijar CO_2 atmosférico, siendo los principales tipos C3, C4 y CAM. Las especies del género *Prosopis* pertenecen al grupo C3, el cual, con relación a los otros tipos metabólicos, posee menor eficiencia en el uso del agua, presenta fotorrespiración y la fotosíntesis neta y la producción de materia seca es inferior al de las plantas C4 (Villagra 2000). Sin embargo, las especies de *Prosopis* representan un grupo especial dentro de los C3, mostrando características adaptativas que los acercan a la eficiencia de las plantas C4.

Entre las especies del género *Prosopis* se ha reportado una buena capacidad fotosintética aún bajo altos niveles de estrés, como lo refieren Mooney et al. (1977), para *Prosopis glandulosa* var. *glandulosa* en el Valle de la Muerte en EU, reportando altas tasas fotosintéticas mientras la planta experimentaba 45°C de temperatura ambiental y un potencial hídrico de -4.5 MPa en el tejido foliar (Tabla 2). De Soyza et al. (1996), reportaron también altas tasas fotosintéticas, para la misma especie, en el desierto Chihuahuense en una zona con una precipitación media anual de 223 mm. Dicho patrón se ha repetido en otras poblaciones de *P. glandulosa* en Norteamérica, como lo demuestran Hansen y Dye (1980), Nielsen et al. (1981) y Ansley et al.(1992) (Tabla 2). Los resultados se encuentran entre las tasas fotosintéticas más altas registradas para especies leñosas, evidenciando la capacidad de las especies para regular sus procesos fotosintéticos aún bajo escenarios altamente estresantes (Corcuera y Butterfield, 1999). Por otra parte, Delatorre et al. (2008), reportaron para las especies sudamericanas *P. chilensis* y *P. tamarugo*, bajas tasas fotosintéticas a 40°C de temperatura ambiental y un potencial hídrico de -2.5 MPa, sugiriendo que estas especies tienen mayor sensibilidad a condiciones extremas (Tabla 2).

Tabla 2.- Patrones fotosintéticos en especies del género *Prosopis* a través de su distribución natural y como planta introducida.

Especie	**Área**	**T (°C)***	**Pot. Hid (MPa)**	**Factor**	**Respuesta (µmol CO_2 m^{-2} s^{-1})**	**Cita**
P. juliflora	India	30 - 45	NR	A_N	16 - 10	Shirke y Pathre (2003)
P. juliflora	Sudan	33 - 45	NR	A_N	17 - 7	Elfadl y Luukkanen (2006)
P. juliflora	Brasil	NR	-4 a - 2.4	A_N	8.7 - 16	Oliveira et al. (2017)
P. chilensis	Argentina	24 - 40	-0.3 a -2.4	A_N	23.5 - 9.4	Delatorre et al. (2008)
P. tamarugo	Argentina	25 - 40	-0.3 a -2.5	A_N	17.9 - 2.6	Delatorre et al. (2008)
P. glandulosa var. *glandulosa*	EU	45	-4.5	A_N	18	Money et al. (1977)
P. glandulosa var. *glandulosa*	EU	NR	NR	A_N	22	De Soyza et al. (1996)
P. glandulosa var. *glandulosa*	EU	NR	-3.3 a -3.7	A_N	19 - 7	Hansen y Dye (1980)

T (°C) *: Temperatura ambiental; **NR**: No reportado; **A_N**: Fotosíntesis Neta

La adaptabilidad existente a través del género muestra una relación estrecha con la capacidad de captación y aprovechamiento del agua en las especies en escenarios de déficit hídrico. En este sentido, se ha reportado que los sistemas radiculares en especies de *Prosopis* pueden alcanzar una profundidad de hasta 53 m (Phillips 1963). Sin embargo, es probable que las raíces más profundas no contribuyan de manera activa a la captación hídrica y desarrollo de las plantas, como lo reportó Meinzer (1927), para *P. glandulosa* var. *glandulosa*, mostrando que las plantas que crecían bajos fuentes de agua superficiales a tres metros de profundidad variaban entre 3.6 y 6 m de altura, mientras las plantas que crecían bajo aguas subterráneas de hasta 14 m de profundidad variaban entre 0.6 y 0.9 m en altura.

La condición de freatofitas en las especies de *Prosopis* es una característica ampliamente relacionada con las características competitivas de algunas especies del género, como lo demostraron Mooney et al. (1977), para *P. glandulosa* var. *glandulosa*, reportando el cierre estomático hasta temperaturas de 45°C y un potencial hídrico foliar de -4.5 MPa, evidenciando una gran eficiencia en el uso del agua. De la misma manera, en *P. juliflora* se ha reportado un comportamiento más competitivo como invasora en la India y Sudán, al establecerse en sitios asociados a fuentes de agua, reportando altas tasas fotosintéticas, que representan mayores capacidades reproductivas y por ende de colonización (Shirke y Pathre 2003; Elfadl y Luukkanen 2006). Así mismo, Oliveira et al. (2017), reportan una alta capacidad fotosintética y amplia variación morfoanatómica a nivel de hojas en poblaciones de la invasora *P. juliflora* en Brasil, sugiriendo que esta especie muestra características adaptativas y/o plasticidad fenotípica más eficientes bajo escenarios adversos en relación con sus competidoras nativas, que han sido desplazadas de amplias zonas.

Además, se han registrado respuestas diferenciales en algunas especies a través de gradientes hídricos. Verzino et al. (2003), evaluaron el crecimiento de plántulas de *P. chilensis* provenientes de distintas localidades de Sudamérica, reportando una asociación de la precipitación y variables geográficas con las tasas iniciales de crecimiento y la resistencia al frío, sugiriendo la existencia de una adaptación genética relacionada con factores macro ambientales. Weber et al. (2008) evaluaron la sobrevivencia de plantas provenientes de un gradiente hídrico latitudinal y longitudinal en la distribución de *P. africana* en Burkina Faso y Níger, reportando mayor supervivencia en plantas de zonas secas en relación con las de zonas húmedas. Por su parte, Montes y Weber (2009), al analizar la densidad de la madera de *P. africana* en Níger, registraron una mayor densidad en la madera en los sitios más secos *vs.* los sitios más húmedos, y propusieron la posible existencia de adaptaciones genéticas para la producción de madera de mayor densidad en zonas secas.

El género *Prosopis* en México

En México, el género *Prosopis* está representado por entre 10 y 14 taxa, tres de las cuales pertenecen a la sección *Strombocarpa* (*Prosopis palmeri*, *P. reptans* var. *cinerascens y P. pubescens*), 11 a la sección *Algarobia* de acuerdo con Palacios (2006): *P. articulata, P. glandulosa , P. mayana, P. odorata, P. tamaulipana, P. velutina, P. vidalina, P. yaquiana, P. juliflora, P. mezcalana* y *P. laevigata,* mientras que Rzedowski (1988) y Burkart (1976), unicamente reconocen seis especies de algarobios: *P. articulata, P. glandulosa , P. tamaulipana, P. velutina, , P. juliflora* y *P. laevigata,* no existiendo un consenso definitivo acerca del número de especies de algarobios en México.

Dentro de las especies del complejo norteamericano destaca *Prosopis laevigata* (Willd.) M. C. Johnst, el cual es el “mezquite” típico del centro de México (Burkart 1976; Rzedowski 1988). *Prosopis laevigata* es un árbol o arbusto, de 3 hasta 12 m de altura, tronco de 30 cm a 1 m de diámetro, corteza gruesa, de color café negruzco, fisurada, armada de espinas estipulares de 1 a 4 cm de largo; hojas pecioladas, con 1 a 3 pares de pinnas, cada una con 10 a 20 pares de foliolos sésiles, linear-oblongos, de 5 a 15 mm de largo por 1 a 2 mm de ancho, flores dispuestas en espigas densas de 5 a 10 cm de largo; flores blanco amarillentas, sésiles o casi sésiles; cáliz de 1 mm de largo, glabro o puberulento; corola de 2 a 3 mm de largo, pétalos agudos, tomentosos en el margen y en el interior; estambres de 4 a 5 mm de largo. Fruto, legumbre linear de 7 a 20 cm de largo por 8 a 15 mm de ancho, comprimida, glabra, de color café-amarillento, a veces rojizo, algo constreñida entre las semillas; éstas oblongas, comprimidas, de 8 a 10 mm de largo, de color blanco amarillento (Burkart, 1976; Calderón y Rzedowski 2001).

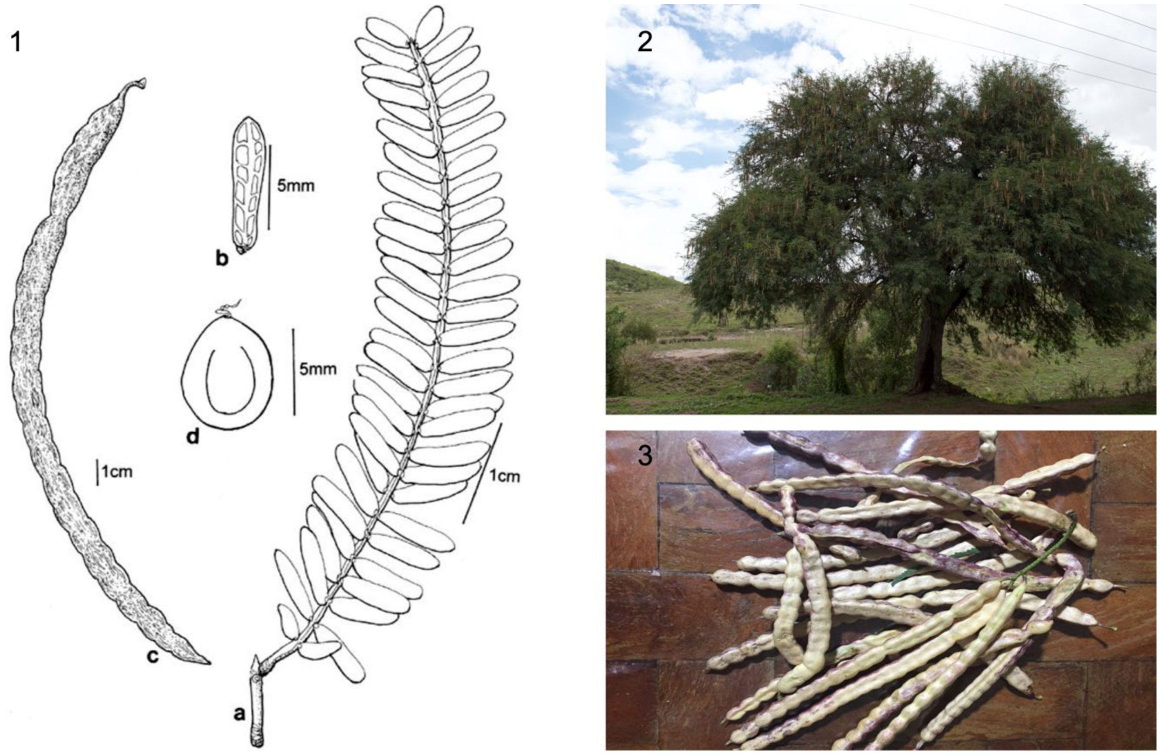


Figura. 3.- *Prosopis laevigata*: 1).- *a*) pinna; b) foliolo; c) fruto; d) semilla (Tomado de Palacios, 2006); 2) Arbol de *Prosopis laevigata;* 3) Frutos de *Prosopis laevigata*

Prosopis laevigata es la especie de más amplia distribución del género en México (Rzedowski 1988, Palacios 2006). Presenta una gran variación morfológica en hojas, altura y forma de crecimiento a través de su distribución, posiblemente asociada a las condiciones ambientales locales experimentadas por las poblaciones a lo largo de su distribución (Rzedowski 1988; Palacios 2006), ya que la especie puede encontrarse en climas semihúmedos, selva baja o en matorrales xerófilos en altitudes cercanas a los 2500 msnm al norte del país (Rzedowski, 1988). La distribución geográfica de *P. laevigata* incluye las zonas áridas del centro y nororiente del país, así como zonas semiáridas del sur como los valles centrales de Oaxaca y el Valle de Tehuacán-Cuicatlán (Rzedowski 1988; Palacios 2006). Su distribución se encuentra fraccionada por la Faja Volcánica Transmexicana (FVTM), cadena montañosa que divide las porciones Norte y Sur de México, y por la Sierra Madre Oriental, que divide a las poblaciones del centro-norte de aquellas de la Planicie Tamaulipeca. A pesar de las disyunciones en su distribución, no existen particularidades morfológicas asociadas a las áreas de distribución, por lo tanto, se acepta que es la misma especie (Rzedowski 1988).

Objetivos generales

En el presente trabajo se exploraron diferentes aspectos ecológico-evolutivos de *Prosopis laevigata*, la cual representa un referente ecológico y cultural en las zonas áridas y semiáridas de noreste, centro y sur de México. Por lo tanto, la evaluación se centró en . i) Evaluar la diversidad genética neutral, demografía y distribución histórica (Capitulo 1), ii) Analizar las respuestas fisiológicas a contrastes ambientales durante la germinación de su semillas (Capitulo2), iii) Determinar los patrones de asignación de biomasa y crecimiento en su estadio de plántula (Capitulo 3) y iv) Estudiar el efecto de la sequía en sus estrategias funcionales de atributos de biomasa, crecimiento y fisiológicos, a partir de germoplasma proveniente de diferentes poblaciones que cubren su distribución en México (Capitulo 4).

En el **primer capítulo**, se exploraron los patrones de diversidad y estructura genética de poblaciones cubriendo el área de distribución de la especie. Asimismo, se evaluaron los patrones de demografía histórica y distribución potencial histórica a través de su distribución en México. En este estudio, el principal objetivo fue contribuir a la comprensión de la biogeografía histórica de las zonas áridas y semiáridas mexicanas. De manera particular, los objetivos fueron determinar si la diferenciación poblacional a nivel genético en *P. laevigata* está asociada con su distribución; por otra parte evaluar si los patrones de demografía histórica y la distribución geográfica de la especie durante el último interglacial (LIG), último máximo glacial (LGM) así como el Holoceno medio (MH) se ajustan a la hipótesis de los refugios glaciales (GRH) o a la hipótesis de los refugios interglaciares (IRH), previamente reportados para otras especies de zonas áridas en México.

En el **segundo capítulo**, se exploró la existencia de un primer filtro selectivo de la vida de las plantas, la germinación. Para evaluar los patrones de germinación de *P. laevigata*, se usaron modelos de Tiempos Termales (Thermal Time Models) e Hidro Temporales (Hydrotime Models) para examinar la respuesta fisiológica de semillas provenientes de 15 poblaciones bajo diferentes niveles de temperatura, disponibilidad hídrica y salinidad. Simultáneamente, se evaluó si la disyuntiva entre las estrategias de explotación y tolerancia a recursos y condiciones promueve la diferenciación entre las poblaciones durante de germinación de la semilla. Finalmente, se exploró si las respuestas fisiológicas durante la germinación están relacionadas con las condiciones ambientales locales experimentadas por las poblaciones.

En el **tercer capítulo** se abordaron las estrategias de asignación de biomasa y crecimiento durante el establecimiento a través de la distribución de *P. laevigata,* mediante la medición de atributos funcionales simples en plántulas. Esto, bajo la hipótesis de que la existencia de asignación diferencial de biomasa y patrones de crecimiento en plántulas a lo largo de la distribución de *P. laevigata* se asocia con los contrastes ambientales experimentados por la especie. Por lo tanto, los principales objetivos fueron determinar la asignación de biomasa y los patrones de crecimiento en las plántulas de las poblaciones de *P. laevigata* e identificar las variables ambientales que han moldeado los patrones de asignación de biomasa y crecimiento en las poblaciones de *P. laevigata* a través de su distribución durante el establecimiento de las plántulas.

Finalmente, en el **cuarto capítulo** se evaluó la respuesta funcional de las plántulas de *P. laevigata* a condiciones contrastantes de disponibilidad hídrica (-0.12 MPa y -1.25 MPa, respectivamente). En particular, bajo la predicción de que los atributos morfológicos y fisiológicos de poblaciones de *P. laevigata* se expresarían a través de un eje funcional de explotación y tolerancia en relación al gradiente ambiental experimentado por la especie a traves de su distribución. Los objetivos particulares fueron: evaluar la diferenciación poblacional expresada en los atributos funcionales el alta y baja disponibilidad hídrica, asi como explorar las estrategias funcionales expresadas respecto a la disponibilidad hídrica en las de poblaciones a través de su distribución. Finalmente, se determinó si la variación funcional encontrada en poblaciones de *P. laevigata* está correlacionada con la variación ambiental experimentada por la especie a través de su distribución.

Capítulo I:
Genetic structure, phylogeography and potential distribution modeling suggest a population expansion in the mesquite *Prosopis laevigata* since the last interglacial

Aceptado en: Plant Systematics and Evolution

Plant Systematics and Evolution (2021) 307:22
https://doi.org/10.1007/s00606-021-01744-5

ORIGINAL ARTICLE

Genetic structure, phylogeography and potential distribution modeling suggest a population expansion in the mesquite *Prosopis laevigata* since the last interglacial

Gonzalo Contreras-Negrete[1] · **Luis Letelier**[2] · **Javier Piña-Torres**[3] · **Antonio González-Rodríguez**[1]

Received: 17 February 2020 / Accepted: 1 February 2021 / Published online: 5 March 2021

Abstract

Patterns of genetic and phylogeographic structure and recent population history of plant species in the Mexican arid zones have been scarcely investigated. *Prosopis laevigata* is the most widely spread species of mesquite in Mexico, with extensive populations in the arid and semiarid zones of the central and northern plateaus and scattered presence in southern Mexico. We evaluated the genetic and phylogeographic structure of this species to infer its recent demographic history. We genotyped six nuclear microsatellite loci and sequenced the psbA3´-trnH chloroplast DNA (cpDNA) region in individuals from 21 populations covering the whole distribution of the species. Nuclear genetic diversity was moderately high ($H_E = 0.527$), and genetic differentiation was moderate ($F_{ST} = 0.16$). A positive correlation between genetic diversity and latitude was observed. The cpDNA analyses indicated a lack of phylogeographic structure in *P. laevigata* ($G_{ST} = 0.090$, $N_{ST} = 0.101$; $P = 0.497$). Historical demography statistics indicated a population expansion supported by a skyline plot analysis, the star-like shape of the haplotype network, and the unimodal shape of the mismatch distribution. Ecological niche modeling suggested a contracted distribution into west-central Mexico during the Last Interglacial (~ 140 Ka), followed by an expansion in both northwards and southwards directions in the Last Glacial Maximum (~ 22 Ka), which continued in the mid-Holocene (~ 6 Ka) and the present. Results are congruent with a recent population growth and colonization of newly opened arid zones by *P. laevigata* populations. This pattern is consistent with the high capacity of colonization of nutrient-poor areas, high germination rates and resistance to drought reported for *Prosopis* species.

Keywords Arid zones · Phylogeography · Population expansion · Population genetics · *Prosopis*

Introduction

During the Pleistocene and the beginning of the Holocene many territories experienced the effects of climatic and ecological instability produced by the advance and retreat of glaciers, triggering drastic changes in plant communities (Metcalfe et al. 2000; Metcalfe 2006). This transition has been recognized as a main factor that influenced the distribution, population dynamics, and the current patterns of genetic diversity of plant species (Ramírez-Barahona and Eguiarte 2013; Pedersen et al. 2015). For the Nearctic, paleoecological records and genetic patterns show the migration of temperate forests toward lower latitude and altitude in response to the advance of the glacial layers from north to south (Roberts and Hamann 2015; Napier et al. 2019). In contrast, in the subtropical and tropical regions within the Mexican territory, during glaciations, the establishment and geographic expansion of plants with

---

Handling Editor: Giuseppe Pellegrino.

✉ Antonio González-Rodríguez
agrodrig@cieco.unam.mx

[1] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México (UNAM), Antigua Carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, México

[2] Instituto de Ciencias Biológicas y Núcleo Científico Multidisciplinario, Universidad de Talca, 1 Poniente 1141, Casilla 747- 721, Talca, Chile

[3] Escuela Nacional de Estudios Superiores Morelia, Universidad Nacional Autónoma de México (UNAM), Antigua Carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, México

higher affinity to cooler climates have been described, while tropical species were restricted to refugia where conditions allowed them to persist (Gugger et al. 2011; Ornelas et al. 2013; Ramírez-Barahona and Eguiarte 2013, 2014).

In recent years, efforts also have been made to understand the effect of glacial cycles on the genetic diversity and structure of plant species in Mexico, mainly in temperate and mountain cloud forests (e.g., González-Rodríguez et al. 2004; Gugger et al. 2011; Gutiérrez-Rodríguez et al. 2011; Ornelas et al. 2013; Ruiz-Sanchez and Ornelas 2014; Pérez-Crespo et al. 2017; Rodríguez-Correa et al. 2017). The impact of these climatic fluctuations on the population history of plant species in arid zones has been less studied but was apparently dramatic (Nason et al. 2002; Garrick et al. 2009; Ruiz-Sánchez et al. 2012; Vásquez-Cruz and Sosa 2016; Angulo et al. 2017; Cornejo-Romero et al. 2017; Loera et al. 2017; Scheinvar et al. 2017; Ornelas et al. 2018, 2019). Available evidence indicates that, because of climate cycles, the distribution ranges of xerophytic species expanded and contracted/fragmented recurrently, with concomitant lineage divergence and historical demography changes. Areas where populations of such species survived during climatically adverse periods have been called 'xerophilous refugia'. However, contrasting results have been obtained on whether the maximum range contraction occurred during the periods of glacial maxima or during interglacial periods. The first pattern has been considered consistent with the glacial refugia hypothesis (GRH; Hewitt 2000, 2004), while the second has been named the interglacial refugia hypothesis (IRH; Hewitt 2004; Ornelas et al. 2018). In general, the IRH has been supported by results of ecological niche modeling and phylogeographic analysis for several species in the Chihuahuan and Sonoran deserts, the Tehuacán-Cuicatlán Valley and the Oaxaca Central Valleys, which have shown marked southwards range retractions or shifts during the last interglacial (LIG, ~ 120–140 Ka), followed by northwards expansions during the last glacial maximum (LGM, ~ 22 Ka) and the Holocene. Genetic signatures of these processes include historical demography evidence of population expansions and latitudinal gradients of genetic diversity, with northern populations showing genetic depauperation in comparison to southern populations (Ruiz-Sánchez et al. 2012; Angulo et al. 2017; Scheinvar et al. 2017). However, the opposite pattern (i.e., expansion during the LIG and contraction during the LGM), consistent with the GRH has also been found (Cornejo-Romero et al. 2017). Therefore, extensive research is still needed to better understand the biogeographic history of the arid zones of Mexico, considering that they constitute nearly 50% of the country surface (Challenger 1998) and have a floristic diversity of around 6,000 plant species (Rzedowski et al. 1993; Cervantes 2005) with a large number of endemisms, representing a set of natural resources that offer multiple alternatives for appropriation of timber, food and other goods (Cervantes 2005).

Mesquites (genus *Prosopis* L.) are among the most important tree groups in arid and semiarid areas across Mexico. The genus probably originated in tropical Africa (Burkart 1976), given the existence of *Prosopis africana* (Guill. & Perr.) Taub. 1893 the most basal of the species in the phylogeny of *Prosopis* (Pohill and Raven 1981). For the Americas, the presence of 43 species of *Prosopis* has been documented, with South America, and particularly Argentina, representing the main diversity center with 34 and 29 species, respectively. In North America, 10 species are known, most of them part of the "Mexico-Texas" complex (Rzedowski 1988; Palacios 2006). In México, *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C.Johnst is the most widespread species, and the "typical" mesquite of the central region of the country (Burkart 1976; Rzedowski 1988). This species represents an excellent study system to analyze the population history of arid-adapted plant species in Mexico, given its wide distribution and high abundance. The geographic distribution of *P. laevigata* includes several physiographic regions in Mexico characterized by arid or semiarid climate, such as the Tamaulipas Plains, the Mexican Altiplano, parts of the Trans-Mexican Volcanic Belt, the Balsas Depression, the Tehuacán-Cuicatlán Valley and the Oaxaca Central Valleys (Rzedowski 1988; Palacios 2006). These physiographic regions are characterized by geological elements that could have acted as barriers or corridors for *P. laevigata* at different historical periods but, at present, the distribution of the species is partially interrupted by areas with temperate vegetation characteristic of the highlands of the Trans-Mexican Volcanic Belt, and by the Sierra Madre Oriental, a mountain chain that separates the populations from the Mexican Altiplano from those of the Tamaulipas Plains. However, there are no morphological peculiarities in the populations associated with the distribution areas, and therefore, they are considered as the same species (Rzedowski 1988).

In this study, our main goal was to analyze the genetic diversity and structure of *P. laevigata* throughout its distribution in Mexico to gain insight into the evolutionary history of the species and contribute to the understanding of the historical biogeography of the Mexican arid zones. In particular, we aimed at i) determining if population differentiation in *P. laevigata* is associated with its distribution in different physiographic regions, and ii) testing if the historical demography and geographic distribution of the species during the LIG, LGM and middle-Holocene (MH) periods conforms to the GRH or the IRH.

Materials and methods

Study system

Prosopis laevigata (Fabaceae, Mimosoideae) is a tree or bush up to 12 m in height, trunk 0.3 to 1 m in diameter, with thick bark of blackish brown color (Calderón and Rzedowski 2001). *Prosopis* species have been characterized as self-compatible (Simpson 1977; Masuelli and Balboa 1989; Genise et al. 1990) with percentages of self-fertilization between 65 and 85% (Galindo-Almanza 1992). The main pollination syndrome of the genus is entomophily, with hymenopterans such as *Ahsmaediella*, *Calicodoma* (Megachillidae), *Coletes* (Colletidae) and *Apis mellifera* (Apidae) being the most frequent pollinators (Galindo-Almanza 1992). Mammalochory and hydrochory have been reported as the main seed dispersal syndromes in *Prosopis* species (Campos and Ojeda 1997; de Noir et al.2002; Pasiecznik et al. 2002).

Sampling methods

We collected fresh leaves of 220 individuals from 21 populations of *P. laevigata* covering the whole distribution of the species (Table 1), including the Oaxaca Central Valleys (OCV), the Tehuacán-Cuicatlán Valley (TCV), the Balsas Depression (BD), the Trans-Mexican Volcanic Belt (TMBV), the Mexican Altiplano (MA) and the Tamaulipas Plains (TP). In each population, seven to 12 adult trees were collected, with a distance of at least 50 m between individuals. The fresh leaves were kept on ice for subsequent storage at -70 °C. Additionally, voucher samples were collected from each of the populations, that were processed for later storage at the IEB Herbarium of the Instituto de Ecología A. C. (Pátzcuaro, Michoacán, México).

Laboratory procedures

Genomic DNA was extracted using a modified CTAB protocol (Otero-Arnaiz et al. 2005). We amplified six polymorphic microsatellite loci (Mo05, Mo07, Mo08, Mo09, Mo13 and Mo016) originally designed for *Prosopis chilensis* (Molina) Stuntz and *Prosopis flexuosa* DC. (Mottura et al. 2005). The PCR reactions were carried out using Platinum

Table 1 Geographic data of the populations collected of *Prosopis laevigata.*

Number	Physiographic region	State	Sample size	Latitude N	Longitude W	Elevation (m a.s.l.)
1	BD	Guerrero	10	17° 55′ 41.45″	99° 35′ 28.25″	515
2	BD	Guerrero	9	18° 03′ 22.1″	100° 49′ 41.85″	1373
3	OCV	Oaxaca	11	18° 06′ 10.59″	97° 20′ 8.50″	1708
4	TCV	Puebla	7	18° 35′ 18.19"	97° 24′ 30.99"	2075
5	TCV	Puebla	8	18° 33′ 41.69"	97° 55′ 29.79"	1778
6	TMBV	Hidalgo	11	20° 34′ 16.65″	98° 36′ 12.54″	2280
7	TMBV	Hidalgo	11	20° 04′ 38.69″	99° 20′ 58.78″	2293
8	TMBV	Querétaro	11	20° 41′ 54.91″	99° 47′ 36.06″	1921
9	TMBV	Michoacán	12	19° 48′ 36.77″	100° 57′ 23″	2249
10	TMBV	Guanajuato	12	20° 24′ 0.18″	101° 34′ 33″	1733
11	TMBV	Jalisco	12	21° 04′ 53.82″	102° 24′ 43.21″	1902
12	TMBV	Michoacán	12	20° 13′ 53.2″	102° 25′ 48.17″	1693
13	TMBV	Jalisco	10	19° 56′ 53.06″	103° 29′ 15.5″	1419
14	TMBV	Aguascalientes	9	21° 53′ 13″	102° 24′ 50.4″	1870
15	MA	San Luis P	11	21° 44′ 56.7″	100° 41′ 47.52″	1852
16	MA	San Luis P	12	22° 37′ 54″	101° 44′ 22.2″	2084
17	MA	San Luis P	11	23° 30′ 23.24″	100° 37′ 37.48″	2168
18	TP	Veracruz	12	22° 09′ 25.62″	98° 04′ 39.06″	32
19	TP	Nuevo León	12	24° 53′ 06.76″	99° 35′ 54.29″	888
20	TP	Tamaulipas	10	23° 44′ 56.32″	99° 02′ 29.58″	900
21	TP	Tamaulipas	11	23° 27′ 10.14″	98° 03′ 0.40″	54

BD Balsas Depression; *OCV* Oaxaca Central Valleys; *TCV* Tehuacán-Cuicatlán Valley; *TMBV* Trans-Mexican Volcanic Belt; *MA* Mexican Altiplano; *TP* Tamaulipas Plains higher values of K, we tested K values from 1 to 5, with 20 iterations for each K. Every run was done using 50,000 iterations as burn-in and 100,000 repetitions of the Markov chain after burn-in. The options of correlated allele frequencies and possible admixture among individuals in the populations were used. The determination of the most probable K value was executed using the maximum value of ΔK according to Evanno et al. (2005) through the online software Structure Harvester (Earl and vonHoldt 2012) As recommended by Janes et al. (2017), we conducted further analysis to test for substructure within the main genetic groups identified, using similar settings and procedures. Results of multiple runs for each K value were summarized using CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007). Finally, we plotted the CLUMPP results with DISTRUCT 1.1 (Rosenberg 2004).

CpDNA sequence analysis

The electropherograms obtained were analyzed and edited using the software BIOEDIT (Hall 1999). The edited sequences were aligned manually using MEGA 4 (Tamura et al. 2007). The analyses of genetic variation were carried out considering nucleotide substitutions only, while the haplotype level analysis considered both nucleotide substitutions and insertion/deletions (indels). We calculated nucleotide diversity (π) and haplotype diversity (h_S) using the software DNAsp 5.0 (Librado and Rozas 2009) and the rarefied haplotype richness with the software SPAGeDi (Hardy and Vekemans 2002) We built a statistical parsimony network with the TCS software (Clement et al. 2000), through the parsimony algorithm of Templeton et al. (1992) using a connection limit of 95% and considering gaps as fifth state. The network was edited using TCS Beautifier (Múrias Dos Santos et al. 2016).

To evaluate the partitioning of haplotype diversity within and among populations and regions, we carried out an AMOVA in Arlequin 3.5 (Excoffier and Lischer 2010) with 10,000 permutations to determine the significance of the test. Populations were grouped according to the six physiographic regions, as previously described for the microsatellite analyses. The presence of phylogeographic structure in the populations was assessed through the comparison of population differentiation with unordered (G_{ST}) and ordered alleles (N_{ST}). If N_{ST} is significantly higher than G_{ST} it means that genealogically close haplotypes tend to occur together in the same populations (i.e., there is phylogeographic structure) (Pons and Petit 1996). This test was performed in SPAGeDi (Hardy and Vekemans 2002) with 20,000 permutations.

The demographic history of the populations was investigated by calculating Tajima's D and Fu's Fs (Tajima 1989; Fu 1997) with the software DNAsp 5.0 (Librado and Rozas 2009) with 10,000 permutations. Additionally, we performed a mismatch distribution analysis, which assesses the relative frequency of the number of nucleotide differences among all pairs of haplotypes and compares it to the unimodal distribution expected under a recent demographic expansion (Rogers and Harpending 1998; Excoffier et al. 2009). This analysis was carried out in Arlequin 3.5.1.3 (Excoffier and Lischer 2010). The statistical test of no difference between the observed distribution and the distribution expected under the population expansion model was performed through the comparison of the sum of squares differences (SSD).

As an additional historical demography test, we ran a Bayesian Skyline Plot (BSP; Drummond et al. 2005) by means of the software BEAST 1.8.1 implemented online (http://www.phylo.org), to evaluate the effective population size variation over time. We performed two independent runs of 100 million generations using the substitution model GTR + I based on empirical frequencies, a log-normal relaxed clock model and a Bayesian Skyline tree with constant size using 10 initial groups. The parameters and trees were sampled every 1000 iterations with a burn-in of 10%. The time axis was adjusted using rates of 1.0×10^{-9} and 3.0×10^{-9} substitutions per site per year (s/s/y), encompassing the range reported for chloroplast DNA in many angiosperms (Wolfe et al. 1987; Gutiérrez-Rodríguez et al. 2011; Ruiz-Sánchez and Ornelas 2014) The results of every run were analyzed by the software TRACER 1.5 (Drummond and Rambaut 2007) in order to ensure effective sample sizes (ESS) > 200.

Ecological niche modeling (ENM)

The ecological niche of *P. laevigata* was modeled under present climate conditions using the maximum entropy algorithm implemented in MAXENT 3.3.3e (Phillips et al. 2006). One hundred and twenty-nine records of the presence of *P. laevigata* were used, coming from the MEXU herbarium database, the CONABIO database (available at http://www.conabio.gob.mx/informacion/gis/; accessed September 10, 2020) and the GBIF database (available at https://doi.org/10.15468/00000000; accessed September 10, 2020) and after excluding non-georeferenced data, duplicated records, and non-credible data. For each presence record, associated data for 19 bioclimatic variables were taken from WorldClim 2.1 (Fick and Hijmans 2017) for current climate conditions (1970–2000) with 30 arcsec resolution (available at http://worldclim.org/version2). A variance inflation factor (VIF, Brauner and Shacham 1998) analysis was applied to select the least redundant bioclimatic layers (variables with VIF > 0.8 were included). The variables finally used in the niche model were mean diurnal range, isothermality, temperature annual range, mean temperature of coldest quarter, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter and precipitation of warmest quarter.

The model was implemented using the cross-validation resampling method with 50 replicates. As a threshold-independent method of model validation, we used the receiver operating characteristic (ROC) curve analysis. If the value of the area under the curve (AUC) of the ROC is close to 1 it indicates a good model, while values of 0.5 indicate models that are no better than a random model (Phillips et al. 2006). Also, as an additional threshold-dependent method of model validation, we used the true skill statistic (TSS; Allouche et al. 2006). The ecological niche model (ENM) of the present climate conditions was then projected to past climate scenarios, one for the Last Interglacial (LIG, ~ 120 to 140 Ka) (Otto-Bliesner et al. 2006) and two Last Glacial Maximum (LGM, ~ 22 Ka) models provided by the Paleoclimate Modeling Intercomparison Project Phase II (Braconnot et al. 2007), the Community Climate System Model (CCSM4; Collins et al. 2006) and the Model for Interdisciplinary Research on Climate (MIROC-ESM; Hasumi 2007). The LIG and LGM climate models have a resolution of 2.5 arcmin. Additionally, we used the MIROC-ESM and CCSM4 climate scenarios for the mid-Holocene (~ 6 Ka) with a 30 arcsec resolution.

Results

Genetic structure

According to MICROCHECKER, all microsatellite loci showed null alleles, varying in frequency in the populations from 0.09 (Mo07) to 0.29 (Mo13). The results of the statistical power analysis showed that for the different effective population sizes, the six microsatellite markers have sufficient power to detect genetic differentiation of $F_{ST} = 0.01$ at least, which corresponds to low levels of genetic differentiation and high amounts of connectivity (Online Resource 1).

The results of the analysis with FreeNA showed a proportion of null alleles from 0 to 0.38 depending on the locus and the population; however, null alleles did not affect the estimation of genetic differentiation ($F_{ST} = 0.152$ and 0.155 with and without the ENA correction, respectively). In general, genetic diversity levels were moderately high. We found a total of 96 alleles, summed across the six microsatellite loci

Table 2 Parameters of genetic diversity at six microsatellite loci for 21 populations of *Prosopis laevigata* in Mexico

Population	A	N_{EA}	AR	H_O	H_E	H_{EC}	F
1	3.5	2.32	1.54	0.372	0.514	0.544	0.330*
2	2.33	2.01	1.21	0.148	0.195	0.207	0.297
3	4.83	3.25	1.6	0.386	0.565	0.596	0.367*
4	4.33	3.62	1.63	0.444	0.579	0.63	0.319*
5	2.83	2.46	1.54	0.235	0.482	0.543	0.602*
6	3.33	2.19	1.48	0.318	0.455	0.476	0.344*
7	4.83	2.78	1.61	0.449	0.58	0.612	0.277*
8	4.33	3.19	1.61	0.43	0.064	0.612	0.310*
9	5.33	2.93	1.59	0.427	0.564	0.589	0.285*
10	4.33	2.87	1.6	0.481	0.569	0.598	0.205
11	3.83	2.44	1.47	0.334	0.445	0.468	0.297*
12	4	2.47	1.46	0.23	0.119	0.462	0.515*
13	2.66	1.59	1.32	0.267	0.303	0.319	0.172
14	3.83	3.61	1.55	0.317	0.508	0.547	0.441*
15	4	2.55	1.52	0.436	0.485	0.515	0.167
16	5.16	3.66	1.67	0.42	0.639	0.669	0.385*
17	5.5	4.51	1.66	0.45	0.629	0.659	0.328*
18	4.83	3.61	1.64	0.559	0.611	0.639	0.132
19	6	4.6	1.71	0.551	0.68	0.71	0.233*
20	5.5	3.43	1.66	0.518	0.625	0.66	0.226
21	5.83	3.7	1.65	0.495	0.62	0.65	0.247*
Total	4.33	3.03	1.55	0.393	0.487	0.557	0.323

*Significant deviation from Hardy–Weinberg equilibrium ($P < 0.05$)

A mean number of alleles per locus; N_{EA} mean effective number of alleles per locus; *AR* rarefied allelic richness; H_O observed heterozygosity; H_E expected heterozygosity; H_{EC} expected heterozygosity corrected by sample size (Nei, 1978); *F* fixation index analyzed. The total number of alleles per locus fluctuated from nine (Mo05) to 27 (Mo16), with an average number of alleles per locus of $A = 4.34$. At all loci, we found a few alleles in high frequency and many rare alleles in low frequency (alleles with a frequency > 0.10). The rarefied allelic richness showed an average value of $AR = 1.68$ (Table 2).

The average expected heterozygosity (H_E) was 0.527, ranging from $H_E = 0.195$ (population 21) to $H_E = 0.680$ (population 4). The average observed heterozygosity (H_O) was 0.393, varying between $H_O = 0.148$ (population 21) and $H_O = 0.558$ (population 17). The percentage of polymorphic loci was 100% in most populations, except for populations 1, 2, 19 ($P = 83.33$) and 21 ($P = 33.33$) (Table 2). The regression analysis between genetic diversity estimates and latitude indicated positive and significant relations for N_{EA} ($R^2 = 0.45$, $P = 0.008$), A ($R^2 = 0.47$, $P = 0.006$), AR ($R^2 = 0.20$, $P = 0.01$), H_O ($R^2 = 0.38$, $P = 0.003$), and H_{Ec} ($R^2 = 0.29$, $P = 0.01$), showing substantial evidence of increased genetic diversity in populations northwards. In addition, we found positive correlations of AR ($R^2 = 0.19$, $P = 0.04$) and H_O ($R^2 = 0.19$, $P = 0.04$) with longitude, showing an increased value of these parameters in eastern populations (Fig. 1).

The software INest revealed a significant contribution of null alleles to inbreeding values according to the DIC value for the nfb (8214.56) and fb (8286.39) models. The revised estimate of inbreeding ($F = 0.177$), was considerably lower than the estimate without correcting for null alleles ($F = 0.323$).

The AMOVA using the F_{ST} estimator revealed a moderate overall genetic structure ($F_{ST} = 0.16$; $P < 0.001$). We found slight differences between the six physiographic regions indicating that only 3% ($F_{CT} = 0.03$; $P < 0.001$) of the genetic diversity is found among regions and that 13% ($F_{SC} = 0.13$; $P < 0.001$) is found among populations within regions, while 84% is within populations. The value of the R_{ST} estimator was higher than the F_{ST} value (0.20; $P < 0.001$), with 0% ($R_{CT} = -0.01$; $P = 0.983$) of the genetic diversity being due to differences among regions, and 20% ($R_{SC} = 0.2$; $P < 0.001$) due to differences among populations within regions (Table 3). The Mantel test between log geographic distances and the pairwise F_{ST} values showed a non-significant relationship ($r = 0.064$; $P = 0.257$), indicating no isolation by distance among populations.

The ΔK statistic showed $K = 2$ as the most probable number of genetic groups in the data set (Fig. 2a, b; Online Resource 2a, b). Populations in the Balsas Depression (i. e. 1, 2) were almost completely assigned to the light green cluster (proportion of ancestry = 0.97), whereas populations in the western Trans-Mexican Volcanic Belt (9, 10, 11, 12 and 13) had high proportions (> 0.7) of the dark green cluster. The other populations had mixed proportions of both clusters (Fig. 2a, b).

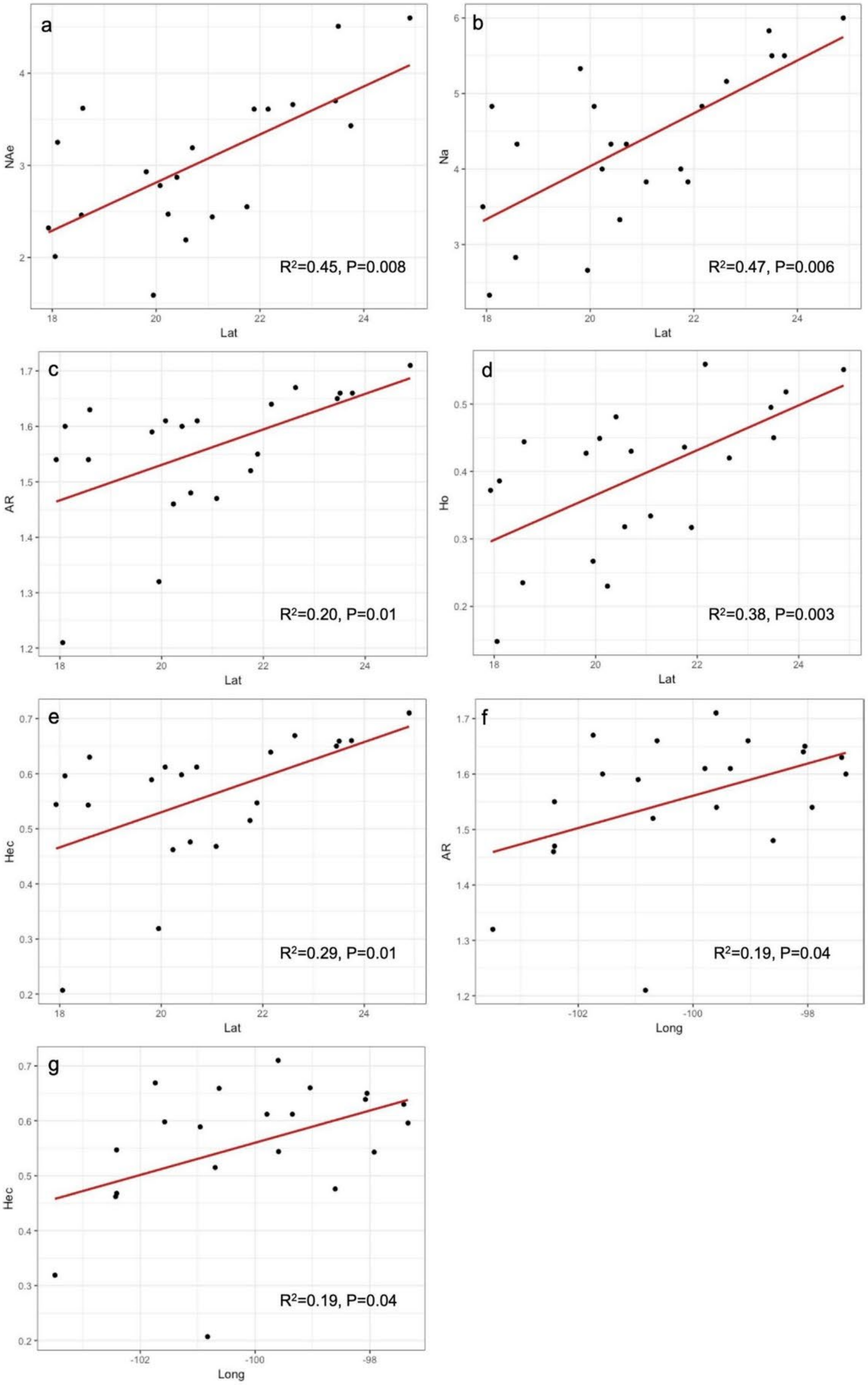
When testing for substructure within the two main genetic clusters, we found that $K = 3$ was the most probable number of genetic groups within the dark green group (Fig. 2c, d; Online Resource 2c, d). In this case, populations from the TP (18, 19, 20, 21), the east of the MA (17) and the TCV (4, 5) showed a high frequency of the light blue genetic group and the rest of the populations showed more or less equal proportions of the other genetic groups, except for populations 6 and 11 in which the dark blue genetic group predominated and population 13, which showed a high frequency of the purple genetic group (Fig. 2c, d). The analysis also suggested $K = 3$ as the optimal number of groups within the light green main genetic cluster (Fig. 2e, f; Online Resource 2e, f). Population 2 from the BD had an almost complete assignment (94%) to the brown genetic group, while the rest of the populations had in general less than 10% assignment to this group. Meanwhile, the yellow genetic group was predominant in the other population from the BD (1) and in population 6, while the red group was frequent in MA (14, 16) and TP populations (21) (Fig. 2f).

Chloroplast DNA and haplotype network

We sequenced 427 bp of the intergenic spacer region psbA3′-trnH in 109 individuals belonging to 19 populations of *P. laevigata* covering the whole distribution. A total of 18 haplotypes were found, which formed a network with a star-like shape, with the most common haplotype (77 individuals) located at the center of the network (Table 4, Fig. 3). This haplotype was found in all the populations sampled. Most of the other haplotypes were separated by one mutational step from the central haplotype, although, there were some haplotypes separated by two to six mutational steps from the central haplotype (Fig. 3).

Most of the derived haplotypes were exclusive to a single population (private haplotypes), except for the haplotypes H2 (found in populations 1, 3, 10, 12, 15 and 17), H3 (found in populations 18, 20 and 21) and H4 (found in populations 18 and 21). Eight populations were monomorphic for the most common haplotype. On the other hand, the populations with the highest number of haplotypes were 1, 12, 20 and 21, located at the southwest, center and northeast of the distribution of the species (Table 4, Fig. 3).

The haplotype diversity (h_S) ranged between 0 and 1 in the populations and was on average moderate (0.4). The nucleotide diversity (π) was in general low, ranging between 0 and 0.00392 with an average of 0.0013 (Table 4). The results of the AMOVA indicated an $F_{ST} = 0.09$ ($P < 0.001$), meaning that 9% of the genetic diversity is found among populations, while 91% of the genetic diversity is found within populations (Table 5). Differences among regions were low and non-significant ($F_{CT} = 0.043$; $P = 0.06$) signaling a high genetic similarity of *P. laevigata* populations


a
NAe
Lat
R²=0.45, P=0.008
b
Na
Lat
R²=0.47, P=0.006
c
AR
Lat
R²=0.20, P=0.01
d
Ho
Lat
R²=0.38, P=0.003
e
Hec
Lat
R²=0.29, P=0.01
f
AR
Long
R²=0.19, P=0.04
g
Hec
Long
R²=0.19, P=0.04

◂**Fig. 1** Regression analysis between genetic diversity parameters of *Prosopis laevigata* populations and geographic variables: **a** mean effective number of alleles (N_{EA}) per locus versus latitude; **b** mean number of alleles per locus (A) versus latitude; **c** rarefied allelic richness (AR) versus latitude; **d** observed heterozygosity (H_O) versus latitude; **e** expected heterozygosity corrected by sample size (H_{Ec}) versus latitude; **f** rarefied allelic richness (AR) versus longitude; **g** expected heterozygosity corrected by sample size (H_{Ec}) versus longitude

along its distribution. The G_{ST} value (0.090) also indicated a low level of genetic structure across the distribution of *P. laevigata*. The differentiation value considering distances among haplotypes (ordered alleles) was $N_{ST} = 0.101$ and was not significantly different from G_{ST} ($P = 0.497$), denoting a lack of phylogeographic structure in this species.

The values of Tajima's D and Fu's Fs were not significant for individual populations but both overall values were negative and significant ($D = -2.018$, $P < 0.001$; $Fs = -10.868$, $P < 0.001$), suggesting a recent demographic expansion in *P. laevigata*. The mismatch analysis showed a unimodal distribution, with a main peak located on a single difference between pairs of haplotypes (Online Resource 3). The sum of square deviations (SSD) did not indicate significant differences in comparison to a constant expansion model ($SSD = 0.058$; $P = 0.312$), therefore supporting a recent demographical expansion. Likewise, the Bayesian Skyline Plot analysis showed a slight increase in effective population size of the species from 70 Ka to the beginning of the LGM, followed by a more marked expansion from around 20 Ka to the beginning of the Holocene (10 Ka) (Fig. 4).

Ecological Niche model

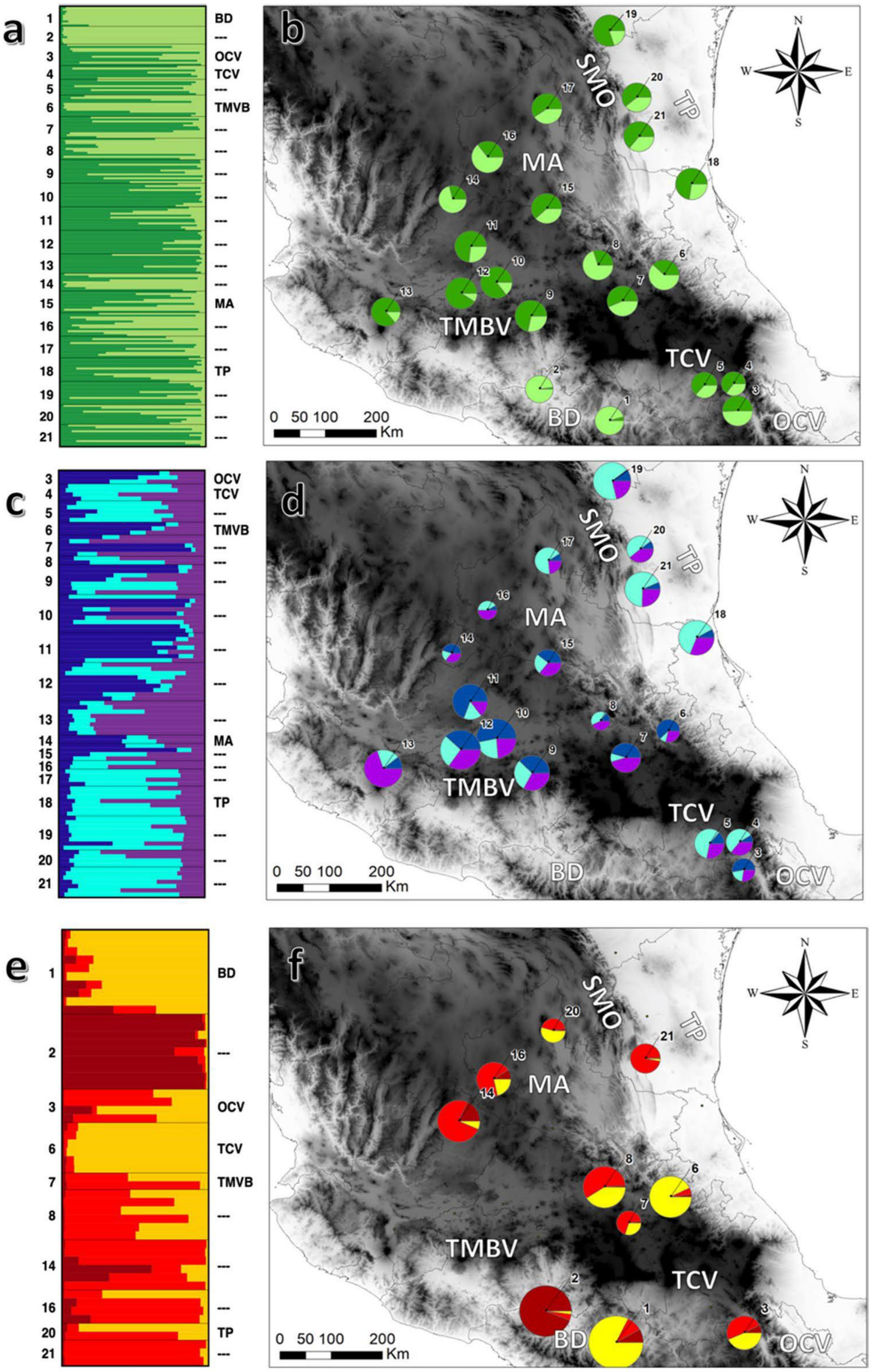
The potential distribution map based on the ENM of *P. laevigata* for the present-day climate conditions corresponded well to the known distribution of the species ($AUC = 0.954$ and $TSS = 0.825$) (Fig. 5a). When the model was projected onto the LIG, we found a substantial reduction of the suitable area for *P. laevigata*, which appeared mainly restricted to the western portion of the Balsas Depression (BD), with scattered small predicted areas in the central BD, the westernmost part of the TMBV and the OCV (Fig. 5b). For the LGM, somewhat different results were obtained with the MIROC-ESM and CCSM4 models (Fig. 5c, d). In the warmer and dryer MIROC-ESM model, a larger area of suitable habitat was predicted in comparison to the LIG, including most of the BD, a large portion of the Sierra Madre del Sur (SMS), the OCV and even the Central Depression of Chiapas; and to the north, some parts of the TMBV, the SMO and the MA (Fig. 5c). In contrast, the CCSM4 model suggested fragmented areas of suitable habitat in the westernmost and the central part of the BD, the OCV, the northwestern Pacific coastal plain and the MA (Fig. 5d). For the MH, differences between the MIROC-ESM and CCSM4 models were less marked (Fig. 5e, f), both showing suitable habitat for *P. laevigata* in the western and eastern parts of the BD and in the OCV, the TMBV, the MA (in the south eastern and central portions) and the western ridges of the SMO. The whole set of models suggests a refugial area for *P. laevigata* in the west of the BD during the LIG, an expansion to the east and the south in the LGM, and a northwards expansion in the MH and the present.

Discussion

In this study, we used nuclear and chloroplast DNA markers to assess genetic diversity and structure of *Prosopis laevigata* throughout its distribution in Mexico. Despite the ecological and economic importance of *Prosopis* species in the arid zones of North America, this is the first study focusing on the evolutionary history of a species of the genus in this geographic region. Overall, we found moderate levels of genetic diversity in *P. laevigata* ($H_E = 0.527$) which are similar or lower than the values previously reported for a few other *Prosopis* species from South America calculated also from nuclear microsatellites (*Prosopis alba* Griseb, *P. chilensis* and *P. flexuosa*), with H_E values of 0.67, 0.55 and 0.71, respectively (Bessega et al. 2016, 2019; Moncada et al. 2019). Genetic differentiation values are more difficult to compare given the different geographic scales and number of populations analyzed and, unfortunately, analyses of cpDNA diversity based on sequences have not been published yet for any other mesquite species, making comparisons impossible. Nevertheless, some of the shared biological characteristics of *Prosopis* species (pollination by bees, self-compatible, animal dispersed seeds) may explain to some extent the similarities in their patterns of genetic diversity (Duminil et al. 2007).

Interestingly, topographic elements associated with the limits of the physiographic regions, and particularly areas such as the highlands of the TMBV and the SMO that represent interruptions to the continuity of the Mexican arid zones and, therefore, were hypothesized to constitute barriers to gene flow among *P. laevigata* populations, were not associated with any significant genetic breaks in the species. Previously, it has been demonstrated that the TMBV impaired historical gene flow between northern and southern populations of trees such as *Liquidambar styraciflua* L. (Ruiz-Sanchez and Ornelas 2014) and even promoted species diversification in plants and animals (McCormack et al. 2011; Gándara and Sosa 2014). However, the lower elevation parts of the TMBV are probably permeable for some species of drier habitats, providing connectivity between populations to the south and the north.

Fig. 2 Genetic structure in the populations of *Prosopis laevigata*, inferred with the STRUCTURE algorithm (Pritchard et al. 2000; Hubisz et al. 2009) from microsatellite data. **a** bar plot showing the assignment of all sampled individuals into two main genetic groups, **b** map showing the geographic distribution of these two main genetic groups, **c** bar plot showing the genetic assignment corresponding to the substructure within the dark green main genetic group, **d** map showing the geographic distribution of these three genetic subgroups, **e** bar plot showing the genetic assignment corresponding to the substructure within the light green genetic group, **f** map showing the geographic distribution of these three genetic subgroups. The numbering of populations follows Table 1. The gray shading indicates elevation with darker tones corresponding to higher elevations. *SMO* Sierra Madre Oriental; *TP* Tamaulipas plains; *MA* Mexican Altiplano; *TMBV* Trans-Mexican Volcanic Belt; *BD* Balsas Depression; *TCV* Tehuacán-Cuicatlán Valley; *OCV* Oaxaca Central Valleys



are also thought to have been very variable in space and time during the end of the Pleistocene and the beginning of the Holocene.

In general, our results seem to support the interglacial refugia hypothesis (IRH). It is probable that during the LIG the distribution of *P. laevigata* was most restricted in extent and located mainly in the western part of the BD, with other smaller potential refugial areas in the central BD, the westernmost part of the TMBV and the OCV. These areas acted as sources for population expansion and migration both

Table 4 Genetic diversity estimates for the psbA3′-trnH region of the cpDNA in populations of *Prosopis laevigata* in Mexico

Population	N	h	AR	h_S	π	D	Fs
1	7	4	2.2	0.7143	0.00538	– 1.0354	0.1255
2	4	1	1	0	0	0	0
3	4	3	2.5	0.8333	0.00118	– 0.6123	– 0.2876
4	7	1	1	0	0	0	0
5	7	1	1	0	0	0	0
6	5	1	1.6	0.4	0	0	1.0404
7	3	2	2	0.67	0.00314	0	1
8	5	2	1.6	0.4	0.00094	– 0.816	0.0902
9	5	1	1	0	0	0	0
10	6	2	1.5	0.33	0.00078	– 0.933	– 0.0027
12	4	4	3	1	0.00392	0.167	– 2.1811
13	4	2	1.75	0.5	0.00118	– 0.6123	1.0986
15	6	2	1.9	0.6	0.00141	1.445	0.7951
16	6	1	1	0	0	0	0
17	5	3	2.2	0.7	0.00282	– 1.0484	– 0.1858
18	6	3	2.25	0.7333	0.0022	0.3106	– 0.3041
19	6	1	1	0	0	0	0
20	9	4	2.46	0.8056	0.00249	– 1.1499	– 1.5044
21	9	3	2.31	0.75	0.00183	0.1959	– 1.0387
Total		2.05	1.68	0.4	0.0013	– 2.018***	– 10.868***

***P < 0.001

N number of individuals analyzed; *h* number of haplotypes; *AR* rarefied haplotypic richness; h_S haplotype diversity (Pons and Petit, 1996); *π* nucleotide diversity; *D* Tajima´s D; *Fs* Fu's Fs

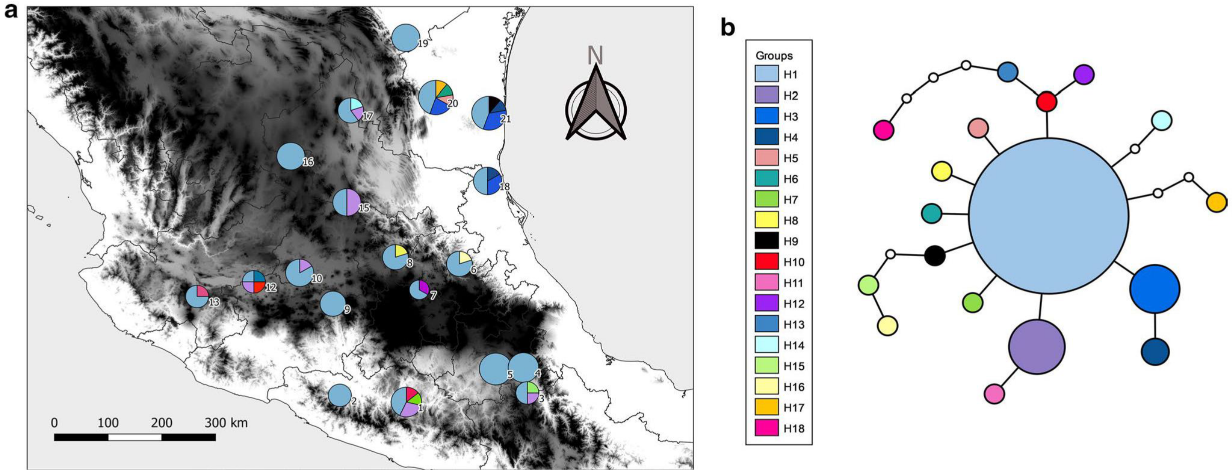


Fig. 3 **a** Geographic distribution of the haplotypes observed in the psbA3′-trnH region of the cpDNA in *Prosopis laevigata*. The numbering of populations follows Table 1. Note that no data are presented for populations 11 and 14 due to amplification problems. The gray shading indicates elevation with darker tones corresponding to higher elevations. **b** Haplotype network obtained with statistical parsimony in TCS (Clement et al. 2000). Each circle indicates a haplotype, with circle size proportional to the frequency of the haplotype. White dots indicate mutational steps

northwards and southwards with the aridification trends that occurred in Mexico toward the LGM and the present, and particularly with the combination of warming and aridification of the Pleistocene/Holocene transition. However, as is frequently observed (e. g. Ornelas et al. 2018; Guevara 2020; Peñaloza-Ramírez et al. 2020), the MIROC-ESM and CCSM4 scenarios differed in the extent of the predicted suitable area for *P. laevigata*, even though the two suggested the same trend. In contrast, the two models for the MH were much more concordant.

Table 5 Analysis of molecular variance for the psbA3′-trnH region of the cpDNA in *Prosopis laevigata* populations in Mexico. The proportions of genetic variation among regions and within and between populations are shown

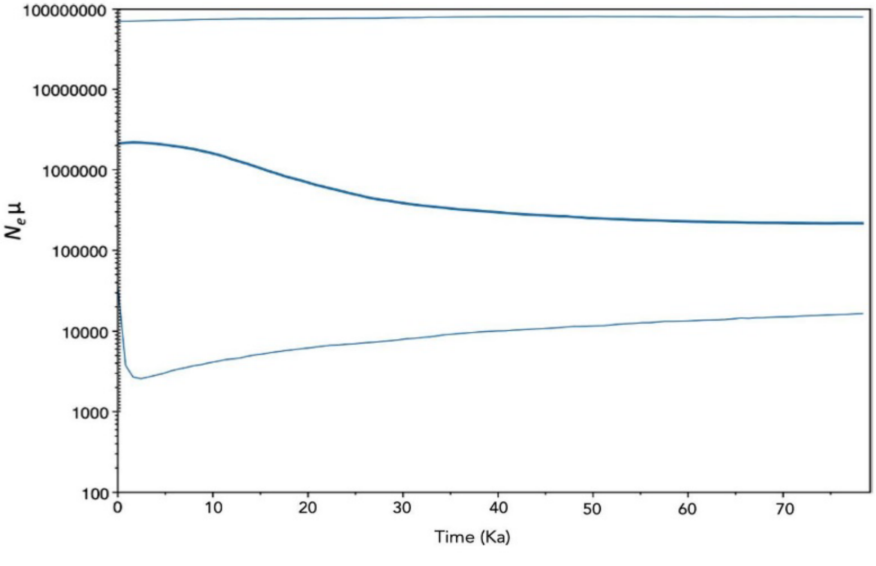
Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of the variance
Among Regions	5	3.979	0.01803	4.36%
Among populations within Regions	13	6.307	0.01914	4.63%
Within Populations	90	33.90	0.3767	91.02%
Total	108	44.19	0.4171	100%

$F_{ST}=0.089$ ($P<0.001$); $F_{SC}=0.048$ ($P=0.08$); $F_{CT}=0.043$ ($P=0.06$)

Interestingly, genetic diversity levels calculated from the nuclear microsatellites were positively correlated with latitude. Usually, areas within the geographic range of a species that have been recently colonized, harbor less genetic diversity in comparison to areas that sustained stable populations over time (i. e. refugia) because of successive founder effects during the process of colonization (Hewitt 2000; Gugger et al. 2008). However, our available evidence favors the scenario in which the central-west portions of the current range of *Prosopis laevigata* acted as refugial areas during the LIG, while southern, eastern and northern areas were more recently colonized. Still, the latitudinal trend in genetic diversity might be explained by current differences in effective population size rather than a historical signature of the colonization process. Indeed, during the collection trips in the north, we could observe very large populations with many thousands of individuals, while the current populations in the BD, the TCV and the OCV are small and scattered, even making it difficult to sample ten individuals in some of them. This pattern also suggests that the 'leading edge' populations of *P. laevigata* may be still expanding while the 'rear edge' populations may be decreasing. Additionally, recent ecophysiological studies of *P. laevigata* in populations from the whole distribution have shown better performance in germination under water deficit, salinity and temperature, as well as photosynthetic performance under drought conditions in northern populations in relation to southern ones (Contreras-Negrete et al. unpublished data), probably leading to more effective regeneration of northern populations.

The range shift and expansion in the distribution of *P. laevigata* during these historical climate transitions are also congruent with the ecology of the species. The seed dispersal of *Prosopis* species is carried out mainly by mammalians as rabbits, hares, humans, and by water courses (Campos and Ojeda 1997; de Noir et al. 2002; Pasiecznik et al. 2002). Endozoochory has been identified as an efficient mechanism in long-distance dispersal, and the seed dispersal of some species of *Prosopis* by the megafauna in the last 12.000 years has been proposed (Janzen and Martin 1982), which could have allowed the rapid expansion of *P. laevigata* populations under favorable ecological conditions during the large-scale warming and aridification process of the Holocene. Mesquites are known to be effective colonizers of open areas, since these plants have high light requirements and show high germination rates and resistance to drought and another stressful conditions typical of arid zones (Zimmermann 1991; Golubov et al. 2001; Pasiecznik et al. 2002).

Fig. 4 Bayesian skyline plot of *Prosopis laevigata* effective population size through time in Mexico, based on psbA3′-trnH cpDNA sequences from 109 individuals. The thick solid blue line is the median estimate, and the area among the light blue lines shows the 95% highest probability density (HPD) (Drummond et al., 2005)



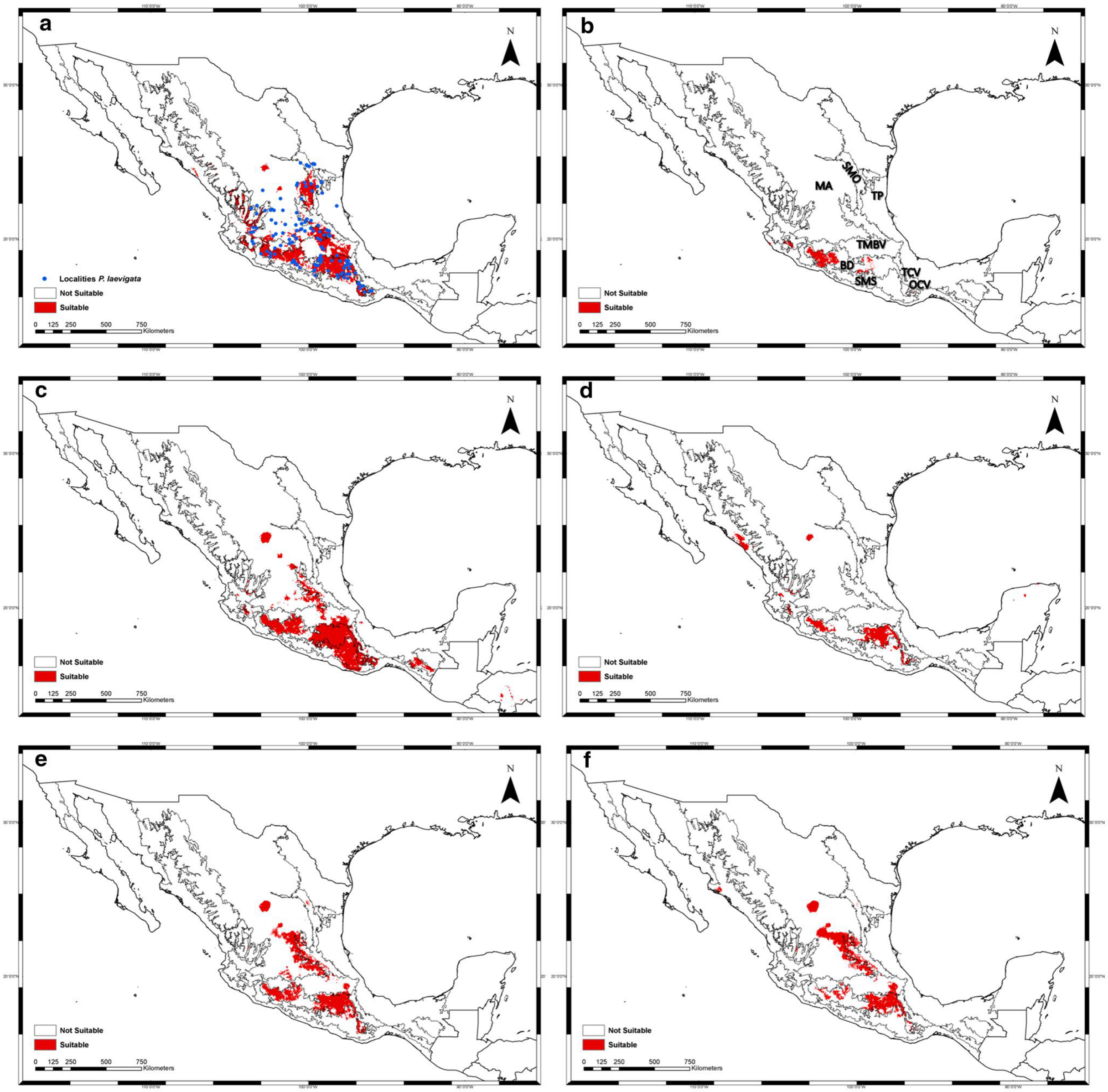


Fig. 5 Ecological niche models for *Prosopis laevigata* in Mexico, **a** contemporary climate conditions, **b** Last interglacial (LIG) climatic conditions, **c** Last Glacial Maximum (LGM) under the MIROC-ESM model, **d** LGM under the CCSM4 model, **e** Mid-Holocene under the MIROC-ESM model, **f** Mid-Holocene under the CCSM4 model. The red area represents the potential distribution of the species in each period. *SMO* Sierra Madre Oriental; *TP* Tamaulipas Plains; *MA* Mexican Altiplano; *TMBV* Trans-Mexican Volcanic Belt; *BD* Balsas Depression; *SMS* Sierra Madre del Sur; *TCV* Tehuacán-Cuicatlán Valley; *OCV* Oaxaca Central Valleys

These ecological characteristics are responsible for the rapid spread of some *Prosopis* species in contemporary time and some of them have become invasive in arid zones of the Middle East, Africa and Australia (Pasiecznik et al. 2002).

Conclusion

In conclusion, we observe that the recent demographic history, as well as the current patterns of genetic diversity and structure found in *P. laevigata,* have been decisively shaped by the climatic fluctuations experienced by the species since the LIG, following a pattern consistent with the IRH for dryland species. Likewise, the spread of *P. laevigata* to the north and south of its current distribution since the LIG is consistent with the ecological characteristics of species of the genus, which have been recognized as effective colonizers, even under adverse environmental conditions. Given the widespread distribution of *P. laevigata* as well as its ecological importance, the present study represents relevant information on the ecological and environmental historical patterns that have shaped the biogeographic history of the arid zones of Mexico.

Data archiving statement

Sequence data have been deposited in the Genbank (accession numbers MK618446- MK618463). Microsatellite data and the sequence alignment file have been deposited in the Dryad database (https://doi.org/10.5061/dryad.w3r2280pr).

Information on Electronic Supplementary Material

Online Resource 1. Results of the POWSIM analysis to evaluate the statistical power of our data for six microsatellite loci to detect different values of genetic differentiation in *Prosopis laevigata* populations..
Online Resource 2. Values of ΔK and mean Ln P (D) as a function of K from STRUCTURE analysis for **a**, **b** the main genetic structure, **c**, **d** the genetic substructure with the dark green main genetic group and **e**, **f** the genetic structure within the light green main genetic group.
Online Resource 3. Mismatch distribution analysis. The plot shows the frequency distribution of the observed number of pairwise differences among haplotypes (blue line) compared to the distribution expected under a recent population expansion (red line).

Supplementary Information The online version of this article (https://doi.org/10.1007/s00606-021-01744-5).

Acknowledgements The authors are grateful to Mariana Hernández-Leal, Yesenia Vega-Sánchez, Tamara Ochoa, Eduardo Ruiz-Sánchez and Aly Valderrama for field assistance, laboratory analysis and data processing. Jesús Llanderal, Víctor Rocha and Goretty Mendoza provided help with DNA sequencing. We also thank Alejandro Casas and Juan Francisco Ornelas for useful suggestions during the development of this work. Gonzalo Contreras-Negrete thanks the National Council of Science and Technology CONACyT (CVU 549242). This article represents a partial fulfillment of the Graduate Program in Biological Sciences of UNAM. The authors thank the funding provided by the Instituto de Investigaciones en Ecosistemas y Sustentabilidad, UNAM, for this research.

Compilance with ethical standards

Ethical statement The authors have no conflicts of interest to declare. The sample collection for this study was performed under permit SGPA-DGGFS-712-2912-17 issued by Secretaría de Medio Ambiente y Recursos Naturales de México.

References

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Angulo DF, Amarilla LD, Anton AM, Sosa V (2017) Colonization in North American arid lands: The journey of Agarito (*Berberis trifoliolata*) revealed by multilocus molecular data and packrat midden fossil remains. PLoS ONE 12:1–26. https://doi.org/10.1371/journal.pone.0168933

Bessega C, Cony M, Saidman BO et al (2019) Genetic diversity and differentiation among provenances of *Prosopis flexuosa* DC (Leguminosae) in a progeny trial: Implications for arid land restoration. Forest Ecol Managem 443:59–68. https://doi.org/10.1016/j.foreco.2019.04.016

Bessega C, Pometti CL, Ewens M et al (2016) Fine-scale spatial genetic structure analysis in two Argentine populations of *Prosopis alba* (Mimosoideae) with different levels of ecological disturbance. Eur J Forest Res 135:495–505. https://doi.org/10.1007/s10342-016-0948-9

Braconnot P, Otto-Bliesner B, Harrison S et al (2007) Results of PMIP2 coupled simulations of the Mid-Holocene and last glacial maximum - Part 1: Experiments and large-scale features. Clim Past 3:261–277. https://doi.org/10.5194/cp-3-261-2007

Burkart A (1976) A monograph of the genus *Prosopis* (Leguminosae subfam. Mimosoideae). J Arnold Arbor 57:219–249

Brauner N, Shacham M (1998) Role of Range and Precision of the Independent Variable in Regression of Data. AIChE J 44:603–611. https://doi.org/10.1002/aic.690440311

Caballero-Rodríguez D, Correa-Metrio A, Lozano-García S et al (2018) Late-Quaternary spatiotemporal dynamics of vegetation in Central Mexico. Rev Palaeobot Palynol 250:44–52. https://doi.org/10.1016/j.revpalbo.2017.12.004

Caballero M, Lozano García S, Vázquez Selem L, Ortega B (2010) Evidencias de cambio climático y ambiental en registros glaciales y en cuencas lacustres del centro de México durante el último máximo glacial. Bol Soc Geol Mex 62:359–377. https://doi.org/10.18268/bsgm2010v62n3a4

Calderón G, Rzedowski J (2001) Flora fanerogámica del Valle de México. Instituto de Ecología, A.C. y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Pátzcuaro

Campos CM, Ojeda RA (1997) Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. J Arid Environm 35:707–714. https://doi.org/10.1006/jare.1996.0196

Cervantes M (2005) Plantas de importancia económica en zonas áridas y semiáridas de México. X Encuentro de Geógrafos de América Latina, São Paulo, Brasil, 20 al 25 de marzo de 2005. Invest Geogr 57:3388–3407

Challenger A (1998) La zona ecológica árida y semiárida In: Utilización y conservación de los ecosistemas terrestres de México. Pasado, presente y futuro. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad/Instituto de Biología, UNAM/Agrupación Sierra Madre, México, DF, pp 617–713

Chapuis MP, Estoup A (2007) Microsatellite null alleles and estimation of population differentiation. Molec Biol Evol 24:621–631. https://doi.org/10.1093/molbev/msl191

Chávez-Lara CM, Roy PD, Caballero MM et al (2012) Lacustrine ostracodes from the Chihuahuan desert of Mexico and inferred late quaternary paleoecological conditions. Revista Mex Ci Geol 29:422–431

Chybicki IJ, Burczyk J (2009) Simultaneous estimation of null alleles and inbreeding coefficients. J Heredity 100:106–113. https://doi.org/10.1093/jhered/esn088

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Molec Ecol 9:1657–1659. https://doi.org/10.1046/j.1365-294x.2000.01020.x

Cohen J (1988) Statistical Power Analysis for the Behavioral Sciences. Routledge, New York. https://doi.org/10.4324/9780203771587

Collins WD, Bitz CM, Blackmon ML et al (2006) The Community Climate System Model Version 3 (CCSM3). J Clim 19:2122–2143. https://doi.org/10.1175/JCLI3761.1

Cornejo-Romero A, Vargas-Mendoza CF, Aguilar-Martínez GF et al (2017) Alternative glacial-interglacial refugia demographic hypotheses tested on *Cephalocereus columna-trajani* (Cactaceae) in the intertropical Mexican drylands. PLoS ONE 12:1–17. https://doi.org/10.1371/journal.pone.0175905

Correa-Metrio A, Lozano-García S, Xelhuantzi-López S, Sosa-Najera S, Metcalfe SE (2012) Vegetation in western Central Mexico during the last 50 000 years: Modern analogs and climate in the Zacapu Basin. J Quatern Sci 27:509–518. https://doi.org/10.1002/jqs.2540

de Noir, F. Bravo, S. Abdala R (2002) Mecanismos de dispersión de algunas especies de leñosas nativas del Chaco Occidental y Serrano. Quebracho Revista Ci Forest 140–150

Domínguez-Vázquez G, Osuna-Vallejo V, Castro-López V, Israde-Alcántara I, Bischoff J (2019) Changes in vegetation structure during the Pleistocene-Holocene transition in Guanajuato, central Mexico. Veg Hist Archaeobot 28:81–91. https://doi.org/10.1007/s00334-018-0685-8

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol Biol 7:1–8. https://doi.org/10.1186/1471-2148-7-214

Drummond AJ, Rambaut A, Shapiro B, Pybus OG (2005) Bayesian coalescent inference of past population dynamics from molecular sequences. Molec Biol Evol 22:1185–1192. https://doi.org/10.1093/molbev/msi103

Duminil J, Fineschi S, Hampe A, Jordano P, Salvani D, Vendramin GG, Petit RJ (2007) Can population genetic structure be predicted from life-history traits? Amer Naturalist 169:662–672. https://doi.org/10.1086/513490

Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genet Resources 4:359–361. https://doi.org/10.1007/s12686-011-9548-7

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molec Ecol 14:2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Excoffier L, Foll M, Petit RJ (2009) Genetic consequences of range expansions. Annual Rev Ecol Evol Syst 40:481–501. https://doi.org/10.1146/annurev.ecolsys.39.110707.173414

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molec Ecol Resources 10:564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315. https://doi.org/10.1002/joc.5086

Fu YX (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925

Galindo-Almanza S (1992) Potencial de Hibridacion natural en el Mezquite (*Prosopis laevigata* y *P.glandulosa* Var. *torreyana*, Leguminosae) De La Altiplanicie De San Luis Potosi. Acta Bot Mex 20:101–117. https://doi.org/10.1017/CBO9781107415324.004

Gándara E, Sosa V (2014) Spatio-temporal evolution of *Leucophyllum pringlei* and allies (Scrophulariaceae): A group endemic to North American xeric regions. Molec Phylogen Evol 76:93–101. https://doi.org/10.1016/j.ympev.2014.02.027

Garrick RC, Nason JD, Meadows CA, Dyer RJ (2009) Not just vicariance: Phylogeography of a Sonoran Desert euphorb indicates a major role of range expansion along the Baja peninsula. Molec Ecol 18:1916–1931. https://doi.org/10.1111/j.1365-294X.2009.04148.x

Genise J, Palacios RA, Hoc PS, Carrizo R, Moffat L, Mom MP, Torregrosa S (1990) Observaciones sobre la biología floral de *Prosopis* (Leguminosae, Mimosoideae). II. Fases florales y visitantes en el Distrito Chaqueño Serrano. Darwiniana 30:71–85.

Golubov J, Mandujano MC, Eguiarte LE (2001) La paradoja de mezquites (*Prosopis* spp.): La invasión de especies o potenciadores de la biodiversidad? Bot Sci 69:23–30. https://doi.org/10.17129/botsci.1644

González-Rodríguez A, Bain JF, Golden JL, Oyama K (2004) Chloroplast DNA variation in the *Quercus affinis*-*Q. laurina* complex in Mexico: Geographical structure and associations with nuclear and morphological variation. Molec Ecol 13:3467–3476. https://doi.org/10.1111/j.1365-294X.2004.02344.x

Guevara L (2020) Altitudinal, latitudinal, and longitudinal responses of cloud forest species to Quaternary glaciations in the northern Neotropics. Biol J Linn Soc 130:615–625. https://doi.org/10.1093/biolinnean/blaa070

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl Acids Symp Ser 41:95–98

Gugger PF, Gonzalez-Rodriguez A, Rodriguez-Correa H, Sugita S, Cavender-Bares J (2011) Southward Pleistocene migration of Douglas-fir into Mexico: Phylogeography, ecological niche modeling, and conservation of "rear edge" populations. New Phytol 189:1185–1199. https://doi.org/10.1111/j.1469-8137.2010.03559.x

Gugger PF, McLachlan JS, Manos PS, Clark JS (2008) Inferring long-distance dispersal and topographic barriers during postglacial colonization from the genetic structure of red maple (*Acer rubrum* L.) in New England. J Biogeogr 35:1665–1673. https://doi.org/10.1111/j.1365-2699.2008.01915.x

Gutiérrez-Rodríguez C, Ornelas JF, Rodríguez-Gómez F (2011) Chloroplast DNA phylogeography of a distylous shrub (*Palicourea padifolia*, Rubiaceae) reveals past fragmentation and demographic expansion in Mexican cloud forests. Molec Phylogen Evol 61:603–615. https://doi.org/10.1016/j.ympev.2011.08.023

Hallatschek O, Nelson DR (2008) Gene surfing in expanding populations. Theor Popul Biol 73:158–170. https://doi.org/10.1016/j.tpb.2007.08.008

Hardy OJ, Vekemans X (2002) spagedi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Molec Ecol Notes 2:618–620. https://doi.org/10.1046/j.1471-8286.2002.00305.x

Hewitt G (2000) The genetic legacy of the quaternary ice ages. Nature 405:907–913. https://doi.org/10.1038/35016000

Hewitt GM (2004) Genetic consequences of climatic oscillations in the Quaternary. Philos Trans Roy Soc B Biol Sci 359:183–195. https://doi.org/10.1098/rstb.2003.1388

Hofer T, Ray N, Wegmann D, Excoffier L (2009) Large allele frequency differences between human continental groups are more likely to have occurred by drift during range expansions than by selection. Ann Hum Genet 73:95–108. https://doi.org/10.1111/j.1469-1809.2008.00489.x

Hubisz MJ, Falush D, Stephens M, Pritchard JK (2009) Inferring weak population structure with the assistance of sample group information. Molec Ecol Resources 9:1322–1332. https://doi.org/10.1111/j.1755-0998.2009.02591.x

Jakobsson M, Rosenberg NA (2007) CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Janes JK, Miller JM, Dupuis JR, Malenfant RM, Gorrell JC, Cullingham CI, Andrew LI (2017) The K = 2 conundrum. Molec Ecol 26:3594–3602. https://doi.org/10.1111/mec.14187

Janzen DH, Martin PS (1982) Neotropical anachronisms: The fruits the gomphotheres ate. Science 215:19–27. https://doi.org/10.1126/science.215.4528.19

Keinan A, Mullikin JC, Patterson N, Reich D (2007) Measurement of the human allele frequency spectrum demonstrates greater genetic drift in East Asians than in Europeans. Nat Genet 39:1251–1255. https://doi.org/10.1038/ng2116

Librado P, Rozas J (2009) DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25:1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Loera I, Ickert-Bond SM, Sosa V (2017) Pleistocene refugia in the Chihuahuan Desert: the phylogeographic and demographic history of the gymnosperm *Ephedra compacta*. J Biogeogr 44:2706–2716. https://doi.org/10.1111/jbi.13064

Mantel N (1967) The Detection of Disease Clustering and a Generalized Regression Approach. Cancer Res 27:64–71

Masuelli RS, Balboa O (1989) Self-incompatibility in *Prosopis flexuosa*. Pl Cell Incompat Newslett 21:44–48

McCormack JE, Heled J, Delaney KS, Peterson AT, Knowles LL (2011) Calibrating divergence times on species trees versus gene trees: Implications for speciation history of *Aphelocoma* jays. Evolution 65:184–202. https://doi.org/10.1111/j.1558-5646.2010.01097.x

Metcalfe SE (2006) Late Quaternary environments of the northern deserts and central transvolcanic belt of Mexico. Ann Missouri Bot Gard 93:258–273. https://doi.org/10.3417/0026-6493(2006)93[258:LQEOTN]2.0.CO;2

Metcalfe SE, O'Hara SL, Caballero M, Davies SJ (2000) Records of Late Pleistocene-Holocene climatic change in Mexico - A review. Quatern Sci Rev 19:699–721. https://doi.org/10.1016/S0277-3791(99)00022-0

Moncada X, Plaza D, Stoll A, Payacan C, Seelenfreund D, Martínez E, Bertin A, Squeo FA (2019) Genetic diversity and structure of the vulnerable species *Prosopis chilensis* (Molina) Stuntz in the Coquimbo region, Chile. Gayana Bot 76:91–104. https://doi.org/10.4067/S0717-66432019000100091

Mottura MC, Finkeldey R, Verga AR, Gailing O (2005) Development and characterization of microsatellite markers for *Prosopis chilensis* and *Prosopis flexuosa* and cross-species amplification. Molec Ecol Notes 5:487–489. https://doi.org/10.1111/j.1471-8286.2005.00965.x

Múrias Dos Santos A, Cabezas MP, Tavares AI, Xavier R, Branco M (2016) TcsBU: A tool to extend TCS network layout and visualization. Bioinformatics 32:627–628. https://doi.org/10.1093/bioinformatics/btv636

Napier JD, de Lafontaine G, Heath KD, Hu FS (2019) Rethinking long-term vegetation dynamics: multiple glacial refugia and local expansion of a species complex. Ecography 42:1056–1067. https://doi.org/10.1111/ecog.04243

Nason JD, Hamrick JL, Fleming TH (2002) Historical Vicariance and Postglacial Colonization Effects on the Evolution of Genetic Structure in Lophocereus, a Sonoran Desert Columnar Cactus. Evolution 56:2214. https://doi.org/10.1554/0014-3820(2002)056[2214:hvapce]2.0.co;2

Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590

Ornelas JF, García JM, Ortiz-Rodriguez AE, Licona-Vera Y, Gándara E, Molina-Freaner F, Vásquez-Aguilar AA (2019) Tracking host trees: The phylogeography of endemic *Psittacanthus sonorae* (loranthaceae) mistletoe in the Sonoran desert. J Heredity 110:229–246. https://doi.org/10.1093/jhered/esy065

Ornelas JF, Licona-Vera Y, Vásquez-Aguilar AA (2018) Genetic differentiation and fragmentation in response to climate change of the narrow endemic *Psittacanthus auriculatus*. Trop Conserv Sci 11:1–15. https://doi.org/10.1177/1940082918755513

Ornelas JF, Sosa V, Soltis DE, Daza JM, González C, Soltis PS, Gutiérrez-Rodríguez C, Espinosa de los Monteros A, Castoe TA, Bell C, Ruiz-Sanchez E, (2013) Comparative Phylogeographic Analyses Illustrate the Complex Evolutionary History of Threatened Cloud Forests of Northern Mesoamerica. PLoS ONE 8:1–9. https://doi.org/10.1371/journal.pone.0056283

Ortega B, Vázquez G, Caballero M, Israde I, Lozano-García S, Schaaf P, Torres E (2010) Late Pleistocene: Holocene record of environmental changes in Lake Zirahuen, Central Mexico. J Paleolimnol 44:745–760. https://doi.org/10.1007/s10933-010-9449-x

Otero-Arnaiz A, Casas A, Hamrick JL, Cruse-Sanders J (2005) Genetic variation and evolution of *Polaskia chichipe* (Cactaceae) under domestication in the Tehuacán Valley, central Mexico. Molec Ecol 14:1603–1611. https://doi.org/10.1111/j.1365-294X.2005.02494.x

Otto-Bliesner BL, Marshall SJ, Overpeck JT, Miller GH, Hu A (2006) Simulating arctic climate warmth and icefield retreat in the last interglaciation. Science 311:1751–1753. https://doi.org/10.1126/science.1120808

Palacios R (2006) Los Mezquites mexicanos: Biodiversidad y Distribución Geográfica. Bol Soc Argent Bot 41:99–121

Pasiecznik N, Felker P, Harsh HP, LN, Cruz G, Tewari JC, Cadoret K, Maldonado LJ, (2002) The'*Prosopis juliflora*'-'*Prosopis pallida*'complex: a monograph. For Trees Livelihoods 12:229–229

Peakall R, Smouse PE (2012) GenALEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research-an update. Bioinformatics 28:2537–2539. https://doi.org/10.1093/bioinformatics/bts460

Pedersen MW, Overballe-Petersen S, Ermini L, SarkissianC D, Haile J, Hellstrom M, Spens J, Thomsen PF, Bohmann K, Cappellini E, Schnell IB, Wales NA, Carøe C, Campos PF, Schmidt AMZ, Gilbert TP, Hansen AJ, Orlando L, Willerslev E (2015) Ancient and modern environmental DNA. Philos Trans Roy Soc B Biol Sci 370:1–12. https://doi.org/10.1098/rstb.2013.0383

Peñaloza-Ramírez JM, Rodríguez-Correa H, González-Rodríguez A, Rocha-Ramírez V, Oyama K (2020) High genetic diversity and stable Pleistocene distributional ranges in the widespread Mexican red oak *Quercus castanea* Née (1801) (Fagaceae). Ecol Evol 10:4204–4219. https://doi.org/10.1002/ece3.6189

Pérez-Crespo MJ, Ornelas JF, González-Rodríguez A, Ruiz-Sanchez E, Vasquez-Aguilar AA¸ Ramírez-Barahona S, (2017) Phylogeography and population differentiation in the *Psittacanthus calyculatus* (Loranthaceae) mistletoe: a complex scenario of climate–volcanism interaction along the Trans-Mexican Volcanic Belt. J Biogeogr 44:2501–2514. https://doi.org/10.1111/jbi.13070

Phillips SB, Aneja VP, Kang D, Arya SP (2006) Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. Int J Glob Environ Issues 6:231–252. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Polhill RM, Raven PH, Stirton CH (1981) Evolution and systematics of the Leguminosae. Advances Legume Syst 1:1–26

Pons O, Petit RJ (1996) Measuring and testing genetic differentiation with ordered versus unordered alleles. Genetics 144:1237–1245

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959. https://doi.org/10.1007/s10681-008-9788-0

Ramírez-Barahona S, Eguiarte LE (2013) The role of glacial cycles in promoting genetic diversity in the Neotropics: The case of cloud forests during the Last Glacial Maximum. Ecol Evol 3:725–738. https://doi.org/10.1002/ece3.483

Ramírez-Barahona S, Eguiarte LE (2014) Changes in the distribution of cloud forests during the last glacial predict the patterns of genetic diversity and demographic history of the tree fern *Alsophila firma* (Cyatheaceae). J Biogeogr 41:2396–2407. https://doi.org/10.1111/jbi.12396

Rhode D (2002) Early Holocene juniper woodland and chaparral taxa in the Central Baja California Peninsula, Mexico. Quatern Res 57:102–108. https://doi.org/10.1006/qres.2001.2287

Roberts DR, Hamann A (2015) Glacial refugia and modern genetic diversity of 22 western North American tree species. Proc Roy Soc B Biol Sci. https://doi.org/10.1098/rspb.2014.2903

Rodríguez-Correa H, Oyama K, Quesada M, Fuchs EJ, Quezada M, Ferrufino M, Valencia-Ávalos S, Cascante-Marín A, González-Rodríguez A (2017) Complex phylogeographic patterns indicate Central American origin of two widespread Mesoamerican *Quercus* (Fagaceae) species. Tree Genet Genomes 13:1–14. https://doi.org/10.1007/s11295-017-1147-7

Rogers AR, Harpending H (1992) Population growth makes waves in the distribution of pairwise genetic differences. Molec Biol Evol 9:552–569. https://doi.org/10.1093/oxfordjournals.molbev.a040727

Rosenberg NA (2004) Distruct MANUAL. Molec Ecol Notes 4:137–138

Ruiz-Sanchez E, Ornelas JF (2014) Phylogeography of *Liquidambar styraciflua* (Altingiaceae) in Mesoamerica: Survivors of a Neogene widespread temperate forest (or cloud forest) in North America? Ecol Evol 4:311–328. https://doi.org/10.1002/ece3.938

Ruiz-Sanchez E, Rodriguez-Gomez F, Sosa V (2012) Refugia and geographic barriers of populations of the desert poppy, *Hunnemannia fumariifolia* (Papaveraceae). Organisms Diversity Evol 12:133–143. https://doi.org/10.1007/s13127-012-0089-z

Ryman N, Palm S (2006) POWSIM: a computer program for assessing statistical power when testing for genetic differentiation. Molec Ecol Notes 6:600–602. https://doi.org/10.1111/j.1471-8286.2006.01378.x

Rzedowski J (1988) Análisis de la distribución geográfica del complejo *Prosopis* (Leguminosae, Mimosoideae) en Norteamérica. Acta Bot Mex 3:7. https://doi.org/10.21829/abm3.1988.566

Rzedowski J (1993) Diversity and origins of the phanerogamic flora of Mexico. In: Ramamoorthy TP, Bye R, Lot A, Fa J (eds) Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York, pp 129–144

Scheinvar E, Gámez N, Castellanos-Morales G, Aguirre-Planter E, Eguiarte LE (2017) Neogene and Pleistocene history of *Agave lechuguilla* in the Chihuahuan Desert. J Biogeogr 44:322–334. https://doi.org/10.1111/jbi.12851

Shadik CR, Cárdenes-Sandí GM, Correa-Metrio A, Edwards RL, Min A, Bush MB (2017) Glacial and interglacials in the Neotropics: a 130,000-year diatom record from central Panama. J Paleolimnol 58:497–510. https://doi.org/10.1007/s10933-017-0006-8

Shaw J, Lickey EB, Schilling EE, Small RL (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The Tortoise and the hare III. Amer J Bot 94:275–288. https://doi.org/10.3732/ajb.94.3.275

Simpson BB (1977) Mesquite, its biology in two desert scrub ecosystems. US/IBP Synthesis Series. Dowden, Hutchinson & Ross, New York

Stefenon VM, Klabunde G, Lemos RPM, Rogalski M, Nodari RO (2019) Phylogeography of plastid DNA sequences suggests post-glacial southward demographic expansion and the existence of several glacial refugia for *Araucaria angustifolia*. Sci Rep 9:1–13. https://doi.org/10.1038/s41598-019-39308-w

Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molec Biol Evol 24:1596–1599. https://doi.org/10.1093/molbev/msm092

Templeton AR, Crandall KA, Sing CF (1992) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III Cladogram estimation. Genetics 132:619–633

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. Molec Ecol Notes 4:535–538. https://doi.org/10.1111/j.1471-8286.2004.00684.x

Vásquez-Cruz M, Sosa V (2016) New insights on the origin of the woody flora of the Chihuahuan Desert: The case of Lindleya. Amer J Bot 103:1694–1707. https://doi.org/10.3732/ajb.1600080

Wolfe KH, Li WH, Sharp PM (1987) Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. Proc Natl Acad Sci USA 84:9054–9058. https://doi.org/10.1073/pnas.84.24.9054

Xun H, Li H, Li S, Wei S, Zhang L, Song F, Jiang P, Yang H, Han F, Cai W (2016) Population genetic structure and post-LGM expansion of the plant bug *Nesidiocoris tenuis* (Hemiptera: Miridae) in China. Sci Rep 6:1–11. https://doi.org/10.1038/srep26755

Zimmermann HG (1991) Biological control of mesquite, *Prosopis spp.* (Fabaceae), in South Africa. Agric Ecosyst Environm 37:175–186. https://doi.org/10.1016/0167-8809(91)90145-N

Capítulo II

Differences in germination response to temperature, salinity, and water availability among mesquite (*Prosopis laevigata*) populations from Mexico are guided by the tolerance-exploitation trade-off

Aceptado en: Flora: Morphology, Distribution, Functional Ecology of Plants

Flora 285 (2021) 151963

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Highlighted Student Research

Differences in germination response to temperature, salinity, and water potential among *Prosopis laevigata* populations are guided by the tolerance-exploitation trade-off.

Gonzalo Contreras-Negrete [a], Fernando Pineda-García [b], Sergio Nicasio-Arzeta [a], Erick De la Barrera [a], Antonio González-Rodríguez [a,*]

[a] *Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, Mexico*

[b] *Escuela Nacional de Estudios superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, Mexico*

ARTICLE INFO

Edited by Hermann Heilmeier

Keywords:
Arid zones
Cardinal temperatures
Environmental gradients
Hydrotime
Local adaptation
Mesquite
Thermal time

ABSTRACT

Exploring the mechanisms that promote population divergence represents a central point in evolutionary ecology. Along their distribution, species commonly experience contrasting environmental conditions, which impose local selection pressures to which populations tend to adapt resulting, for example, in ways to deal with resource shortage or abundance. In this study, we explored if germination performance varies under different levels of temperature, water potential and salinity among populations of *Prosopis laevigata*, a widespread mesquite species from the arid and semi-arid zones of Mexico. Given the wide distribution of *P. laevigata* and the sensitivity of the germination phase to environmental conditions, we hypothesized the existence of differential responses during this crucial stage of plant development. Thus, we expected germination in populations of *P. laevigata* from more arid zones to be less sensitive to high temperatures, salinity, and water deficit. Also, we explored if the exploitation–tolerance trade-off guides the differentiation of *P. laevigata* populations in germination performance under varying conditions. Germination of all populations was very sensitive to water scarcity but not to variation in temperature or salinity. We identified two major axes of trait covariation in germination physiology: one defined by tolerance of germination to water and saline stress versus germination velocity, and the other defined by the tolerance to extreme temperatures. We found evidence that variation in tolerance among the populations was related with their distribution along environmental gradients. Overall, populations with a higher capacity to germinate under water deficit stress, salinity, and extreme temperatures inhabit warmer and more saline areas. Our study provides strong evidence of existing local adaptations during germination of *P. laevigata* from across its distribution in the arid lands of Mexico.

1. Introduction

Determining the mechanisms that promote population divergence is a central question in evolutionary ecology. Populations often experience contrasting environmental conditions across the distribution of species, especially for those with wide ranges (Cochrane et al., 2015; Jung et al., 2010). This environmental variation frequently imposes local selection pressures to which populations tend to adapt (Torres-Martínez et al., 2017), possibly generating divergent patterns of variation in life history traits and physiological tolerance (Cochrane et al., 2015; Vergeer and Kunin, 2011). Additionally, this variation between populations is expected to be observed since early stages of plant development (Barton et al., 2020; Cochrane et al., 2015; Morar et al., 2019), such as seed germination. In particular, the evaluation of differential responses during the germination process in relation to the patterns of environmental variation is imperative to understand and predict adaptation mechanisms of species along environmental gradients (Duarte et al., 2018; Qiu et al., 2010; Seal et al., 2017).

A fundamental trade-off has been proposed that describes a continuum of plant strategies for surviving under different regimes of resource

---

Edited by: Hermann Heilmeier

* Corresponding author.

E-mail address: agrodrig@iies.unam.mx (A. González-Rodríguez).

https://doi.org/10.1016/j.flora.2021.151963
Received 7 May 2021; Received in revised form 20 September 2021; Accepted 29 October 2021

availability (Reich, 2014). Specifically, this trade-off expresses the conflict between maximizing resource uptake and use (i. e. exploitation strategy), against the capacity of tolerating and surviving under resource scarcity. It has been observed that plants with a tolerance strategy have low metabolic rates therefore with a reduced demand for resources (Meira-Neto et al., 2019; Roach and Smith, 2020). In addition, tolerant plants invest in mechanisms that enable them to grow and survive under stressful conditions but with a concomitant investment cost that impacts developmental rates. For example, plants from arid areas with low growth rate produce and accumulate osmolytes to maintain water status (Farooq et al., 2009; Hossain et al., 2016; Kapoor et al., 2020) as reported for different *Prosopis* species (Carman et al., 1974), such as *P. strombulifera* (Llanes et al., 2013; Reginato et al., 2012) and *P. ruscifolia* (Meloni and Martínez, 2009). In contrast, plants with an exploitation strategy would maximize growth and resource uptake, as for example, drought deciduous species that maximize water uptake during water pulses in arid zones. Additionally, it has been stated that the trade-off expresses at the different plant constituents, that is, the trade-off would guide plant differentiation at the above- and below-ground organs and at different stages of its life cycle (Reich, 2014). Therefore, it would be expected to observe the exploitation–tolerance trade-off in seed germination, since it is one of the most important events in the life cycle of a plant, representing a stage in which the new individual experiences a drastic physiological transition (Baskin and Baskin, 2014a; Donohue et al., 2010). Also, strong selective pressures on germination physiology are expected, given the sensitivity of the germination process to environmental variation and the high mortality rates observed at this stage (Donohue et al., 2010).

Some of the adaptations related to germination include the response to cues associated with a sequence or even specific environmental signals that trigger the breaking of dormancy (Barga et al., 2017; Baskin and Baskin, 2014a; Cochrane, 2016; Donohue et al., 2010). Particularly, temperature, water potential and salinity are among the main factors driving seed germination, influencing germination rate and the final germination percentage (Baskin and Baskin, 2014b; Bewley et al., 2013). All plant species exhibit thresholds for these three factors during seed germination (Dürr et al., 2015; Mesgaran et al., 2017). For example, seeds germinate above a minimum temperature and below a maximum temperature (representing the species thermal range of germination), reaching their maximum germination rate and highest percentage of germination at an optimal temperature (Alvarado and Bradford, 2002; El-Keblawy et al., 2020; Elnaggar et al., 2018; Gao et al., 2021; Garcia-Huidobro et al., 1982; Onofri et al., 2018; Washitani, 1987). Similarly, each species would exhibit responses to water potential and salinity during seed germination (Bradford and Still, 2004; Gummerson, 1986; Mesgaran et al., 2017). Evaluating the influence of temperature, water potential and salinity on the germination of different populations or species is fundamental to predict their responses to future climate scenarios and to model potential changes in their distribution (Cochrane, 2020; Dürr et al., 2015; El-Keblawy et al., 2020; Elnaggar et al., 2018; Gao et al., 2021; Seal et al., 2017; Stevens et al., 2014).

Arid and semi-arid zones constitute approximately 30% of the Earth's surface (Zalibekov, 2011). These zones experience high temperatures, spatially and temporally unpredictable rains, and variable soil salinity, altogether representing adverse scenarios for plant recruitment (Cavallaro et al., 2016; Cochrane, 2016; Lai et al., 2018; Miranda et al., 2014). In many of these areas, the species from the *Prosopis* genus (mesquites) are considered ecological keystones due to the numerous interactions that sustain with other organisms and also constitute a valuable resource for local human populations (Golubov et al., 2001; Pasiecznik et al., 2002).

Several previous studies have focused on germination responses in *Prosopis* species, including experiments evaluating variation in performance under different temperatures, salinities, and water potentials. High germination percentages in many *Prosopis* species have been found in a wide range of temperatures (i.e., 10 to 40 °C), with maximum values often observed around 30 °C (Cony and Trione, 1996; Flores et al., 2017; Flores and Briones, 2001a; Miranda et al., 2014). Tolerance of germination to salinity has been found in *P. chilensis, P. argentina* and *P. alpataco* in experiments using NaCl solutions (Villagra, 1997; Westphal et al., 2015), and in *P. strombulifera, P. chilensis* and *P. flexuosa* subjected to different salinizing agents (Cony and Trione, 1998; Sosa et al., 2005). In general, a decrease in the germination percentage of these species was observed beyond a concentration of 400 mM NaCl or an osmotic potential of below −1.2 MPa. Water deficit stress experiments using polyethylene glycol (PEG) as osmotic agent have shown a high germination percentage at a water potential of −1 MPa in *P. flexuosa* and *P. chilensis*, with a decrease at −1.4 MPa and reaching the lowest value at −2 MPa (Cony and Trione, 1998). In contrast, Miranda et al. (2014) found high germination in *P. juliflora* at −0.5 MPa, but only 5% germination at −0.75 MPa and no germination at all at −1 MPa. For *P. laevigata* from northern Mexico germination percentage was high at 0, −0.2, −0.4 and −0.6 MPa but decreased below −0.8 MPa in a temperature range from 32 to 36 °C (Flores et al., 2017). However, such studies have rarely compared germination responses among populations from the whole distribution range of the study species, in association with the variation in local environmental conditions.

Table 1

Sites of the 15 populations of *Prosopis laevigata* from which seeds were collected. The table shows the population name and the state of Mexico where it belongs, the code we assigned to the population, the geographical location and the salinity levels measured in soil samples collected in each site.

Code	Population	State	Latitude	Longitude	Salinity (mM)
MAT	Matehuala	San Luis P	23.6302	−100.6401	13
HUI	Huizachal	Tamaulipas	23.5884	−99.2247	4.8
VA	Villa de Arista	San Luis P	22.6439	−100.8452	24.5
HM	Huizache-Mante	San Luis P	22.5505	−99.8059	24
LAG	Lagos	Jalisco	21.3695	−101.9623	16.1
PN	Peña de B	Querétaro	20.7452	−99.9474	8
IXM	Ixmiquilpan	Hidalgo	20.4605	−99.3393	31.4
NOV	Novillero	Guanajuato	20.3889	−101.5918	19.6
SP	San Pedro T	Jalisco	20.2214	−103.3954	16.6
CUI	Cuitzeo	Michoacán	19.9615	−101.2022	10.7
SY	Sayula	Jalisco	19.9270	−103.5283	8.7
IND	Indaparapeo	Michoacán	19.7947	−100.9687	13.5
TEH	Tehuixtla	Morelos	18.5861	−99.263	5.5
ZIN	Zinacatepec	Puebla	18.3242	−97.2518	35.9
SMA	Santa María Ayú	Oaxaca	17.8925	−97.8229	8.1

In Mexico, *Prosopis laevigata* (Humb. et Bonpl. ex Willd) is the most widely distributed species of the genus (Rzedowski, 1988). The species is found in the arid zones of the center and north-east of Mexico, as well as in the semi-arid zones at the south of the country. Throughout the distribution range of the species, *P. laevigata* populations experience contrasting environmental conditions. For example, across its range, annual mean temperature exhibits a difference of 9 °C (15 to 24 °C) and a difference in annual precipitation of 500 mm (360 to 860 mm). Additionally, variation in leaf size and maximum tree height has been observed among mesquite populations (Rzedowski, 1988). This evidence could imply that *P. laevigata* populations have diverged in their functional strategies because of local environmental conditions. Given the sensitivity of seed germination to environmental cues, we hypothesized that populations of *P. laevigata* differ in their response to abiotic factors during this crucial stage of plant development. In particular, we predicted that germination of seeds from *P. laevigata* populations located in more arid areas would be less sensitive to high temperatures, salinity and water deficit. To test this hypothesis, we explored germination responses of *P. laevigata* seeds from across the distribution range of the species under different levels of temperature, water potential and salinity. At the same time, we sought to document whether the exploitation–tolerance trade-off guides differentiation among *P. laevigata* populations at the seed germination stage. This is one of the first studies to document germination responses in a considerable number of populations of a plant species throughout most of its distribution area and to relate observed patterns of variation to local environmental conditions from an evolutionary ecology perspective.

2. Materials and methods

2.1. Seed sampling

We collected *Prosopis laevigata* Humb. et Bonpl. ex Willd (Fabaceae) seeds from 15 localities covering the whole geographic distribution of the species (Table 1). During the summer of 2016, we sampled seeds from at least five mother plants haphazardly selected at each locality, except for the population from Morelos state, in which only three mother plants could be sampled (Table 1). Mother plants were separated from each other by at least 100 m to reduce any possible genetic relatedness effects on samples. At least 100 mature pods were obtained from each mother plant. Once removed from the pods, the seeds were washed with 0.5% sodium hypochlorite and left to dry at room temperature (Arriaga et al., 1994). We stored the seeds in sealed vials with 0.5 g of commercial fungicide until use. At the same time, in order to determine soil salinity at each of the localities, we collected between three and five samples from the first 25 cm of soil in the area surrounding each of the mother plants, which were then combined to obtain a composite sample per population (Westphal et al., 2015). The electrical conductivity (EC) of the soil, which represents the total concentration of ionized solutes in an aqueous sample, was determined by the method described in Rhoades et al. (1999). Then, salinity values of saturated soil were calculated using as a reference the molecular weight of sodium chloride (NaCl) (Table 1).

2.2. Germination experiments

Since physical dormancy has been reported for the seeds of *Prosopis* species, we scarified seeds mechanically using sandpaper because this method has been shown to result in high germination percentages (> 80%; Ortega-Baes et al., 2002). We germinated the seeds in plastic Petri dishes of 9 cm in diameter containing a disk of filter paper Whatman No. 1 (except in the water potential experiment, see below). To explore the effect of temperature, salinity and water potential on seed germination among the different populations, we performed three different experiments, each lasting 12 days, which represent the average germination time reported for *Prosopis* species (Catalán et al., 1994; Cony and Trione, 1998; Sosa et al., 2005). We used five Petri dishes for each population, each one containing ten seeds (i. e. two seeds per mother plant). Therefore, for each treatment of temperature, salinity and water potential, 50 seeds per population were used. The Petri dishes were sealed using parafilm to prevent the evaporation of water or the test solution in the case of the water potential and salinity experiments, respectively. In all cases, seeds were considered germinated when the radicle reached a length of 2 mm (Cony and Trione, 1998). The germination assays were carried out in Lumistell® ICP-09 model incubators, with a 12 h photoperiod for all the experiments. The Petri dishes were placed randomly within the incubator and moved daily to minimize possible position effects on germination patterns.

The temperature experiment consisted of six levels (15, 20, 25, 30, 35 and 40 °C), representing the range of temperatures experienced during the germination period at field conditions across the distribution range of *P. laevigata* (Flores and Briones, 2001a; Palacios, 2006; Flores et al., 2017). Also, these levels of experimental temperatures have been frequently used in analysis of germination in other *Prosopis* species (Cony and Trione, 1998; El-Keblawy and Al-Rawai, 2005; Miranda et al., 2014). During the experimental period, humidity in the Petri dishes was maintained constant by soaking the filter paper every two days.

In a second experiment, we evaluated seed germination under different salinity scenarios. The experimental treatments were based on the results of the soil salinity quantified from the soil samples for each of the collection sites (Table 1). The salinity levels were established by using sodium chloride (NaCl) solutions. Germination was evaluated in concentrations of 5, 16 and 36 mM of NaCl, representing the lower value, the average, and the higher value of the soil salinity found across collection sites, respectively. Also, to simulate extreme stressful conditions, we established two levels of higher salinity (50 and 100 mM NaCl). We transformed the NaCl concentration of each experimental level to osmotic potential ($\Psi_{O;}$ MPa) using van't Hoff's relation (Ferreira Marques et al., 2015). The resulting experimental osmotic potentials (Ψ_O) were 0, −0.025, −0.075, −0.18, −0.25 and −0.45 MPa. To avoid temperature effects on osmotic potential, the germination at all the salinity levels was done at the same temperature (35 °C), which was the temperature where the highest percentage of germination was detected for all populations in the previous experiment (see Results).

Finally, we tested for differences in germination performance among *P. laevigata* populations under different water potentials, previously reported for other species of the genus (Cony and Trione, 1998; De Villalobos and Peláez, 2001; Flores et al., 2017; Miranda et al., 2014). Five different levels of water potential (hereafter referred to as Ψ_H) were established: 0, −0.2, −0.5, −0.8 and −1 MPa by using PEG 8000 (polyethylene glycol with a molecular weight of 8000) solutions, based on Michel (1983). In this experiment filter paper was not included in the Petri dishes to prevent modifications in the treatment water potentials (Hardegree and Emmerich, 1990) and the same volume (10 mL) was used in all cases. This experiment was also conducted at 35 °C.

2.3. Germination assessment

Variation in germination performance among *P. laevigata* populations under the different experimental levels for each of the three experiments (i.e., response to temperature, salinity, and water deficit) was assessed by calculating germinability (*GRP*). The germinability represents the percentage of seeds germinated at the end of the germination process, and is calculated as follows:

$$GRP = \frac{\sum_{i=1}^{k} ni}{N}$$

where n_i = number of germinated seeds in the i^{th} time, k = last germination time and N = number of seeds of the experimental unit. *GRP* was evaluated with the GerminaQuant software (Ferreira Marques et al., 2015).

2.4. Thermal time model

For each temperature treatment, germination percentage was plotted against time to generate cumulative germination curves. We fitted a three-parameter log-logistic function

$$G(t) = \frac{G_{max}}{1 + exp\ \{b[log\ (t) - log\ (t_{50})]\}}$$

to the data in which: G(t) = cumulative germination over time, *t*; *b* = slope at the inflection point; Gmax = maximum germination as *t* approaches infinity; and t_{50} = time at which germination reaches half the Gmax (Mesgaran et al., 2013; Onofri et al., 2018). From each cumulative curve we calculated the germination rate (GR), which is the reciprocal of the time required to reach 50% germination ($GR = 1/t_{50}$) (Chen et al., 2021; Covell et al., 1986; Martínez-Villegas et al., 2018; Picapietra et al., 2020). The germination rate ($1/t_{50}$) for all the treatments was plotted against temperature (*x* axis). We performed a nonlinear least squares (nls) analysis to assess the x-intercept of both the suboptimal and supra-optimal temperature ranges, giving estimates of the base temperature (T_b) below which germination rate ($1/t_{50}$) is zero and ceiling temperature (T_C) above which germination rate ($1/t_{50}$) is also zero

Table 2

Differences in germination performance of the *Prosopis laevigata* populations for the temperature, salinity and water potential treatment analyzed with a generalized linear model. Model details in Methods section. Abbreviations: K = number of parameters; QAICc = quasi-Akaike's Information Criterion; ΔQAICc = difference in quasi-Akaike's Information Criterion compared to the best-fit model; QAICcWt = quasi Akaike weight, describes the relative support of models; Quasi.LL = likelihood value for the quasi-Akaike's Information Criterion; %E.D. = percentage of explained deviance.

Experiment	Model	K	QAICc	ΔQAICc	QAICcWt	Quasi.LL	%E.D.
Temperature							
	Pop + Treatment	17	235.79	0	0.74	−96.64	73.42
	Pop	16	237.91	2.12	0.26	−99.23	71.73
	Pop * Treatment	31	273.51	37.73	0	−88.65	78.62
	Treatment	3	420.45	184.66	0	−207.09	1.47
	1	2	422.83	187.05	0	−209.35	0
Salinity							
	Pop + Treatment	17	204.97	0	1	−81.24	59.02
	Pop	16	222.61	17.63	0	−91.58	49.03
	Pop* Treatment	31	239.15	34.17	0	−71.47	68.47
	Treatment	3	273.28	68.31	0	−133.5	8.48
	1	2	288.69	83.72	0	−142.28	0
Water potential							
	Pop + Treatment	17	128.34	0	1	−39.88	93.21
	Pop	16	585.45	457.11	0	−270.4	7.97
	Pop * Treatment	31	197.75	69.41	0	−32.45	95.96
	Treatment	3	173.59	45.25	0	−83.58	77.05
	1	2	588.13	459.79	0	−291.96	0

(Covell et al., 1986). From the intersection of the non-linear regression of suboptimal and supra-optimal temperature, we estimated the optimal temperature (T_O) at which GR is maximized (Washitani, 1987; Hardegree, 2006; Chen et al., 2021). Also, the thermal-time at 50% of the final germination (Growing Degree Day = GDD_{50}) for the sub-optimal temperatures was calculated as the reciprocal of the slope of the nonlinear regression (Covell et al., 1986; Giolo et al., 2019; López et al., 2019; Martínez-Villegas et al., 2018; Picapietra et al., 2020).

2.5. Hydrotime and osmotime models

Hydrotime and osmotime models describe the relation of water potential (Ψ_H, MPa) from the water potential experiment and of the osmotic potential (Ψ_O, MPa) from the salinity experiment with germination percentage. Germination percentages from each level of water potential and osmotic potential were plotted against time to generate cumulative curves. In both cases, we fitted a three parameters logistic function

$$G(t) = \frac{G_{max}}{1 + exp\left[-\frac{(t)-t_{50}}{b}\right]}$$

in which: G(t) = cumulative germination over time, *t*; *b* = slope around the inflection point; Gmax = maximum germination as *t* approaches infinity; and t_{50} = time at which germination reaches half the Gmax (Mesgaran et al., 2013; Watt et al., 2010). We calculated the germination rate (GR) as $1/t_{50}$ for each cumulative curve, then we plotted the GR against water potential or osmotic potential. A nonlinear least squares regression analysis was performed between GR ($1/t_{50}$) and Ψ, the x-intercept was calculated to estimate the base water (ΨH_{b50}) and osmotic potential (ΨO_{b50}) below which GR is zero, and the standard deviations of the base water ($\sigma\Psi H_b$) and osmotic potential ($\sigma\Psi O_b$) were estimated (Gummerson, 1986; Mesgaran et al., 2017, 2013; Watt et al., 2010). Base water and osmotic potential are theoretical thresholds below which germination is inhibited, and the more negative values indicate higher tolerance to both conditions, and their standard deviation represents the uniformity of germination under the water potential and salinity levels, respectively (Duncan et al., 2019; Mesgaran et al., 2017, 2013). The hydrotime and osmotime constants (θ_H MPa and θ_O MPa, respectively) were estimated as the reciprocal of the slopes (Bradford, 1997; Gummerson, 1986); both are indicative of the germination velocity (smaller values are the faster) (Alvarado and Bradford, 2002; Bradford, 2002, 1997; Cristaudo et al., 2019; Mesgaran et al., 2017; Trudgill et al., 2005; Washitani, 1987) and represent the MPa days needed to germinate (Bochenek et al., 2010; Mesgaran et al., 2013; Onofri et al., 2014). Finally, for all models (thermal time, osmotime and hydrotime) we estimated the pseudoR^2 as a measure of goodness-of-fit (Laitila, 1993). We performed the entire procedure with the *R* software (Developmental Core Team, 2018).

2.6. Statistical analysis

Differences in *GRP* between *P. laevigata* populations under the different experimental treatments were evaluated through generalized linear models (GLM). We employed a binomial distribution and corrected the binomial models for overdispersion using the quasi- Akaike information criterion (QAICc). To explore if *GRP* differs between populations or treatments, we built models with one and two explanatory variables (Population and Treatment) plus the null model (only the intercept). Then, we ranked the models according to QAICc scores (lowest = best) and selected those models with a difference in QAICc lower than two ($\Delta QAICc < 2$) as the best supported by the data (Burnham and Anderson, 2002). We labeled the null model as 1 for all cases. Also, we estimated the percentage of explained deviance of the models as a measure of goodness-of-fit of each model (Crawley, 2007). We performed the entire procedure with the *R* software (Developmental Core Team, 2018).

To explore whether populations differentiate along the exploitation–tolerance trade-off we performed a principal components analysis (PCA) based on mean values for each population of the cardinal temperature traits (T_b, T_O, T_C, and GGD_{50}), hydrotime traits (θ_H, ΨH_{b50}, and $\sigma\Psi H_b$) and osmotime traits (θ_O, ΨO_{b50} and $\sigma\Psi O_b$).

The association between germination traits and the environment was explored under two approaches. First, we extracted 19 bioclimatic variables for each of the collection localities from high-resolution monthly climate surfaces of the study area, available at https://github.com/AngelaCrow/variables-bioclimatica (Cuervo-Robayo et al., 2014). Then, we eliminated highly correlated variables by calculating pairwise Pearson correlation coefficients and discarding one variable from each pair with $r \geq 0.8$ (Aguilar-Romero et al., 2016; Marquínez et al., 2003). Afterwards, we included the following variables in the analysis: isothermality (bio3); maximum temperature of the warmest month (bio5); minimum temperature of the coldest month (bio6); annual precipitation (bio12); precipitation of the wettest month (bio13);

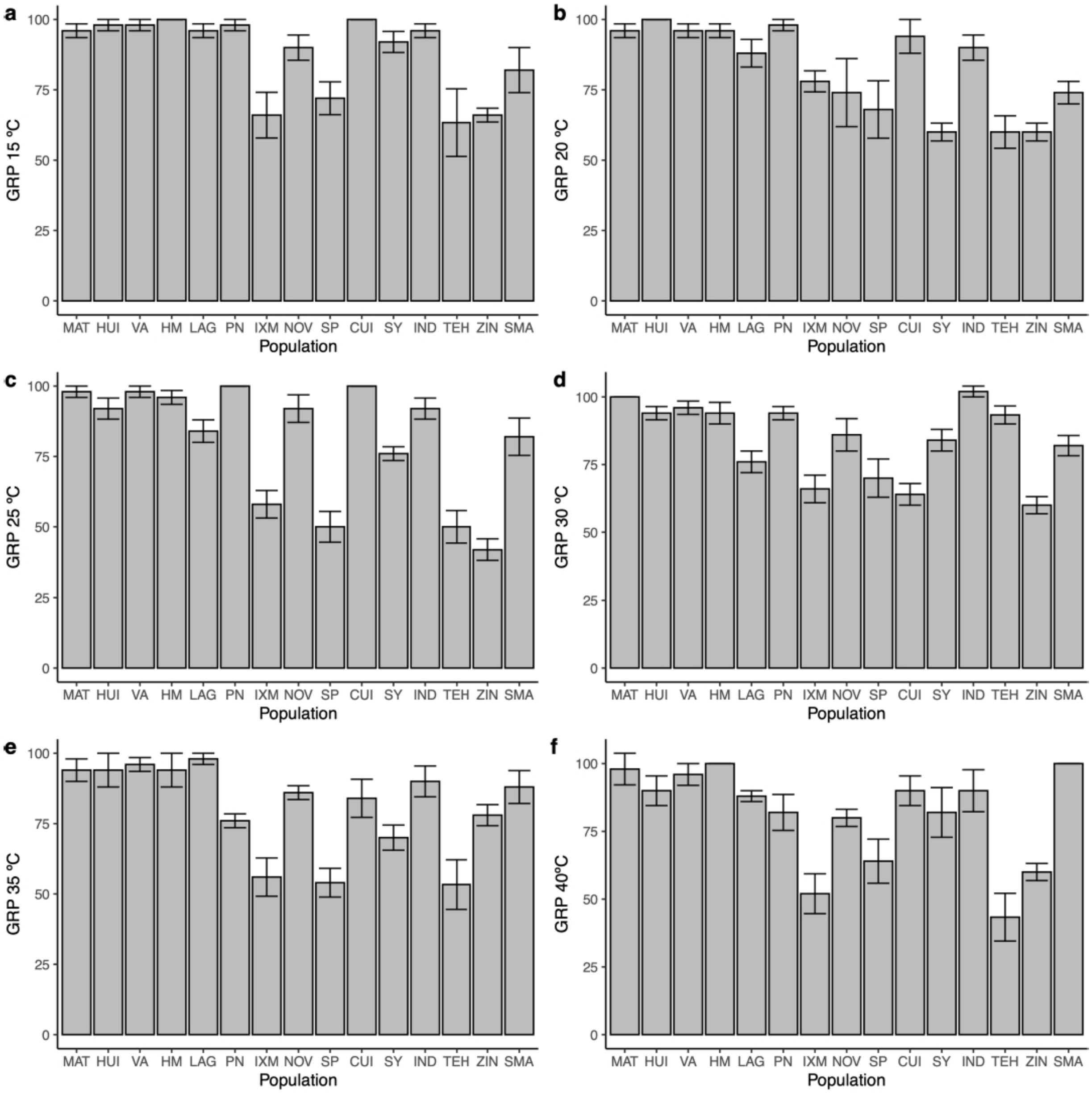


Fig. 1. *GRP* results for 15 populations of *Prosopis laevigata* under six experimental temperatures: a) *GRP* at 15 °C; b) *GRP* at 20 °C; c) *GRP* at 25 °C; d) *GRP* at 30 °C; e) *GRP* at 35 °C and f) *GRP* at 40 °C.

precipitation seasonality (bio15); precipitation of the driest quarter (bio17) and precipitation of the warmest quarter (bio18). For the first approach, we explored the correlation of these eight bioclimatic variables plus soil salinity with the population scores extracted from the two principal components from the analysis described above. For the second approach, we correlated the thermal traits (T_b, T_O, T_C and GDD_{50}) only with temperature variables (bio3, bio5, bio6). Similarly, we explored the correlation of osmotime traits (θ_O, ΨO_{b50} and $\sigma\Psi O_b$) with soil salinity from the population sites. Finally, hydrotime traits (θ_H, ΨH_{b50} and $\sigma\Psi H_b$) were correlated against precipitation variables (bio12, bio13, bio15, bio17 and bio18).

3. Results

3.1. Differences in germination response under experimental treatments

3.1.1. Effect of temperature on germination patterns of P. laevigata

The GLM analysis showed the best supported model was the additive effect of population and treatment (lower QAICc), which explained nearly 74% of the deviance (Table 2). In general, we found relatively high levels of germination in all temperature treatments (> 40%; Fig. 1). Northern populations (MAT, HUI, VA, and HM) reached a *GRP* from 90 to 100% in all the temperatures tested (Fig. 1a–f). In contrast, the germination response from central and southern populations was very

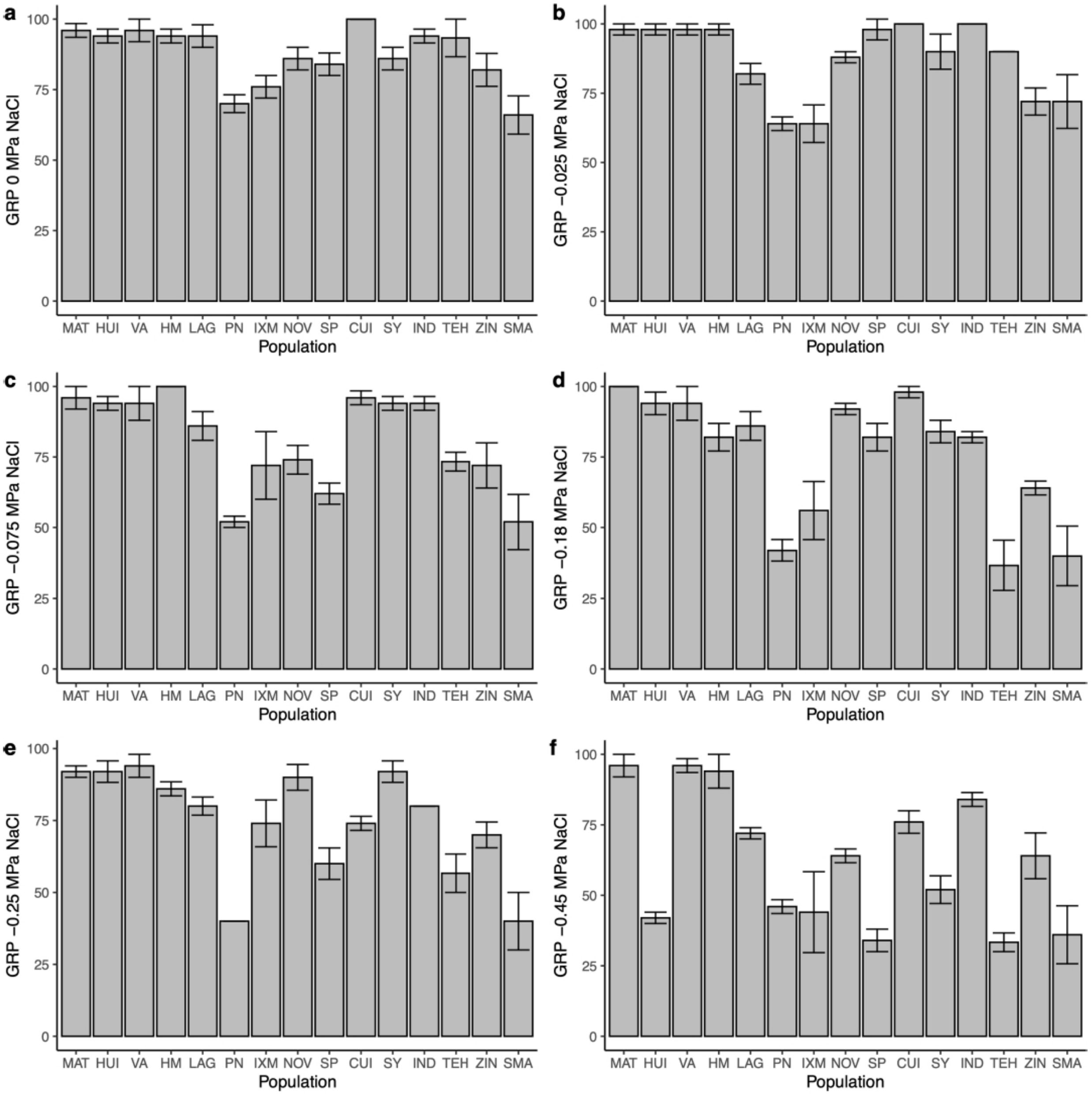


Fig. 2. *GRP* results for 15 populations of *Prosopis laevigata* under six experimental salinities (MPa NaCl): a) *GRP* at 0 MPa NaCl; b) *GRP* at −0.025 MPa NaCl; c) *GRP* at −0.075 MPa NaCl; d) *GRP* at −0.18 MPa NaCl; e) *GRP* at −0.25 MPa NaCl; f) *GRP* at −0.45 MPa NaCl.

variable depending on temperature. The southern population SMA maintained germination levels greater than 80% at all treatments, while the CUI population reached a *GRP* close to 100% at the 25 °C treatment, in contrast to SP and ZIN that only reached 50% and 40%, respectively, under the same temperature treatment (Fig. 1a–f).

3.1.2. Effect of salinity on the germination patterns of *P. laevigata*

The GLM analysis for *GRP* under the salinity treatments showed that the additive model was the best supported one, explaining 59% of the deviance of *GRP* (Table 2). The population and treatment factors explained 49 and 8.5% of the deviance of *GRP*, respectively (Table 2). At the control and the Ψ_O treatments of −0.025 and −0.075 MPa the *GRP* was ca. 80% (Fig. 2a–c). The Ψ_O treatments of −0.18 and −0.25 MPa resulted in a global *GRP* of ca. 70% (Fig. 2d,e), while at Ψ_O of −0.45 MPa *GRP* was only 60% (Fig. 2f). At the population level, the northern populations under the Ψ_O of 0 to −0.25 MPa treatments reached a *GRP* between 70 and 100% (Fig. 2a–e), and at Ψ_O of −0.45 MPa the MAT, VA, and HM populations exhibited values of *GRP* close to 100%. In contrast, the populations from the center and the south showed highly variable patterns among salinity treatments. Population CUI at the Ψ_O of −0.075 MPa treatment reached a GRP close to 100%; in contrast, the *GRP* of the SP population decreased to less than 50% from the Ψ_O of −0.18 to −0.45 MPa treatments.

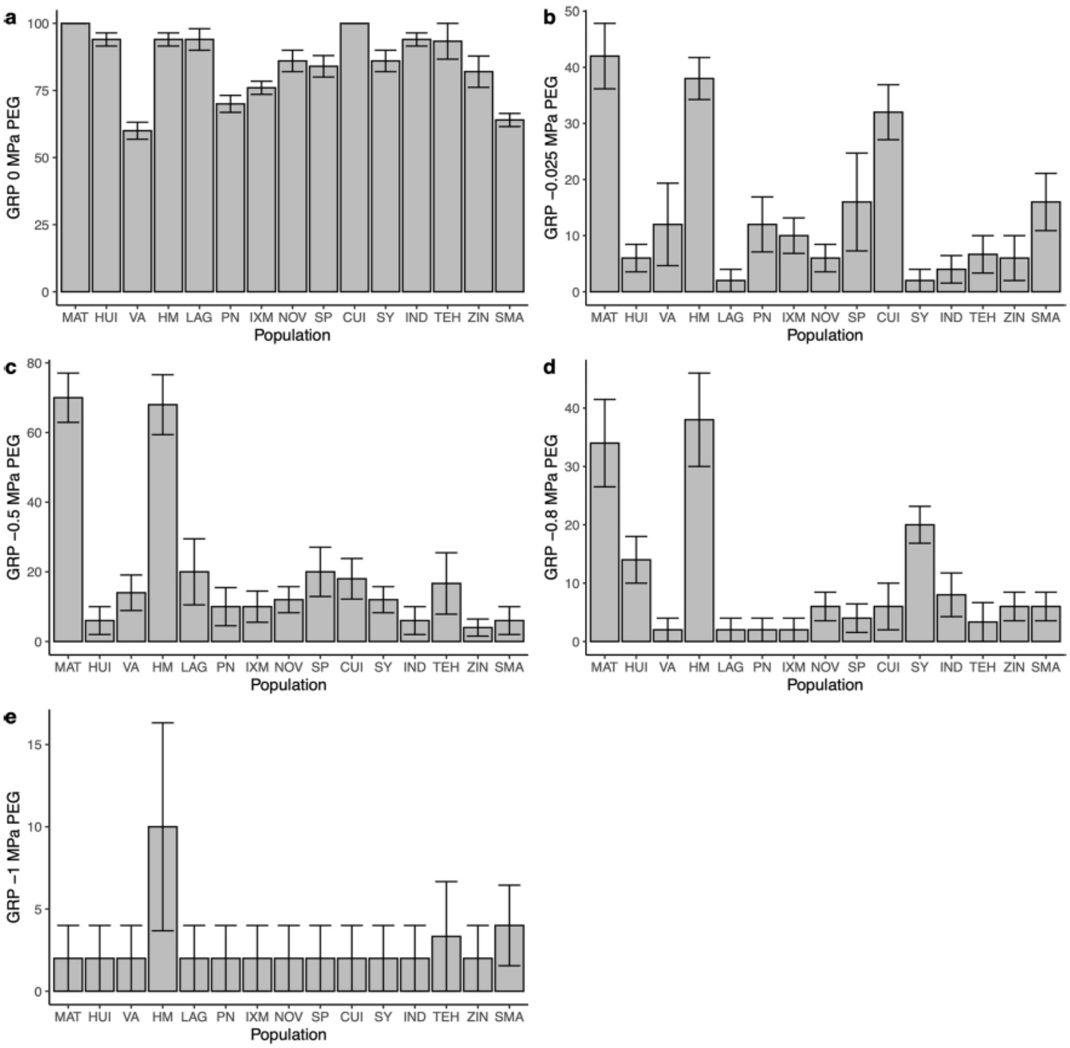


Fig. 3. *GRP* results for 15 populations of *Prosopis laevigata* under five experimental water potentials (MPa PEG 8000): a) *GRP* at 0 MPa; b) *GRP* at −0.2 MP; c) *GRP* at −0.5 MPa ; d) *GRP* at −0.8 MPa ; e) *GRP* at −1 MPa.

3.1.3. Effect of water potential on the germination patterns of *P. laevigata*

The GLM analysis for the water potential experiment showed that the additive model (Population + Treatment) was the best supported and explained 93% of the deviance of *GRP* (Table 2). In this case, the treatment factor explained 77% of the deviance and the population factor only 8% (Table 2). Overall, the *GRP* was very sensitive to water potential (Fig. 3a–e). The *GRP* in the control was ca. 80%, and at Ψ_H of −0.8 MPa it reached ca. 10% only. Most of the populations experienced a substantial reduction in *GRP* under all the treatments (Fig. 3b–e). The populations of the center and south of the species distribution showed *GRP* values of 4 to 18% at −0.5 MPa, while northern populations as MAT and HM reached levels between 50% and 68% in the same treatment. Under the Ψ_H of −0.8 MPa treatment the northern populations (MAT, HUI, and HM) showed a *GRP* near 38%, while the rest of the populations reached levels generally below 8% only (Fig. 3d).

3.2. Thermal time, hydrotime and osmotime models

The nonlinear least squares regression analysis showed that the optimum temperature for germination (T_O) did not vary largely among populations, ranging from 31.79 °C in the TEH population to 34.52 °C in the SMA population (Table S1a). In contrast, the base temperature (T_b) had a larger variation between populations (−6.38 °C for the LAG population to 7.96 °C for the IND population) (Table S1a). The IND population had the lowest ceiling temperature (T_C) (44.79 °C) and the SP population the highest (50.34 °C). The GDD_{50} showed a considerable variation among the populations, ranging from 38.32°-days for the TEH population to 160.52°-days for the PN population (Table S1a).

The osmotime constant (θ_O) and the base osmotic potential (ΨO_{b50}) varied greatly between the populations (1.22 MPa-days in TEH and 10.77 MPa-days in HM and −4.33 MPa-days in HM to −0.40 MPa-days in SMA, respectively) (Table S1b). Germination in the water potential experiment showed the hydrotime constant (θ_H) values fluctuated between 0.03 MPa-days in NOV and 2.32 MPa-days in HM, and the base water potential (ΨH_{b50}) ranged between −0.83 MPa in HM and −0.01 MPa in NOV (Table S1c).

3.3. Multiple trait covariation

In the principal component analysis, the first axis explained 44% of the variation. In this axis, populations with a lower (more negative) base osmotic and water potential and requiring a higher number of MPa-days

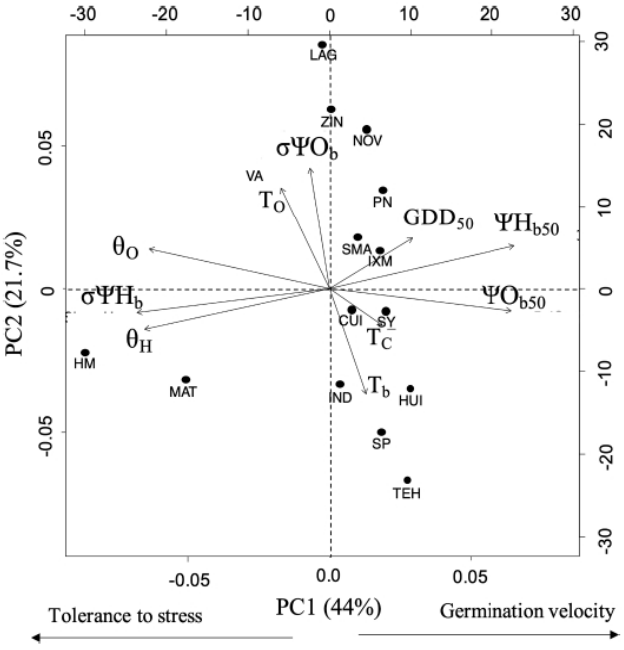


Fig. 4. Principal components analysis showing the two main axes of trait covariation. The analysis included the following germination traits: osmotic time constant (θ_O), base osmotic potential (ΨO_{b50}), standard deviation of the base osmotic potential ($\sigma\Psi O_b$), hydrotime constant (θ_H), base water potential (ΨH_{b50}), standard deviation of the base water potential ($\sigma\Psi H_b$), growing degree day at 50% of final germination (GDD_{50}), optimal temperature for germination (T_O), base temperature for germination (T_b) and ceiling temperature for germination (T_C). The population codes are as in Table 1.

to germinate (i.e., slow germination velocity) and a more variable germination under water shortage were in the negative side of the axis (Fig. 4; Table S2). Conversely, populations that germinated under higher (less negative) osmotic and water potential, with a faster germination rate under higher salinity and lower water potential treatments but with a higher GDD_{50} were located at the positive side of the axis (Fig. 4; Table S2). The second principal component explained 21.7% of the total variation and was mostly related to the germination response to temperature conditions. Populations with a higher optimum temperature and with a more variable germination under the salinity treatments were at the positive side of the axis. Populations that had higher base and ceiling temperatures were at the negative side of the axis (Fig. 4; Table S2).

3.4. *Correlation of germination responses and local environmental conditions*

The correlation analysis between population scores on the two first axes of the principal components analysis and bioclimatic variables showed a positive association of the PC1 with precipitation seasonality (PSeas) and a negative association with the precipitation of the driest quarter (PDQ) (Fig 5a and b), indicating that populations which experience more seasonal precipitation germinate faster and that populations with higher precipitation in the driest quarter germinate more slowly.

Also, associations between individual traits and environmental variables were detected (Fig 5; Table 3). We found a negative correlation between maximum temperature of the warmest month and GDD_{50}: seeds of populations from warmer areas required fewer growing degree-days to germinate (Fig. 5c). On the other hand, the osmotic time constant (θ_O) and the standard deviation of the base osmotic potential ($\sigma\Psi O_b$) were positively correlated with the levels of salinity experienced by the populations in the field. Populations from sites with more saline soils had a lower germination velocity and had lower uniformity in their germination under higher salinity conditions (Fig. 5d and e). In the case of hydrotime variables, we detected that populations with a more negative base water potential (ΨH_{b50}), with higher variability ($\sigma\Psi H_b$) of germination and those which required more MPa-days to germinate (θ_H) are the ones from sites with higher precipitation during the driest quarter and a lower seasonal pattern of precipitation (i.e., MAT, VA, HM; Fig. 5f–i; Table 3).

4. Discussion

It its widely recognized that abiotic environmental conditions exert strong selective pressures that usually result in patterns of local adaptation among populations. In the present study, we explored whether germination performance varies between populations of *P. laevigata* across its distribution range, examining the possible existence of local adaptations to deal with contrasting environmental regimes. Overall, the populations exhibited contrasting responses in several of the experimental treatments. In general, germination of all populations was very sensitive to water shortage but not to high temperature or salinity. The patterns of variation among the populations, as synthesized by two main principal components, suggested segregation among a tolerance–exploitation axis. Likewise, we provided evidence that the patterns of variation among the populations were related to their distribution along environmental gradients.

Though the optimum temperature (T_O) for germination was similar between the populations (it differed by 3 °C only), the minimum and maximum temperatures (T_b and T_C, respectively) that allow germination exhibited a higher variation. Additionally, some populations like MAT, HUI, VA, and HM sustained a high germination percentage under the six experimental temperatures, and others (i.e., ZIN and TEH) had a more heterogeneous response to the variation in temperature. However, most of the populations exhibited a *GRP* above 50% under the different temperatures. Other *Prosopis* species have also shown high *GRP* values in a wide range of temperatures (Cony and Trione, 1996; Miranda et al., 2014; Palacios et al., 2001; Zeng, 2006).

On the other hand, though germination decreased with increased salinity, it sustained relatively high percentages (>50%) even in the highest salinity levels evaluated (except for populations HUI, PN, SP and TEH). Additionally, the base osmotic potential (ΨO_{b50}) reached theoretical values as negative as −4.33 MPa and $\sigma\Psi O$ showed a value up to −0.7 MPa, indicating high tolerance of *P. laevigata* germination to salinity. Other species of the *Prosopis* genus have also shown high tolerance to salinity (Cony and Trione, 1998; El-Keblawy and Al-Rawai, 2006; Ramawat, 2010; Westphal et al., 2015). In contrast, germination in most of the populations was very sensitive to the decrease in water potential. Only some populations germinated at mild levels of water deficit stress and germination decreased drastically at −0.8 and −1 MPa. Though the base water potential was very high for some populations, the northern populations showed a higher germination percentage under low water potential. Taken together, the variation in the response to temperature, salinity, and water potential among the populations is indicative of divergent patterns of adaptation to local environmental pressures.

Interestingly, we found evidence to support the hypothesis that the variation in seed germination patterns among populations of *P. laevigata* was constrained along the trade-off between tolerance to stress and exploitation. Remarkably, we detected that a group of populations (i.e., HM and MAT) showed a higher germination percentage at more negative osmotic potential in the salinity experiment and more negative water potential in the water potential experiment (ΨO_{b50} and ΨH_{b50}) but had a lower germination velocity. This indicates that for these populations, germination is not completely inhibited under stressful conditions, that is, they can tolerate the stress. Conversely, on the other side of the axis, the germination of a group of populations (i.e., HUI, SP and TEH) was faster but sensitive to both water deficit stress and salinity

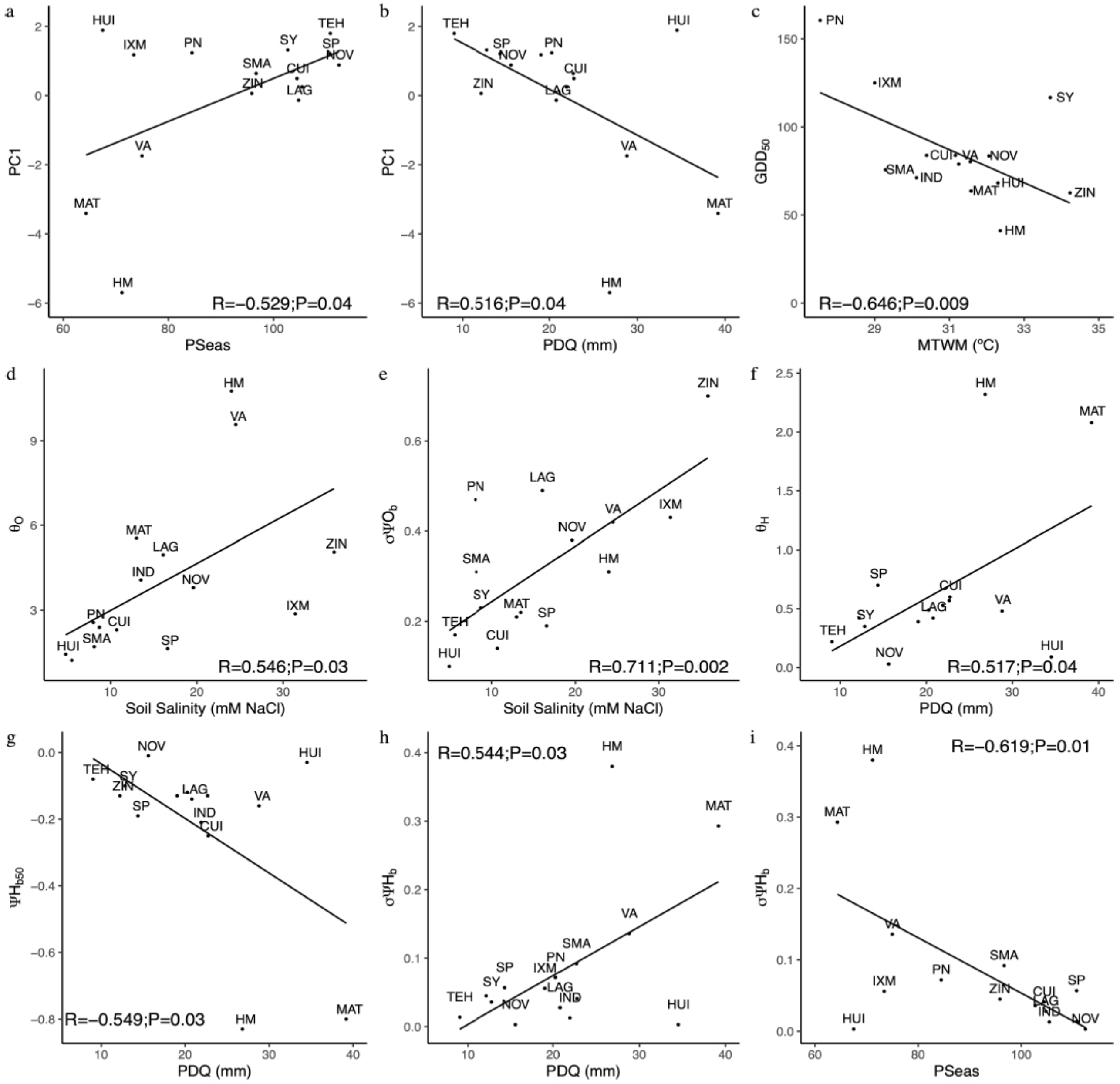


Fig. 5. Relationships of principal components scores and individual germination traits with environmental variables at the collection localities; a) precipitation seasonality (PSeas) and the first principal component (PC1); b) precipitation during the driest quarter (PDQ) and the first principal component (PC1); c) maximum temperature of the warmest month (MTWM) and the growing degree day at 50% of final germination (GDD_{50}); d) soil salinity (mM NaCl) and osmotic time constant (θ_O); e) soil salinity (mM NaCl) and the standard deviation of the base osmotic potential ($\sigma\Psi O_b$); f) precipitation during the driest quarter (PDQ) and hydrotime constant (θ_H); g) precipitation during the driest quarter (PDQ) and base water potential (ΨH_{b50}); h) precipitation during the driest quarter (PDQ) and standard deviation of the base water potential ($\sigma\Psi H_b$); i) seasonality of precipitation (PSeas) and standard deviation of the base water potential ($\sigma\Psi H_b$). The population codes are as in Table 1.

and needed a higher accumulation of temperature to germinate, suggesting that their germination physiology is more adapted to optimum conditions and they do not tolerate stress. In contrast, the second axis of differentiation was mostly defined by the germination response to temperature. A group of populations (i.e., LAG and ZIN) germinated at lower temperatures, but at higher temperatures germination was inhibited. On other hand, the rest of the populations showed a higher optimum temperature (i.e., IND and CUI), but germination was initiated at higher and inhibited at lower temperatures. The PCA allowed to detect that the variation patterns in the germination response to drought, salinity and temperature are not entirely independent. This association in the response to the three environmental factors could be promoted by the same or similar physiological mechanisms. For example, high and low temperatures, drought and salinity directly impact the water status of cells and plants respond by modifying their metabolism to maintain the hydric balance in cells (Balfagón et al.,

Table 3

Relationships between environmental variables and germination traits modeled under the a) thermal time, b) osmotime and c) hydrotime models explored through Pearson correlation analysis. Correlation coefficient (r) and probability (*P*) are shown. Significant values are in bold. Symbols: bio3 = isothermality; bio5 = maximum temperature of warmest month; bio6 = minimum temperature of the coldest month; bio12 = annual precipitation; bio13 = precipitation of wettest month; bio15 = precipitation seasonality; bio17 = precipitation of the driest quarter; bio18 = precipitation of warmest quarter; mM NaCl = salinity from the population sites. T_b = base temperature; T_O = optimum temperature; T_C = ceiling temperature; GDD_{50} =thermal time at 50% of final germination. θ_O = osmotime constant; ΨO_{b50} = median base osmotic potential; $\sigma\Psi O_b$ = standard deviation of the median base osmotic potential. θ_H = hydrotime constant; ΨH_{b50} = median base water potential; $\sigma\Psi H_b$ = standard deviation of the median base water potential.

	Environmental variable	r	*P*	r	*P*	r	*P*	r	*P*
a)		T_O		T_C		T_b		GDD_{50}	
	bio3	0.27	0.32	−0.19	0.47	0.15	0.58	0.22	0.41
	bio5	−0.41	0.12	0.43	0.10	−0.09	0.73	**−0.64**	**0.009**
	bio6	−0.17	0.53	0.30	0.26	−0.02	0.91	−0.35	0.18
b)		θ_O		ΨO_{b50}		$\sigma\Psi O_b$			
		r	*P*	r	*P*	r	*P*		
	Salinity (mM NaCl)	0.546	**0.03**	−0.46	0.08	**0.71**	**0.002**		
		θ_H		ΨH_{b50}		$\sigma\Psi H_b$			
c)		r	*P*	r	*P*	r	*P*		
	bio12	−0.33	0.20	0.318	0.20	−0.481	0.06		
	bio13	−0.414	0.12	0.406	0.13	−0.540	0.05		
	bio15	−0.505	0.05	0.509	0.05	**−0.619**	**0.01**		
	bio17	**0.517**	**0.04**	**−0.549**	**0.03**	**0.544**	**0.03**		
	bio18	−0.316	0.25	0.258	0.35	−0.420	0.11		

2020b; Kapoor et al., 2020; Yang and Guo, 2018). One of such mechanisms is the synthesis of compatible solutes such as polyols, sugars, or amino acids that serve as osmolytes or osmo-protectors, which organize proteins and cellular structures to maintain hydration status of cells through osmotic adjustment and stabilization of chemical bonds (Fathi and Tari, 2016; Munns and Tester, 2008; Sadura and Janeczko, 2018). Therefore, osmolyte production and accumulation could diminish the effect of the three types of stress.

Interestingly, we found that germination parameters obtained for the three experiments were associated to certain environmental variables of the collection localities. In contrast with populations from more temperate areas, populations from warmer areas required a lower accumulation of temperature across the days to germinate (Andrade and Cardoso, 2016; Dürr et al., 2015; Hu et al., 2015; Simão et al., 2010; Trudgill et al., 2005). Similar results were reported by Seal et al. (2017) for different cacti species from the Americas, recording higher GDD_{50} values and slower germination in seeds from more temperate zones, possibly to prevent the risk of late frosts, while in warmer areas a faster germination and lower GDD_{50} values were observed, probably to ameliorate the risk of drought. Also, Arana et al. (2016) reported for three *Nothofagus* species from the Patagonian Andes that seeds at higher elevations delayed germination until the spring, reaching higher GDD_{50} values, preventing seedling freezing, a response which possibly contributes to maintain the distribution pattern across the elevational gradient. Conversely, López et al. (2019) reported for the perennial grass *Festuca pallescens* from North Patagonia higher GDD_{50} values for arid eastern populations and a decrease in GDD_{50} towards the temperate Andean zone at the west. These patterns of variation along temperature gradients are attributable to specific responses to environmental cues. For example, thermal signals could influence the quantity, mass, dormancy and germination of seeds through various mechanisms, including the evolution of genetic differences or via phenotypic plasticity, including "thermal memory" which is the adjustment resulting from the past thermal environment experienced by the seed and its recent ancestors (Fernández-Pascual et al., 2019; Kijowska-Oberc et al., 2020).

On the other hand, we found that populations from more saline sites (i.e., HM and VA) had lower germination velocity under conditions of higher salinity than populations from less saline sites. Similarly, Duncan et al. (2019) reported a marked reduction in germination velocity under water limitation in *Atriplex rhagodioides* and *Hakea leucoptera* from arid lands in Australia, for which slowed germination represents a strategy to avoid greater risk of desiccation. Additionally, we observed that *P. laevigata* populations from sites with a more seasonal pattern of precipitation and with some events of precipitation during the driest period had a better germination performance under water deficit stress. Hydrotime studies in *Festuca pallescens* from North Patagonia have shown higher θ_H at the extremes of the distribution gradient, possible related to delayed germination in suboptimal conditions. However, no correlations were found in this case among hydrotime values and precipitation variables (López et al., 2021).

Together, these results suggest the germination physiology of the *P. laevigata* populations that inhabit more arid and saline sites is adapted to continue despite the levels of stress (Alvarado and Bradford, 2002; Bradford and Still, 2004; Bradford, 1997). The marked decrease in germination velocity found in more stressful salinity and water potential are consistent with reports about seed hydration memory, caused by the discontinuous imbibition process which guarantees successful germination under water shortage conditions (Dubrovsky, 1998, 1996; Lima and Meiado, 2018). Also, the presence of seed hydration memory depends on the climate where individuals occur, for which seed germination of some species is influenced by environmental conditions imposed to parental plants (Contreras-Quiroz et al., 2016).

5. Conclusion

We compared germination performance under different levels of water deficit stress, salinity, and temperature among 15 populations of *P. laevigata* and we found significant variation in their germination response under the experimental conditions. We found germination was more sensitive to water deficit than to variation in salinity and temperature. Our study provides evidence of existing local adaptations at the germination level among *P. laevigata* populations from the arid lands of Mexico. We detected two major axes of trait covariation; one defined by the tolerance of germination physiology to water deficit and saline stress versus the velocity to germinate and the other defined by the tolerance of the germination physiology to extreme temperatures. Our study contributes to the growing evidence that the fundamental trade-off constricts population and species differentiation at the different plant components and phases of development. Populations whose seeds show a higher germination performance under water deficit stress, salinity and extreme temperatures inhabit warmer and more saline areas. Overall, our study evidenced different responses in the germination process, suggesting divergent patterns of adaptations triggered by local environmental conditions between *P. laevigata* populations.

CRediT authorship contribution statement

Gonzalo Contreras-Negrete: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft. **Fernando Pineda-García:** Conceptualization, Methodology, Data curation, Formal analysis, Funding acquisition, Resources. **Sergio Nicasio-Arzeta:** Methodology, Data curation, Formal analysis. **Erick De la Barrera:** Methodology, Formal analysis. **Antonio González-Rodríguez:** Conceptualization, Methodology, Data curation, Formal analysis, Funding acquisition, Resources, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Funding

This study was supported by Presupuesto Operativo from Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES), UNAM to A. González-Rodríguez and by Programa de Apoyos a Proyectos de Investigación e Innovación Tecnológica (PAPIIT) (IA203221) to F. Pineda-García.

Acknowledgments

The authors thank Florencio Mosqueda-Ruíz, Oscar de Luna, Ricardo Gaytán, Saddan Morales and Mariana Hernández for field assistance and Tamara Ochoa, Griselda Pérez, and Claudia Guerrero for laboratory assistance. The comments by two anonymous reviewers and Hermann Heilmeier to previous versions of the manuscript are greatly appreciated. Dr. Rafael Aguilar-Romero provided technical assistance in the assembly of the experiments. Gonzalo Contreras-Negrete thanks the National Council of Science and Technology CONACyT (CVU 549242) and the Postgraduate Program in Biological Sciences UNAM (PCBiol UNAM) for the facilities provided. This article represents a partial requirement of the Postgraduate Program in Biological Sciences of the UNAM.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2021.151963.

References

Aguilar-Romero, R., García-Oliva, F., Pineda-García, F., Torres, I., Peña-Vega, E., Ghilardi, A., Oyama, K., 2016. Patterns of distribution of nine *Quercus* species along an environmental gradient in a fragmented landscape in central Mexico. Bot. Sci. 94, 471–482. https://doi.org/10.17129/botsci.620.

Alvarado, V., Bradford, K.J., 2002. A hydrothermal time model explains the cardinal temperatures for seed germination. Plant Cell Environ. 25, 1061–1069. https://doi.org/10.1046/j.1365-3040.2002.00894.x.

Andrade, L.F.D., Cardoso, V.J.M., 2016. Does thermal time for germination vary among populations of a tree legume (*Peltophorum dubium*)? Braz. J. Biol. 76, 592–599. https://doi.org/10.1590/1519-6984.18714.

Arana, M.V., Gonzalez-Polo, M., Martinez-Meier, A., Gallo, L.A., Benech-Arnold, R.L., Sánchez, R.A., Batlla, D., 2016. Seed dormancy responses to temperature relate to *Nothofagus* species distribution and determine temporal patterns of germination across altitudes in Patagonia. New Phytol. 209, 507–520. https://doi.org/10.1111/nph.13606.

Arriaga, V., Cervantes, V., Vargas-Mena, A., 1994. Manual de reforestación con especies nativas: colecta y preservación de semillas, propagación y manejo de plantas. Univ. Nac. Auton. México 186, 111–130.

Balfagón, D., Zandalinas, S.I., Mittler, R., Gómez-Cadenas, A., 2020. High temperatures modify plant responses to abiotic stress conditions. Physiol. Plant. 170, 335–344. https://doi.org/10.1111/ppl.13151.

Barga, S., Dilts, T.E., Leger, E.A., 2017. Climate variability affects the germination strategies exhibited by arid land plants. Oecologia 185, 437–452. https://doi.org/10.1007/s00442-017-3958-5.

Barton, K.E., Jones, C., Edwards, K.F., Shiels, A.B., Knight, T., 2020. Local adaptation constrains drought tolerance in a tropical foundation tree. J. Ecol. 108, 1540–1552. https://doi.org/10.1111/1365-2745.13354.

Baskin, C.C., Baskin, J.M., 2014a. Biogeographical and evolutionary aspects of seed dormancy. In: Baskin, C.C., Baskin, J.M. (Eds.), Seeds. Ecology, Biogeography, and, Evolution of Dormancy and Germination, 2nd ed. Academic Press, San Diego, pp. 1005–1073. https://doi.org/10.1016/b978-0-12-416677-6.00012-3.

Baskin, C.C., Baskin, J.M., 2014b. Variation in seed dormancy and germination within and between individuals and populations of a species. In: Baskin, C.C., Baskin, J.M. (Eds.), Seeds. Ecology, Biogeography, and, Evolution of Dormancy and Germination, 2nd ed. Academic Press, San Diego, pp. 277–373. https://doi.org/10.1016/b978-0-12-416677-6.00008-1.

Bewley, J.D., Bradford, K.J., Hilhorst, H.W.M., Nonogaki, H., 2013. Seeds: physiology of development, germination and dormancy, 3rd ed. 10.1007/978-1-4614-4693-4.

Bochenek, A., Gołaszewski, J., Giełwanowska, I., 2010. Hydrotime model analysis of *Matricaria maritima* ssp. *inodora* seed dormancy. Plant Species Biol. 25, 136–148. https://doi.org/10.1111/j.1442-1984.2010.00276.x.

Bradford, K., 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. Weed Sci. 50, 248–2360. https://doi.org/10.1614/0043-1745(2002)050.

Bradford, K.J., 1997. The hydrotime concept in seed germination and dormancy. In: Ellis, R.H., Black, M., Murdoch, A.J., Hong, T.D. (Eds.), Basic and Applied Aspects of Seed Biology. Springer Science+Business Media, Dordrecht, pp. 349–360. https://doi.org/10.1007/978-94-011-5716-2_39.

Bradford, K., Still, D., 2004. Application of hydrotime analysis in seed testing. Seed Technol. 26, 75–85.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a practical information-theoretic approach. Ecological Modelling, 2nd ed. Springer-Verlag, Heidelberg. https://doi.org/10.1016/j.ecolmodel.2003.11.004.

Carman, N.J., Dossaji, S.F., Mabry, T.J., 1974. A populational survey of amino acids in *Prosopis* species from North and South America. Biochem. Syst. Ecol. 2, 73–74. https://doi.org/10.1016/0305-1978(74)90007-6.

Catalán, L., Balzarini, M., Taleisnik, E., Sereno, R., Karlin, U., 1994. Effects of salinity on germination and seedling growth of *Prosopis flexuosa* (D.C.). For. Ecol. Manag. 63, 347–357. https://doi.org/10.1016/0378-1127(94)90116-3.

Cavallaro, V., Barbera, A.C., Maucieri, C., Gimma, G., Scalisi, C., Patanè, C., 2016. Evaluation of variability to drought and saline stress through the germination of different ecotypes of carob (*Ceratonia siliqua* L.) using a hydrotime model. Ecol. Eng. 95, 557–566. https://doi.org/10.1016/j.ecoleng.2016.06.040.

Chen, D., Chen, X., Wang, J., Zhang, Z., Wang, Y., Jia, C., Hu, X., 2021. Estimation of thermal time model parameters for seed germination in 15 species: the importance of distribution function. Seed Sci. Res. 31, 83–90. https://doi.org/10.1017/S0960258521000040.

Cochrane, A., 2016. Can sensitivity to temperature during germination help predict global warming vulnerability? Seed Sci. Res. 26, 14–29. https://doi.org/10.1017/S0960258515000355.

Cochrane, A., Yates, C.J., Hoyle, G.L., Nicotra, A.B., 2015. Will among-population variation in seed traits improve the chance of species persistence under climate change? Glob. Ecol. Biogeogr. 24, 12–24. https://doi.org/10.1111/geb.12234.

Cochrane, J.A., 2020. Thermal requirements underpinning germination allude to risk of species decline from climate warming. Plants 9, 1–22. https://doi.org/10.1007/978-3-319-95885-9_300028.

Contreras-Quiroz, M., Pando-Moreno, M., Jurado, E., Flores, J., Bauk, K., Gurvich, D.E., 2016. Is seed hydration memory dependent on climate? Testing this hypothesis with Mexican and Argentinian cacti species. J. Arid Environ. 130, 94–97. https://doi.org/10.1016/j.jaridenv.2016.03.001.

Cony, M.A., Trione, S.O., 1996. Germination with respect to temperature of two Argentinian *Prosopis* species. J. Arid Environ. 33, 225–236. https://doi.org/10.1006/jare.1996.0058.

Cony, M.A., Trione, S.O., 1998. Inter- and intraspecific variability in *Prosopis flexuosa* and *P. chilensis*: seed germination under salt and moisture stress. J. Arid Environ. 40, 307–317. https://doi.org/10.1006/jare.1998.0448.

Covell, S., Ellis, R.H., Roberts, E.H., Summerfield, R.J., 1986. The influence of temperature on seed germination rate in grain legumes: I. A comparison of chickpea, lentil, soyabean and cowpea at constant temperatures. J. Exp. Bot. 37, 705–715. https://doi.org/10.1093/jxb/37.5.705.

Crawley, M.J., 2007. The R Book. John Wiley and Sons. pp. 1–942. doi: 10.1002/9780470515075.

Cristaudo, A., Catara, S., Mingo, A., Restuccia, A., Onofri, A., 2019. Temperature and storage time strongly affect the germination success of perennial *Euphorbia* species in Mediterranean regions. Ecol. Evol. 9, 10984–10999. https://doi.org/10.1002/ece3.5535.

Cuervo-Robayo, A.P., Téllez-Valdés, O., Gómez-Albores, M.A., Venegas-Barrera, C.S., Manjarrez, J., Martínez-Meyer, E., 2014. An update of high-resolution monthly climate surfaces for Mexico. Int. J. Climatol. 34, 2427–2437. https://doi.org/10.1002/joc.3848.

Developmental Core Team, R., 2018. A Language and Environment for Statistical Computing. R Found. Stat. Comput. 2 https://www.R-project.org.

De Villalobos, A.E., Peláez, D.V., 2001. Influences of temperature and water stress on germination and establishment of *Prosopis caldenia* Burk. J. Arid Environ. 49, 321–328. https://doi.org/10.1006/jare.2000.0782.

Donohue, K., Rubio De Casas, R., Burghardt, L., Kovach, K., Willis, C.G., 2010. Germination, postgermination adaptation, and species ecological ranges. Annu. Rev. Ecol. Evol. Syst. 41, 293–319. https://doi.org/10.1146/annurev-ecolsys-102209-144715.

Duarte, A.A., de Lemos Filho, J.P., Marques, A.R., 2018. Seed germination of bromeliad species from the campo rupestre: thermal time requirements and response under predicted climate-change scenarios. Flora Morphol. Distrib. Funct. Ecol. Plants 238, 119–128. https://doi.org/10.1016/j.flora.2017.05.016.

Dubrovsky, J.G., 1996. Seed hydration memory in Sonoran Desert cacti and its ecological implication. Am. J. Bot. 83, 624–632. https://doi.org/10.2307/2445922.

Dubrovsky, J.G., 1998. Discontinuous hydration as a facultative requirement for seed germination in two cactus species of the Sonoran Desert. J. Torrey Bot. Soc. 125, 33–39. https://doi.org/10.2307/2997229.

Duncan, C., Schultz, N.L., Good, M.K., Lewandrowski, W., Cook, S., 2019. The risk-takers and -avoiders: germination sensitivity to water stress in an arid zone with unpredictable rainfall. AoB Plants 11, 1–12. https://doi.org/10.1093/aobpla/plz066.

Dürr, C., Dickie, J.B., Yang, X.Y., Pritchard, H.W., 2015. Ranges of critical temperature and water potential values for the germination of species worldwide: contribution to a seed trait database. Agric. For. Meteorol. 200, 222–232. https://doi.org/10.1016/j.agrformet.2014.09.024.

El-Keblawy, A., Al-Rawai, A., 2005. Effects of salinity, temperature and light on germination of invasive *Prosopis juliflora* (Sw.) D.C. J. Arid Environ. 61, 555–565. https://doi.org/10.1016/j.jaridenv.2004.10.007.

El-Keblawy, A., Al-Rawai, A., 2006. Effects of seed maturation time and dry storage on light and temperature requirements during germination in invasive *Prosopis juliflora*. Flora Morphol. Distrib. Funct. Ecol. Plants 201, 135–143. https://doi.org/10.1016/j.flora.2005.04.009.

El-Keblawy, A., Elnaggar, A., Tammam, A., Mosa, K.A., 2020. Seed provenance affects salt tolerance and germination response of the habitat-indifferent *Salsola drummondii* halophyte in the arid Arabian deserts. Flora Morphol. Distrib. Funct. Ecol. Plants 266, 151592. https://doi.org/10.1016/j.flora.2020.151592.

Elnaggar, A., El-Keblawy, A., Mosa, K.A., Soliman, S., 2018. Drought tolerance during germination depends on light and temperature of incubation in *Salsola imbricata*, a desert shrub of Arabian deserts. Flora Morphol. Distrib. Funct. Ecol. Plants 249, 156–163. https://doi.org/10.1016/j.flora.2018.11.001.

Farooq, M., Wahid, A., Kobayashi, N., , S.M.A., Fujita, D.B., 2009. Plant drought stress : effects, mechanisms and management. Agron. Sustain. Dev. 29, 185–212.

Fathi, A., Tari, D.B., 2016. Effect of drought stress and its mechanism in plants. Int. J. Life Sci. 10, 1–6. https://doi.org/10.3126/ijls.v10i1.14509.

Fernández-Pascual, E., Mattana, E., Pritchard, H.W., 2019. Seeds of future past: climate change and the thermal memory of plant reproductive traits. Biol. Rev. 94, 439–456. https://doi.org/10.1111/brv.12461.

Ferreira Marques, F.R., Vinicius Meiado, M., Corte Real de Castro, N.M., Lins de Oliveira Campos, M., Rego Mendes, K., de Oliveira dos Santos, O., Pompelli, M.F., 2015. Germina quant : a new tool for germination measurements. J. Seed Sci. 1–8. https://doi.org/10.1590/2317-1545v37n3145605.

Flores, J., Briones, O., 2001. Plant life-form and germination in a Mexican inter-tropical desert: effects of soil water potential and temperature. J. Arid Environ. 47, 485–497. https://doi.org/10.1006/jare.2000.0728.

Flores, J., Pérez-Sánchez, R.M., Jurado, E., 2017. The combined effect of water stress and temperature on seed germination of Chihuahuan Desert species. J. Arid Environ. 146, 95–98. https://doi.org/10.1016/j.jaridenv.2017.07.009.

Gao, C., Liu, F., Zhang, C., Feng, D., Li, K., Cui, K., 2021. Germination responses to water potential and temperature variation among provenances of *Pinus yunnanensis*. Flora Morphol. Distrib. Funct. Ecol. Plants 276–277, 151786. https://doi.org/10.1016/j.flora.2021.151786.

Garcia-Huidobro, J., Monteith, J.L., Squire, G.R., 1982. Time, temperature and germination of Pearl Millet (*Pennisetum typhoides* S. & H.). J. Exp. Bot. 33, 288–296.

Giolo, M., Benincasa, P., Anastasi, G., Macolino, S., Onofri, A., 2019. Effects of sub-optimal temperatures on seed germination of three warm-season turfgrasses with perspectives of cultivation in transition zone. Agronomy 9, 421. https://doi.org/10.3390/agronomy9080421.

Golubov, J., Mandujano, M.C., Eguiarte, L.E., 2001. La paradoja de mezquites (*Prosopis* spp.): la invasión de especies o potenciadores de la biodiversidad? Bot. Sci. 30, 23. https://doi.org/10.17129/botsci.1644.

Gummerson, R.J., 1986. The effect of constant temperatures and osmotic potentials on the germination of sugar beet. J. Exp. Bot. 37, 729–741. https://doi.org/10.1093/jxb/37.6.729.

Hardegree, S.P., 2006. Predicting germination response to temperature. I. Cardinal-temperature models and subpopulation-specific regression. Ann. Bot. 97, 1115–1125. https://doi.org/10.1093/aob/mcl071.

Hossain, M.A., Wani, S.H., Bhattacharjee, S., Burritl, D.J., Tran, L.S.P., 2016. Drought Stress Tolerance in Plants, Vol 1: Physiology and Biochemistry. Springer, Switzerland. https://doi.org/10.1007/978-3-319-28899-4.

Hu, X.W., Fan, Y., Baskin, C.C., Baskin, J.M., Wang, Y.R., 2015. Comparison of the effects of temperature and water potential on seed germination of Fabaceae species from desert and subalpine grassland. Am. J. Bot. 102, 649–660. https://doi.org/10.3732/ajb.1400507.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., Muller, S., 2010. Intraspecific variability and trait-based community assembly. J. Ecol. 98, 1134–1140. https://doi.org/10.1111/j.1365-2745.2010.01687.x.

Kapoor, D., Bhardwaj, S., Landi, M., Sharma, Arti, Ramakrishnan, M., Sharma, Anket, 2020. The impact of drought in plant metabolism: how to exploit tolerance mechanisms to increase crop production. Appl. Sci. 10, 5692. https://doi.org/10.3390/app10165692.

Kijowska-Oberc, J., Staszak, A.M., Kamiński, J., Ratajczak, E., 2020. Adaptation of forest trees to rapidly changing climate. Forests 11, 1–23. https://doi.org/10.3390/f11020123.

Lai, L., Chen, L., Jiang, L., Zhou, J., Zheng, Y., Shimizu, H., 2018. Seed germination of seven desert plants and implications for vegetation restoration. AoB Plants 8. https://doi.org/10.1093/aobpla/plw031/2609579.

Laitila, T., 1993. A pseudo-R2 measure for limited and qualitative dependent variable models. J. Econ. 56, 341–355. https://doi.org/10.1016/0304-4076(93)90125-O.

Lima, A.T., Meiado, M.V., 2018. Effects of seed hydration memory on initial growth under water deficit of cactus from two populations that occur in different ecosystems in Northeast Brazil. Plant Species Biol. 33, 268–275. https://doi.org/10.1111/1442-1984.12219.

Llanes, A., Bertazza, G., Palacio, G., Luna, V., 2013. Different sodium salts cause different solute accumulation in the halophyte *Prosopis strombulifera*. Plant Biol. 15, 118–125. https://doi.org/10.1111/j.1438-8677.2012.00626.x.

López, A.S., López, D.R., Arana, M.V., Batlla, D., Marchelli, P., 2021. Germination response to water availability in populations of *Festuca pallescens* along a Patagonian rainfall gradient based on hydrotime model parameters. Sci. Rep. 11, 1–11. https://doi.org/10.1038/s41598-021-89901-1.

López, A.S., Marchelli, P., Batlla, D., López, D.R., Arana, M.V., 2019. Seed responses to temperature indicate different germination strategies among *Festuca pallescens* populations from semi-arid environments in North Patagonia. Agric. For. Meteorol. 272–273, 81–90. https://doi.org/10.1016/j.agrformet.2019.04.002.

Marquínez, J., Lastra, J., García, P., 2003. Estimation models for precipitation in mountainous regions: the use of GIS and multivariate analysis. J. Hydrol. 270, 1–11. https://doi.org/10.1016/S0022-1694(02)00110-5.

Martínez-Villegas, J.A., Castillo-Argüero, S., Márquez-Guzmán, J., Orozco-Segovia, A., 2018. Plant attributes and their relationship to the germination response to different temperatures of 18 species from central Mexico. Plant Biol. 20, 1042–1052. https://doi.org/10.1111/plb.12882.

Meira-Neto, J.A.A., Nunes Cândido, H.M., Miazaki, Â., Pontara, V., Bueno, M.L., Solar, R., Gastauer, M., 2019. Drivers of the growth-survival trade-off in a tropical forest. J. Veg. Sci. 30, 1184–1194. https://doi.org/10.1111/jvs.12810.

Meloni, D.A., Martínez, C.A., 2009. Glycinebetaine improves salt tolerance in vinal (*Prosopis ruscifolia* Griesbach) seedlings. Braz. J. Plant Physiol. 21, 233–241. https://doi.org/10.1590/s1677-04202009000300007.

Mesgaran, M.B., Mashhadi, H.R., Alizadeh, H., Hunt, J., Young, K.R., Cousens, R.D., 2013. Importance of distribution function selection for hydrothermal time models of seed germination. Weed Res. 53, 89–101. https://doi.org/10.1111/wre.12008.

Mesgaran, M.B., Onofri, A., Mashhadi, H.R., Cousens, R.D., 2017. Water availability shifts the optimal temperatures for seed germination: a modelling approach. Ecol. Modell. 351, 87–95. https://doi.org/10.1016/j.ecolmodel.2017.02.020.

Michel, B.E., 1983. Evaluation of the water potentials of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. Plant Physiol. 72, 66–70. https://doi.org/10.1104/pp.72.1.66.

Miranda, R.D.Q., Correia, R.M., De Almeida-Cortez, J.S., Pompelli, M.F., 2014. Germination of *Prosopis juliflora* (Sw.) D.C. seeds at different osmotic potentials and temperatures. Plant Species Biol. 29, E9–E20. https://doi.org/10.1111/1442-1984.12025.

Morar, I.M.T., González-orenga, S., Sestras, A.F., Prohens, J., Vicente, O., Sestras, R.E., Boscaiu, M., 2019. Screening for salt and water stress tolerance in fir (*Abies alba*) populations. Notulae 47, 1063–1072. https://doi.org/10.15835/nbha47411348.

Munns, R., Tester, M., 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59, 651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911.

Onofri, A., Benincasa, P., Mesgaran, M.B., Ritz, C., 2018. Hydrothermal-time-to-event models for seed germination. Eur. J. Agron. 101, 129–139. https://doi.org/10.1016/j.eja.2018.08.011.

Onofri, A., Mesgaran, M.B., Neve, P., Cousens, R.D., 2014. Experimental design and parameter estimation for threshold models in seed germination. Weed Res. 54, 425–435. https://doi.org/10.1111/wre.12095.

Ortega-Baes, P., De Viana, M.L., Sühring, S., 2002. Germination in *Prosopis ferox* seeds: Effects of mechanical, chemical and biological scarificators. J. Arid Environ. 50, 185–189. https://doi.org/10.1006/jare.2001.0859.

Palacios, A., 2006. Los mezquites mexicanos : biodiversidad y distribución geográfica. Bol. Soc. Argent. Bot. 41, 99–121.

Palacios, A., Pasiecznik, N., Felker, P., Harris, P., Harsh, L., Cruz, G., Tewari, J., Cadoret, K., Maldonado, L., Miranda, R.D.Q., Correia, R.M., De Almeida-Cortez, J.S., Pompelli, M.F., Flores, J., Briones, O., Simão, E.E., Takaki, M., Cardoso, V.J.M., Jordan, G.L., Haferkamp, M.R., Batlla, D., Benech-Arnold, R.L., 2001. A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy. Seed Sci. Res. 25, 147–158. https://doi.org/10.1017/S0960258514000452.

Pasiecznik, N., Felker, P., Harris, P., Harsh, L., Cruz, G., Tewari, J., Cadoret, K., Maldonado, L., 2002. The'*Prosopis juliflora*'-'*Prosopis pallida*' complex: a monograph. For. Trees Livelihoods 12, 229. –229.

Picapietra, G., González-Andújar, J.L., Acciaresi, H.A., 2020. Predicting junglerice (*Echinochloa colona* L.) emergence as a function of thermal time in the humid pampas of Argentina. Int. J. Pest Manag. 67, 328–337. https://doi.org/10.1080/09670874.2020.1778811.

Qiu, J., Bai, Y., Fu, Y.B., Wilmshurst, J.F., 2010. Spatial variation in temperature thresholds during seed germination of remnant *Festuca hallii* populations across the Canadian prairie. Environ. Exp. Bot. 67, 479–486. https://doi.org/10.1016/j.envexpbot.2009.09.002.

Ramawat, K.G., 2010. Desert Plants: Biology and Biotechnology. Springer, Berlin Heidelberg. https://doi.org/10.1007/978-3-642-02550-1.

Reginato, M., Sgroy, V., Llanes, A., Cassán, F., Luna, V., 2012. The American halophyte *Prosopis strombulifera*, a new potential source to confer salt tolerance to crops. Crop Prod. Agric. Improv. 9789400741, 115–143. https://doi.org/10.1007/978-94-007-4116-4_5.

Reich, P.B., 2014. The world-wide "fast-slow" plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301. https://doi.org/10.1111/1365-2745.12211.

Rhoades, J.D.D., Chanduvi, F., Lesch, S., 1999. Soil Salinity assessment. Methods and Interpretation of Electrical Conductivity Measurements. FAO Irrigation and Drainage Paper 57. FAO Irrig, Drain. Pap.

Roach, D.A., Smith, E.F., 2020. Life-history trade-offs and senescence in plants. Funct. Ecol. 34, 17–25. https://doi.org/10.1111/1365-2435.13461.

Rzedowski, J., 1988. Análisis de la distribución geográfica del complejo *Prosopis* (Leguminosae, Mimosoideae) en Norteamérica. Acta Bot. Mex. 3, 7. https://doi.org/10.21829/abm3.1988.566.

Sadura, I., Janeczko, A., 2018. Physiological and molecular mechanisms of brassinosteroid-induced tolerance to high and low temperature in plants. Biol. Plant. 62, 601–616. https://doi.org/10.1007/s10535-018-0805-4.

Seal, C.E., Daws, M.I., Flores, J., Ortega-Baes, P., Galíndez, G., León-Lobos, P., Sandova, A., 2017. Thermal buffering capacity of the germination phenotype across the environmental envelope of the Cactaceae. Glob. Chang. Biol. 12, 5309–5317. https://doi.org/10.1111/ijlh.12426.

Simão, E.E., Takaki, M., Cardoso, V.J.M., 2010. Germination response of *Hylocereus setaceus* (Salm-Dyck ex DC.) Ralf Bauer (Cactaceae) seeds to temperature and reduced water potentials. Braz. J. Biol. 70, 135–144. https://doi.org/10.1590/s1519-69842010000100019.

Sosa, L., Llanes, A., Reinoso, H., Reginato, M., Luna, V., 2005. Osmotic and specific ion effects on the germination of *Prosopis strombulifera*. Ann. Bot. 96, 261–267. https://doi.org/10.1093/aob/mci173.

Stevens, N., Seal, C.E., Archibald, S., 2014. Increasing temperatures can improve seedling establishment in arid-adapted savanna trees. Oecologia 175, 1029–1040. https://doi.org/10.1007/s00442-014-2958-y.

Torres-Martínez, L., Weldy, P., Levy, M., Emery, N.C., 2017. Spatiotemporal heterogeneity in precipitation patterns explain population-level germination strategies in an edaphic specialist. Ann. Bot. 119, 253–265. https://doi.org/10.1093/aob/mcw161.

Trudgill, D.L., Honek, A., Li, D., Van Straalen, N.M., 2005. Thermal time-concepts and utility. Ann. Appl. Biol. 146, 1–14. https://doi.org/10.1111/j.1744-7348.2005.04088.x.

Vergeer, P., Kunin, W.E., 2011. Life history variation in *Arabidopsis lyrata* across its range: effects of climate, population size and herbivory. Oikos 120, 979–990. https://doi.org/10.1111/j.1600-0706.2010.18944.x.

Villagra, P.E., 1997. Germination of *Prosopis argentina* and *P. alpataco* seeds under saline conditions. J. Arid Environ. 37, 261–267. https://doi.org/10.1006/jare.1997.0275.

Washitani, I., 1987. A convenient screening test system and a model for thermal germination responses of wild plant seeds: behaviour of model and real seeds in the system. Plant Cell Environ. 10, 587–598. https://doi.org/10.1111/1365-3040.ep11604111.

Watt, M.S., Xu, V., Bloomberg, M., 2010. Development of a hydrothermal time seed germination model which uses the Weibull distribution to describe base water potential. Ecol. Modell. 221, 1267–1272. https://doi.org/10.1016/j.ecolmodel.2010.01.017.

Westphal, C., Gachón, P., Bravo, J., Navarrete, C., Salas, C., Ibáñez, C., 2015. The potential of Algarrobo (*Prosopis chilensis* (Mol.) Stuntz) for regeneration of desertified soils: assessing seed germination under saline conditions. Environ. Manag. 56, 209–220. https://doi.org/10.1007/s00267-015-0490-4.

Yang, Y., Guo, Y., 2018. Unraveling salt stress signaling in plants. J. Integr. Plant Biol. 60, 796–804. https://doi.org/10.1111/jipb.12689.

Zalibekov, Z.G., 2011. The arid regions of the world and their dynamics in conditions of modern climatic warming. Arid Ecosyst. 1, 1–7. https://doi.org/10.1134/S2079096111010094.

Zeng, Y.J., 2006. Response of South African indigenous grass species to drought stress induced by polyethylene glycol (PEG) 6000. South Afr. J. Bot. 72, 284–286. https://doi.org/10.1016/j.sajb.2005.07.006.

Capítulo III:
Develop patterns in *Prosopis laevigata* seedlings are determined by local environmental conditions across the Mexican arid and semiarid zones

Develop patterns in *Prosopis laevigata* seedlings are determined by local environmental conditions across the Mexican arid and semiarid zones

Gonzalo Contreras-Negrete[1]; Fernando Pineda-García[2]; Antonio González-Rodríguez[1]
[1] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, México.

[2] Escuela Nacional de Estudios superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, México.

Abstract

Widespread species frequently experience contrasting environmental conditions across their distribution, which exert selection pressures to which populations tend to adapt. Plants from arid and semiarid zones are exposed to extreme abiotic factors, as high temperatures and unpredictable water availability. Seedlings are particularly susceptible to these factors, which is reflected in high rates of mortality during this stage and, therefore, strong impacts on the parental fitness. In the present study, we looked for the existence of differential strategies in growth and resource allocation in *P. laevigata* seedlings from populations covering the distribution of the species in Mexico. We hypothesized the existence of differential biomass assignment and growth patterns associated to the environmental local conditions experienced by the populations. We found significant differences among populations in all the traits analyzed and we identified the environmental variables which influence the allocation and growth patterns in *P. laevigata* seedlings. Overall, we found differential strategies in resource allocation to below-ground and above-ground tissues, strongly influenced by temperature and soil and environmental moisture and following a geographical trend: an evasive strategy in which the seedlings allocate more resources to the root in southernmost populations, and an exploitation strategy, investing resources in growth of aerial tissues to take advantage of pulses of favorable conditions, as observed in northern populations.

Keywords: water availability, biomass assignment, growth, trade off, local adaptation

Introduction

Widespread species are often subjected to contrasting environmental conditions along their distribution (Cochrane et al. 2015; Jung et al. 2010), which exert selection pressures to which populations tend to adapt (Fréjaville et al. 2020; Pedlar and McKenney 2017). Thus, geographic variation in the functional traits of plants represents the evolutionary response to local environments (Poorter et al. 2012, 2015; Reich 2014; Reich et al. 2003).

The establishment, growth and survival of plants depend more on water availability than on any other environmental factor (Kozlowski, 1964), and the seedling stage represents one of the most vulnerable periods of the life cycle (Vange, Heuch, and Vandvik 2004) due to their root system only reaches the upper layers of the soil. For this reason, seedlings experience a larger water availability in comparison to mature trees, whose roots can access the deep layers of the soil. Consequently, the existence of functional strategies during the seedling stage which allow coping with limited water availability is expected (Vizcaíno-Palomar et al. 2020), particularly in arid and semiarid environments. In this type of environments, precipitation regimes usually follow unpredictable patterns (Noy-Mier 1973; Rewald et al. 2010), and seedlings are exposed to frequent droughts resulting in high rates of mortality (Fenner 1987; Moles and Westoby 2004), that directly affect parental fitness (Gross 1984; Wulff 1986).

Differential biomass assignment between belowground or aboveground plant parts is frequently related with the location of the most limiting factor for growth (Poorter et al. 2012). Therefore, in arid and semiarid zones, the relative resource investment in roots versus aerial parts is expected to be directly related to water availability (Padilla, Miranda, and Pugnaire 2007) since a larger root means greater absorption surface for water acquisition (Carlson and Miller 1990; Arnold et al. 2014). On the other hand, under conditions of higher soil moisture plants tend to allocate more resources into the development of shoots and leaves (Padilla et al. 2007), because competition for aerial resources among seedlings and other plants could be the main limiting factor (Grossnickle 2012).

Species in the *Prosopis* (Leguminosae) genus have developed functional adaptations to arid and semiarid environments (Felker 2009; Pasiecznik et al. 2002; Rzedowski 1988), showing a high resistance to water stress, high germination rates, as well as a high colonization potential in these environments (Felker 2009; Golubov et al. 2001; Villagra et al. 2010). Interest in these species also arises because of the multiple products obtained from them, their high yield in poor soils and their value in agroforestry systems given their high capacity for vegetative regeneration (Pasiecznik et al. 2002; Rzedowski 1988). So far, several reports have focused on the seed germination dynamics of *Prosopis* species, evaluating the effects of temperature variation (Cony and Trione 1996; Wan and Sosebee 1991; Westphal et al. 2015), salinity and drought (Cony and Trione 1998; Miranda et al. 2014; Villagra 1997; Westphal et al. 2015), mainly for South American *Prosopis* species.

However, there is no information for the North American *Prosopis* species complex evaluating the effect of environmental variation in the recruitment of new individuals.

In Mexico, *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C.Johnst., is the most widely distributed species, which inhabits warm arid and semiarid zones of the north, center and south of the country (Palacios 2006; Rzedowski 1988) Across its distribution, *P. laevigata* is a highly valuable resource from an ecological and economic perspective (Pasiecznik et al. 2002; Rzedowski 1988). Also, along its distribution, *P. laevigata* experiences a wide environmental and climatic variation mainly in temperature and rainfall patterns, which could have potentially influenced local adaptation processes for biomass allocation and growth during the first developmental stages. Therefore, we hypothesize the existence of differential biomass assignment and growth patterns during the first development in seedlings of the populations of *P. laevigata* from across its distribution, associated with the environmental variation experienced by the species. Therefore, our main goals were: 1) to determine and compare biomass allocation and growth patterns in seedling of *P. laevigata* populations from across its distribution and, 2) to identify the environmental variables that have shaped the biomass allocation and growth patterns in *P. laevigata* populations

Materials and methods

Fruit collection

Fruits were collected in fifteen *P. laevigata* populations during 2016 (Fig. 1; Table 1) covering the whole distribution area of the species. At each locality fruits were collected according to their availability (200 to 500 fruits per population), ensuring a distance of at least 100 m between mother plants to reduce possible genetic relatedness between sampled individuals. Seeds were extracted from the pods and subsequently washed and disinfected with 5% sodium hypochlorite. Afterwards, seeds were stored at room temperature in transparent vials adding 5g of commercial fungicide, until used.

Growth under greenhouse conditions

Seeds were sown during November 2016 in 50-well germination trays 10 cm in depth with a total of 750 seeds sown (50 seeds per population). The substrate used consisted of 30% vermiculite, 30% perlite and 40% peat moss. Seeds were sown at a depth not greater than 1cm. The trays were arranged in a completely random arrangement to standardize the conditions between the different populations. Irrigations were carried out twice a week, to maintain ideal humidity levels that guarantee the optimal development of the seedlings. The germination trays were moved periodically during the germination to homogenize the growth conditions. The whole experiment was carried out under greenhouse conditions at the Escuela Nacional de Estudios Superiores UNAM, Campus Morelia.

Harvest and trait measurement of seedlings

Between 20 and 30 healthy seedlings were harvested from each population 14 weeks after sowing. The harvest was carried out minimizing damage to the seedlings during the collection. During harvesting, we measured the height (SH), the diameter at the height of the collar (DC) and the root length (RL) for each seedling. Then, we separated the seedlings into root, stem and leaves, of which we recorded the fresh weight. Subsequently, the different plant parts were placed in paper bags and dried at 80 °C for at least 72 hours (Ecoshel 9025H). Afterwards, the dry weights of root, stem and leaves were recorded for each individual.

We estimated eight functional traits based on the size and weight measures of the seedlings. First, we calculated the mass fractions for leaves, shoot and root (LMF, SMF, RMF, respectively), defined as the ratio among the mass fraction (leaves, shoot, root) and the total biomass. These biomass distribution patterns have been used in the evaluation of the responses of plants to contrasting environmental conditions to examine ontogenetic trends and the comparison of performance between populations and species, being fundamental to reveal the underlying components in the analysis of the plant growth rates (Poorter et al. 2012, 2015). Also, we estimated the dry matter content in the leaves (DMCL) and roots (DMCR), defined as the ratio between root or leaves dry mass and root or leaves fresh mass. The DMCL is an important predictor of the above-ground net primary production (Smart et al. 2017). Otherwise, we calculated the root-shoot ratios R:S and RL:SL, defined as the ratios between root dry mass and shoot dry mass and root length and shoot length, respectively, which represent the biomass investment in support and growth functions. Plants with greater investment in roots compete effectively for nutrients and water in the soil, while those with greater aerial growth can collect more light energy (Agathokleous et al. 2019; Sharma et al. 2020). In Addition, we measured specific shoot density (DEN) using the cylinder volume formula ($V = h*\pi*r^{\wedge 2}$), and then obtained the ratio among the shoot dry weight and the shoot volume. The specific shoot density represents an important functional attribute about the stability, defense, architecture, hydraulic characteristics, C uptake and plant growth (Pérez-Harguindeguy et al. 2013). Also, to predict the potential success of the seedling under field conditions through the analysis of functional attributes of biomass assignment and growth, we use the Dickson Quality Index (DQI; (Dickson, Leaf, and Hosner 1960), which was calculated according to (Bayala et al. 2009). The DQI represents a measure of quality based on simple measures of growth which has been widely associated with the potential to survive and grow, for which the performance of the seedlings increases as DQI values get higher (Bayala et al. 2009; Dickson et al. 1960; Tsakaldimi, Ganatsas, and Jacobs 2013).

Statistical analysis

We used the Box-Cox function transformation to normalize the data set of functional traits when needed, using the software R (Core R Team 2019). One-way ANOVAs were carried out to test the differences for each individual traits at the population level and in all cases $P < 0.05$ was considered to be significant; mean populations comparisons were done with Tukey's HSD tests. To establish the partitioning of the total variance for each functional trait among populations a, we fit separate random intercept models using Restricted Maximum Likelihood (REML) for each trait with population as random effect. A principal components analysis (PCA) was performed using the mean values of each trait per population to reduce the axes of variation of the eight functional traits. Also, we carried out correlation analysis among the first two principal components and the Dickson Quality Index (DQI) with the 19 bioclimatic variables, the Actual Evapotranspiration (AET) and Soil Water Content (SWC) monthly and yearly data (Cuervo-Robayo et al. 2014; Trabucco and Zomer 2010). To reduce the levels of collinearity among variables (bioclimatic, AET and SWC), we assessed pairwise correlations and discarding the more specific variable in each pair of highly correlated for each set of variables ($r \geq 0.8$). Subsequently, a Variance Inflation Factor (VIF) analysis (Brauner and Shacham 1998), was carried out for the choice of variables that would help avoid redundancies in the correlation analysis. Variables with VIF values <5 were selected as suitable for the model. We repeated the analyses independently for the first two Principal Components analyzed (PC1 and PC2) and the DQI data for the bioclimatic variables and AET and SWC datasets. The variables with low levels of collinearity according to VIF (VIF <5) for the Bioclimatic variables and AET and SWC monthly and yearly data are summarized in the supplementary tables S1, S2 and S3. Additionally, we carried out correlation analysis among PC1, PC2 and DQI with the geographical variables Latitude and Longitude.

Results

The results of the one-way ANOVAs showed significant differences in all traits among the populations analyzed (Table 2; Fig. 2 and 3). The mean differences among populations showed and slightly increase in aerial develop for populations northwards the distribution (i.e SMF; Fig. 2), while southern populations tend to increase the below growth develop (i.e., RMF, RL/SL, R/S; Fig. 2). Overall, an increase in seedling quality was recorded in populations nortwards the distribution according to the DQI (i.e., MAT, HUI, LAG; Fig. 2). The partition of the variance showed different results in function of the trait analyzed. According to the REML, the traits that showed the highest percentage of variance among populations were DMCR, RL:SL, DMCL and RMF, while the rest of the traits reached values lower than 15 % (Table 3). The first two axes of the PCA explained respectively 50.1% and 21.8 % of the variation among traits for the 15 populations. RMF, R:S and

RL:SL had large positive loadings on the PC1 and LMF and DMCL and DMCR negative loadings. D and SMF showed a large negative loading on the PC2 (Fig. 4).

Correlation Analysis

The correlation analysis for PC1 showed only a significant correlation with Mean Temperature of Coldest Quarter (bio11; R = 0.66; P=0.006; Fig. 5a), the Soil Water Content of the third month (SWC_3; R= -0.71; P= 0.002; Fig. 5b), and the Actual Evapotranspiration of the third month (AET_3; R= -0.63; P= 0.01; Fig. 5c). No significant correlations were found for the PC2 and DQI data. However, a markedly trend among PC1 and DQI with Latitude were found (R= -0.48; P=0.05 and R=0.50; P=0.05; Fig. 5d and e respectively).

Discussion

In the present study we measured functional traits related to the biomass assignment and growth patterns in *P. laevigata* seedlings under uniform conditions, to test for the existence of differences among populations, as well as the relationship between the functional variation and geographic and bioclimatic gradients along the distribution of the species. Across its distribution in Mexico *P. laevigata* experiences a wide and marked environmental variation, defined mainly by differential patterns of temperature and rainfall (For example, across its range, annual mean temperature exhibits a difference of 9 °C (15 to 24°C) and a difference in annual precipitation of 500 mm (360 to 860 mm). Thus, we predicted the existence of variation in biomass assignment and growth at the seedling stage related to the environmental conditions of the sites of origin. We found significant differences in all the traits analyzed and we identified the environmental variables which influence the allocation and growth patterns in *P. laevigata* seedlings. Overall, we found a differential pattern in resources allocation to belowground and aboveground tissues strongly influenced by temperature regimes and following a geographical pattern: the southernmost populations invest in root development while northern populations tend to assign more resources to the aerial development.

Among population differences were the main source of variation in almost all the traits analyzed (Table 3), strongly evidencing the existence of functional strategies in the biomass assignment and growth during the first stages of development of *P. laevigata* seedlings from across its distribution. In widespread species subjected to contrasting environmental conditions, divergent patterns of variation in phenotypic traits are usually observed, mainly in response to directional stress experienced locally, generating variation patterns across geographical scales (Cochrane et al. 2015; Jung et al. 2010; Matías, Pérez-Ramos, and Gómez-Aparicio 2019; Vergeer and Kunin 2011). Our results suggest a marked separation among the populations with higher relative investment in belowground or aboveground tissues (Figs. 2, 3 and 4). Differential biomass assignment patterns in plants are related to the most limiting growth factor (i.e., water, CO_2, light). Therefore, plants allocate more resources to roots under low water availability and allocate more resources to shoots and leaves if the limiting factor is found aboveground (i.e. light, CO_2) (Poorter et al. 2012, 2015).

We observed higher values of R:S, RL:SL and RMF traits in southern populations (Figs. 2 and 3c and d). A high R:S ratio is crucial during the establishment stage in desert plants, given the short periods of water availability during rain pulses, mainly for phreatophytes as *Prosopis* species, which tend to develop deep root systems (Felker 2009; Smith-Martin et al. 2020), demonstrating a potential strategy to cope with high temperatures and low water availability. As the soil superficial layer gets dry, the seedlings need to invest resources into root development to guarantee ground water acquisition (Padilla et al. 2007). A larger root system provides a greater absorptive surface for water uptake (Smith-Martin et al. 2020; Vizcaíno-Palomar et al. 2020). Also, it is expected that plants that inhabit zones with low nutrient availability and low water supply tend to show increased overall root length as well as higher R:S ratio (Agathokleous et al. 2019; Carvajal et al. 2019; Prado-Tarango et al. 2019; Reich 2014). Our results suggest that higher R:S and RL:SL ratios as well as RMF in the southern populations express the prioritization on the investment in root tissue with respect to the aerial part, probably because the limiting factor for growth is below ground (i.e., water acquisition).

Under high soil moisture, plants do not prioritize the investment in root biomass and frequently tend to allocate higher biomass to aerial development, reflected in a lower R:S ratio (Padilla et al. 2007; Prado-Tarango et al. 2019; Shen et al. 2019). Our results were consistent with this pattern, for which populations northwards showed a higher investment in aerial development as indicated by DQI and SMF (Figs. 2b and 3). Thus, the shoot system development could be important when nutrients and water are not limiting and the competition for aerial resources such as light among seedlings and other plants could be the main factors limiting growth (Grossnickle 2012; Poorter et al. 2012; Reich 2014). Previous reports have shown that the potential to survive and grow, as well as the performance of the seedlings, increase as DQI values get higher (Bayala et al. 2009; Tsakaldimi et al. 2013). In this manner, seedlings with faster initial growth can develop greater shoot system (del Campo, Navarro, and Ceacero 2009) and thus display greater photosynthetically active surface area (Grossnickle 2012; Luis et al. 2009) promoting a higher success under field conditions.

After establishment, seedlings performance is related to their inherent ecophysiological attributes, as well as its individual response to site environmental conditions that determine the success of the new plants in field (Baldocchi et al. 2014; Poorter et al. 2012, 2015; Reich et al. 2003). Our results suggest that the biomass assignment and growth patterns in the seedlings of *P. laevigata* across its distribution have inherent characteristics related with the sites of origin. In an energy investment spectrum, under water deficit some species produce less dense leaves and roots in order to promote greater absorption area per unit of biomass, resulting in a rapid return of investment in tissue and a large relative growth (Reich 2014; Salguero-Gómez 2017). On the other hand, species that invest in dense leaves and roots tend to have a slow growth but a larger longevity of the tissues and high tolerance to stress, which can promote survival under adverse environmental scenarios (López-Iglesias et al. 2014; Reich 2014; Poorter et al. 2015; Díaz et al. 2016; Salguero-Gómez 2017; Rüger et al. 2018)

We found that *P. laevigata* seedlings trait differences showed a functional axis of trait variation represented by two main strategies, in order to maintain its persistence across its distribution and cope with the environmental variation and the resources constraint (Poorter et al. 2012, 2015), an evasive strategy in which the seedling invest in a greater development of the root as well as less dense leaves and shoot as shown for the southernmost populations (Reich 2014; Siefert et al. 2015), and a exploitation strategy in which the seedlings invest resources in aerial development thus promoting rapid growth, as shown for northwards populations (Poorter and Bongers 2006; Ryser 1996).

This pattern is consistent with widely distributed species, for which is possible to find morphological and functional adaptations among populations which reflect patterns of clinal variation in traits associated with environmental gradients (Carvajal et al. 2019; Greenwood et al. 2017; Ramírez-Valiente et al. 2017). Plants species that inhabit areas with contrasting environmental conditions tend to adopt multiple strategies, evidenced in the modification of the organ's physiology and their growth patterns (García-Nogales et al. 2016). Consequently, environmental disparity promotes divergent variation in phenotypic attributes across geographical scales (Cochrane et al. 2015; Matías et al. 2019; Vergeer and Kunin 2011). Thus, the functional response of the of plants evidence the evolutionary response to specific environmental variation (Cavender-Bares and Ramírez-Valiente 2017; Poorter et al. 2015, 2016; Reich 2014; Reich et al. 2003; Salguero-Gómez 2017). For *P.*

laevigata populations we found a positive correlation among the two allocation strategies and the mean temperature of the coldest quarter (bio11) manifesting that populations which experience higher temperatures tend to allocate more resources to the root development while the populations experience lower temperatures allocates more resource to the aerial grow (Fig 4a). Also, negative correlations were found among these strategies and the Actual Evapotranspiration and Soil Water Content of the third month (AET_3 and SWC_3), strongly suggest a major root develop in plants from populations which experiments lower moisture levels during the dry season, as reported for other *Prosopis* species (Felker 2009; Villagra et al. 2010). A trend which was found also latitudinally, the northern populations showed greater investment in aerial development and the southernmost populations showed a greater investment in root development at the seedling stage (Fig. 5d and e).

Across the distribution of *P. laevigata* it has been previously reported the existence of geographic variation in the genetic diversity patterns, which increases northern the distribution (Contreras-Negrete et al. 2021). In this connection, high genetic diversity could help during the establishment of the populations by increasing the probability to cope with stressful conditions and allowing an efficient use of available resources (Crawford and Whitney 2010; Huston and Huston 1996; Loreau M. and Hector. A. 2001). In an ecological timescale, high genetic diversity could aid the new individuals to establish in new habitats with environmentally variable conditions, allowing to increase the chances to survive, growth and reproduce, mainly for colonizing species (Crawford and Whitney 2010). Overall, the trait variation observed among the populations analyzed evidence that the plant performance, and allocation patterns has been shaped by selective pressures alongside environmental gradients experience by the species suggesting genetic adaptation processes to local conditions (Eckert et al. 2015; García-Nogales et al. 2016; Kolb et al. 2016; Ramírez-Valiente et al. 2017; Reich et al. 2003)

Conclusions

Through the analysis of functional traits of *P. laevigata* seedlings we found the existence of differential patterns in biomass allocation and growth associated with the environmental variation across the distribution of the species, mainly in function of temperature and precipitation patterns. In this way, two main strategies in resources assignment were found: an evasive strategy in which the seedling allocate more resource to root develop as well as less dense aerial tissues, to promote greater absorption area per unit of biomass, as shown for southernmost populations and an exploitation strategy, investing resources in growth in order to tolerate variable conditions, as shown for the Northwards populations. Finally, according to the DQI our results suggest an increase of quality in seedlings northwards the distribution, probably associated with an increase in genetic diversity (Contreras-Negrete et al. 2021). Across its distribution *P. laevigata* represents a highly valuable resource, having a great potential to multipurpose exploitation, as agroforestry systems and ecological restoration programs. Thus, our findings represent the first approach in the evaluation of the eco-functional strategies of *P. laevigata* seedlings during the establishment throughout its distribution, representing relevant information for the exploitation, management, and conservation of this species in the arid and semiarid zones of Mexico.

Acknowledgments

The authors thank Saddan Morales, Oscar de Luna, Ricardo Gaytán, and Mariana Hernández for field assistance and, Griselda Pérez, and Claudia Guerrero for laboratory assistance. Dr. Rafael Aguilar-Romero provided technical assistance in the assembly of the experiments. Gonzalo Contreras-Negrete thanks the National Council of Science and Technology CONACyT (CVU 549242) and the Postgraduate Program in Biological Sciences UNAM (PCBiol UNAM) for the facilities provided. This article represents a partial requirement of the Postgraduate Program in Biological Sciences of the UNAM.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Agathokleous E., Belz RG., Kitao M, Koike T, and Calabrese EJ. 2019. “Does the Root to Shoot Ratio Show a Hormetic Response to Stress? An Ecological and Environmental Perspective.” *Journal of Forestry Research* 30(5):1569–80.

Sven A., Kailichova Y, and Baumgartl T. 2014. “Germination of *Acacia Harpophylla* (Brigalow) Seeds in Relation to Soil Water Potential: Implications for Rehabilitation of a Threatened Ecosystem.” *PeerJ* 2014(1):1–15.

Baldocchi, D. D., Kattge J., Reichstein M., Mahecha M. D., and Bahn M. 2014. “Linking Plant and Ecosystem Functional Biogeography.” *Proceedings of the National Academy of Sciences* 111(38):13697–702.

Bayala, J., M. Dianda, Wilson J., Ouédraogo S. J., and Sanon K. 2009. “Predicting field performance of five irrigated tree species using seedling quality assessment in Burkina Faso, West Africa.” *New Forests* 38(3):309–22.

Brauner N., and Shacham M. 1998. “Role of Range and Precision of the Independent Variable in Regression of Data.” *AIChE Journal* 44(3):603–11.

del Campo A.D., Navarro R.M., and Ceacero C.J. 2009. “Seedling quality and field performance of commercial stocklots of containerized Holm Oak (*Quercus ilex*) in Mediterranean Spain: An Approach for Establishing a Quality Standard.” *New Forests* 39(1):19–37.

Carlson W.C. and Miller D.E. 1990. “Target seedling root system size, hydraulic conductivity, and water use during seedling establishment.” *In: Proceedings, Western Forest Nursery Association, Roseburg, OR. General Technical Report RM-200, US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO* 53–65.

Carvajal, D.E, Loayza, P, Rios R.S., Delpiano A., Squeo, F. 2019. “A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies.” *Journal of Ecology* 107(3):1079–92.

Cavender-Bares J., and Ramírez-Valiente J.A. 2017. “Physiological evidence from common garden experiments for local adaptation and adaptive plasticity to climate in american live oaks (*Quercus* Section *Virentes*): Implications for Conservation Under Global Change.” 107–35.

Cochrane, A, Yates, C.H., Gand Nicotra AB. 2015. “Will among-population variation in seed traits improve the chance of species persistence under climate change?” *Global Ecology and Biogeography* 24(1):12–24.

Contreras-Negrete, G, Letelier, L, Piña-Torres J, and González-Rodríguez, A. 2021. “Genetic structure, phylogeography and potential distribution modeling suggest a population expansion in the mesquite *Prosopis laevigata* since the Last Interglacial.” *Plant Systematics and Evolution* 307(2):1–18.

Cony, M. A., and. Trione S. O. 1996. “Germination with respect to temperature of two argentinian *Prosopis* species.” *Journal of Arid Environments* 33(2):225–36.

Cony, M. A. and Trione S. O. 1998. “Inter- and intraspecific variability in *Prosopis flexuosa* and *P. chilensis*: seed germination under salt and moisture stress.” *Journal of Arid Environments* 40(3):307–17.

Core R Team. 2019. “A Language and Environment for Statistical Computing.” *R Foundation for Statistical Computing* 2(2.11.1):https://www.R--project.org.

Crawford, K. M. and Whitney, K. D.. 2010. “Population Genetic Diversity Influences Colonization Success.” *Molecular Ecology* 19(6):1253–63.

Cuervo-Robayo, .P., Téllez-Valdés O, Gómez-Albores MA, Venegas-Barrera SC, Manjarrez J, and Martínez-Meyer, E. 2014. “An update of high-resolution monthly climate surfaces for Mexico.” *International Journal of Climatology* 34(7):2427–37.

Díaz S, Kattge J, J Cornelissen J, Wright I, Lavorel S, Dray S, Reu B, Kleyer M, Wirth, I. Prentice C, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB,. Moles A, Dickie J, Gillison AN, Zanne A, et. al. 2016. “The Global Spectrum of Plant Form and Function.” *Nature* 529(7585):167–71.

Dickson A, Leaf A, and Hosner JF. 1960. “Quality Appraisal of White Spruce and White Pine Seedling Stock in Nurseries.” *The Forestry Chronicle* 36(1):10–13.

Eckert, A.J., Maloney P.E, Vogler D.R, Jensen C.E, Delfino A, and Neale D.B. 2015. "Local Adaptation at Fine Spatial Scales: An Example from Sugar Pine (*Pinus lambertiana*, Pinaceae)." *Tree Genetics and Genomes* 11(3).

Felker P. 2009. "Unusual Physiological Properties of the Arid Adapted Tree Legume Prosopis and Their Applications in Developing Countries." Pp. 221–55 in *Perspectives in biophysical plant ecophysiology: a tribute to Park S. Nobel*, edited by S. de la Barrera, E; Smith. Mexico city: Universidad Nacional Autonoma de Mexico.

Fenner, M. 1987. "Seedlings." *New Phytologist* 106:35–47.

Fréjaville T., Vizcaíno-Palomar N., Fady B., Kremer A., and Benito-Garzón M. 2020. "Range Margin Populations Show High Climate Adaptation Lags in European Trees." *Global Change Biology* 26(2):484–95.

García-Nogales, A., Linares J.C., Laureano R.G., Seco J.I., and Merino J. 2016. "Range-Wide Variation in Life-History Phenotypes: Spatiotemporal Plasticity across the Latitudinal Gradient of the Evergreen Oak *Quercus ilex*." *Journal of Biogeography* 43(12):2366–79.

Golubov J., Mandujano M.C., and. Eguiarte L.E. 2001. "La Paradoja de Mezquites (*Prosopis* spp.): La Invasión de Especies o Potenciadores de La Biodiversidad?" *Botanical Sciences* 30(69):23.

Greenwood S., Ruiz-Benito P., Martínez-Vilalta J., Lloret F., Kitzberger T., Allen C.D., Fensham R., Laughlin D.C., Kattge J., Bönisch G., Kraft N., and Jump A.S. 2017. "Tree Mortality across Biomes Is Promoted by Drought Intensity, Lower Wood Density and Higher Specific Leaf Area." *Ecology Letters* 20(4):539–53.

Gross, K.L. 1984. "Effects of Seed Size and Growth Form on Seedling Establishment of Six Monocarpic Perennial Plants." *The Journal of Ecology* 72(2):369.

Grossnickle, Steven C. 2012. "Why Seedlings Survive: Influence of Plant Attributes." *New Forests* 43(5–6):711–38.

Huston M.A, and Huston M.A,. 1996. "International Association for Ecology Hidden Treatments in Ecological Experiments: Re-Evaluating the Ecosystem Function of Biodiversity Published by : Springer in Cooperation with International Association for Ecology Stable URL : Http://Www.Jstor.Org/St." 110(4):449–60.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S. 2010. "Intraspecific Variability and Trait-Based Community Assembly." *Journal of Ecology* 98(5):1134–40.

Kolb, T.E., Grady K.C., McEttrick M.P., and Herrero A. 2016. "Local-Scale Drought Adaptation of Ponderosa Pine Seedlings at Habitat Ecotones." *Forest Science* 62(6):641–51.

López-Iglesias, B., Villar R., and Poorter L. 2014. "Functional Traits Predict Drought Performance and Distribution of Mediterranean Woody Species." *Acta Oecologica* 56:10–18.

Loreau M., and Hector. A. 2001. "Partitioning Selection and Complementarity in Biodiversity Experiments." *Nature* 412(6842):72–76.

Luis V.C., Puértolas J., Climent J., Peters J., González-Rodríguez A.M., Morales D., and Jiménez M. S. 2009. "Nursery Fertilization Enhances Survival and Physiological Status in Canary Island Pine (*Pinus canariensis*) Seedlings Planted in a Semiarid Environment." *European Journal of Forest Research* 128(3):221–29.

Matías L., Pérez-Ramos I.G., and Gómez-Aparicio L. 2019. "Are Northern-Edge Populations of Cork Oak More Sensitive to Drought than Those of the Southern Edge?" *Environmental and Experimental Botany* 163(April):78–85.

Miranda R., Moura Correia R., Silva De Almeida-Cortez J, and Pompelli M.P. 2014. "Germination of *Prosopis Juliflora* (Sw.) D.C. Seeds at Different Osmotic Potentials and Temperatures." *Plant Species Biology* 29(3).

Moles A.T., and Westoby W. 2004. "Seedling Survival and Seed Size: A Synthesis of the Literature." *Journal of Ecology* 92(3):372–83.

Noy-Mier, I. 1973. "Desert Ecosystems: Environment and Producers." 4:25–51.

Padilla, F.M., Miranda J., and Pugnaire F.I. 2007. "Early Root Growth Plasticity in Seedlings of Three Mediterranean Woody Species." *Plant and Soil* 296(1–2):103–13.

Palacios A. 2006. "Los Mezquites Mexicanos : Biodiversidad y Distribución Geográfica." *Bol. Soc. Argent. Bot.* 41(1–2):99–121.

Pasiecznik, N.M, Felker P., Harris P.J.C., Harsh L.N., Cruz G., Tewari J.C., Cadoret K., and Maldonado L.J. 2002. "The' *Prosopis juliflora*'-'*Prosopis pallida*'complex: A Monograph." *Forests Trees and Livelihoods* 12:229–229.

Pedlar, J.H. and McKenney D.W. 2017. "Assessing the Anticipated Growth Response of Northern Conifer Populations to a Warming Climate." *Scientific Reports* 7(March):1–10.

Pérez-Harguindeguy, N., Díaz S., Garnier E., Lavorel S., Poorter H., Jaureguiberry P., Bret-Harte M. S., Cornwell W. K., Craine J. M., Gurvich D. E., Urcelay C., Veneklaas E. J., Reich P. B., Poorter L., Wright , Ray P., Enrico L., Pausas J. G., de Vos A. C., Buchmann N., Funes G., Quétier F., Hodgson J. G., Thompson K., Morgan H. D., ter

Steege H., Sack L., Blonder B., Poschlod P., Vaieretti M. V., Conti G., Staver A. C., Aquino S., and Cornelissen J. H. C.. 2013. “New handbook for standardised measurement of plant functional traits worldwide.” *Australian Journal of Botany* 61(3):167.

Poorter H., Fiorani F., Pieruschka R., Wojciechowski T. van der Putten W.H., Kleyer, Uli Schurr W, and Postma J. 2016. “Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field.” *New Phytologist* 212(4):838–55.

Poorter H., Jagodzinski A.M., Ruiz-Peinado R., Kuyah S., Luo Y., Oleksyn J., Usoltsev V.A., Buckley T.N., Reich P.B., and Sack L. 2015. “How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents.” *New Phytologist* 208(3):736–49.

Poorter H., Niklas K.J., Reich P.B., Oleksyn J., Poot P., and Mommer L. 2012. “Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control.” *New Phytologist* 193(1):30–50.

Poorter L., and Bongers F. 2006. “Leaf traits are good predictors of plant performance across 53 rain forest species.” *Ecology* 87(7):1733–43.

Prado-Tarango D., Mata-González R., Melgoza-Castillo A., Elias S.G., and Santellano-Estrada E. 2019. “Simulated rainfall sequences affect germination and biomass allocation of chihuahuan desert native plants.” *Arid Land Research and Management* 33(1):22–36.

Ramírez-Valiente, J.A., Center A., Sparks J.P., Sparks K.L., Etterson J.R., Longwell T, Pilz G, and Cavender-Bares J. 2017. “Population-level differentiation in growth rates and leaf traits in seedlings of the neotropical live oak *Quercus oleoides* grown under natural and manipulated precipitation regimes.” *Frontiers in Plant Science* 8(May):1–14.

Reich, P. 2014. “The World-Wide ‘fast-Slow’ Plant Economics Spectrum: A Traits Manifesto.” *Journal of Ecology* 102(2):275–301.

Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. “The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies.” *International Journal of Plant Sciences* 164(SUPPL. 3).

Rewald B., Michopoulos P., Dalsgaard L., Jones D.L., and Godbold D.L. 2010. “Hydrological effects on below ground processes in temperate and mediterranean forests.” 5–29.

Rüger N., Comita L.S., Condit R., Purves D., Rosenbaum B., Visser M.D., Wright S.J., and Wirth C. 2018. "Beyond the Fast–Slow Continuum: demographic dimensions structuring a tropical tree community." *Ecology Letters* 21(7):1075–84.

Ryser, P. 1996. "The Importance of Tissue Density for Growth and Life Span of Leaves and Roots: A Comparison of Five Ecologically Contrasting Grasses." *Functional Ecology* 10(6):717.

Rzedowski, J. 1988. "Análisis de La Distribución Geográfica Del Complejo Prosopis (Leguminosae, Mimosoideae) En Norteamérica." *Acta Botanica Mexicana* 3(3):7.

Salguero-Gómez, Roberto. 2017. "Applications of the fast–slow continuum and reproductive strategy framework of plant life histories." *New Phytologist* 213(4):1618–24.

Sharma A., Kumar V., Shahzad B., Ramakrishnan M., Sidhu G., Bali A. S., and Zheng B. 2020. "Photosynthetic Response of Plants Under Different Abiotic Stresses: A Review." *Journal of Plant Growth Regulation* 39(2):509–31.

Yong S., Gilbert G.S, Li W., Fang, M, Lu H, and Yu H. 2019. "Linking Aboveground Traits to Root Traits and Local Environment: Implications of the Plant Economics Spectrum." *Frontiers in Plant Science* 10(October):1–12.

Siefert A., Violle C., Chalmandrier L., Albert C.H., Taudiere A., Fajardo A., Aarssen L.W., Baraloto C., Carlucci M.B., Cianciaruso M.V., Dantas M.L., de Bello F., Duarte L.D.S., Fonseca C.R., Freschet G.T., Gaucherand S., Gross N., Hikosaka K., Jackson B., Jung V., Kamiyama C., Katabuchi M., Kembel S.W., Kichenin E., Kraft N.J., Lagerström A., Bagousse-Pinguet Y.L., Li Y., Mason N., Messier J., Nakashizuka T., Overton J.M., Peltzer D.A., Pérez-Ramos I.M., Pillar V.D., Prentice H.C., Richardson S., Sasaki T., Schamp B.S., Schöb C., Shipley B., Sundqvist M., Sykes M.T., Vandewalle M., and Wardle D.A. 2015. "A global meta-analysis of the relative extent of intraspecific trait variation in plant communities." *Ecology Letters* 18(12):1406–19.

Smart, S.M., Glanville H.C., Blanes M.C., Mercado L.M., Emmett B.A., Jones D.L., Cosby J., Marrs R.H., Butler A., Marshall M.R., Reinsch S., Herrero-Jáuregui C., and Hodgson G. 2017. "Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area." *Functional Ecology* 31(6):1336–44.

Smith-Martin C.M., Xiangtao X., Medvigy D., Schnitzer S.A., and Powers J.S. 2020. "Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees." *New Phytologist* 226(3):714–26.

Trabucco A., and Zomer R.J. 2010. "High-Resolution global soil-water balance explicit for climate - standard vegetation and soil conditions." *CGIAR Consortium for Spatial Information* 2010(June).

Tsakaldimi M., Ganatsas P., and Jacobs D.F. 2013. “Prediction of planted seedling survival of five mediterranean species based on initial seedling morphology.” *New Forests* 44(3):327–39.

Vange V., Heuch I., and Vandvik V. 2004. “Do seed mass and family affect germination and juvenile performance in *Knautia arvensis*? A Study Using Failure-Time Methods.” *Acta Oecologica* 25(3):169–78.

Vergeer P., and Kunin W.E. 2011. “Life history variation in arabidopsis lyrata across its range: effects of climate, population size and herbivory.” *Oikos* 120(7):979–90.

Villagra P.E. 1997. “Germination of *Prosopis Argentina* and *P. Alpataco* seeds under saline conditions.” *Journal of Arid Environments* 37(2):261–67.

Villagra P.E., Vilela A., Giordano C., and Alvarez J.A. 2010. “Ecophysiology of *Prosopis* species from the arid lands of argentina: what do we know about adaptation to stressful environments?” Pp. 321–40 in *Desert Plants*. Berlin, Heidelberg: Springer Berlin Heidelberg.

Vizcaíno-Palomar N., Fady B., Alía R., Raffin A., Mutke S., and Garzón M.B. 2020. “The legacy of climate variability over the last century on populations’ phenotypic variation in tree height.” *Science of the Total Environment* 749.

Wan C., and Sosebee R. 1991. “Water relations and transpiration of honey mesquite on 2 sites in West Texas.” *Journal of Range Management* 44(2):156.

Westphal C., Gachón P., Bravo J., Navarrete C., Salas C., and Ibáñez C. 2015. “The potential of Algarrobo (*Prosopis Chilensis* (Mol.) Stuntz) for regeneration of desertified soils: Assessing Seed Germination Under Saline Conditions.” *Environmental Management* 56(1):209–20.

Wulff R.D. 1986. “Seed Size Variation in *Desmodium Paniculatum*: II. Effects on Seedling Growth and Physiological Performance.” *The Journal of Ecology* 74(1):99.

Table 1. *Prosopis laevigata* populations collected along its distribution in the arid and semiarid zones of Mexico. The name, code, state, and geographical location of each site are shown

Population	**Code**	**State**	**Latitud**	**Longitud**
Matehuala	MAT	San Luis P	23.63021	-100.64014
Huizachal	HUI	Tamaulipas	23.5884	-99.22468
Villa de Arista	VA	San Luis P	22.6439	-100.8452
Lagos Moreno	LAG	Jalisco	21.36951	-101.96226
Peña de Bernal	PÑ	Querétaro	20.74523	-99.94743
Ixmiquilpan	IXM	Hidalgo	20.460455	-99.33933
Novillero	NOV	Guanajuato	20.388887	-101.59178
San Pedro T	SP	Jalisco	20.22138	-103.39535
Cuitzeo	CUI	Michoacán	19.961482	-101.20221
Sayula	SAY	Jalisco	19.926994	-103.5283
Indaparapeo	IND	Michoacán	19.79466	-100.96873
Tehuixtla	TEH	Morelos	18.586123	-99.263001
Zinacatepec	ZIN	Puebla	18.32423	-97.25181
Sta. María Ayú	SMA	Oaxaca	17.892532	-97.822939
San Nicolás	SN	Oaxaca	16.843833	-96.779097

Table 2. Results of the one-way variance analysis for the evaluated biomass and growth for seedling of *P. laevigata* populations from the arid and semiarid zones of Mexico grown under greenhouse conditions. DEN= Shoot Density DMCL= Dry Matter Content in Leaves; DMCR: Dry Matter Content in Roots; RL:SL= Lenght Root:Shoot ratio; R/S= biomass Root:Shoot ratio; LMF= Leaves Mass Fraction; SMF= Shoot Mass Fraction; RMF= Roots Mass Fraction; DQI= Dickson Quality Index. Significance level: $P \leq 0.05$

Trait	$F_{14, 425}$	P
LMF	3.5754	<0.0001***
SMF	4.8694	<0.0001***
RMF	6.4812	<0.0001***
DMCL	6.965	<0.0001***
DMCR	19.1762	<0.0001***
R:S	4.8838	<0.0001***
RL:SL	15.2922	<0.0001***
DEN	3.9688	<0.0001***
DQI	3.8789	<0.0001***

Table 3. Restricted maximum likelihood (REML) variance components (percentage of total variation) for nine functional traits of seedling of *P. laevigata* populations from the arid and semiarid zones of Mexico. Variation among populations, and residual variance was considered. LMF= Leaves Mass Fraction; SMF= Shoot Mass Fraction; RMF= Roots Mass Fraction; DMCL= Dry Matter Content in Leaves; DMCR: Dry Matter Content in Roots; R:S= biomass Root:Shoot ratio; DEN= Wood Density; RL:SL= Length Root: Shoot ratio; DQI= Dickson Quality Index (*Significant according to Wald´s P ($P \leq 0.05$)).

Trait	**Populations**	**Residual**
LMF	8.29	91.71
SMF	12.19*	87.8
RMF	16.88*	83.1
DMCL	19.34*	80.66
DMCR	40.35*	59.65
R:S	12.38*	87.62
RL:SL	35.95*	64.05
DEN	9.43*	90.57
DQI	9.27	90.73

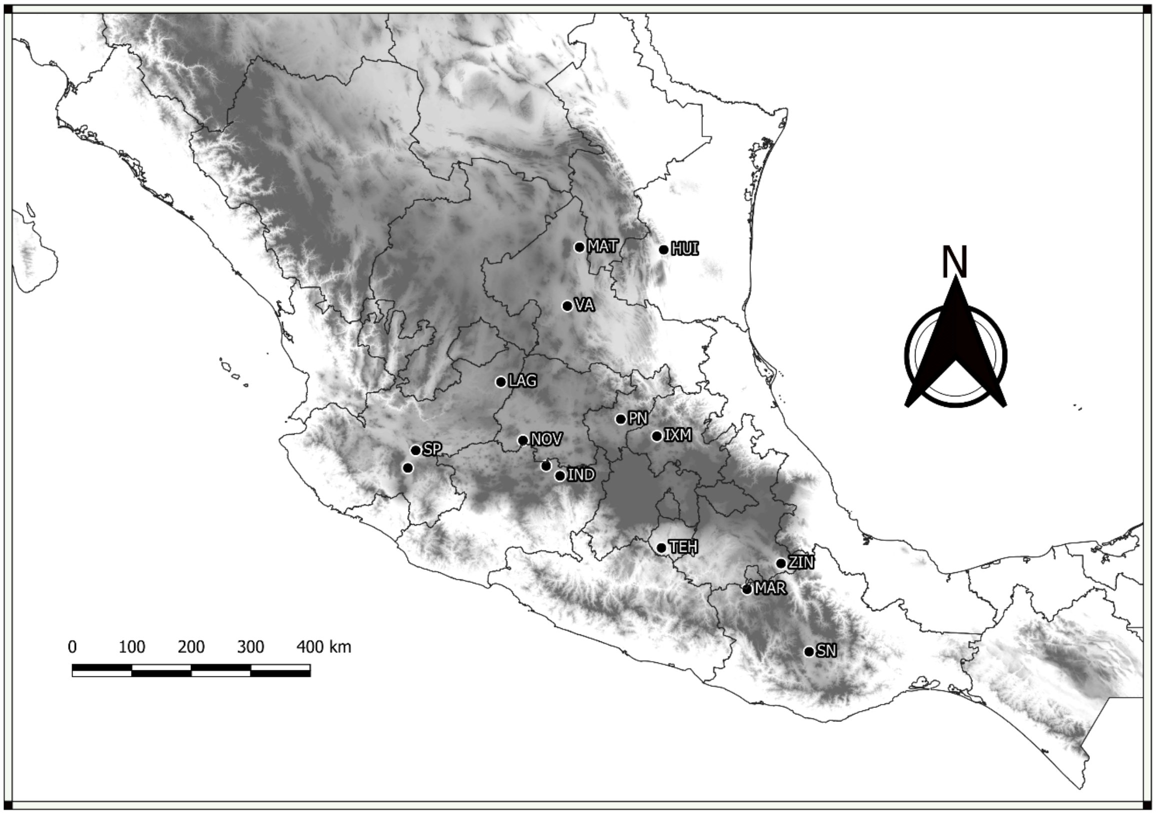


Figure 1. Geographical distribution of *Prosopis laevigata* populations from along the arid and semiarid zones of Mexico sampled in this study.

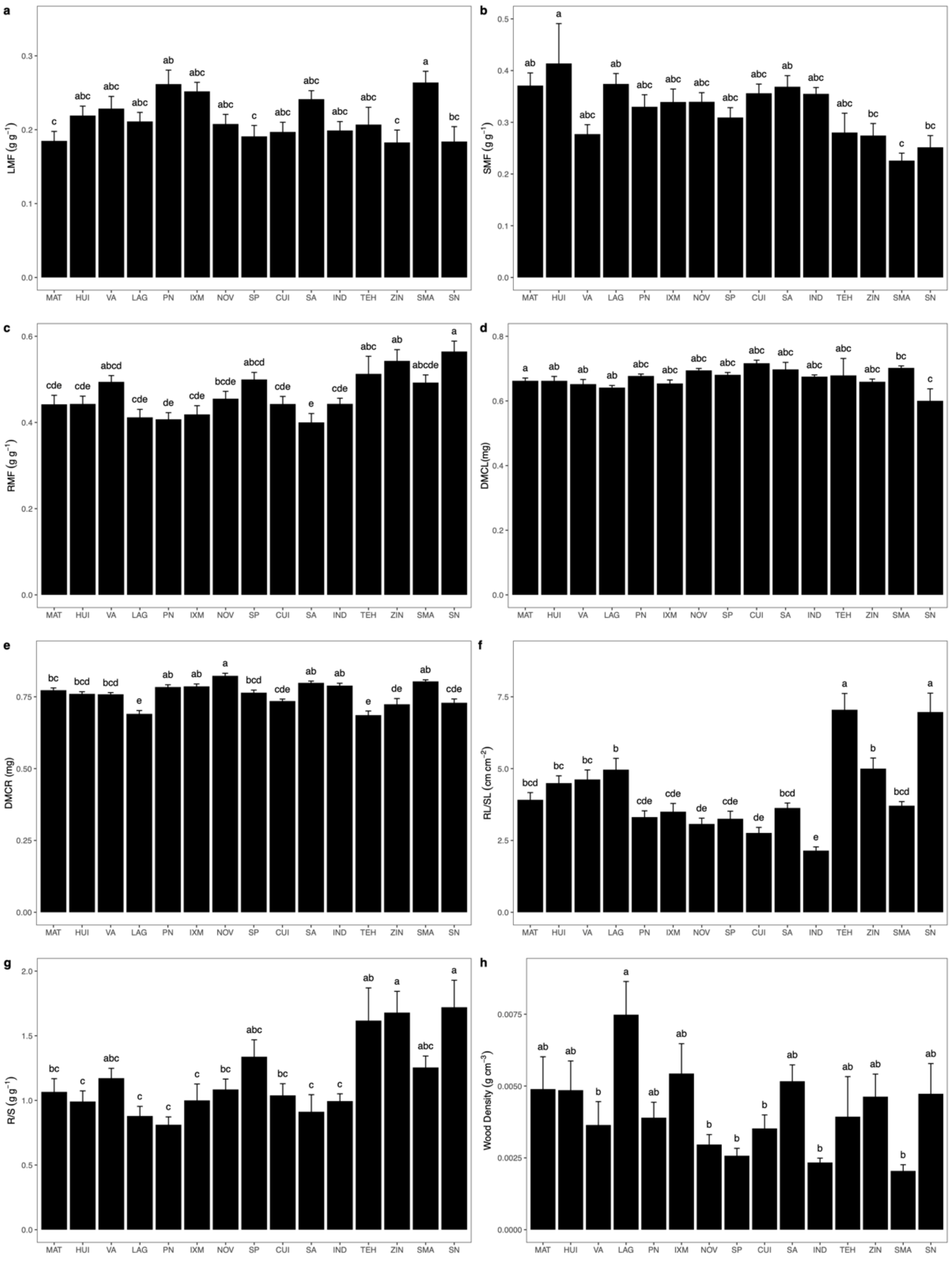


Figure 2. Functional traits for biomass assignment and growth for seedlings of *P. laevigata* populations from the arid and semiarid zones of Mexico, grown under greenhouse conditions: a) LMF= Leaf mass fraction (g g^{-1}); b) SMF= Shoot mass fraction (g g^{-1}); c)

RMF= Root mass fraction (g g^{-1}); d) DMCL= Dry matter content in leaves; e) DMCR= Dry matter content in roots; f) RL/SL= Length Root:Shoot ratio (cm cm^{-1}); g) R:S= biomass Root:Shoot ratio (g g^{-1}); h) D= Wood density (g cm^{-3}). Error bars = SE. The order of the populations follows their latitudinal placement. *Post hoc* (Tukey HSD) results are represented as letters in each case.

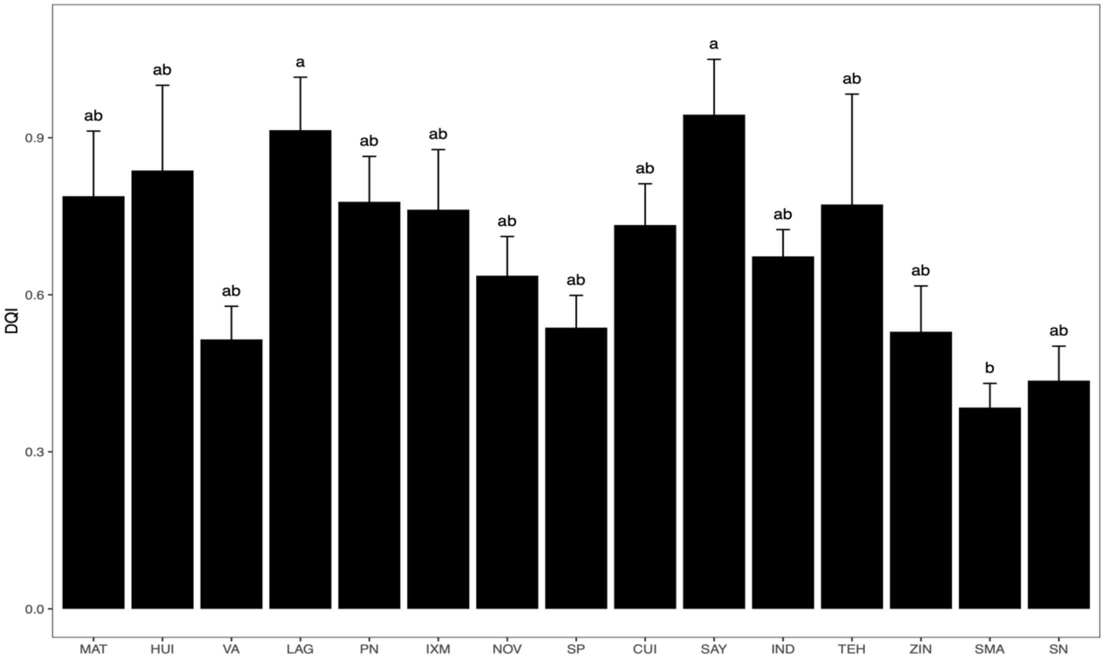


Figure 3. Dickson Quality Index (DQI) mean values for seedlings of 15 populations of *P. laevigata* from the arid and semiarid zones of Mexico, grown under greenhouse conditions. Error bars = SE). The order of the populations follows their latitudinal placement. *Post hoc* (Tukey HSD) results are represented as letters in each case.

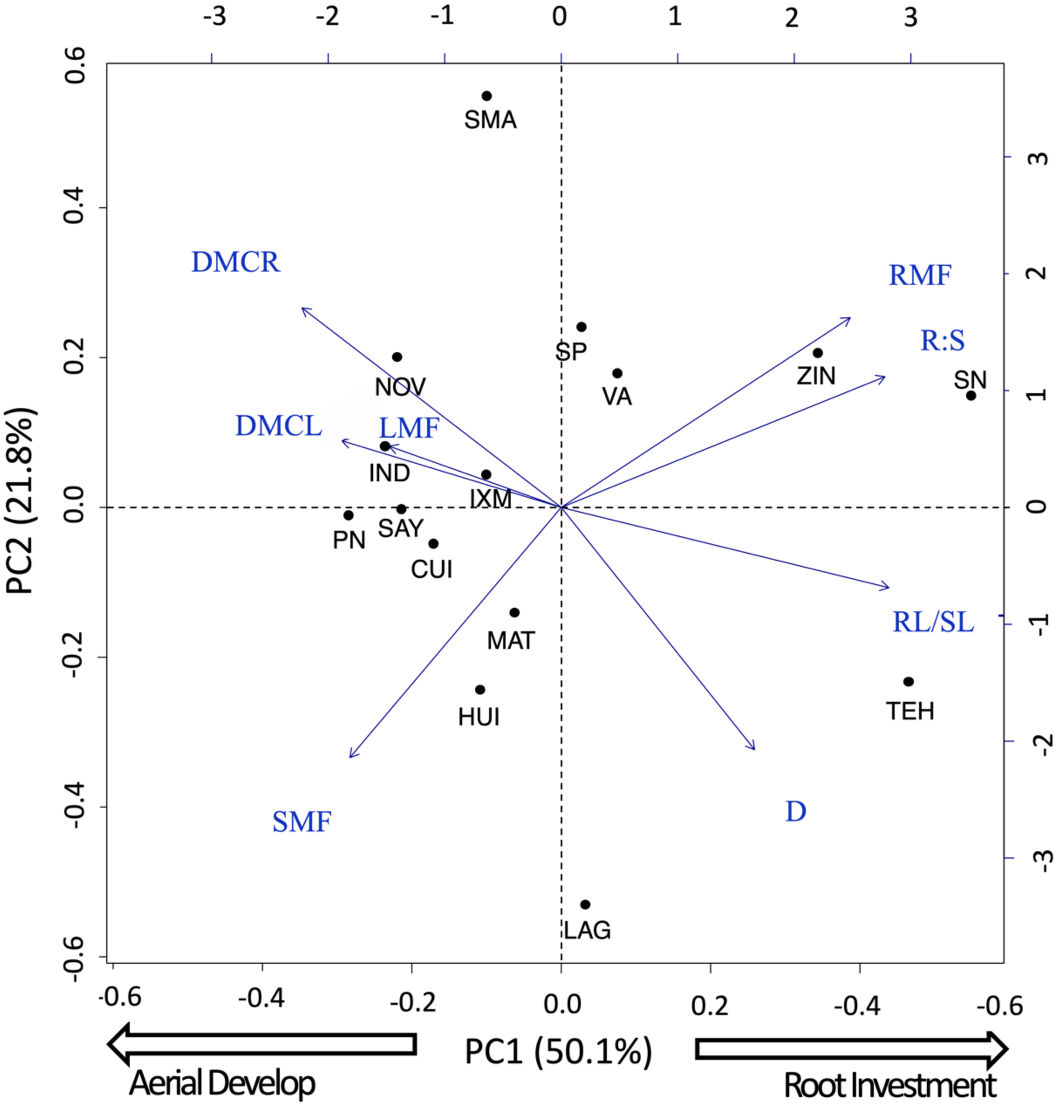


Figure 4. Principal Components Analysis showing the two axes of trait covariation for traits of biomass assignment and growth traits of seedling of *P. laevigata* populations from the arid and semiarid zones of Mexico grown under greenhouse conditions. The analysis included the following traits: DEN= Shoot Density DMCL= Dry Matter Content in Leaves; DMCR: Dry Matter Content in Roots; RI:SI= Length Root: Shoot ratio; R/S= biomass Root: Shoot ratio; LMF= Leaves Mass Fraction; SMF= Shoot Mass Fraction; RMF= Root Mass Fraction. The populations codes are shown in black corresponding to Table 1.

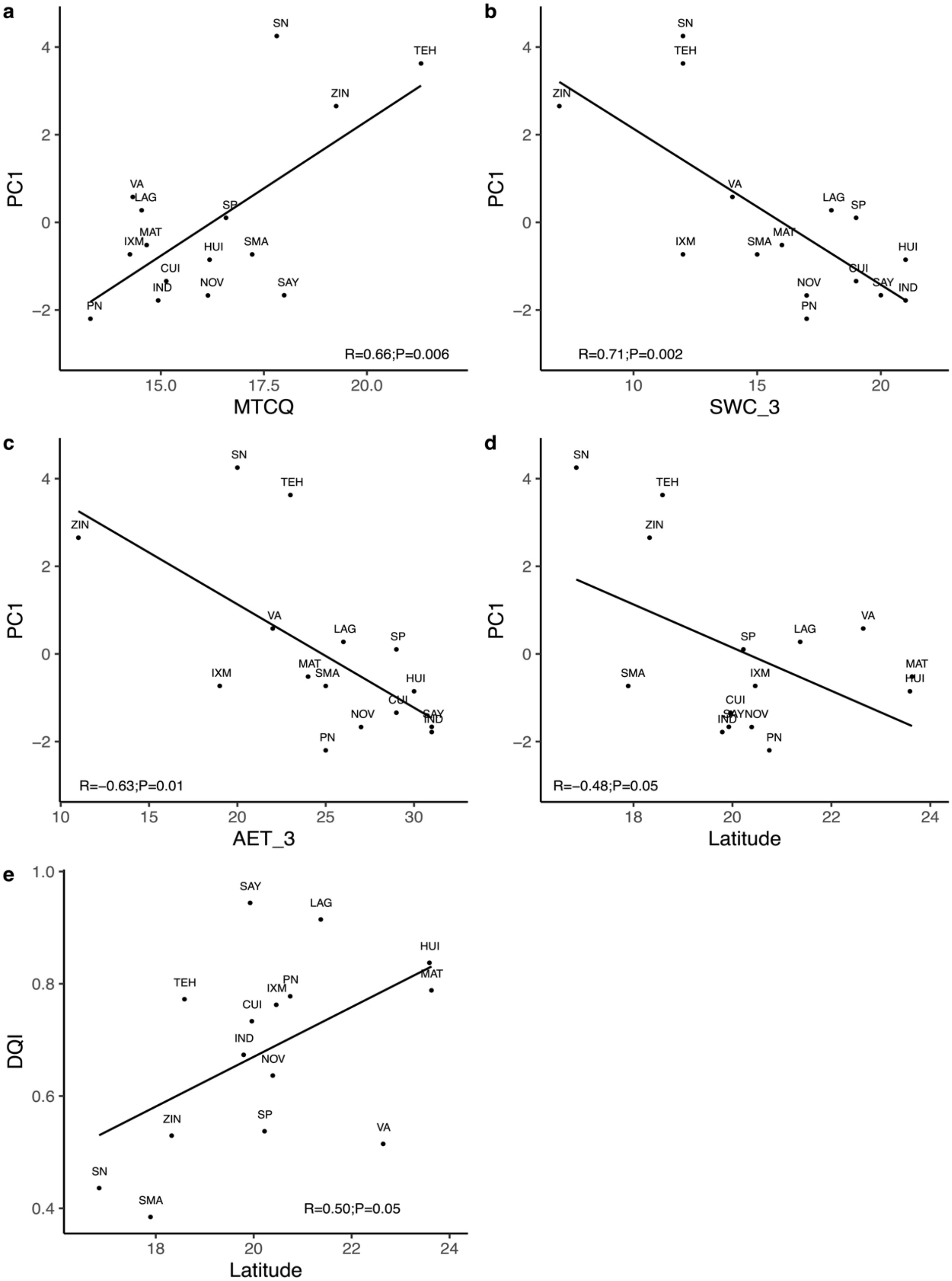


Figure 5. Correlation analysis among bioclimatic and geographical variables and the first two Principal Components for biomass assignment and growth traist and the Dickson

Quality Index of seedlings of *P. laevigata* populations from the arid and semiarid zones of Mexico grown under greenhouse conditions: (DQI). a) PC1 vs MTCQ (Mean Temperature of Coldest Quarter); b) PC1 vs SWC_3 (Soil Water Content of the third month); c) PC1 vs AET_3 (actual evapotranspiration of the third month); d) PC1 and Latitude; e) DQI (Dickson Quality Index) *vs* Latitude.

Supplementary Material

Table S1. Variance Inflation Factor among the two first Principal Components for the biomass assignment and growth traits of seedlings of *P. laevigata* populations from the arid and semiarid zones of Mexico, grown under greenhouse conditions and the Bioclimatic variables. VIF values in bold represents bioclimatic variables suitable for our models.

PC	Variable	R^2	Tolerance	VIF
PC1	bio12	0.822	0.177	5.622
	bio15	0.810	0.189	5.265
	bio14	0.750	0.249	**4.013**
	bio19	0.728	0.271	**3.678**
	bio18	0.708	0.291	**3.429**
	bio3	0.650	0.349	**2.863**
	bio11	0.598	0.401	**2.488**
	bio7	0.329	0.670	**1.491**

PC2	bio15	0.810	0.189	5.288
	bio4	0.770	0.229	**4.361**
	bio14	0.767	0.232	**4.308**
	bio18	0.722	0.277	**3.602**
	bio19	0.626	0.373	**2.676**
	bio5	0.533	0.466	**2.145**
	bio2	0.263	0.736	**1.358**

Table S2. Variance Inflation Factor among the two first Principal Components for the biomass assignment and growth traits of seedlings of *P. laevigata* populations from the arid and semiarid zones of Mexico, grown under greenhouse conditions and the Actual Evapotranspiration monthly data (AET). VIF values in bold represents AET variables suitable for our models.

PC	**AET**	**R^2**	**Tolerance**	**VIF**
PC1	AET_6	0.313	0.686	**1.456**
	AET_5	0.306	0.693	**1.442**
	AET_3	0.069	0.930	**1.075**
PC2	AET_5	0.920	0.079	12.656
	AET_6	0.918	0.081	12.261
	AET_9	0.886	0.113	8.804
	AET_4	0.775	0.224	**4.454**

Table S3. Variance Inflation Factor among the two first Principal Components for the biomass assignment and growth traits of seedling of *P. laevigata* populations from the arid and semiarid zones of Mexico grown under greenhouse conditions and the Soil Water Content monthly data (SWC). VIF values in bold represents the SWC variables suitable for our models.

PC	**SWC**	**R^2**	**Tolerance**	**VIF**
PC1	SWC_5	0.881	0.118	8.406
	SWC_6	0.875	0.125	8.008
	SWC_8	0.862	0.137	7.289
	SWC_3	0.771	0.228	**4.371**
PC2	SWC_6	0.960	0.039	25.207
	SWC_7	0.943	0.056	17.767
	SWC_5	0.926	0.073	13.590
	SWC_3	0.790	0.209	**4.764**

Capítulo IV

Los patrones de variación climática determinan la respuesta funcional a la sequía en las poblaciones de mezquite (*Prosopis laevigata*) de las zonas áridas y semiáridas de México

Los patrones de variación climática determinan la respuesta funcional a la sequía en las poblaciones de mezquite (*Prosopis laevigata*) de las zonas áridas y semiáridas de México

Gonzalo Contreras-Negrete; Fernando Pineda-García; Antonio González-Rodríguez

Resumen

El estudio de los procesos de aislamiento y divergencia de las poblaciones a través de gradientes ambientales representa uno de los principales temas de la ecología evolutiva. Cambios súbitos en el ambiente alteran la dirección y magnitud de la selección, modificando la distribución geográfica, diversidad genética y la variación de rasgos adaptados localmente en las especies. La adaptación local surge cuando las poblaciones experimentan gradientes ambientales contrastantes más fuertes que el flujo génico, promoviendo rasgos que incrementan la aptitud de los individuos bajo condiciones locales. En el presente estudio se evaluó la respuesta funcional de 15 poblaciones de *P. laevigata*, especie de mayor distribución del género en México, a dos escenarios contrastantes de disponibilidad hídrica. Particularmente, se hipotetizó que los atributos morfológicos y fisiológicos evaluados en poblaciones de *P. laevigata* provenientes de zonas áridas serían menos sensibles a la sequía en comparación con poblaciones de zonas semiáridas. En general, se registraron diferencias morfológicas y fisiológicas entre las poblaciones de *P. laevigata*. Estas diferencias se pueden interpretar como estrategias para afrontar la sequía a través de su distribución, expresadas como un eje funcional de explotación-tolerancia mediante un continuo rápido-lento en la adquisición de recursos: algunas poblaciones generan tejidos poco densos pero con altas tasas de adquisición de recursos (explotación-rápido), mientras otras desarrollan tejidos densos y longevos, con una tasa lenta de adquisición de recursos (tolerante-lento). En condiciones óptimas de disponibilidad de agua, los patrones de temperatura guían las estrategias funcionales; sin embargo, bajo condiciones de sequía, los patrones de precipitación de las localidades de origen determinan la expresión de los rasgos funcionales a lo largo del eje de explotación-tolerancia.

Palabras clave: sequía, atributos funcionales, adaptación local, explotación-tolerancia,

Introducción

La evaluación de los procesos de aislamiento y divergencia de las poblaciones través de gradientes ambientales representa uno de los principales temas de estudio de la ecología evolutiva. Particularmente, en especies de amplia distribución la variación ambiental ejerce presiones selectivas que suscitan procesos adaptativos que originan estrategias para afrontar las restricciones ambientales (Keller et al. 2011; Ramírez-Valiente et al. 2011, 2017; Llanderal-Mendoza et al. 2017). A diferencia de procesos evolutivos neutrales (mutación, migración , deriva) que ocasionan cambios estocásticos en las frecuencias alélicas, la selección direccional origina tendencias divergentes que pueden asociarse con los patrones de adaptación local (Excoffier et al. 2009; Pometti et al. 2019). La adaptación local surge cuando las poblaciones experimentan condiciones ambientales contrastantes que superan el efecto homogeneizador del flujo de genes, favoreciendo rasgos que aumentan la aptitud de los individuos en su entorno local (Izuno et al. 2017; Garot et al. 2020). Por lo tanto, cambios repentinos en el ambiente generan cambios en la dirección y magnitud de la selección, modificando la distribución geográfica, diversidad genética y la variación de rasgos adaptados localmente en las especies (Excoffier et al. 2009; Keller et al. 2011; Kolb et al. 2016). Consecuentemente, la magnitud de la interacción especie-ambiente varía a lo largo de la distribución y la cuantificación de dicha variación podría reflejar la fuerza de la selección natural en rasgos fenotípicos particulares (Helsen et al. 2017; Pometti et al. 2019). Así, a través del desarrollo de múltiples estrategias que conducen a modificar los patrones de crecimiento y respuestas fisiológicas (García-Nogales et al. 2016) la variación entre poblaciones asociada con la variación climática puede interpretarse como adaptación local

(Eckert et al. 2015; Cavender-Bares y Ramírez-Valiente 2017; Ramírez-Valiente et al. 2017).

Mediante dichas estrategias, las plantas manifiestan su historia evolutiva mientras ajustan su desempeño para afrontar contrastes ambientales experimentados a través de gradientes ambientales y a lo largo de su vida (López-Iglesias et al. 2014; Reich 2014; Díaz et al. 2016; Cavender-Bares y Ramírez-Valiente 2017). En este sentido, se ha propuesto una disyuntiva principal expresada a través de un continuo de estrategias en las plantas para subsistir bajo regímenes contrastantes de disponibilidad de recursos, exteriorizando la disyuntiva entre maximizar la obtención de recursos a través de estrategias de explotación y la capacidad de tolerar y persistir bajo escasez
a través de estrategias conservadoras de recursos (Reich 2014; Dias et al. 2017; Salguero-Gómez 2017). Muchas plantas se ajustan a la hipótesis de la disyuntiva explotación-tolerancia manifestando estrategias contrastantes respecto a la disponibilidad de recursos a través de un continuo de aprovechamiento rápido-lento: algunas plantas desarrollan tejidos poco densos, de vida útil corta, pero experimentan altas tasas de adquisición recursos (explotación-rápido), mientras que otras plantas desarrollan tejidos densos longevos y tolerantes, a costa de una tasa lenta de adquisición de recursos (tolerante-lento) (López-Iglesias et al. 2014; Reich 2014; Poorter et al. 2015; Díaz et al. 2016; Salguero-Gómez 2017; Rüger et al. 2018; Lara-De La Cruz et al. 2020).

En las plantas, la disponibilidad de agua regula en mayor medida el establecimiento, crecimiento y supervivencia en relación con cualquier otro factor ambiental (Kozlowski 1964). Particularmente en ambientes áridos y semiáridos, la disponibilidad de agua se asocia a variaciones regionales en las precipitaciones, la topografía y las características del suelo, lo que hace de este recurso limitado y esporádico (Nobel et al. 1996, de la Barrera 1997, Nobel 1998, Wiegeand et al.1998, Galindo-Jaimes et al.2013). Por lo tanto, las plantas de zonas áridas y semiáridas están expuestas a factores abióticos extremos, como altas temperaturas y lluvias espaciales y temporalmente impredecibles (Noy-Mei 1973, Rewald et al.2010), representando escenarios adversos que determinan el establecimiento y desarrollo de las comunidades vegetales, además de promover el surgimiento de estrategias de respuesta en las plantas para afrontar condiciones contrastantes (Fenner 1987, Moles y Westoby 2004a).

En México, las zonas áridas y semiáridas se distribuyen en el norte, centro y sur, representando aproximadamente la mitad de la superficie de nacional (Challenger 1998). Dentro de los grupos vegetales más conspicuos de las zonas áridas de Norte y Sudamérica, se encuentran los “mezquites”, especies del género *Prosopis* (Rzedowski 1988; Palacios 2006). A largo de su distribución los mezquites se consideran especies ecológicamente claves por la gran cantidad de interacciones que mantienen con otros organismos y con el suelo (AGREGA LAS CITAS), además de constituir recursos apreciados para las poblaciones humanas locales (Golubov et al. 2001; Pasiecznik et al. 2002). En México, *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C.Johnst., es la especie más ampliamente distribuida (Rzedowski 1988; Palacios 2006). A través de su distribución, las poblaciones de *P. laevigata* experimentan una gran variación ambiental. Por ejemplo, la temperatura media anual de las localidades en las que se encuentra la especie va de 15 a 24°C, mientras la precipitación anual varía de 360 a 860 mm. Asimismo, se ha reportado una amplia variación morfológica en la forma de las hojas, la altura y la forma de crecimiento de los árboles a través de su distribución, atribuida a las condiciones ambientales locales experimentadas por las poblaciones (Rzedowski 1988; Palacios 2006). Con base en estas evidencias, así como en reportes previos sobre sus patrones de germinación, desarrollo de plántulas y variación y estructura genética (Contreras-Negrete et al. 2021) se hipotetiza en este estudio la existencia de respuestas funcionales asociadas a la variación climática, particularmente de temperatura y precipitación, experimentada a través del gradiente ambiental experimentado por la especie a través de su distribución. Para probar esta hipótesis, se sometieron 15 poblaciones de *P. laevigata*, cubriendo el área de distribución, así como los contrastes ambientales experimentados por la especie, a dos tratamientos de disponibilidad hídrica con el objetivo de simular escenarios de sequía y precipitaciones constantes. En particular, se predijo que los atributos morfológicos y fisiológicos de poblaciones de *P. laevigata* provenientes de zonas áridas serían menos sensibles a la baja disponibilidad de agua en comparación con poblaciones de zonas semiáridas, siguiendo un eje funcional de explotación y tolerancia. El principal objetivo fue evaluar las estrategias funcionales expresadas por la especie a través de su distribución en respuesta a escenarios contrastantes de disponibilidad hídrica. Los objetivos particulares fueron: 1) evaluar la respuesta funcional a la disponibilidad de hídrica así como los patrones de diferencias poblacionales expresadas; 2) evaluar si la variación funcional encontrada en poblaciones de *P. laevigata* muestra correlación con las variables ambientales experimentadas a través de la distribución de la especie.

Materiales y métodos

Material vegetal

Las semillas fueron colectadas de entre dos y cinco plantas madre en 15 poblaciones de *Prosopis laevigata* que se localizan a lo largo del área total de distribución (Rzedowski 1988; Palacios 2006) y la colecta se hizo durante el verano de 2016 (Tabla 1; Fig. 1). De cada planta madre se colectaron al menos 100 frutos (legumbre en forma de vaina) libres de plagas y patógenos, asegurando una distancia de al menos 100 metros entre plantas (individuos?) para reducir cualquier posible efecto de consanguinidad en las muestras (Arriaga et al. 1994). Una vez removidas de la legumbre, las semillas fueron lavadas y desinfectadas con hipoclorito de sodio al 5.0%, para su posterior secado a temperatura ambiente (Arriaga et al. 1994). Las semillas fueron almacenadas en frascos transparentes sellados a temperatura ambiente, adicionando 0.5 g de fungicida comercial para su posterior uso.

Condiciones de crecimiento y diseño experimental

El experimento se llevó a cabo bajo un diseño de bloque completamente aleatorio con dos factores (población y tratamiento). Las semillas se sembraron durante noviembre de 2016 en charolas de germinación de 50 pozos de 10 cm de profundidad; 90 días después de la siembra de las semillas, las plántulas fueron trasplantadas a tubos de PVC de 50 cm de profundidad y 10 cm de diámetro. Durante el proceso de trasplante se registró el diámetro del tallo, y la longitud de la parte aérea y radicular de cada plántula. El sustrato utilizado consistió en 25% de vermiculita, 25% de perlita y 50% de turba. Para mejorar la disponibilidad de nutrientes en el suelo, se mezclaron con el sustrato 10 g de un fertilizante comercial de liberación lenta a cada tubo de PVC, al inicio del proceso experimental. Las plántulas se irrigaron a capacidad de campo por 3 meses cada 3 días (Al-Rawahy et al., 2003). Una vez uniformizadas las condiciones entre las plantas, estas fueron separadas en dos grupos por población los cuales se sometieron a los dos niveles de disponibilidad de agua. Se utilizaron 8 plántulas por tratamiento de cada población (Tabla 1). Los tratamientos de disponibilidad de agua tuvieron dos niveles: bajo (L), con sustrato al 5% de la capacidad de campo, y alto (H), con sustrato al 40% de la capacidad de campo (Llanderal-Mendoza et al. 2017). Bajo dichos niveles hídricos el contenido medio de agua en el sustrato fue de 3.9 g g^{-1} y 0.73 g g^{-1}, equivalentes a potenciales hídricos de alrededor de -0.12 MPa y -1.25 MPa para los tratamientos de alta y baja disponibilidad hídrica, respectivamente. Dichos valores fueron calculados con base en el contenido de agua del sustrato a través de ecuaciones de curvas de secado y humectación de acuerdo con Buitenwerf et al. (2014). La desviación media y estándar de la temperatura del aire y la humedad relativa a lo largo del experimento fueron 32.5 ± 8.6° C y 73.2 ± 19.78%, respectivamente. Durante el periodo experimental a los contenedores se les realizaron rotaciones cíclicas periódica con el objetivo de uniformizar las condiciones durante el periodo experimental.

Medición de atributos funcionales

Las plantas fueron cosechadas después de siete meses del proceso experimental. Previo a la cosecha, para evaluar el efecto de los tratamientos en el estatus hídrico de las plantas se llevó a cabo la medición del potencial hídrico de al menos 5 plantas por tratamiento en cada población, durante el pre amanecer y el medio día utilizando una cámara de Schölander

(Modelo 1505D; PMS Instrument Company, Albany, USA). Por otra parte, se analizaron los patrones de intercambio de gases y fotosíntesis en cinco plantas por tratamiento para cada población. Las mediciones se llevaron a cabo con un sistema de medición portátil (IRGA LI-6400 Licor® Bioscience) en el que se ajustaron los parámetros en función de las necesidades del presente experimento (flujo de aire, CO_2, temperatura). Dada la morfología foliar de la especie (hojas pinnadas), se realizaron ajustes del área analizada calculando la porción de área de cada hoja analizada en la cámara del IRGA mediante el programa Image J (Schneider et al. 2012). Se evaluó la fotosíntesis neta (A_N =μmol CO_2 m^{-2} s^{-1}), conductancia estomática (g_s= mol H_2O m^{-2} s^{-1}), y la eficiencia instantánea en el uso de agua como la relación entre la tasa fotosintética y la conductancia estomática (A_N/ g_s= μmol CO_2 / mmol H_2O) (Quero et al. 2008). Las mediciones de fotosíntesis e intercambio de gases se llevaron entre las 7:00 y las 10:00 horas para mantener las condiciones de la radiación fotosintéticamente activa en valores de alrededor de 600 μmol m^{-2} s^{-1}.

Una vez cosechadas las plantas, se midieron el largo de la raíz y de la parte aérea, para consecutivamente separarse en raíz, tallo y hojas (Pérez-Harguindeguy et al. 2013; López-Iglesias et al. 2014). Se calculó la densidad del tallo (WD; g cm^{-3}), mediante el método de desplazamiento de agua, al sumergir un trozo de tallo de entre 3 y 5 cm en un matraz aforado para calcular el volumen desplazado. Posteriormente, la porción del tallo fue secada a 70°C por 48 h para calcular WD como la relación entre la masa seca y el volumen del tallo (Pérez-Harguindeguy et al. 2013). Además, se separaron 3 hojas libres de daño para cada individuo las cuales fueron depositadas en papel humedecido dentro de bolsas plásticas para su rehidratación por 24 hrs a 4°C. Concluido el periodo, se retiró el exceso de agua a cada hoja para registrar la masa fresca de las hojas saturadas. Finalmente, las hojas fueron escaneadas (Epson Perfection V850) y el área foliar fue determinada mediante el programa Image J (Schneider et al. 2012).

Una vez separadas del recipiente, las raíces fueron limpiadas y tamizadas cuidadosamente para recuperar las raíces finas (≤ 1mm), e incluirse en las mediciones posteriores. Los segmentos de raíces recuperados fueron depositados en un recipiente transparente con agua para su posterior escaneo (Epson Perfection V850). Una vez procesadas, se registró el peso fresco de la raíz para su secado a 60°C por 48 h para posteriores mediciones de peso. Finalmente, la longitud de raíces finas (< 1mm) para cada individuo fue determinada a través del programa WinRhizo® (Régent Instrument Inc., 2001). Las porciones restantes de raíz, tallo y hojas fueron secadas a 70°C por 48 horas para el registrar el peso seco.

Con base en estas mediciones, se calcularon diferentes rasgos funcionales abordados en el presente estudio (Tabla 2). El área foliar específica (SLA; $cm^2\ g^{-1}$) representa el cociente entre el área foliar (cm^2) y el peso seco de las hojas (g). Asimismo, se calculó el cociente entre área foliar total (TLA) y la longitud total de raíz (< 1mm) (TLA/TRL; $cm\ cm^{-2}$) que representa el cociente de tejidos de consumo y adquisición de agua. TLA se obtuvo al determinar la ecuación de la recta entre el peso seco (X) y el área foliar (Y) para cada población, al sustituir el valor del peso seco del total de hojas por individuo en la ecuación. Por otra parte, se calcularon los cocientes de Raíz:Tallo, determinados por el cociente entre el largo de la raíz y de la parte aérea (RL/SL; $cm\ cm^{-2}$), así como el cociente entre el peso seco de la raíz y el peso seco de la parte aérea (R/S; $g\ g^{-1}$). Además, calculamos la longitud específica de la raíz (SRL; $g\ cm^{-1}$) representada como la longitud de la raíz dividida por su peso seco. Finalmente, se obtuvo la tasa de crecimiento relativo

(RGR, mm day^{-1}), el cual fue determinada mediante la diferencia del logaritmo natural (*ln*) del producto de las mediciones iniciales y finales del largo y diámetro del tallo y el largo de la raíz y su cociente con el número de días desde el trasplante hasta la cosecha de acuerdo con la relación RGR = (*ln*(LTF*DTF*LRF) - *ln*(LTI*DTI*LRI) / NDE, donde LTF y LT son el largo del tallo final e inicial; DTF y DTI son el diámetro del tallo final e inicial; LRF y LRI son el largo de la raíz final e inicial y NDE es el número de días experimentales (Villar et al., 2004; Villegas-Jiménez et al., 2016). Las características de los atributos evaluados se resumen en la Tabla 2.

Análisis estadísticos

Previo a los análisis estadísticos los datos de atributos fisiológicos y de biomasa y crecimiento, se transformaron mediante el método Box-Cox para cumplir con los supuestos de normalidad mediante el paquete MASS del software R (Venables and Ripley 1997; Core R Team 2019). Se realizó un ANOVA de dos vias para cada atributo de biomasa, crecimiento y fisiológicos analizados para evaluar el efecto del tratamiento hidrico y de la población (como efectos fijos) y su interacción, en todos los casos se consideró significativos valores de $P < 0.05$. Para estudiar las asociaciones entre los atributos analizados, se realizaron correlaciones de Pearson entre los promedios poblacionales de los atributos para cada tratamiento hídrico. Posteriormente, para evaluar los posibles patrones de covariación de los atributos funcionales evaluados (asignación de biomasa, crecimiento y fisiológicas), se realizaron dos análisis de componentes principales (PCA) independientes para los tratamientos de baja (L) y alta (H) disponibilidad de hídrica, utilizando el software R (Core R Team 2019)

El efecto de la variación climática experimentada por la especie sobre la expresión de los atributos funcionales analizados en cada tratamiento se evaluó utilizando dos aproximaciones. Se extrajeron 19 variables bioclimáticas para cada una de las localidades a partir de superficies climáticas mensuales de alta resolución (disponibles en https://github.com/AngelaCrow/variables-bioclimatica; Cuervo-Robayo et al. 2014). Posteriormente, se evaluaron las correlaciones por pares de variables bioclimáticas descartandose la mas especifica pero se descartaron la más específica en cada par de variables altamente correlacionadas ($r \geq 0.8$), para evitar cualquier error asociado con la sobrerrepresentación de las variables (Marquínez et al. 2003; Aguilar-Romero et al. 2016). De esta manera, se seleccionaron las variables bio2= rango diurno medio de la temperatura, bio3= isotermalidad, bio5= temperatura máxima del mes más cálido, bio6= temperatura mínima del mes más frío, bio12= precipitación anual, bio14= precipitación del mes más seco, bio15= estacionalidad de la precipitación; bio18= precipitación del trimestre más cálido. Consecutivamente, se exploraron también las correlaciones de las ocho variables bioclimáticas con los valores poblacionales extraídos de los dos primeros componentes del análisis de componentes principales, así como para las medias poblacionales medios de cada atributo para cada tratamiento (L y H).

Adicionalmente, para separar los efectos de la distancia espacial y las variables ambientales sobre la diferenciación de los atributos funcionales analizados se realizaron análisis de redundancia (RDA) independientes para cada uno de los tratamientos (L y H) (van den Wollenberg 1977). El RDA es un método de ordenación restringida, análogo a la regresión lineal para conjuntos de datos con múltiples variables dependientes y múltiples variables independientes. Se evaluaron tres modelos de RDA: i) el modelo completo con variables ambientales y geográficas como variables explicativas; ii) RDA parcial (pRDA1; modelo climático puro), iii) RDA parcial (pRDA2; modelo geográfico puro). La significancia de cada modelo RDA se calculó mediante una prueba de ANOVA con 1,000 permutaciones, en todos los casos se consideró que $P < 0.05$ como significativo. Posteriormente, evaluamos la partición de la varianza para calcular la proporción de variación explicada por las contribuciones independientes de las variables ambientales y geográficas asi como su efecto conjunto (Borcard et al. 1992, Peres-Neto et al. 2006). Adicionalmente, calculamos el coeficiente de determinación múltiple ajustado (R^2_{adj}) para cada modelo (Peres-Neto et al. 2006). El análisis RDA fue realizado utilizando los atributos de biomasa y crecimiento (RGR, SLA, R/S, RL/SL; TLA/TRL, SLR, WD) como variables dependientes y las variables bioclimáticas previamente mencionadas, además de latitud y longitud de las poblaciones como variables independientes. Para todas las variables se utilizó el método Box-Cox de transformación para corregir desviaciones a los supuestos de normalidad, se centraron y estandarizaron antes del análisis. El RDA, la prueba de significancia y el R^2_{adj} realizaron mediante el software R utilizando el paquete "vegan" (Core R Team 2019).

Resultados

Efecto de la disponibilidad de agua en atributos de crecimiento, asignación de biomasa y fisiológicos

Los ANOVA de dos vías indicaron diferencias significativas a nivel de población y tratamiento para A_N, a nivel de tratamiento para g_s, y no se encontraron diferencias para la eficiencia del uso del agua (A_N/g_s) en ninguno de los niveles analizados. Por otra parte, se detectaron diferencias significativas entre poblaciones y tratamientos para la mayoría de los atributos de asignación de biomasa y crecimientos evaluados (Tabla 3); sin embargo, la interacción población*tratamiento únicamente fue significativa para TLA/TRL (Tabla 3; Fig. 2). En general, se registró un aumento en A_N y g_s, así como en SLA, RGR y TLA/TRL en el tratamiento de alta disponibilidad hídrica, y un marcado aumento en atributos relacionados a la raíz como SRL, R/S, RL/SL, así como WD en el tratamiento de baja disponibilidad hídrica (Fig. 2). Las correlaciones de Pearson entre pares de atributos mostraron porcentajes bajos de variables correlacionadas significativamente para ambos tratamientos (24 y 15 % de 45 correlaciones para alta y baja disponibilidad hídrica respectivamente; Fig. 3; Tabla S2), algunas de las cuales se detectaron en ambos tratamientos hídricos (p.ej. A_N vs g_s, RGR vs R/S y R/S vs TLA/TLR). En el tratamiento de alta disponibilidad hídrica, la densidad específica de la madera (WD) se correlacionó positivamente con el área foliar específica (SLA) y negativamente con la longitud específica de la raíz (SRL) (Fig. 3; Tabla S2). Por otra parte, en el tratamiento de baja disponibilidad hídrica hubo correlaciones positivas entre TLA/TRL y la eficiencia del uso del agua (A_N/g_s) y la tasa de crecimiento relativo (RGR), así como correlaciones negativas entre el cociente de longitud raíz/tallo (RL/SL) y la fotosíntesis neta (A_N); el área foliar específica (SLA) y el cociente de masa raíz/tallo (R/S); asi como la densidad específica de la madera (WD) y TLA/TRL (Fig. 3; Tabla S2).

Variación en atributos en función de la disponibilidad hídrica entre poblaciones

El PCA para atributos en el experimento de alta disponibilidad hídrica alcanzó el 48% de la variación para los dos primeros ejes (Fig. 4). El primer eje (PC1) segregó a las poblaciones con una mayor inversión en crecimiento y asignación de biomasa a hojas y crecimiento (RGR y TLA/TLR) hacia el lado positivo del eje (p.ej. NOV, CUI, HUI) y las poblaciones con mayores tasas fotosintéticas (A_N) e inversión en tejido radicular (SRL, R/S) hacia la parte negativa del eje (p.ej. MAT, VA, HM). El PC2 mostró principalmente la variación entre las poblaciones con inversión en formar madera densa (WD) pero con una menor biomasa por unidad de área en hojas (SLA) hacia el lado positivo del eje (SN, TEH, ZIN), y las poblaciones con mayor longitud radicular respecto a la longitud aérea (RL/SL), mayor longitud específica de raíz (SRL) y eficiencia en el uso del agua (A_N/g_s) hacia la parte negativa del eje (SP, SY, PN). Por otra parte, los resultados del PCA para el experimento de baja disponibilidad hídrica explicó el 53% de la variación existente en los dos primeros ejes (Fig. 4). El PC1 se explicó por poblaciones con mayor inversion en atributos relacionados a la raíz (RL/SL y R/S) y la densidad de la madera (WD), hacia el lado positivo del eje (p.ej. MAT, HM, VA, PÑ), y mayor asignación a biomasa foliar (SLA y TLA/TRL) hacia la parte negativa del eje (p.ej. CUI, SP, ZIN). Por otra parte, el PC2 separó a las poblaciones con mayor eficiencia en el uso del agua (A_N/g_s) hacia el lado positivo (CUI, HUI, HM) y poblaciones con mayor inversión en raíces densas (SRL), así como tasas fotosintéticas (A_N) y conductancia estomática mayores (g_s) (SP, SY, IXM), hacia el lado positivo del eje. Los valores propios de los dos primeros componentes para cada tratamiento se resumen en la Tabla S1.

Variación de los atributos funcionales en relación con los patrones climáticos

No se encontraron correlaciones entre las variables ambientales y los componentes principales para ninguno de los dos tratamientos. Sin embargo, a nivel de atributos individuales hubo una correlación positiva entre SLA y temperatura máxima del mes más cálido (bio5) para ambos tratamientos (Fig. 5a y b). Asimismo, el cociente raíz-tallo en biomasa, en el tratamiento de alta disponibilidad hídrica y en longitud en el de baja disponibilidad hídrica mostraron correlaciones positivas con la precipitación del mes más seco (bio14) (Fig. 5c y d). Finalmente, para ambos tratamientos hubo correlaciones negativas entre RL/SL y la estacionalidad de la precipitación (bio15) (Fig. 5e y f).

Los resultados del RDA para el tratamiento de alta disponibilidad hídrica, el modelo completo (RDAfull) y el modelo pRDA1 (efecto climático puro) mostraron valores significativos (P=0.002 y P=0.001, respectivamente), este último contabilizando R^2_{adj}= 17% de la varianza total del modelo (Tabla 4). Las variables más importantes dentro del modelo pRDA1 fueron isotermalidad (bio3) y temperatura máxima del mes más cálido (bio5), mientras que las variables restantes (bio2, bio6, bio12, bio14, bio15 y bio18), no mostraron valores significativos (Tabla 4). Asimismo, el modelo pRDA2 (efecto geográfico) fue significativo aunque explicó una proporción muy baja de la varianza (P=0.04; R^2_{adj}= 3%). El efecto conjunto de clima y geografía explicaron el 54% de la variación.

Por otra parte, en el RDA para el tratamiento de baja disponibilidad hídrica, el modelo completo (RDAfull) y el modelo pRDA1 (efecto climático puro) fueron significativos (P=0.001, para ambos modelos). Este último, contabilizando R^2_{adj}=26% de la varianza total del modelo (Tabla 4). Las variables climáticas más importantes dentro de este modelo fueron la temperatura máxima del mes más cálido (bio5), la precipitación del mes más seco (bio14), la estacionalidad de la precipitación (bio15), la isotermalidad (bio3), y la temperatura mínima del mes más frío (bio6), mientras las variables restantes (bio2, bio12 y bio18) no mostraron valores significativos (Tabla 4). Por su parte, el modelo pRDA2 (efecto geográfico puro) no mostró valores significativos (P=0.4; R^2_{adj}=-0.002). El efecto conjunto de clima y geografía explicaron el 41% de la variación.

Discusión

A lo largo de la distribución de *P. laevigata* se ha descrito una amplia variación morfológica, principalmente en hojas, tamaño y forma de crecimiento debida, de acuerdo con Rzedowski (1988), a las condiciones ambientales del hábitat donde se desarrolla la especie. En el presente estudio, se evaluaron las diferencias en la expresión de atributos funcionales bajo distintos niveles de disponibilidad hídrica entre poblaciones de *P. laevigata*, lo que sugeriría patrones de adaptación local a condiciones ambientales específicas. En general, los resultados revelan diferencias morfológicas y fisiológicas entre las poblaciones de *P. laevigata*. Esto sugiere la existencia de diferentes estrategias para afrontar la sequía a lo largo de la distribución de la especie, expresadas como un eje funcional de explotación-tolerancia mediante un continuo rápido-lento en la adquisición de recursos, acentuado bajo condiciones de sequía. Además, se encontró también evidencia sobre la relación entre la variación de los atributos y el gradiente ambiental experimentado a través de su distribución.

La gran variación morfológica reportada para la especie a lo largo de su distribución se acentúo bajo los tratamientos de disponibilidad hídrica , manifestado en el bajo porcentaje de correlaciones significativas entre atributos, patrón reportado previamente para especies del género (López-Lauenstein et al. 2013; Salazar et al. 2018, 2019). Aun así, las correlaciones atributo-atributo revelaron estrategias para maximizar los recursos disponibles: algunas poblaciones presentan mayor desarrollo radicular en detrimento del desarrollo aéreo y viceversa, evidenciando consistentemente una disyuntiva funcional en ambos tratamientos. Las especies del género *Prosopis* se han identificado como freatofitas, característica fundamental de su éxito en zonas secas (Golubov et al. 2001; Pasiecznik et al. 2002; Felker 2009; Villagra et al. 2010), ya que la optimización de la extracción del agua del suelo requiere un gran desarrollo radicular, el cual es beneficioso aun cuando el agua no es una limitante (Felker 2009; López-Lauenstein et al. 2013; Liese et al. 2017; Agathokleous et al. 2019; Shen et al. 2019). En el tratamiento de déficit hídrico, se registró mayor inversión en raíz (R/S) respecto a la parte aérea (SLA), mientras que en el tratamiento de alta disponibilidad hídrica hubo una menor longitud específica de raíz al aumentar la relación raíz-tallo en longitud. En especies como *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth, *Prosopis chilensis* (Molina) Stuntz y *Prosopis flexuosa* DC (López-Lauenstein et al. 2013; Salazar et al. 2019), se ha reportado que una mayor inversión en raíz incrementa significativamente la captación hídrica mientras reduce la pérdida de agua en tejidos aéreos (Quero et al. 2008; Eziz et al. 2017; Salazar et al. 2019; Hanslin et al. 2020; Dolezal et al. 2021). Un mayor desarrollo radicular representa ventajas independientemente de la disponibilidad hídrica al incorporar estrategias oportunistas para aprovechar pulsos de agua, estrategia observada en *Prosopis juliflora, P. glandulosa* var. *torreyana* y *P. pallida,* distribuidas en hábitats con altos índices de aridez (Palacios et al. 2001; Felker 2009; Salazar et al. 2018). No obstante, el desarrollo foliar es crucial para mantener un estatus hídrico adecuado y maximizar la adquisición y administración de recursos, particularmente en especies con hojas compuestas (Xu et al. 2009; Malhado et al. 2010; Yang et al. 2019). Sin embargo, el desarrollo foliar no mostró correlación con un aumento en los patrones fotosintéticos, pero si se registró un aumento en RGR al aumentar TLA/TLR. Asimismo, se esperaría una relación directa entre el desarrollo radicular y la eficiencia en el uso del agua. Sin embargo, en el tratamiento de baja disponibilidad hídrica hubo una correlación negativa con un mayor desarrollo foliar respecto al desarrollo radicular (TLA/TLR vs R/S), en el tratamiento de baja disponibilidad hídrica, evidenciando el papel del desarrollo foliar en la administración de recursos hídricos (Salazar et al. 2019). Asimismo, cuando la disponibilidad hídrica fue alta, ocurrió un mayor desarrollo foliar en detrimento de tejidos densos (p.ej. WD), pero bajo estrés hídrico el desarrollo foliar (SLA) se redujo mientras aumentó la inversión en raíz (R/S; SRL). De acuerdo con el espectro económico de las hojas, una mayor biomasa foliar por área representa una estrategia conservadora con tejidos densos y longevos, mientras menor biomasa por área representa una estrategia de explotación, presentando tejidos menos densos y de corta duración (Reich 2014; Poorter et al. 2015; Klimešová et al. 2016; Dias et al. 2017; Lara-De La Cruz et al. 2020; Xu et al. 2020). Por otra parte, mayor WD evidencia estrés por sequía, al proteger al tallo de implosiones por escasez hídrica y prevenir embolismos al soportar presiones más negativas de xilema sin experimentar cavitación (Poorter and Markesteijn 2008; Adams et al. 2009; Chave et al. 2009; Woodall et al. 2015; Salazar et al. 2019). En algunas poblaciones hubo aumento de densidad de la madera respecto al desarrollo foliar (p. ej. WD vs TLA/TRL), sugiriendo una estrategia de tolerancia bajo sequía (Chave et al. 2009; Woodall et al. 2015; Verbeeck et al. 2019; Ahrens et al. 2020); sin embargo, cuando disponibilidad hídrica fue alta se redujo la relevancia de invertir en tejidos densos.

A través de estrategias funcionales, las plantas reflejan su historia evolutiva y moldean su desempeño. Consecuentemente, los atributos funcionales evidencian las estrategias de las plantas para hacerle frente a contrastes ambientales experimentados a través de gradientes ambientales y a lo largo de su vida (López-Iglesias et al. 2014; Reich

2014; Díaz et al. 2016; Cavender-Bares and Ramírez-Valiente 2017). El PCA recuperó alrededor del 50% de la variación total en ambos tratamientos. Al respecto, se detectó un grupo de poblaciones con una mayor inversión radicular y tejidos densos (e.g. SRL, WD), mientras que otro grupo muestró una mayor inversión energética al crecimiento y desarrollo aéreo, particularmente al aumentar SLA en el PC1 (p. ej. RGR, TLA/TLR y SLA). Los resultados son consistentes con el postulado de explotación-tolerancia a través de estrategias de un continuo rápido-lento: algunas plantas desarrollan tejidos poco densos, de vida útil corta mediante altas tasas de adquisición recursos (explotación-rápido), mientras otras plantas desarrollan tejidos densos y longevos, tolerantes a condiciones adversas, a costa de una tasa lenta de adquisición de recursos (tolerante-lento) (López-Iglesias et al. 2014; Reich 2014; Poorter et al. 2015; Díaz et al. 2016; Salguero-Gómez 2017; Rüger et al. 2018). En este sentido, poblaciones del norte de la distribución (p. ej. MAT, HM, VA), consistentemente se ubicaron en el eje de tolerancia-lento, mientras que algunas poblaciones del centro y norte (p.ej. CUI, SP y HUI) mantuvieron una estrategia de explotación-rápido. La inversión en los atributos varía en función de las condiciones ambientales, no obstante, una rápida adquisición en un aspecto generalmente demanda ser rápido en otros, por consiguiente, la velocidad de adquisición es una característica general de las poblaciones y su relación con el ambiente (Reich et al. 2003; Ramírez-Valiente et al. 2011; Reich 2014; Cavender-Bares and Ramírez-Valiente 2017; Salguero-Gómez 2017). Aunque no se registró una relación significativa entre los PC y las variables ambientales, en atributos individuales, se registró un incremento de SLA a mayor temperatura del mes más seco (bio5), estrategia asociada a eficientizar la administración de recursos. Previos reportes para árboles tropicales han encontrado mayor masa por área en hojas en condiciones mésicas pero reduciéndose en zonas secas, argumentando diferencias fenológicas en las cuales las plantas de zonas secas desarrollan una estrategia de explotación-rápido con hojas efímeras, mientras que en zonas mésicas, las hojas son más longevas y tolerantes a largo de la temporada de sequía, patrón similar al encontrado en el presente estudio (Cavender-Bares and Ramírez-Valiente 2017; Ramírez-Valiente et al. 2017; Carvajal et al. 2019b). Para *P. laevigata,* se han reportado patrones fenologicos foliares brevideciduos o perennifolios (variando a traves de su distribución), presentando pérdida de hojas durante el invierno (Cervantes 2005). Por otra parte, la asignación de biomasa a raíz aumentó con la precipitación del mes más seco (bio5) y la relación raíz-tallo (RL/SL) disminuyó a mayor estacionalidad de la precipitación (bio15) en ambos tratamientos, manifestando estrategias oportunistas en la adquisición hídrica mediante el desarrollo radicular como en otras especies de *Prosopis* (Palacios et al. 2001; Felker 2009; Salazar et al. 2018). Además, el RDA mostró que la isotermalidad (bio3) y la temperatura máxima del mes más cálido (bio5) representan las variables ambientales que más influencian los atributos en alta disponibilidad hídrica. Sin embargo, el RDA del tratamiento de baja disponibilidad hídrica mostró que la temperatura máxima del mes más cálido (bio5), la precipitación del mes más seco (bio14), la estacionalidad de la precipitación (bio15), son las principales variables que determinan las estrategias de tolerancia-explotación en las poblaciones de *P. laevigata*. En general, se observó que cuando el agua no es la principal limitante, las estrategias subyacentes están determinadas por patrones de temperatura asociados a las localidades de origen. Sin embargo, al existir baja disponibilidad hídrica se expresan las estrategias de asignación de biomasa, crecimiento y fisiológicas asociadas a los patrones de precipitación a través de la distribución de la especie. Consistentemente, los resultados de este estudio sugieren fuertemente la existencia de patrones de adaptación local en las poblaciones de *P. laevigata* asociadas al gradiente ambiental experimentado a lo largo de su distribución (Eckert et al. 2015; Cavender-Bares and Ramírez-Valiente 2017; Ramírez-Valiente et al. 2017; Mantel and Sweigart 2019; Krushelnycky et al. 2020)

En conclusión, a través del análisis de atributos funcionales de asignación de biomasa, crecimiento y fisiológicos, se propone la existencia de estrategias adaptativas asociadas a patrones de variación ambiental a lo largo de la distribución de *P. laevigata* en México. Curiosamente, un eje funcional de explotación -tolerancia, expresado en un continuo rápido-lento de captación y asignación de recursos determinan el éxito de *P. laevigata* a través de las zonas áridas y semiáridas de México. Reportes previos para la especie, han mostrado patrones latitudinales de diversidad genética, así como estrategias asociadas a tolerancia- explotación durante la germinación y las primeras fases del establecimiento, lo que da soporte a la idea de la existencia de estrategias de adaptación a condiciones locales en la distribución de la especie, características que han permitido su dominancia fisionómica e importancia ecológica a través de las zonas áridas de México.

Referencias

Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, et al (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc Natl Acad Sci U S A 106:7063–7066. https://doi.org/10.1073/pnas.0901438106

Agathokleous E, Belz RG, Kitao M, et al (2019) Does the root to shoot ratio show a hormetic response to stress? An ecological and environmental perspective. J For Res 30:1569–1580. https://doi.org/10.1007/s11676-018-0863-7

Aguilar-Romero R, García-Oliva F, Pineda-García F, et al (2016) Patterns of distribution of nine Quercus species along an environmental gradient in a fragmented landscape in central Mexico. Bot Sci 94:471–482. https://doi.org/10.17129/botsci.620

Ahrens CW, Andrew ME, Mazanec RA, et al (2020) Plant functional traits differ in adaptability and are predicted to be differentially affected by climate change. Ecol Evol 10:232–248. https://doi.org/10.1002/ece3.5890

Alvarado V, Bradford KJ (2002) A hydrothermal time model explains the cardinal temperatures for seed germination. Plant, Cell Environ 25:1061–1069. https://doi.org/10.1046/j.1365-3040.2002.00894.x

Alvarado V, Bradford KJ (2005) Hydrothermal time analysis of seed dormancy in true (botanical) potato seeds Hydrothermal time analysis of seed dormancy in true (botanical) potato seeds. Seed Sci Res · 15:77–88. https://doi.org/10.1079/SSR2005198

Alvarez M, Leparmarai P, Heller G, Becker M (2017) Recovery and germination of Prosopis juliflora (Sw .) DC seeds after ingestion by goats and cattle. Arid L Res Manag 31:71–80. https://doi.org/10.1080/15324982.2016.1234521

Andrade LFD, Cardoso VJM (2016) Does thermal time for germination vary among populations of a tree legume (Peltophorum dubium)? Brazilian J Biol 76:592–599. https://doi.org/10.1590/1519-6984.18714

Arriaga V, Cervantes V, Vargas-Mena A (1994) Manual de reforestación con especies nativas: colecta y preservación de semillas, propagación y manejo de plantas. Univ Nac Auton México 186

Balfagón D, Zandalinas SI, Mittler R, Gómez-Cadenas A (2020) High temperatures modify plant responses to abiotic stress conditions. Physiol. Plant. 170:335–344

Barga S, Dilts TE, Leger EA (2017) Climate variability affects the germination strategies exhibited by arid land plants. Oecologia 185:437–452. https://doi.org/10.1007/s00442-017-3958-5

Barton KE, Jones C, Edwards KF, et al (2020) Local adaptation constrains drought tolerance in a tropical foundation tree. J Ecol 108:1540–1552. https://doi.org/10.1111/1365-2745.13354

Baskin CC, Baskin JM (2014a) Biogeographical and Evolutionary Aspects of Seed Dormancy

Baskin CC, Baskin JM (2014b) Variation in Seed Dormancy and Germination within and between Individuals and Populations of a Species

Bessega C, Cony M, Saidman BO, et al (2019) Genetic diversity and differentiation among provenances of Prosopis flexuosa DC (Leguminosae) in a progeny trial: Implications for arid land restoration. For Ecol Manage 443:59–68. https://doi.org/10.1016/j.foreco.2019.04.016

Bessega C, Pometti C, Ewens M, et al (2015) Evidences of local adaptation in quantitative traits in Prosopis alba (Leguminosae). Genetica 143:31–44. https://doi.org/10.1007/s10709-014-9810-5

Bessega C, Pometti CL, Ewens M, et al (2016) Fine-scale spatial genetic structure analysis in two Argentine populations of Prosopis alba (Mimosoideae) with different levels of ecological disturbance. Eur J For Res 135:495–505. https://doi.org/10.1007/s10342-016-0948-9

Bewley JD, Bradford KJ, Hilhorst HWM, Nonogaki H (2013) Seeds: Physiology of development, germination and dormancy, 3rd edition

Bochenek A, Gołaszewski J, Giełwanowska I (2010) Hydrotime model analysis of Matricaria maritima ssp. inodora seed dormancy. Plant Species Biol 25:136–148. https://doi.org/10.1111/j.1442-1984.2010.00276.x

Bradford K (2002) Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. Weed Sci 50:248–2360. https://doi.org/10.1614/0043-1745(2002)050

Bradford K, Still D (2004) Application of hydrotime analysis in seed testing. Seed Technol 26:75–85

Bradford KJ (1997) The Hydrotime Concept in Seed Germination and Dormancy. 349–360. https://doi.org/10.1007/978-94-011-5716-2_39

Buitenwerf R, Kulmatiski A, Higgins SI (2014) Soil water retention curves for the major soil types of the kruger national park. Koedoe 56:1–9. https://doi.org/10.4102/koedoe.v56i1.1228

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed). Springer-Verlag

Calderón G, Rzedowski J (2001) Flora fanerogámica del Valle de México. Instituto de Ecología, A.C. y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Pátzcuaro (Michoacán)

Carevic FS (2014) The role of ecophysiological studies in the genus Prosopis: implications for the conservation of drought-prone species. Idesia (Arica) 32:77–81. https://doi.org/10.4067/s0718-34292014000400010

Carvajal DE, Loayza AP, Rios RS, et al. (2019a) A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies. J Ecol 107:1079–1092. https://doi.org/10.1111/1365-2745.13092

Carvajal DE, Loayza AP, Rios RS, et al (2019b) A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies. J Ecol 107:1079–1092. https://doi.org/10.1111/1365-2745.13092

Castillo ML, Schaffner U, Van Wilgen BW, et al. (2021) Genetic insights into the globally invasive and taxonomically problematic tree genus Prosopis. AoB Plants 13:1–13. https://doi.org/10.1093/aobpla/plaa069

Catalán L, Balzarini M, Taleisnik E, et al. (1994) Effects of salinity on germination and seedling growth of Prosopis flexuosa (D.C.). For Ecol Manage 63:347–357. https://doi.org/10.1016/0378-1127(94)90116-3

Catalano SA, Vilardi JC, Tosto D, Saidman BO (2008) Molecular phylogeny and diversification history of Prosopis (Fabaceae: Mimosoideae). Biol J Linn Soc 93:621–640. https://doi.org/10.1111/j.1095-8312.2007.00907.x

Cavallaro V, Barbera AC, Maucieri C (2016) Evaluation of variability to drought and saline stress through the germination of different ecotypes of carob (*Ceratonia siliqua* L.) using a hydrotime model. Ecol Eng 95:557–566. https://doi.org/10.1016/j.ecoleng.2016.06.040

Cavender-Bares J, Ramírez-Valiente JA (2017) Physiological Evidence from Common Garden Experiments for Local Adaptation and Adaptive Plasticity to Climate in American Live Oaks (Quercus Section Virentes): Implications for Conservation Under Global Change. 107–135. https://doi.org/10.1007/978-3-319-69099-5_4

Cervantes M (2005) Plantas de importancia económica en zonas áridas y semiáridas de México. In: X Encuentro de Geógrafos de América Latina. pp 3388–3407

Chave J, Coomes D, Jansen S, et al (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Cochrane A (2016) Can sensitivity to temperature during germination help predict global warming vulnerability? Seed Sci Res 26:14–29. https://doi.org/10.1017/S0960258515000355

Cochrane A, Yates CJ, Hoyle GL, Nicotra AB (2015) Will among-population variation in seed traits improve the chance of species persistence under climate change? Glob Ecol Biogeogr 24:12–24. https://doi.org/10.1111/geb.12234

Cochrane JA (2020) Thermal Requirements Underpinning Germination Allude to Risk of Species Decline from Climate Warming. Plants 9:1–22. https://doi.org/10.1007/978-3-319-95885-9_300028

Contreras-Negrete G, Letelier L, Piña-Torres J, González-Rodríguez A (2021) Genetic structure, phylogeography and potential distribution modeling suggest a population expansion in the mesquite Prosopis laevigata since the last interglacial. Plant Syst Evol 307:1–18. https://doi.org/10.1007/s00606-021-01744-5

Cony MA, Trione SO (1998) Inter- and intraspecific variability in Prosopis flexuosa and P. chilensis: Seed germination under salt and moisture stress. J Arid Environ 40:307–317. https://doi.org/10.1006/jare.1998.0448

Cony MA, Trione SO (1996) Germination with respect to temperature of two Argentinian Prosopis species. 225–236

Core R Team (2019) A Language and Environment for Statistical Computing. R Found Stat Comput 2:https://www.R--project.org

Covell S, Ellis RH, Roberts EH, Summerfield RJ (1986) The influence of temperature on seed germination rate in grain legumes: I. A comparison of chickpea, lentil, soyabean and cowpea at constant temperatures. J Exp Bot 37:705–715. https://doi.org/10.1093/jxb/37.5.705

Crawley MJ (2007) The R Book. R B 1–942. https://doi.org/10.1002/9780470515075

Cristaudo A, Catara S, Mingo A, et al (2019) Temperature and storage time strongly affect the germination success of perennial Euphorbia species in Mediterranean regions. Ecol Evol 9:10984–10999. https://doi.org/10.1002/ece3.5535

Cuervo-Robayo AP, Téllez-Valdés O, Gómez-Albores MA, et al (2014) An update of high-resolution monthly climate surfaces for Mexico. Int J Climatol 34:2427–2437. https://doi.org/10.1002/joc.3848

De Villalobos AE, Peláez D V. (2001) Influences of temperature and water stress on germination and establishment of Prosopis caldenia Burk. J Arid Environ 49:321–328.

https://doi.org/10.1006/jare.2000.0782

Deinlein U, Stephan AB, Horie T, et al (2014) Plant salt-tolerance mechanisms. Trends Plant Sci 19:371–379. https://doi.org/10.1016/j.tplants.2014.02.001

Dias ATC, Cornelissen JHC, Berg MP (2017) Litter for life: assessing the multifunctional legacy of plant traits. J Ecol 105:1163–1168. https://doi.org/10.1111/1365-2745.12763

Díaz S, Kattge J, Cornelissen JHC, et al (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Dolezal J, Jandova V, Macek M, Liancourt P (2021) Contrasting biomass allocation responses across ontogeny and stress gradients reveal plant adaptations to drought and cold. Funct Ecol 35:32–42. https://doi.org/10.1111/1365-2435.13687

Donohue K, Rubio De Casas R, Burghardt L, et al (2010) Germination, postgermination adaptation, and species ecological ranges. Annu Rev Ecol Evol Syst 41:293–319. https://doi.org/10.1146/annurev-ecolsys-102209-144715

Duarte AA, de Lemos Filho JP, Marques AR (2018) Seed germination of bromeliad species from the campo rupestre: thermal time requirements and response under predicted climate-change scenarios. Flora Morphol Distrib Funct Ecol Plants 238:119–128. https://doi.org/10.1016/j.flora.2017.05.016

Duncan C, Schultz NL, Good MK, et al (2019) The risk-takers and -avoiders: Germination sensitivity to water stress in an arid zone with unpredictable rainfall. AoB Plants 11:1–12. https://doi.org/10.1093/aobpla/plz066

Dürr C, Dickie JB, Yang XY, Pritchard HW (2015) Ranges of critical temperature and water potential values for the germination of species worldwide: Contribution to a seed trait database. Agric For Meteorol 200:222–232. https://doi.org/10.1016/j.agrformet.2014.09.024

Eckert AJ, Maloney PE, Vogler DR, et al (2015) Local adaptation at fine spatial scales: an example from sugar pine (Pinus lambertiana, Pinaceae). Tree Genet Genomes 11:. https://doi.org/10.1007/s11295-015-0863-0

El-Keblawy A, Al-Rawai A (2005) Effects of salinity, temperature and light on germination of invasive Prosopis juliflora (Sw.) D.C. J Arid Environ 61:555–565. https://doi.org/10.1016/j.jaridenv.2004.10.007

El-Keblawy A, Al-Rawai A (2006) Effects of seed maturation time and dry storage on light and temperature requirements during germination in invasive Prosopis juliflora. Flora Morphol Distrib Funct Ecol Plants 201:135–143. https://doi.org/10.1016/j.flora.2005.04.009

Excoffier L, Foll M, Petit RJ (2009) Genetic consequences of range expansions. Annu Rev Ecol Evol Syst 40:481–501.
https://doi.org/10.1146/annurev.ecolsys.39.110707.173414

Eziz A, Yan Z, Tian D, et al (2017) Drought effect on plant biomass allocation: A meta-analysis. Ecol Evol 7:11002–11010. https://doi.org/10.1002/ece3.3630

Farooq M, Wahid A, Kobayashi N, S.M.A. Fujita DB (2009) Plant drought stress : effects , mechanisms and management To cite this version : Review article. Agron Sustain Dev 29:185–212

Fathi A, Tari DB (2016) Effect of Drought Stress and its Mechanism in Plants. Int J Life Sci 10:1–6. https://doi.org/10.3126/ijls.v10i1.14509

Felker P (2009) Unusual physiological properties of the arid adapted tree legume Prosopis and their applications in developing countries. Perspect Biophys plant Ecophysiol A … 221–255
Ferreira Marques FR, Vinicius Meiado M, Corte Real de Castro NM, et al (2015) GerminaQuant : a new tool for germination measurements. J Seed Sci 1–8. https://doi.org/10.1590/2317-1545v37n3145605

Flores J, Briones O (2001a) Plant life-form and germination in a Mexican inter-tropical desert: Effects of soil water potential and temperature. J Arid Environ 47:485–497. https://doi.org/10.1006/jare.2000.0728

Flores J, Briones O (2001b) Plant life-form and germination in a Mexican inter-tropical desert : effects of soil water potential and temperature. 52:485–497. https://doi.org/10.1006/jare.2000.0728

Flores J, Estrada E, Jurado E, Garcı JF (2006) Leguminous seedling establishment in Tamaulipan thornscrub of northeastern Mexico. 221:133–139. https://doi.org/10.1016/j.foreco.2005.09.011

Flores J, Pérez-Sánchez RM, Jurado E (2017) The combined effect of water stress and temperature on seed germination of Chihuahuan Desert species. J Arid Environ 146:95–98. https://doi.org/10.1016/j.jaridenv.2017.07.009

Garcia-Huidobro J, Monteith JL, Squire GR (1982) Time , Temperature and Germination of Pearl Millet (*Pennisetum typhoides* S . & H .). J Exp Bot 33:288–296

García-Nogales A, Linares JC, Laureano RG, et al (2016) Range-wide variation in life-history phenotypes: spatiotemporal plasticity across the latitudinal gradient of the evergreen oak Quercus ilex. J Biogeogr 43:2366–2379. https://doi.org/10.1111/jbi.12849

Garot E, Dussert S, Jo T, et al (2020) Multi-Approach Analysis Reveals Local Adaptation in a Widespread Forest Tree of Reunion Island. 0:1–13. https://doi.org/10.1093/pcp/pcaa160

Golubov J, Mandujano MC, Eguiarte LE (2001) La paradoja de mezquites (Prosopis spp.): La invasión de especies o potenciadores de la biodiversidad? Bot Sci 30:23. https://doi.org/10.17129/botsci.1644

Greenwood S, Ruiz-Benito P, Martínez-Vilalta J, et al (2017) Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. Ecol. Lett. 20:539–553

Gummerson RJ (1986) The effect of constant temperatures and osmotic potentials on the germination of sugar beet. J Exp Bot 37:729–741. https://doi.org/10.1093/jxb/37.6.729

Hanslin HM, Bischoff A, Hovstad KA, et al (2020) Root growth plasticity to drought in seedlings of perennial grasses To cite this version : HAL Id : hal-02463457 Root growth plasticity to drought in seedlings of perennial grasses

Hardegree SP (2006) Predicting Germination Response to Temperature . I . Cardinal-temperature Models and Subpopulation-specific Regression. Ann Bot 97:1115–1125. https://doi.org/https://doi.org/10.1093/aob/mcl071

Hassanein AMA (2015) Assessment of Some Important Tree Species for Production under Arid Zones Conditions. 11:325–330. https://doi.org/10.5829/idosi.wjas.2015.11.5.1876

Helsen K, Acharya KP, Brunet J, et al (2017) Biotic and abiotic drivers of intraspecific trait variation within plant populations of three herbaceous plant species along a latitudinal gradient. BMC Ecol 17:1–12. https://doi.org/10.1186/s12898-017-0151-y

Hossain MA, Wani SH, Bhattacharjee S, et al (2016) Drought stress tolerance in plants, vol 1: Physiology and biochemistry

Hu XW, Fan Y, Baskin CC, et al (2015) Comparison of the effects of temperature and water potential on seed germination of fabaceae species from desert and subalpine Grassland. Am J Bot 102:649–660. https://doi.org/10.3732/ajb.1400507

Izuno A, Kitayama K, Onoda Y, et al (2017) The population genomic signature of environmental association and gene flow in an ecologically divergent tree species Metrosideros polymorpha (Myrtaceae). Mol Ecol 26:1515–1532. https://doi.org/10.1111/mec.14016

Jung V, Violle C, Mondy C, et al (2010) Intraspecific variability and trait-based community assembly. J Ecol 98:1134–1140. https://doi.org/10.1111/j.1365-2745.2010.01687.x

Kapoor D, Bhardwaj S, Landi M, et al (2020) The impact of drought in plant metabolism:

How to exploit tolerance mechanisms to increase crop production. Appl Sci 10:. https://doi.org/10.3390/app10165692

Keller SR, Soolanayakanahally RY, Guy RD, et al (2011) Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, Populus balsamifera L. (Salicaceae). Am J Bot 98:99–108. https://doi.org/10.3732/ajb.1000317

Klimešová J, Nobis MP, Herben T (2016) Links between shoot and plant longevity and plant economics spectrum: Environmental and demographic implications. Perspect Plant Ecol Evol Syst 22:55–62. https://doi.org/10.1016/j.ppees.2016.09.002

Kolb TE, Grady KC, McEttrick MP, Herrero A (2016) Local-scale drought adaptation of ponderosa pine seedlings at habitat ecotones. For Sci 62:641–651. https://doi.org/10.5849/forsci.16-049

Krushelnycky PD, Felts JM, Robichaux RH, et al (2020) Clinal variation in drought resistance shapes past population declines and future management of a threatened plant. Ecol Monogr 90:1–22. https://doi.org/10.1002/ecm.1398

Lai L, Chen L, Jiang L, et al (2018) Seed germination of seven desert plants and implications for vegetation restoration. https://doi.org/10.1093/aobpla/plw031/2609579

Lara-De La Cruz LI, García-Oliva F, Oyama K, González-Rodríguez A (2020) Association of functional trait variation of Quercus castanea with temperature and water availability gradients at the landscape level. Bot Sci 98:16–27. https://doi.org/10.17129/BOTSCI.2449

Liese R, Alings K, Meier IC (2017) Root branching is a leading root trait of the plant economics spectrum in temperate trees. Front Plant Sci 8:1–12. https://doi.org/10.3389/fpls.2017.00315

Lipiec J, Doussan C, Nosalewicz A, Kondracka K (2013) Effect of drought and heat stresses o n plant growth and yield : a review. 463–477. https://doi.org/10.2478/intag-2013-0017

Llanderal-Mendoza J, Gugger PF, Oyama K, et al (2017) Climatic determinants of acorn size and germination percentage of Quercus rugosa (Fagaceae) along a latitudinal gradient in Mexico. Bot Sci 95:37–45. https://doi.org/10.17129/botsci.640

López-Iglesias B, Villar R, Poorter L (2014) Functional traits predict drought performance and distribution of mediterranean woody species. Acta Oecologica 56:10–18. https://doi.org/10.1016/j.actao.2014.01.003

López Lauenstein DA, Fernández ME, Verga AR (2013) Drought stress tolerance of Prosopis chilensis and Prosopis flexuosa species and their hybrids. Trees - Struct

Funct 27:285–296. https://doi.org/10.1007/s00468-012-0798-0

Malhado ACM, Whittaker RJ, Malhi Y, et al (2010) Are compound leaves an adaptation to seasonal drought or to rapid growth? Evidence from the Amazon rain forest. Glob Ecol Biogeogr 19:852–862. https://doi.org/10.1111/j.1466-8238.2010.00567.x

Mantel SJ, Sweigart AL (2019) Divergence in drought-response traits between sympatric species of Mimulus. Ecol Evol 9:10291–10304. https://doi.org/10.1002/ece3.5549

Marquínez J, Lastra J, García P (2003) Estimation models for precipitation in mountainous regions: the use of GIS and multivariate analysis. J Hydrol 270:1–11. https://doi.org/10.1016/S0022-1694(02)00110-5

Matías L, Pérez-Ramos IM, Gómez-Aparicio L (2019) Are northern-edge populations of cork oak more sensitive to drought than those of the southern edge? Environ Exp Bot 163:78–85. https://doi.org/10.1016/j.envexpbot.2019.04.011

Meira-Neto JAA, Nunes Cândido HM, Miazaki Â, et al (2019) Drivers of the growth–survival trade-off in a tropical forest. J Veg Sci 30:1184–1194. https://doi.org/10.1111/jvs.12810

Mesgaran MB, Mashhadi HR, Alizadeh H, et al (2013) Importance of distribution function selection for hydrothermal time models of seed germination. Weed Res 53:89–101. https://doi.org/10.1111/wre.12008

Mesgaran MB, Onofri A, Mashhadi HR, Cousens RD (2017a) Water availability shifts the optimal temperatures for seed germination: A modelling approach. Ecol Modell 351:87–95. https://doi.org/10.1016/j.ecolmodel.2017.02.020

Mesgaran MB, Onofri A, Mashhadi HR, Cousens RD (2017b) Water availability shifts the optimal temperatures for seed germination: A modelling approach. Ecol Modell 351:87–95. https://doi.org/10.1016/j.ecolmodel.2017.02.020

Michel BE (1983) Evaluation of the Water Potentials of Solutions of Polyethylene Glycol 8000 Both in the Absence and Presence of Other Solutes. Plant Physiol 72:66–70. https://doi.org/10.1104/pp.72.1.66

Miranda RDEQ, Correia RM, Pompelli MF (2013) Germination of Prosopis juliflora (Sw .) D . C . seeds at different osmotic potentials and temperatures. https://doi.org/10.1111/1442-1984.12025

Miranda RDQ, Correia RM, De Almeida-Cortez JS, Pompelli MF (2014) Germination of Prosopis juliflora (Sw.) D.C. seeds at different osmotic potentials and temperatures. Plant Species Biol 29:. https://doi.org/10.1111/1442-1984.12025

Moncada X, Plaza D, Stoll A, et al (2019) Genetic diversity and structure of the vulnerable species prosopis chilensis (Molina) Stuntz in the Coquimbo region, Chile. Gayana - Bot 76:91–104. https://doi.org/10.4067/S0717-66432019000100091

Morar IMT, González-orenga S, Sestras AF, et al (2019) Screening for Salt and Water Stress Tolerance in Fir (Abies alba) Populations. Notulae 47:1063–1072. https://doi.org/10.15835/nbha47411348

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911

Oliveira MT, Matzek V, Medeiros CD, et al (2014) Stress tolerance and ecophysiological ability of an invader and a native species in a seasonally dry tropical forest. PLoS One 9:. https://doi.org/10.1371/journal.pone.0105514

Onofri A, Benincasa P, Mesgaran MB, Ritz C (2018) Hydrothermal-time-to-event models for seed germination. Eur J Agron 101:129–139. https://doi.org/10.1016/j.eja.2018.08.011

Onofri A, Mesgaran MB, Neve P, Cousens RD (2014) Experimental design and parameter estimation for threshold models in seed germination. Weed Res 54:425–435. https://doi.org/10.1111/wre.12095

Palacios a (2006) Los Mezquites Mexicanos : Biodiversidad y Distribución Geográfica. Bol Soc Argent Bot 41:99–121

Palacios a, Pasiecznik N, Felker P, et al (2001) A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy. Seed Sci Res 25:147–158. https://doi.org/10.1017/S0960258514000452

Pasiecznik N, Felker P, Harris P, et al (2002) The’Prosopis juliflora’-’Prosopis pallida’complex: a monograph. For Trees Livelihoods 12:229–229

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167. https://doi.org/10.1071/BT12225

Pometti CL, Bessega CF, Cialdella AM, et al (2019) Evidence of local adaptation and stabilizing selection on quantitative traits in populations of the multipurpose American species Acacia aroma (Fabaceae). Bot J Linn Soc 191:128–141. https://doi.org/10.1093/botlinnean/boz023

Poorter H, Fiorani F, Pieruschka R, et al (2016) Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. New Phytol 212:838–855. https://doi.org/10.1111/nph.14243

Poorter H, Jagodzinski AM, Ruiz-Peinado R, et al (2015) How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. New Phytol 208:736–749. https://doi.org/10.1111/nph.13571

Poorter H, Niklas KJ, Reich PB, et al (2012) Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Poorter L, Markesteijn L (2008) Seedling traits determine drought tolerance of tropical tree species. Biotropica 40:321–331. https://doi.org/10.1111/j.1744-7429.2007.00380.x

Prado-Tarango D, Mata-González R, Melgoza-Castillo A, et al (2019) Simulated rainfall sequences affect germination and biomass allocation of Chihuahuan desert native plants. Arid L Res Manag 33:22–36. https://doi.org/10.1080/15324982.2018.1485779

Qiu J, Bai Y, Fu YB, Wilmshurst JF (2010) Spatial variation in temperature thresholds during seed germination of remnant Festuca hallii populations across the Canadian prairie. Environ Exp Bot 67:479–486. https://doi.org/10.1016/j.envexpbot.2009.09.002

Quero JL, Villar R, Marañón T, et al (2008) Relating leaf photosynthetic rate to whole-plant growth: Drought and shade effects on seedlings of four Quercus species. Funct Plant Biol 35:725–737. https://doi.org/10.1071/FP08149

Ramawat KG (2010) Desert plants: Biology and biotechnology

Ramírez-Valiente JA, Center A, Sparks JP, et al (2017) Population-level differentiation in growth rates and leaf traits in seedlings of the neotropical live oak quercus oleoides grown under natural and manipulated precipitation regimes. Front Plant Sci 8:1–14. https://doi.org/10.3389/fpls.2017.00585

Ramírez-Valiente JA, Valladares F, Huertas AD, et al (2011) Factors affecting cork oak growth under dry conditions: Local adaptation and contrasting additive genetic variance within populations. Tree Genet Genomes 7:285–295. https://doi.org/10.1007/s11295-010-0331-9

Reich PB (2014) The world-wide "fast-slow" plant economics spectrum: A traits manifesto. J Ecol 102:275–301. https://doi.org/10.1111/1365-2745.12211

Reich PB, Wright IJ, Cavender-Bares J, et al (2003) The evolution of plant functional variation: Traits, spectra, and strategies. Int J Plant Sci 164:. https://doi.org/10.1086/374368

Rhoades JDD, Chanduvi F, Lesch S (1999) Soil salinity assessment. Methods and interpretation of electrical conductivity measurements. FAO Irrigation and Drainage paper 57. FAO Irrig Drain Pap

Roach DA, Smith EF (2020) Life-history trade-offs and senescence in plants. Funct Ecol

34:17–25. https://doi.org/10.1111/1365-2435.13461

Rüger N, Comita LS, Condit R, et al (2018) Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree community. Ecol. Lett. 21:1075–1084

Rzedowski J (1988) Análisis de la distribución geográfica del complejo *Prosopis* (Leguminosae, Mimosoideae) en Norteamérica. Acta Bot Mex 3:7. https://doi.org/10.21829/abm3.1988.566

Sadura I, Janeczko A (2018) Physiological and molecular mechanisms of brassinosteroid-induced tolerance to high and low temperature in plants. Biol Plant 62:601–616. https://doi.org/10.1007/s10535-018-0805-4

Salazar PC, Navarro-Cerrillo RM, Ancajima E, et al (2018) Effect of climate and ENSO events on Prosopis pallida forests along a climatic gradient. Forestry 91:552–562. https://doi.org/10.1093/forestry/cpy014

Salazar PC, Navarro-Cerrillo RM, Cruz G, et al (2019) Variability in growth and biomass allocation and the phenotypic plasticity of seven Prosopis pallida populations in response to water availability. Trees - Struct Funct 33:1409–1422. https://doi.org/10.1007/s00468-019-01868-9

Salguero-Gómez R (2017) Applications of the fast–slow continuum and reproductive strategy framework of plant life histories. New Phytol 213:1618–1624. https://doi.org/10.1111/nph.14289

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. https://doi.org/10.1038/nmeth.2089

Seal CE, Daws MI, Flores J, et al (2017) Thermal buffering capacity of the germination phenotype across the environmental envelope of the Cactaceae. Glob Chang Biol 12:5309-5317. https://doi.org/10.1111/ijlh.12426

Shen Y, Gilbert GS, Li W, et al (2019) Linking Aboveground Traits to Root Traits and Local Environment: Implications of the Plant Economics Spectrum. Front Plant Sci 10:1–12. https://doi.org/10.3389/fpls.2019.01412

Shirke PA, Pathre U V., Sane P V. (2018) Adaptation strategies of two leaf cohorts of Prosopis juliflora produced in spring and monsoon. Photosynthetica 56:468–477. https://doi.org/10.1007/s11099-018-0794-8

Siefert A, Violle C, Chalmandrier L, et al (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol Lett 18:1406–1419. https://doi.org/10.1111/ele.12508

Simão EE, Takaki M, Cardoso VJM (2010) Germination response of Hylocereus setaceus

(Salm-Dyck ex DC.) Ralf Bauer (Cactaceae) seeds to temperature and reduced water potentials. Brazilian J Biol 70:135–144. https://doi.org/10.1590/s1519-69842010000100019

Solarik KA, Messier C, Ouimet R, et al (2018) Local adaptation of trees at the range margins impacts range shifts in the face of climate change. Glob Ecol Biogeogr 27:1507–1519. https://doi.org/10.1111/geb.12829

Sosa L, Llanes A, Reinoso H, et al (2005) Osmotic and specific ion effects on the germination of Prosopis strombulifera. Ann Bot 96:261–267. https://doi.org/10.1093/aob/mci173

Stevens N, Seal CE, Archibald S (2014) Increasing temperatures can improve seedling establishment in arid - adapted savanna trees. 1029–1040. https://doi.org/10.1007/s00442-014-2958-y

Szymańska R, Ślesak I, Orzechowska A, Kruk J (2017) Physiological and biochemical responses to high light and temperature stress in plants. Environ Exp Bot. https://doi.org/10.1016/j.envexpbot.2017.05.002

Torres-Martínez L, Weldy P, Levy M, Emery NC (2017) Spatiotemporal heterogeneity in precipitation patterns explain population-level germination strategies in an edaphic specialist. Ann Bot 119:253–265. https://doi.org/10.1093/aob/mcw161

Trudgill DL, Honek A, Li D, Van Straalen NM (2005) Thermal time - Concepts and utility. Ann Appl Biol 146:1–14. https://doi.org/10.1111/j.1744-7348.2005.04088.x

Usman K, Abu-Dieyeh MH, Al-Ghouti MA (2019) Evaluating the invasive plant, Prosopis juliflora in the two initial growth stages as a potential candidate for heavy metal phytostabilization in metalliferous soil. Environ Pollut Bioavailab 31:145–155. https://doi.org/10.1080/26395940.2019.1585958

van den Wollenberg AL (1977) Redundancy analysis an alternative for canonical correlation analysis. Psychometrika 42:207–219. https://doi.org/10.1007/BF02294050

Venables WN, Ripley BD (1997) Tree-based Methods. pp 413–430

Verbeeck H, Bauters M, Jackson T, et al (2019) Time for a Plant Structural Economics Spectrum. Front For Glob Chang 2:1–5. https://doi.org/10.3389/ffgc.2019.00043

Vergeer P, Kunin WE (2011) Life history variation in Arabidopsis lyrata across its range: Effects of climate, population size and herbivory. Oikos 120:979–990. https://doi.org/10.1111/j.1600-0706.2010.18944.x

Villagra PE (1997) Germination of Prosopis argentina and P . alpataco seeds under saline conditions. 261–267

Villagra PE, Vilela A, Giordano C, Alvarez JA (2010) Ecophysiology of Prosopis Species From the Arid Lands of Argentina: What Do We Know About Adaptation to Stressful Environments? In: Desert Plants. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 321–340

Villar R, Ruiz-Robleto J, Quero JL, et al (2004) Tasas de crecimiento en especies leñosas: aspectos funcionales e implicaciones ecológicas

Villegas-Jiménez De, Rodríguez-Ortiz G, Chávez-Servia Jl, et al (2016) Variación del crecimiento en vivero entre procedencias de Pinus pseudostrobus Lindl. Gayana Botánica 73:113–123. https://doi.org/10.4067/s0717-66432016000100013

Vizcaíno-Palomar N, Fady B, Alía R, et al (2020) The legacy of climate variability over the last century on populations' phenotypic variation in tree height. Sci Total Environ 749:. https://doi.org/10.1016/j.scitotenv.2020.141454

Washitani I (1987) A convenient screening test system and a model for thermal germination responses of wild plant seeds: behaviour of model and real seeds in the system. Plant Cell Environ 10:587–598. https://doi.org/10.1111/1365-3040.ep11604111

Westphal C, Gachón P, Bravo J, et al (2015) The Potential of Algarrobo (Prosopis chilensis (Mol.) Stuntz) for Regeneration of Desertified Soils: Assessing Seed Germination Under Saline Conditions. Environ Manage 56:209–220. https://doi.org/10.1007/s00267-015-0490-4

Woodall CW, Russell MB, Walters BF, et al (2015) Forest production dynamics along a wood density spectrum in eastern US forests. Trees - Struct Funct 29:299–310. https://doi.org/10.1007/s00468-014-1083-1

Xu F, Guo W, Xu W, et al (2009) Leaf morphology correlates with water and light availability: What consequences for simple and compound leaves. Prog Nat Sci 19:1789–1798. https://doi.org/10.1016/j.pnsc.2009.10.001

Xu GQ, Arndt SK, Farrell C (2020) Leaf traits of drought tolerance for 37 shrub species originating from a moisture gradient. Water (Switzerland) 12:. https://doi.org/10.3390/w12061626

Yang D, Zhang YJ, Song J, et al (2019) Compound leaves are associated with high hydraulic conductance and photosynthetic capacity: Evidence from trees in Northeast China. Tree Physiol 39:729–739. https://doi.org/10.1093/treephys/tpy147

Yang Y, Guo Y (2018) Unraveling salt stress signaling in plants. J Integr Plant Biol 60:796–804. https://doi.org/10.1111/jipb.12689

Zimmermann HG (1991) Biological control of mesquite, Prosopis spp. (Fabaceae), in South Africa. Agric Ecosyst Environ 37:175–186. https://doi.org/10.1016/0167-8809(91)90145-N

Tablas

Tabla 1. Sitios de colecta de semillas de las 15 poblaciones *Prosopis laevigata* evaluadas en el presente estudio. Se muestra el nombre, código y estado de cada localidad, así como la ubicación geográfica.

Población	**Código**	**Estado**	**Latitud**	**Longitud**
Matehuala	MAT	San Luis P	23.630211	-100.64014
Huizachal	HUI	Tamaulipas	23.588411	-99.224681
Villa de Arista	VA	San Luis P	22.64391	-100.84521
Charco B	HM	San Luis P	22.550488	-99.805877
Lagos	LAG	Jalisco	21.369511	-101.96226
Peña de B	PÑ	Querétaro	20.745231	-99.947431
Ixmiquilpan	IXM	Hidalgo	20.460455	-99.339331
Novillero	NOV	Guanajuato	20.388887	-101.59178
San Pedro T	SP	Jalisco	20.221381	-103.39535
Cuitzeo	CUI	Michoacán	19.961482	-101.20221
Sayula	SY	Jalisco	19.926994	-103.52829
Tehuixtla	TEH	Morelos	18.586123	-99.263001
Zinacatepec	ZIN	Puebla	18.32423	-97.251811
Santa María	SMA	Oaxaca	17.892532	-97.822939
San Nicolás	SN	Oaxaca	16.843833	-96.779097

Tabla 2.- Variables estudiadas en plantasde 15 poblaciones de *Prosopis laevigata* a través de su distribución en las zonas áridas y semiáridas de México, cultivadas en condiciones de invernadero bajo dos tratamientos de disponibilidad hídrica. Se muestran los grupos de variables, nombre completo, abreviatura y unidades.

	Variable	**Abreviatura**	**Unidades**
Fisiológicas	Fotosíntesis neta	A_N	$\mu mol\ CO_2\ m^{-2}\ s^{-1}$
	Conductancia estomática	g_s	$mol\ H_2O\ m^{-2}\ s^{-1}$
	Eficiencia instantanea en el uso de agua	$A_N/\ g_s$	$\mu mol\ CO_2$ / mmol H_2O
Biomasa y crecimiento	Densidad del tallo	WD	$g\ cm^{-3}$
	Área foliar específica	SLA	$cm^2\ g^{-1}$
	Cociente de área foliar total y la longitud total de raíz	TLA/TRL	$cm\ cm^{-2}$
	Cociente raíz-tallo (longitud)	RL/SL	$cm\ cm^{-2}$
	Cociente raíz-tallo (biomasa)	R:S	$g\ g^{-1}$
	Longitud específica de la raíz	SRL	$g\ cm^{-1}$
	Tasa de crecimiento relativo	RGR	$mm\ day^{-1}$

Tabla 3. Resultados de los ANOVA de dos vías para la comparación de 10 atributos funcionales entre 15 poblaciones de *P. laevigata* a través de su distribución en las zonas áridas y semiáridas de México, cultivadas en condiciones de invernadero bajo dos tratamientos de disponibilidad hídrica: A_N= fotosíntesis neta; g_s= conductancia estomática; $A_N/\ g_s$= Eficiencia del uso del agua instantanea; WD= densidad especifica de la madera; SLA= área foliar especifica; TLA/TRL= cociente de área foliar total y longitud total de raíz; RL/SL= cociente entre el largo de la raíz y parte aérea; R/S= cociente entre el peso seco de la raíz y peso seco de la parte aérea; SRL= longitud específica de la raíz; RGR= Tasa de crecimiento relativo. Nivel de significancia: P<0.05.

Atributo		**Pop**	**Tratamiento**	**Pop*Trat**
A_N	$F_{14,138}$	2.0989	131.7876	0.8413
	P	0.0146*	<0.0001*	0.6303
g_s	$F_{14,138}$	1.2881	43.3422	0.5136
	P	0.221	<0.0001*	0.9288
$A_N/\ g_s$	$F_{14,138}$	0.6531	0.7664	0.7344

	P	0.8245	0.3832	0.7452
RGR	$F_{14,215}$	4.7115	237.5115	1.251
	P	<0.0001*	<0.0001*	0.2421
SLA	$F_{14,215}$	4.9111	249.1928	0.9052
	P	<0.0001*	<0.0001*	0.5542
TLA/TLR	$F_{14,215}$	43.1972	89.7895	6.3406
	P	<0.0001*	<0.0001*	<.0001*
WD	$F_{14,215}$	5.2996	229.7579	1.0583
	P	<.0001*	<.0001*	0.3984
R/S	$F_{14,215}$	3.3264	160.1258	0.4709
	P	<0.0001*	<.00001*	0.9462
RL/SL	$F_{14,215}$	4.0276	233.4623	1.6599
	P	<0.0001*	<0.0001*	0.0673
SRL	$F_{14,215}$	54.5146	68.2488	1.5389
	P	<0.0001*	<0.0001*	0.1009

Tabla 4. Resultados del análisis de redundancia (RDA) para la asociación entre la variación de atributos funcionales, ubicación geografía y variación climática en 15 poblaciones de *P. laevigata* a través de su distribución en las zonas áridas y semiáridas de México,cultivadas bajo condiciones de invernadero en dos tratamientos de disponibilidad hídrica. Para cada tratamiento (a= alta disponibilidad hídrica; b= baja disponibilidad hídrica), se muestran los análisis parciales (pRDA1= efecto de las variables climáticas al controlar efectos geográficos y pRDA2= efecto de la distribución geográfica al controlar la variación climática), así como la proporción de varianza conjunta explicada por los efectos geográficos y climáticos (clima / geografía conjunta). La proporción restringida corresponde a la varianza dividida en relación con la varianza restringida del modelo RDA completo. Nivel de significancia: P<0.05.

a	**Inercia**	**Proporción**	R^2_{adj}	P
Total	7.7337	1	0.182	0.002
Climática	1.82859	0.23645	0.177	0.001
Geográfica	1.66399	0.21516	0.031	0.041
Climática/geográfica conjunta	4.24	0.54	0.026	

b	**Inercia**	**Proporción**	**R^2_{adj}**	***P***
Total	180098	1	0.2408589	0.001
Climática	55757	0.309595	0.2581429	0.001
Geográfica	53856	0.29904	-0.002099	0.41
Climática/geográfica conjunta	70485	0.4121	0.0151847	

Figuras

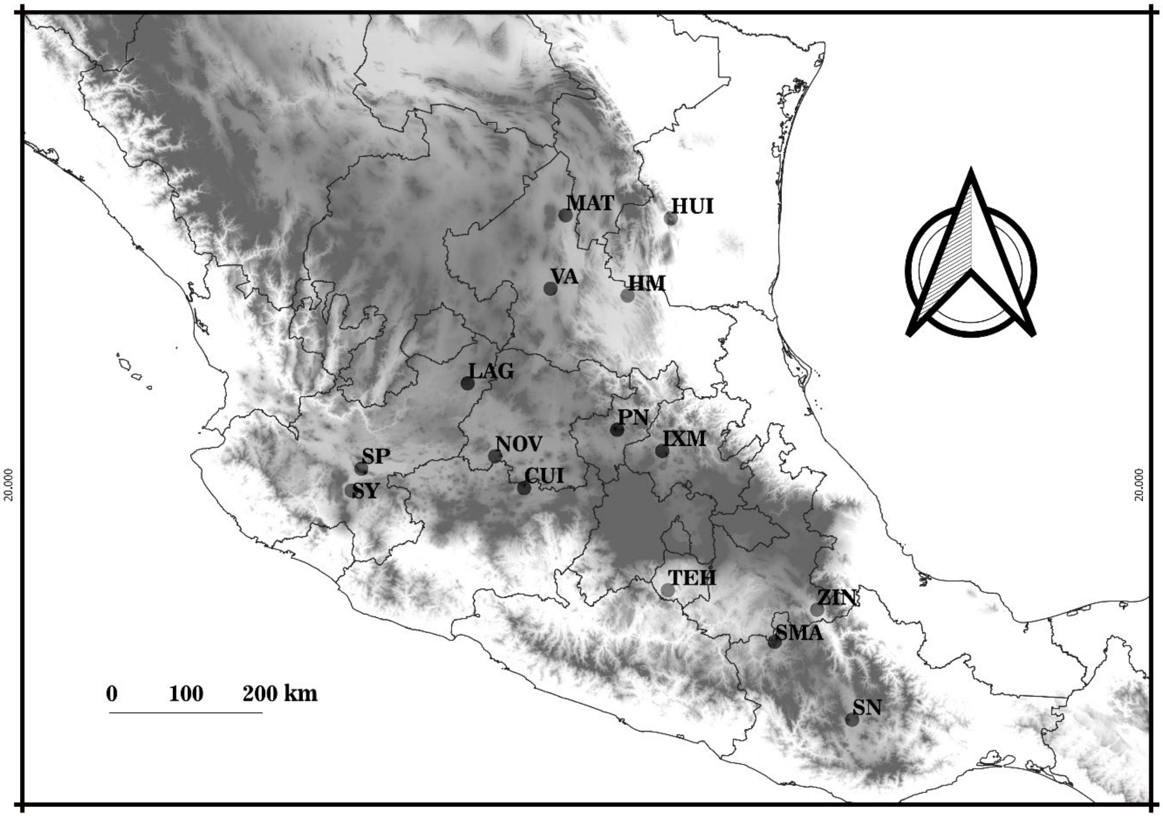


Figura 1. Distribución espacial de las poblaciones colectadas en el presente estudio de *Prosopis laevigata* en las zonas áridas y semiáridas de México. El código de cada población corresponde a la Tabla 1.

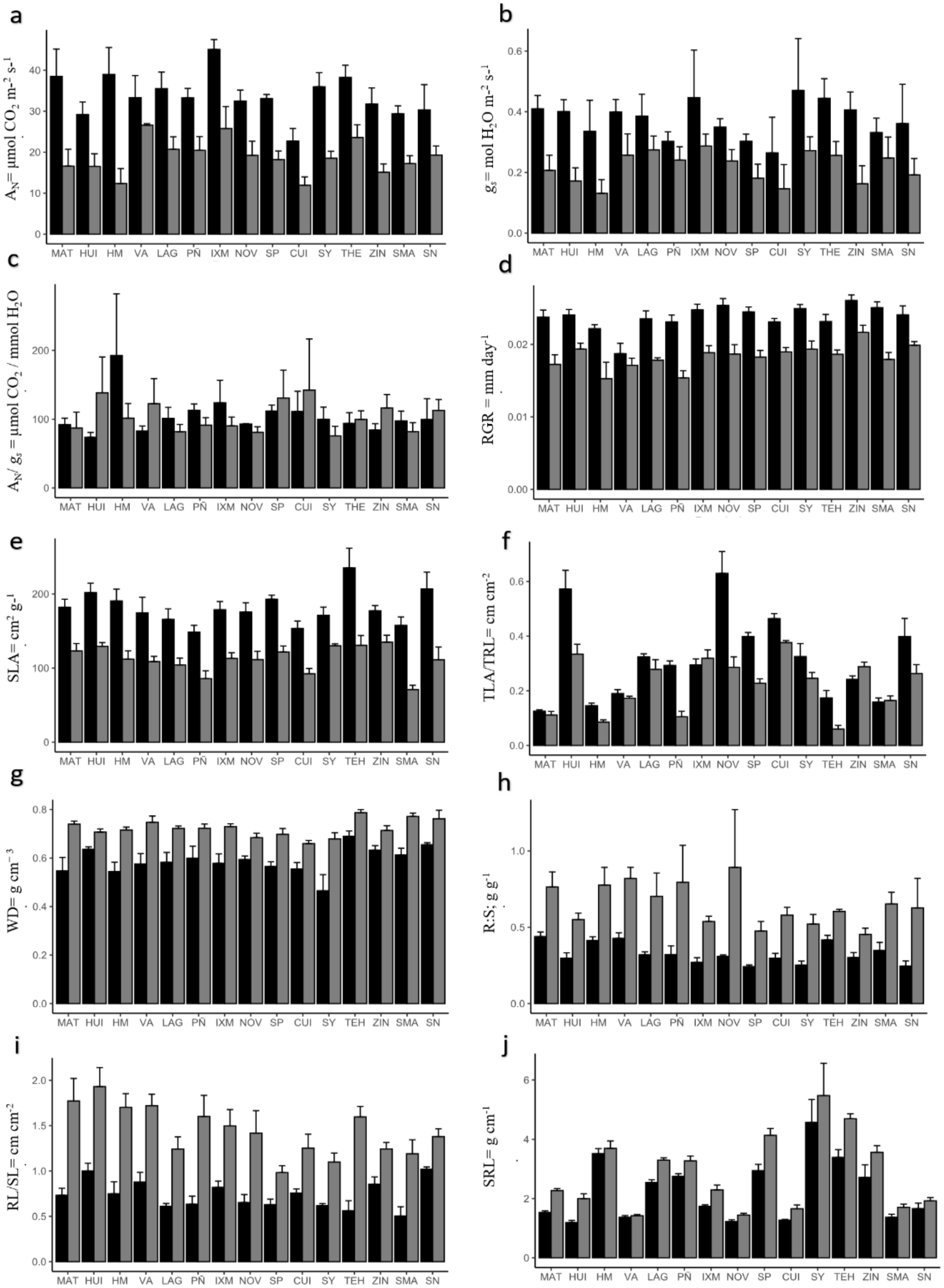

a
A_N= µmol CO_2 m^-2 s^-1
0
10
20
30
40
b
g_s = mol H_2O m^-2 s^-1
0.0
0.2
0.4
0.6
MAT HUI HM VA LAG PÑ IXM NOV SP CUI SY THE ZIN SMA SN
c
A_N/ g_s = µmol CO_2 / mmol H_2O
0
100
200
MAT HUI HM VA LAG PÑ IXM NOV SP CUI SY THE ZIN SMA SN
d
RGR = mm day^-1
0.00
0.01
0.02
MAT HUI HM VA LAG PÑ IXM NOV SP CUI SY TEH ZIN SMA SN
e
SLA= cm^2 g^-1
0
100
200
f
TLA/TRL= cm cm^-2
0.0
0.2
0.4
0.6
MAT HUI HM VA LAG PÑ IXM NOV SP CUI SY TEH ZIN SMA SN
g
WD= g cm^-3
0.0
0.2
0.4
0.6
0.8
h
R:S; g g^-1
0.0
0.5
1.0
MAT HUI HM VA LAG PÑ IXM NOV SP CUI SY TEH ZIN SMA SN
i
RL/SL= cm cm^-2
0.0
0.5
1.0
1.5
2.0
j
SRL= g cm^-1
0
2
4
6
MAT HUI HM VA LAG PÑ IXM NOV SP CUI SY TEH ZIN SMA SN

Figura 2. Atributos de asignación de biomasa, crecimiento y fisiológicos evaluados en las poblaciones de *Prosopis laevigata* cubriendo su area de distribución en las zonas áridas y semiáridas de México, cultivadas bajo condiciones de invernadero y su respuesta a la disponibilidad hídrica alta (barras negras) y baja (barras grises). A_N= fotosíntesis neta; g_s= conductancia estomática; A_N/ g_s= Eficiencia del uso del agua instantanea; WD= densidad especifica de la madera; SLA= área foliar especifica; TLA/TRL= cociente de área foliar total y longitud total de raíz; RL/SL= cociente entre el largo de la raíz y parte aérea; R/S= cociente entre el peso seco de la raíz y peso seco de la parte aérea; SRL= longitud específica de la raíz; RGR= Tasa de crecimiento relativo.

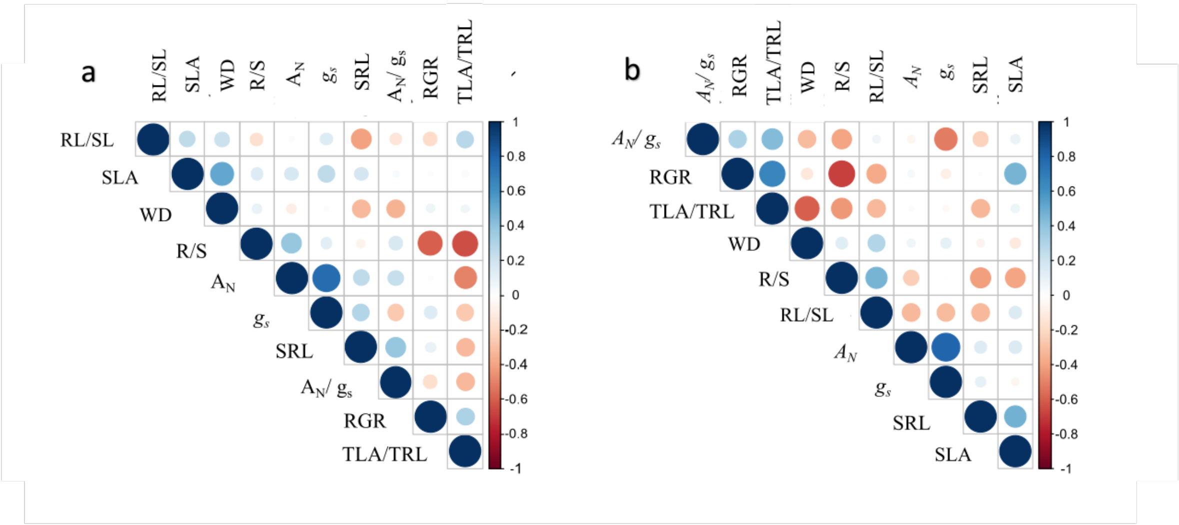


Figura 3. Matriz de correlación bivariado entre atributos funcionales evaluados en 15 poblaciones de *P. laevigata* cubriendo su area de distribución en las zonas áridas y semiáridas de México, cultivadas en condiciones de invernadero bajo disponibilidad hídrica alta (a) y baja (b). A_N= fotosíntesis neta; g_s= conductancia estomática; A_N/g_s= Eficiencia del uso del agua instantanea; WD= densidad especifica de la madera; SLA= área foliar especifica; TLA/TRL= cociente de área foliar total y longitud total de raíz; RL/SL= cociente entre el largo de la raíz y parte aérea; R/S= cociente entre el peso seco de la raíz y peso seco de la parte aérea; SRL= longitud específica de la raíz; RGR= Tasa de crecimiento relativo.

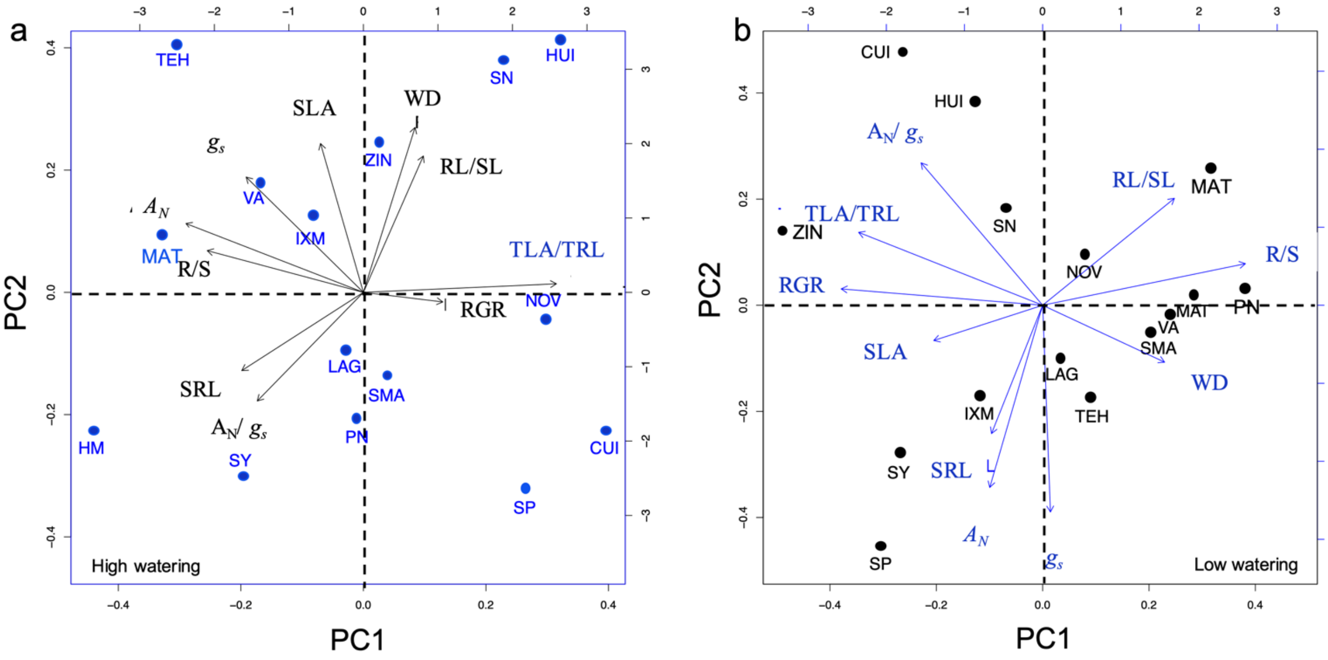


Figura 4. Análisis de componentes principales que muestra los dos ejes de la covariación de atributos en 15 poblaciones *P. laevigata* a través cubriendo su area de distribución en las zonas áridas y semiáridas de México, cultivadas en condiciones de invernadero bajo dos tratamientos de disponibilidad hídrica: a) alta disponibilidad hídrica; b) baja disponibilidad hídrica. A_N= fotosíntesis neta; g_s= conductancia estomática; A_N/ g_s= Eficiencia del uso del agua instantanea; WD= densidad especifica de la madera; SLA= área foliar especifica; TLA/TRL= cociente de área foliar total y longitud total de raíz; RL/SL= cociente entre el largo de la raíz y parte aérea; R/S= cociente entre el peso seco de la raíz y peso seco de la parte aérea; SRL= longitud específica de la raíz; RGR= Tasa de crecimiento relativo.

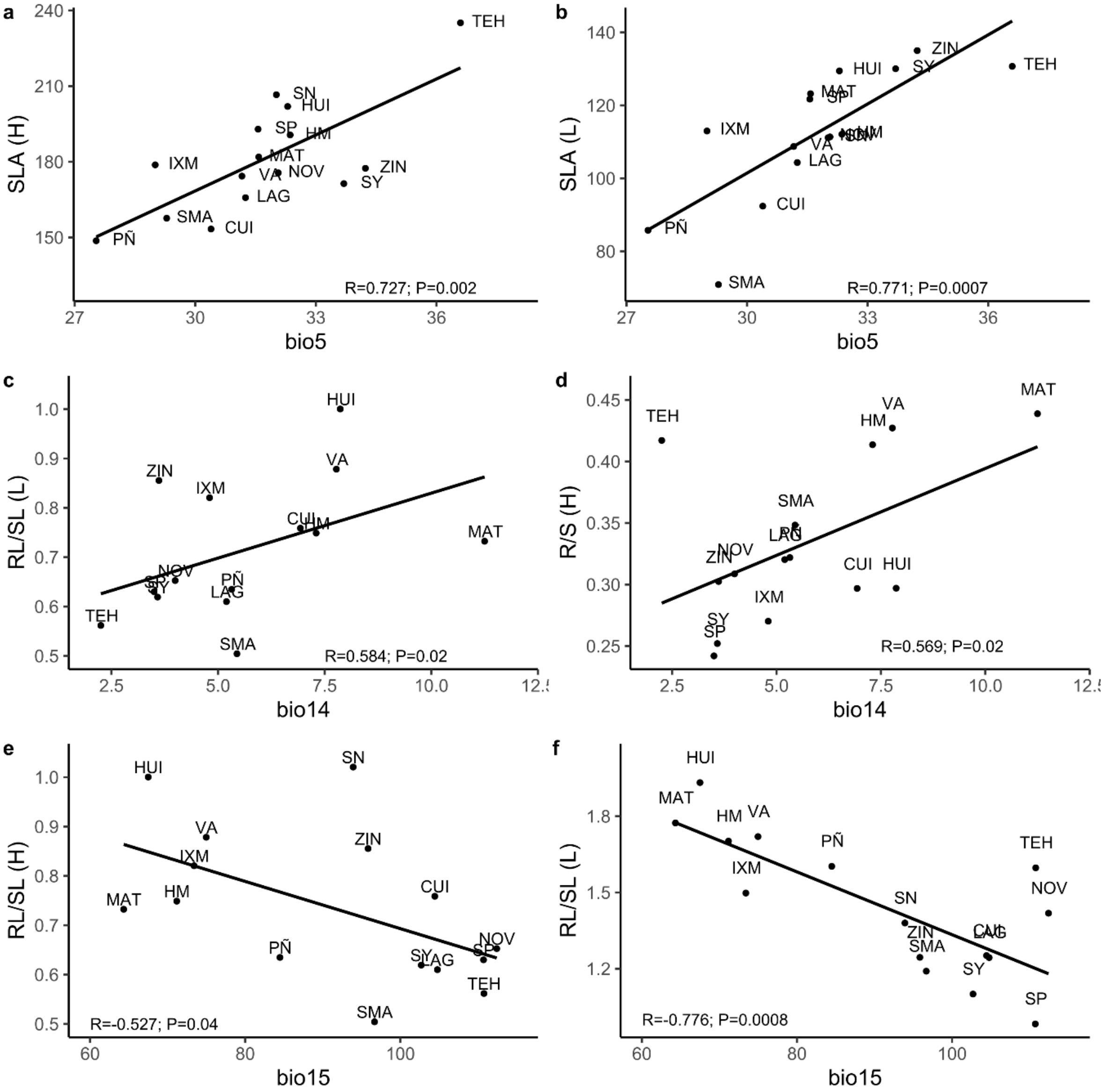


Figura 5. Relación entre atributos funcionales y variables ambientales experimentadas a través de la distribución de 15 poblaciones de *Prosopis laevigata* cubriendo su area de distribución a traves de las zonas áridas y semiáridas en México, cultivadas en condiciones de invernadero bajo dos tratamientos de disponibilidad hídrica: a) Temperatura máxima del mes más cálido (bio5) y área foliar especifica en alta disponibilidad hídrica (SLA (H)); b) Temperatura máxima del mes más cálido (bio5) y área foliar especifica en baja disponibilidad hídrica (SLA (H)); c) Precipitación del mes más seco (bio14) y cociente entre el largo de la raíz y parte aérea en baja disponibilidad hídrica (RL/SL (L)); d) Precipitación del mes más seco (bio14) y cociente entre el peso seco de la raíz y peso seco de la parte aérea en x disponibilidad hídrica (R/S (H)); e) Estacionalidad de las precipitaciones (bio15) y cociente entre el largo de la raíz y parte aérea en alta disponibilidad hídrica (RL/SL (H)); f) Estacionalidad de las precipitaciones (bio15) y cociente entre el largo de la raíz y parte aérea en alta disponibilidad hídrica (RL/SL (H)).

Material suplementario

Tabla S1. Vectores propios representando la correlación entre atributos de 15 poblaciones de *Prosopis laevigata* cubriendo su area de distribución a traves de las zonas áridas y semiáridas en México, cultivadas en condiciones de invernadero bajo dos tratamientos de disponibilidad hídrica, en los dos componentes que explican la mayor proporción de variación en el análisis de componentes principales para cada tratamiento: alta disponibilidad hídrica (a) y baja disponibilidad hídrica (b). El análisis incluyó os atributos: A_N= fotosíntesis neta; g_s= conductancia estomática; A_N/g_s= Eficiencia del uso del agua instantanea; WD= densidad especifica de la madera; SLA= área foliar especifica; TLA/TRL= cociente de área foliar total y longitud total de raíz; RL/SL= cociente entre el largo de la raíz y parte aérea; R/S= cociente entre el peso seco de la raíz y peso seco de la parte aérea; SRL= longitud específica de la raíz; RGR= Tasa de crecimiento relativo.

a	**Atributo**	**PC1 (27.63%)**	**PC2 (19.62%)**
	A_N	0.46	0.21
	g_s	0.31	0.35
	A_N/g_s	0.28	-0.33
	RGR	-0.21	-0.03
	WD	-0.13	0.51
	SLA	0.11	0.46
	TLA/TRL	-0.50	0.03
	RL/SL	-0.16	0.42
	R/S	0.41	0.13
	SRL	0.32	-0.24
b	**Atributo**	**PC1 (30.6%)**	**PC2 (23.25%)**
	A_N	0.12	0.49
	g_s	-0.02	0.56
	A_N/g_s	0.29	-0.39
	RGR	0.47	-0.04
	WD	-0.29	0.15
	SLA	0.26	0.10
	TLA/TRL	0.43	-0.20
	RL/SL	-0.31	-0.29
	R/S	-0.48	-0.11
	SRL	0.12	0.35

Tabla S2. Correlaciones pareadas entre atributos de 15 poblaciones de *Prosopis laevigata* cubriendo su area de distribución a traves de las zonas áridas y semiáridas en México, cultivadas en condiciones de invernadero en diferentes niveles de disponibilidad hídrica: alta disponibilidad hídrica (a) y baja disponibilidad hídrica (b). El análisis incluyó los atributos: A_N= fotosíntesis neta; g_s= conductancia estomática; A_N/g_s= Eficiencia instantanea del uso del agua; WD= densidad especifica de la madera; SLA= área foliar especifica; TLA/TRL= cociente de área foliar total y longitud total de raíz; RL/SL= cociente entre el largo de la raíz y parte aérea; R/S= cociente entre el peso seco de la raíz y peso seco de la parte aérea; SRL= longitud específica de la raíz; RGR= Tasa de crecimiento relativo.

a) alta	***Atributos***		***R***	***P***	***b) baja***	***Atributos***		***R***	***P***
	A_N	g_s	0.89	0.000		A_N	g_s	0.83	0.003
	RGR	TLA/TRL	0.84	0.003		RGR	R/S	-0.81	0.004
	RL/SL	R/S	0.73	0.018		R/S	TLA/TRL	-0.86	0.002
	A_N/g_s	TLA/TRL	0.71	0.020		AN	TLA/TRL	-0.81	0.004
	SLA	SRL	0.65	0.042		RL/SL	SRL	-0.71	0.022
	RL/SL	A_N	-0.63	0.050		WD	SLA	0.64	0.047
	g_s	A_N/g_s	-0.66	0.040		WD	SRL	-0.63	0.049
	R/S	TLA/TRL	-0.67	0.035		WD	A_N/g_s	-0.62	0.054
	SLA	R/S	-0.67	0.034		R/S	A_N	0.62	0.056
	WD	TLA/TRL	-0.81	0.004		SRL	A_N/g_s	0.59	0.071
	RGR	R/S	-0.90	0.000		AN/gs	TLA/TRL	-0.56	0.090
	RL/SL	RGR	-0.62	0.058		RGR	TLA/TRL	0.56	0.093
	RGR	A_N/g_s	0.60	0.066		SRL	TLA/TRL	-0.54	0.106
	WD	A_N/g_s	-0.60	0.066		SRL	A_N	0.47	0.166
	SLA	RGR	0.60	0.068		g_s	TLA/TRL	-0.47	0.168
	WD	RGR	-0.56	0.092		RL/SL	A_N/g_s	-0.46	0.183
	RL/SL	TLA/TRL	-0.54	0.106		RL/SL	TLA/TRL	0.46	0.184

R/S	A_N/g_s	-0.52	0.123	RL/SL	WD	0.44	0.205
WD	R/S	0.50	0.138	RGR	A_N/g_s	-0.40	0.256
RL/SL	g_s	-0.48	0.156	R/S	A_N/g_s	0.37	0.289
R/S	SRL	-0.48	0.162	SRL	g_s	0.35	0.317
RL/SL	WD	0.47	0.172	WD	A_N	-0.35	0.319
RL/SL	SRL	-0.44	0.201	AN	A_N/g_s	0.31	0.384
SRL	A_N	0.36	0.302	RGR	A_N	-0.30	0.394
R/S	A_N	-0.32	0.368	R/S	g_s	0.28	0.441
WD	SLA	-0.32	0.373	RL/SL	SLA	0.27	0.448
AN	A_N/g_s	-0.31	0.389	WD	TLA/TRL	0.26	0.465
SRL	g_s	0.27	0.443	RL/SL	A_N	-0.25	0.486
SRL	$\mathrm{A_N}/g_s$	-0.27	0.451	SLA	R/S	0.24	0.513
SLA	TLA/TRL	0.25	0.490	SLA	RGR	-0.23	0.529
SLA	$\mathrm{A_N}/g_s$	0.25	0.491	RL/SL	R/S	-0.22	0.545
RL/SL	SLA	-0.22	0.543	g_s	A_N/g_s	-0.19	0.597
SRL	TLA/TRL	-0.21	0.559	SLA	A_N/gs	-0.17	0.634
WD	g_s	0.19	0.602	SLA	g_s	0.17	0.637
gs	TLA/TRL	-0.18	0.623	RL/SL	RGR	-0.16	0.660
RGR	g_s	-0.17	0.635	WD	g_s	-0.14	0.690
RGR	SRL	0.17	0.648	SLA	TLA/TRL	-0.13	0.716
SLA	g_s	-0.16	0.653	R/S	SRL	0.13	0.722
RGR	A_N	0.10	0.788	SLA	AN	0.06	0.879
RL/SL	A_N/g_s	-0.08	0.825	RGR	SRL	0.05	0.888

SLA	A_N	0.07	0.847	RL/SL	g_s	-0.04	0.908
A_N	TLA/TRL	0.04	0.902	SLA	SRL	-0.04	0.919
WD	SRL	-0.03	0.925	RGR	g_s	0.02	0.955
R/S	g_s	0.01	0.981	WD	RGR	0.01	0.981
WD	A_N	0.00	0.998	WD	R/S	0.01	0.986

Discusión General y Conclusiones

Las especies del género *Prosopis* representan elementos de gran valor ecológico y cultural a través de las zonas áridas y semiáridas en que se distribuyen (Felker, 2009; Golubov et al., 2001; Pasiecznik et al., 2002; Rzedowski, 1988; Villagra et al., 2010). Desde las primeras fases de ocupación del continente americano, los colonizadores identificaron el potencial de aprovechamiento de las especies del género, las cuales representan (principalmente las especies de la sección Algarobia) recursos agroforestales multipropósito (Pasiecznik et al., 2002). Desde una perspectiva ecológica, se consideran especies clave dada la gran cantidad de interacciones que mantienen con animales y otras plantas, llegando a describirse como islas de diversidad y fertilidad a través distribución (Golubov et al., 2001; Felker, 2009; Perroni-Ventura et al. 2010; Villagra et al., 2010; Cruz-Rodríguez et al. 2017; García-Sánchez et al. 2012; Bernal-Ramírez et al. 2019). Por otra parte, dado su alto potencial de aprovechamiento, algunas especies han sido introducidas en regiones áridas fuera de su distribución natural, muchas de las cuales se han convertido en especies invasoras que frecuentemente amenazan la estabilidad ecosistémica de los lugares donde se han introducido (Alvarez et al., 2017; Oliveira et al., 2014; Palacios et al., 2001; Pasiecznik et al., 2002; Shirke et al., 2018; Zimmermann, 1991). Consecuentemente, las especies del género *Prosopis* representan modelos idóneos para abordar cuestiones acerca de la biogeografía histórica, interacciones ecológicas, así como estrategias funcionales y fisiológicas a través de las zonas áridas.

Aunque las especies del genero *Prosopis* no han sido ajenas al estudio de aproximaciones filogenéticas, microevolutivas, fisiológicas y funcionales, principalmente desde la finales del siglo XX (Catalano et al., 2008; Cony and Trione, 1998; Rzedowski, 1988; Villagra, 1997; Zimmermann, 1991), en años recientes se ha incrementado notablemente la atención a estas especies con afinidades termo xerófilas, de gran importancia bajo los escenarios actuales de degradación ambiental y cambio climático (Bessega et al., 2019, 2016, 2015; Castillo et al., 2021; Moncada et al., 2019; Salazar et al., 2019, 2018; Westphal et al., 2015; Fontana et al., 2018). En el presente estudio se exploraron algunos aspectos relevantes sobre la historia natural de *Prosopis laevigata* con énfasis en la diversidad genética neutral y aspectos funcionales y fisiológicos de la germinación, primeras fases del establecimiento, así como sus estrategias adaptativas a la sequía.

En el primer capítulo, mediante el uso de marcadores moleculares de núcleo y cloroplasto se contribuyó a comprender la historia evolutiva reciente de *Prosopis laevigata*. Se detectaron valores relativamente altos de diversidad genética, baja estructura y una gran cantidad de alelos raros, además de una amplia evidencia de una expansión poblacional "reciente" datada ca. 140 Ka durante el último interglacial (Contreras-Negrete et al., 2021). De manera interesante, los patrones latitudinales de diversidad genética registrados: al norte de la distribución las poblaciones son genéticamente más diversas, lo que permite proponer que el límite sur original de la distribución está desapareciendo mientras el límite norte muestra un proceso, potencialmente activo hasta el presente, de expansión poblacional.

Estos resultados, indirectamente manifestaron la existencia de estrategias funcionales que han promovido la persistencia y dominancia de la especie a lo largo de su distribución actual (Golubov et al., 2001; Palacios et al., 2001; Pasiecznik et al., 2002; Villagra et al., 2010). En el capítulo dos, se abordó la respuesta de la germinación de *P. laevigata* a la temperatura, salinidad y déficit hídrico. La germinación representa el mayor cuello de botella poblacional de las especies vegetales (Baskin and Baskin, 2014; Donohue et al., 2010), por lo cual, la principal predicción fue la existencia de correlaciones entre las respuestas germinativas y la variación ambiental experimentada en los sitios de origen. A partir del modelaje del termo tiempo (Thermal Time models) para tratamientos de temperatura y tiempo hídrico (Hydrotime y Osmotime models) para tratamientos de déficit hídrico y salinidad (Washitani 1987; Alvarado and Bradford 2002, 2005; Trudgill et al. 2005; Cochrane 2020), se encontró que la germinación fue más sensible al estrés hídrico que a la salinidad y las temperaturas extremas. Asimismo, se detectaron dos ejes principales de covariación de los atributos; uno definido por la tolerancia de la germinación al estrés hídrico y salino versus la velocidad de germinación y el otro definido por la tolerancia a temperaturas extremas (Reich, 2014; Reich et al., 2003; Salguero-Gómez, 2017). En general, las poblaciones con mayor capacidad para germinar bajo estrés hídrico, salinidad y temperaturas extremas, habitan áreas más cálidas y salinas.

Asimismo, en el tercer capítulo se evaluó la existencia de estrategias diferenciales en plántulas durante las primeras fases del establecimiento, a través de la evaluación de atributos de asignación de biomasa y crecimiento (López-Iglesias et al., 2014; Pérez-Harguindeguy et al., 2013; Salazar et al., 2019). De esta manera, se hipotetizó la existencia de asignación diferencial de biomasa y en el crecimiento en plántulas de *P. laevigata*, asociados a la variación ambiental experimentada en las localidades de origen. En general, las estrategias diferenciales en la asignación de recursos a los tejidos subterráneos y aéreos están fuertemente influenciados por la temperatura, además de seguir tendencia geográfica: una estrategia evasiva en la que las plántulas asignan más recursos a la raíz para promover una mayor área de absorción por unidad de biomasa (Dias et al., 2017; Díaz et al., 2016;

Poorter et al., 2015) en las poblaciones del sur de la distribución y una estrategia de explotación, invirtiendo recursos en crecimiento para aprovechar pulsos de condiciones favorables, en las poblaciones del norte.

Finalmente, en el cuarto capítulo se evaluó el efecto del déficit hídrico en la respuesta funcional (López-Iglesias et al., 2014; Pérez-Harguindeguy et al., 2013). Para este estudio, se hipotetizó que los atributos morfológicos y fisiológicos evaluados en poblaciones provenientes de zonas áridas sería menos sensible a la sequía o en comparación con poblaciones de zonas menos áridas (semiáridas). Las diferencias en los atributos fisiológicos de biomasa y crecimiento entre las poblaciones de *P. laevigata* revelan diferentes estrategias de esta especie para afrontar la sequía a través de su distribución. De manera interesante, la respuesta de *P. laevigata* a la sequía se expresó como un eje funcional de explotación-tolerancia a través de un continuo rápido-lento para adquirir recursos: algunas poblaciones generan tejidos poco densos, pero con altas tasas de adquisición recursos (explotación-rápido; p.ej. CUI, SP, NOV), mientras que otras plantas desarrollan tejidos densos y longevos, bajo una tasa lenta de adquisición de recursos (tolerante-lento; p.ej. MAT, HM, VA) (Cavender-Bares and Ramírez-Valiente, 2017; Ramírez-Valiente et al., 2011; Reich, 2014; Reich et al., 2003; Salguero-Gómez, 2017). Asimismo, los resultados evidenciaron que bajo condiciones hídricas óptimas, los patrones de temperatura guían las estrategias funcionales, pero al acentuarse la sequía, los patrones de precipitación de las poblaciones de origen determinan el eje funcional de explotación-tolerancia (Cavender-Bares and Ramírez-Valiente, 2017; Eckert et al., 2015; Krushelnycky et al., 2020; Mantel and Sweigart, 2019; Ramírez-Valiente et al., 2017)

En general, los diferentes enfoques de investigacion sobre la biologia e historia natural de *Prosopis laevigata* abordados en el presente estudio indican que:

- La distribucion historica de *Prosopis laevigata* ha mostrado un constante avance hacia el norte de Mexico (120 ka), evidenciado en patrones de diversidad genética (núcleo y cloroplasto), en los cuales las poblaciones del norte en la actualidad albergan los mayores niveles de diversidad y mayores números efectivos poblacionales.
- La germinación de las poblaciones muestra mayor tolerancia a la temperatura y salinidad que a la escasez de agua. La variacion esta determina por la tolerancia al estrés hídrico y salino frente a la velocidad de germinación, y por la amplia tolerancia a temperaturas extremas. Ademas, laa diferenciación en la germinación entre las poblaciones está relacionada con los gradientes ambientales experimentados por la especie a lo largo de la distribucíon.
- Durante el establecimiento existen estrategias diferenciales en la asignación de recursos a los tejidos subterráneos y aéreos, fuertemente influenciadas por la temperatura y la humedad del suelo y del medio ambiente y siguiendo una tendencia geográfica: una estrategia de evasión en la que las plántulas asignan más recursos a la raíz en las poblaciones al sur, y una estrategia de explotación, invirtiendo recursos en el crecimiento de los tejidos aéreos para aprovechar los pulsos de condiciones favorables, como se observa en las poblaciones del norte.
- Bajo sequia se manifiestan diferencias morfológicas y fisiológicas entre las poblaciones de *P. laevigata*, que se pueden interpretar como estrategias para afrontar la escasez hídrica a través de su distribución. En condiciones óptimas de

disponibilidad hídrica, los patrones de temperatura guían las estrategias funcionales; sin embargo, bajo condiciones de sequía, los patrones de precipitación de las localidades de origen determinan la expresión de los rasgos funcionales a lo largo del eje de explotación-tolerancia.

En conjunto los resultados de esta tesis proporcionan evidencias sólidas acerca de los patrones de adaptación local existentes a nivel de germinación, asignación de biomasa y respuestas funcionales a la sequía en las poblaciones de *P. laevigata* en México. Aún al abordar diferentes enfoques metodológicos los resultados reportados son consistentes: *Prosopis laevigata* es una especie genéticamente diversa, que ha sufrido una expansión poblacional reciente. Además, la diversidad genética muestra una marcada relación con las evidencias funcionales encontradas en las diferentes aproximaciones: las poblaciones hacia el norte de su distribución en México muestran un desempeño mayor a nivel de germinación, producen plántulas con mejores características adaptativas (p.ej. mayores valore de DQI), así como estrategias funcionales asociadas al sitio de origen de las poblaciones, como se demostró bajo el experimento de disponibilidad hídrica (p.ej. MAT, HM, VA). Estas características, además de su gran importancia ecológica a través de su distribución, pueden promover que la especie se vuelva más común y aumente su área de distribución , principalmente hacia el norte, en escenarios de cambio climático como lo proponen Flores et al. (2017). Por lo tanto, *P. laevigata* representa un modelo ideal para la evaluación de los efectos de un medio ambiente cambiante sobre la dinámica ecológica de especies de zonas áridas y semiáridas, así como un recurso altamente explotable en áreas altamente empobrecidas que ocupan estás regiones de México. En este sentido, esta tesis ofrece información relevante sobre los patrones históricos, ecológicos y ambientales que han dado forma a la historia biogeográfica y evolutiva de las zonas áridas y semiáridas de México.

Referencias

Alvarado, V., Bradford, K.J., 2005. Hydrothermal time analysis of seed dormancy in true (botanical) potato seeds. Seed Sci. Res. 15, 77–88. https://doi.org/10.1079/ssr2005198

Alvarado, V., Bradford, K.J., 2002. A hydrothermal time model explains the cardinal temperatures for seed germination. Plant, Cell Environ. 25, 1061–1069. https://doi.org/10.1046/j.1365-3040.2002.00894.x

Alvarez, M., Leparmarai, P., Heller, G., Becker, M., 2017. Recovery and germination of Prosopis juliflora (Sw .) DC seeds after ingestion by goats and cattle. Arid L. Res. Manag. 31, 71–80. https://doi.org/10.1080/15324982.2016.1234521

Baskin, C.C., Baskin, J.M., 2014. Biogeographical and Evolutionary Aspects of Seed Dormancy, Seeds. https://doi.org/10.1016/b978-0-12-416677-6.00012-3

Bessega, C., Cony, M., Saidman, B.O., Aguiló, R., Villagra, P., Alvarez, J.A., Pometti, C., Vilardi, J.C., 2019. Genetic diversity and differentiation among provenances of Prosopis flexuosa DC (Leguminosae) in a progeny trial: Implications for arid land restoration. For. Ecol. Manage. 443, 59–68. https://doi.org/10.1016/j.foreco.2019.04.016

Bessega, C., Pometti, C., Ewens, M., Saidman, B.O., Vilardi, J.C., 2015. Evidences of local adaptation in quantitative traits in *Prosopis alba* (Leguminosae). Genetica 143, 31–44. https://doi.org/10.1007/s10709-014-9810-5

Bessega, C., Pometti, C.L., Ewens, M., Saidman, B.O., Vilardi, J.C., 2016. Fine-scale spatial genetic structure analysis in two Argentine populations of Prosopis alba (Mimosoideae) with different levels of ecological disturbance. Eur. J. For. Res. 135, 495–505. https://doi.org/10.1007/s10342-016-0948-9

Bernal-Ramírez, Luis Alberto, José Alejandro Zavala-Hurtado, Monserrat Jiménez, Zenón Cano-Santana, and Juan Fornoni. 2019. “Los Microcosmos de Prosopis Laevigata Albergan Una Alta Diversidad Florística En El Valle de Zapotitlán, Puebla.” Revista Mexicana de Biodiversidad 90.

Cruz-Rodríguez, Juan Antonio, Edmundo García-Moya, Juan Tenorio Frías-Hernández, Genaro Montesinos-Silva, and José Luis Flores-Flores. 2017. “Influencia de Los Mezquites En La Composición y Cobertura de La Vegetación Herbácea de Un Agostadero Semiárido Del Norte de Guanajuato.” Botanical Sciences 30(61):21.

Castillo, M.L., Schaffner, U., Van Wilgen, B.W., Montaño, N.M., Bustamante, R.O., Cosacov, A., Mathese, M.J., Le Roux, J.J., 2021. Genetic insights into the globally invasive and taxonomically problematic tree genus *Prosopis*. AoB Plants 13, 1–13. https://doi.org/10.1093/aobpla/plaa069

Catalano, S.A., Vilardi, J.C., Tosto, D., Saidman, B.O., 2008. Molecular phylogeny and diversification history of *Prosopis* (Fabaceae: Mimosoideae). Biol. J. Linn. Soc. 93, 621–640. https://doi.org/10.1111/j.1095-8312.2007.00907.x

Cavender-Bares, J., Ramírez-Valiente, J.A., 2017. Physiological Evidence from Common Garden Experiments for Local Adaptation and Adaptive Plasticity to Climate in American Live Oaks (Quercus Section Virentes): Implications for Conservation Under Global Change 107–135. https://doi.org/10.1007/978-3-319-69099-5_4

Cochrane, J.A., 2020. Thermal requirements underpinning germination allude to risk of species decline from climate warming. Plants 9, 796. https://doi.org/10.3390/plants9060796

Contreras-Negrete, G., Letelier, L., Piña-Torres, J., González-Rodríguez, A., 2021. Genetic structure, phylogeography and potential distribution modeling suggest a population expansion in the mesquite Prosopis laevigata since the last interglacial. Plant Syst. Evol. 307, 1–18. https://doi.org/10.1007/s00606-021-01744-5

Cony, M.A., Trione, S.O., 1998. Inter- and intraspecific variability in Prosopis flexuosa and P. chilensis: Seed germination under salt and moisture stress. J. Arid Environ. 40, 307–317. https://doi.org/10.1006/jare.1998.0448

Dias, A.T.C., Cornelissen, J.H.C., Berg, M.P., 2017. Litter for life: assessing the multifunctional legacy of plant traits. J. Ecol. 105, 1163–1168. https://doi.org/10.1111/1365-2745.12763

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

Donohue, K., Rubio De Casas, R., Burghardt, L., Kovach, K., Willis, C.G., 2010. Germination, postgermination adaptation, and species ecological ranges. Annu. Rev. Ecol. Evol. Syst. 41, 293–319. https://doi.org/10.1146/annurev-ecolsys-102209-144715

Eckert, A.J., Maloney, P.E., Vogler, D.R., Jensen, C.E., Mix, A.D., Neale, D.B., 2015. Local adaptation at fine spatial scales: an example from sugar pine (Pinus lambertiana, Pinaceae). Tree Genet. Genomes 11. https://doi.org/10.1007/s11295-015-0863-0

Felker, P., 2009. Unusual physiological properties of the arid adapted tree legume Prosopis and their applications in developing countries. Perspect. Biophys. plant Ecophysiol. A … 221–255.

Fontana ML, Pérez VR, Luna CV (2018) Evolutive characteristics of Prosopis spp.: Cytogenetic, genetic and hybridizations. Rodriguesia 69:409–421. https://doi.org/10.1590/2175-7860201869212

Flores, J., Pérez-Sánchez, R.M., Jurado, E., 2017. The combined effect of water stress and temperature on seed germination of Chihuahuan Desert species. J. Arid Environ. 146, 95–98. https://doi.org/10.1016/j.jaridenv.2017.07.009

García-Sánchez, Rosalva, Sara Lucía Camargo-Ricalde, Edmundo García-Moya, Mario Luna-Cavazos, Angélica Romero-Manzanares, and Noé Manuel Montaño. 2012. "Prosopis Laevigata and *Mimosa Biiincifera* (Leguminosae), Jointly Influence Plant Diversity and Soil Fertility of a Mexican Semiarid Ecosystem." Revista de Biologia Tropical 60(1):87–103.

Golubov, J., Mandujano, M.C., Eguiarte, L.E., 2001. La paradoja de mezquites (*Prosopis spp.*): La invasión de especies o potenciadores de la biodiversidad? Bot. Sci. 30, 23. https://doi.org/10.17129/botsci.1644

Krushelnycky, P.D., Felts, J.M., Robichaux, R.H., Barton, K.E., Litton, C.M., Brown, M.D., 2020. Clinal variation in drought resistance shapes past population declines and future management of a threatened plant. Ecol. Monogr. 90, 1–22. https://doi.org/10.1002/ecm.1398

López-Iglesias, B., Villar, R., Poorter, L., 2014. Functional traits predict drought performance and distribution of mediterranean woody species. Acta Oecologica 56, 10–18. https://doi.org/10.1016/j.actao.2014.01.003

Mantel, S.J., Sweigart, A.L., 2019. Divergence in drought-response traits between sympatric species of Mimulus. Ecol. Evol. 9, 10291–10304. https://doi.org/10.1002/ece3.5549

Moncada, X., Plaza, D., Stoll, A., Payacan, C., Seelenfreund, D., Martínez, E., Bertin, A., Squeo, F.A., 2019. Genetic diversity and structure of the vulnerable species prosopis chilensis (Molina) Stuntz in the Coquimbo region, Chile. Gayana - Bot. 76, 91–104. https://doi.org/10.4067/S0717-66432019000100091

Oliveira, M.T., Matzek, V., Medeiros, C.D., Rivas, R., Falcão, H.M., Santos, M.G., 2014.

Stress tolerance and ecophysiological ability of an invader and a native species in a seasonally dry tropical forest. PLoS One 9. https://doi.org/10.1371/journal.pone.0105514

Palacios, a, Pasiecznik, N., Felker, P., Harris, P., Harsh, L., Cruz, G., Tewari, J., Cadoret, K., Maldonado, L., Miranda, R.D.Q., Correia, R.M., De Almeida-Cortez, J.S., Pompelli, M.F., Flores, J., Briones, O., Simão, E.E., Takaki, M., Cardoso, V.J.M., Jordan, G.L., Haferkamp, M.R., Batlla, D., Benech-Arnold, R.L., 2001. A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy. Seed Sci. Res. 25, 147–158. https://doi.org/10.1017/S0960258514000452

Pasiecznik, N., Felker, P., Harris, P., Harsh, L., Cruz, G., Tewari, J., Cadoret, K., Maldonado, L., 2002. The’Prosopis juliflora’-’Prosopis pallida’complex: a monograph. For. Trees Livelihoods 12, 229–229.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167. https://doi.org/10.1071/BT12225

Perroni-Ventura, Yareni, Carlos Montaña, and Felipe García-Oliva. 2010. “Carbon-Nitrogen Interactions in Fertility Island Soil from a Tropical Semi-Arid Ecosystem.” Functional Ecology 24(1):233–42.

Poorter, H., Jagodzinski, A.M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., Usoltsev, V.A., Buckley, T.N., Reich, P.B., Sack, L., 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. New Phytol. 208, 736–749. https://doi.org/10.1111/nph.13571

Ramírez-Valiente, J.A., Center, A., Sparks, J.P., Sparks, K.L., Etterson, J.R., Longwell, T., Pilz, G., Cavender-Bares, J., 2017. Population-level differentiation in growth rates and leaf traits in seedlings of the neotropical live oak quercus oleoides grown under natural and manipulated precipitation regimes. Front. Plant Sci. 8, 1–14. https://doi.org/10.3389/fpls.2017.00585

Ramírez-Valiente, J.A., Valladares, F., Huertas, A.D., Granados, S., Aranda, I., 2011. Factors affecting cork oak growth under dry conditions: Local adaptation and contrasting additive genetic variance within populations. Tree Genet. Genomes 7, 285–295. https://doi.org/10.1007/s11295-010-0331-9

Reich, P.B., 2014. The world-wide “fast-slow” plant economics spectrum: A traits manifesto. J. Ecol. 102, 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., Walters, M.B., 2003. The evolution of plant functional variation: Traits, spectra, and strategies. Int. J. Plant Sci. 164. https://doi.org/10.1086/374368

Rzedowski, J., 1988. Análisis de la distribución geográfica del complejo Prosopis (Leguminosae, Mimosoideae) en Norteamérica. Acta Bot. Mex. 3, 7. https://doi.org/10.21829/abm3.1988.566

Salazar, P.C., Navarro-Cerrillo, R.M., Ancajima, E., Duque Lazo, J., Rodríguez, R., Ghezzi, I., Mabres, A., 2018. Effect of climate and ENSO events on Prosopis pallida forests along a climatic gradient. Forestry 91, 552–562. https://doi.org/10.1093/forestry/cpy014

Salazar, P.C., Navarro-Cerrillo, R.M., Cruz, G., Grados, N., Villar, R., 2019. Variability in growth and biomass allocation and the phenotypic plasticity of seven Prosopis pallida populations in response to water availability. Trees - Struct. Funct. 33, 1409–1422. https://doi.org/10.1007/s00468-019-01868-9

Salguero-Gómez, R., 2017. Applications of the fast–slow continuum and reproductive strategy framework of plant life histories. New Phytol. 213, 1618–1624. https://doi.org/10.1111/nph.14289

Shirke, P.A., Pathre, U. V., Sane, P. V., 2018. Adaptation strategies of two leaf cohorts of Prosopis juliflora produced in spring and monsoon. Photosynthetica 56, 468–477. https://doi.org/10.1007/s11099-018-0794-8

Trudgill, D.L., Honek, A., Li, D., Van Straalen, N.M., 2005. Thermal time - Concepts and utility. Ann. Appl. Biol. 146, 1–14. https://doi.org/10.1111/j.1744-7348.2005.04088.x

Villagra, P.E., 1997. Germination of Prosopis argentina and P. alpataco seeds under saline conditions. J. Arid Environ. 37, 261–267. https://doi.org/10.1006/jare.1997.0275

Villagra, P.E., Vilela, A., Giordano, C., Alvarez, J.A., 2010. Ecophysiology of Prosopis Species From the Arid Lands of Argentina: What Do We Know About Adaptation to Stressful Environments?, in: Desert Plants. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 321–340. https://doi.org/10.1007/978-3-642-02550-1_15

Washitani, I., 1987. A convenient screening test system and a model for thermal germination responses of wild plant seeds: behaviour of model and real seeds in the system. Plant. Cell Environ. 10, 587–598. https://doi.org/10.1111/1365-3040.ep11604111

Westphal, C., Gachón, P., Bravo, J., Navarrete, C., Salas, C., Ibáñez, C., 2015. The

Potential of algarrobo (Prosopis chilensis (Mol.) Stuntz) for regeneration of desertified soils: Assessing seed germination under saline conditions. Environ. Manage. 56, 209–220. https://doi.org/10.1007/s00267-015-0490-4

Zimmermann, H.G., 1991. Biological control of mesquite, Prosopis spp. (Fabaceae), in South Africa. Agric. Ecosyst. Environ. 37, 175–186. https://doi.org/10.1016/0167-8809(91)90145-N

ANEXO:

DIFFERENTIATION IN SEED MASS AND SEEDLING BIOMASS ALLOCATION IN *PROSOPIS LAEVIGATA* THROUGHOUT ITS DISTRIBUTION RANGE IN MEXICO IS ASSOCIATED TO WATER

Aceptado en: **Botanical Science**

Botanical Sciences 100 (2): 1-38. 2022
DOI: 10.17129/botsci.2846

Received: 22 de junio de 2021
Accepted: 1 de diciembre de 2021
First online: xx de xxxxxx de xxxx

Cornisa1: Differentiation in seedling biomass allocation in *Prosopis laevigata*
Cornisa2: Hernández-Madrigal *et al*. / Botanical Sciences 100 (2): 1-38 2022

Section: Ecology

DIFFERENTIATION IN SEED MASS AND SEEDLING BIOMASS ALLOCATION IN *PROSOPIS LAEVIGATA* THROUGHOUT ITS DISTRIBUTION RANGE IN MEXICO IS ASSOCIATED TO WATER AVAILABILITY

LA DIFERENCIACIÓN EN LA MASA DE LA SEMILLA Y LA ASIGNACIÓN DE BIOMASA EN PLÁNTULAS DE *PROSOPIS LAEVIGATA* A LO LARGO DE SU ÁREA DE DISTRIBUCIÓN EN MÉXICO ESTÁ ASOCIADA CON LA DISPONIBILIDAD DE AGUA

Fátima Hernández-Madrigal[1], Gonzalo Contreras-Negrete[1], Rafael Aguilar-Romero[2], Fernando Pineda-García[2] and Antonio González-Rodríguez[1*]

[1]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, México.

[2]Escuela Nacional de Estudios superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro 8701, Morelia, Michoacán 58190, México.

***Author for correspondence**: agrodrig@iies.unam.mx

Abstract

Background: Seedling establishment depends on the quality of the seeds and environmental conditions. Differential biomass allocation in emergent seedlings probably constitutes a relevant adaptive response of populations along environmental gradients.

Questions: Are there differences in seed mass and biomass allocation in seedlings among *Prosopis laevigata* populations? Is this variation correlated with environmental variables?

Studied species: *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C.Johnst (Fabaceae).

Study site and dates: Thirteen localities along the distribution of *P. laevigata* in México. From 2016 to 2020.

Methods: Seeds were collected from four or five mother trees per locality. Seed mass (SM) was obtained in ten seeds per mother and six functional traits indicative of biomass allocation were measured in the seedlings after 10 days of germination. Population mean values were obtained for the six traits plus SM and subjected to a principal component analysis (PCA). Population scores on the first two axis of the PCA were regressed against environmental variables from the collection localities using a stepwise regression model.

Results: Populations displayed functional variation congruent with alternative biomass allocation strategies. The conservative strategy was characterized by larger seeds and seedlings with denser tissues and a higher investment in root biomass, while the opposite characterized the acquisitive strategy. Actual evapotranspiration in May, isothermality and soil water content in February were environmental variables that significantly predicted population scores on the first two axes of the PCA.

Conclusion: Water availability gradients influence seed mass and seedling biomass allocation variation among *P. laevigata* populations.

Keywords: actual evapotranspiration, arid zones, functional traits, germination

Resumen

Antecedentes: El establecimiento de las plántulas depende de la calidad de las semillas y las condiciones ambientales. El patrón de asignación de biomasa en plántulas recién emergidas es probablemente una adaptación relevante en gradientes ambientales.

Preguntas: ¿Existen diferencias en masa de la semilla y asignación de biomasa de plántulas entre poblaciones de *Prosopis laevigata*? ¿Se correlaciona esta variación con factores ambientales?

Especie de estudio: *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C.Johnst (Fabaceae).

Sitio y años de estudio: Trece localidades de *P. laevigata*. 2016-2020.

Métodos: Se colectaron semillas de cinco árboles por localidad. Se determinó la masa (MS) en diez semillas por árbol y se midieron seis rasgos funcionales en plántulas de 10 días de edad. Las medias por población para los siete atributos se analizaron mediante componentes principales (PCA). Se hicieron regresiones multivariadas de los puntajes de las poblaciones en los dos primeros ejes del PCA contra las variables ambientales de las localidades.

Resultados: Las poblaciones desplegaron variación congruente con estrategias alternativas de asignación de biomasa. La estrategia conservativa mostró una alta biomasa de semilla y plántulas con tejidos densos y un mayor tejido radicular, mientras que el patrón opuesto caracterizó la estrategia adquisitiva. La evapotranspiración en mayo, la isotermalidad y el contenido de agua en el suelo en febrero fueron variables ambientales que predijeron los puntajes de las poblaciones en los dos primeros ejes del PCA.

Conclusión: Los gradientes de disponibilidad de agua influyen en la masa de las semillas y la asignación de biomasa en *P. laevigata*.

Palabras clave: evapotranspiración, germinación, rasgos funcionales, zonas áridas.

Seedling establishment is preceded by key transition states such as germination and seedling emergence (Fenner & Thompson 2005), whose success depends on the quality of the seeds and the environmental conditions (Lloret *et al.* 1999, Barak *et al.* 2018, Larson *et al.* 2015, Gardarin *et al*. 2016). During seed production, the environment experienced by mother plants may have a significant impact, since climatic factors such as temperature and precipitation, among others, can affect seed quality (Nemani *et al.* 2003). In turn, seed quality (*i.e.*, seed mass) is correlated positively with rates of germination and seedling emergence (Moles & Westoby 2004). Additionally, at the first stages of growth, seedlings are not capable of acquiring all necessary resources from the environment, so they depend almost exclusively on seed reserves for establishment (Nadeem *et al*. 2013).

Besides seed traits, plants have developed a multitude of adaptations to deal with the restrictions imposed by the environment. One of the main mechanisms is biomass allocation (Ackerly *et al.* 2000, Poorter *et al*. 2012, Donohue *et al.* 2010). It has been proposed that plants adapted to resource-rich environments but with high aboveground competition in general assign a higher biomass proportion to leaves and shoots, and species from resource-poor environments but with high below ground competition assign more biomass to roots (Tilman 1985).

Functional traits such as seed mass and patterns of biomass allocation influence seedling establishment and performance (Costa-Saura *et al.* 2016, Reich *et al.* 2003). Since functional traits are under selection by biotic and abiotic factors, spatial variation in these factors may translate into divergent selection driving differences in adaptations among populations (Petit &Thompson 1998, Fajardo & Piper 2011). Therefore, functional variation may be observed among populations and different strategies deployed to optimize resource use (Jung *et al*. 2010, Salazar *et al.* 2018). On one side, an acquisitive strategy, characterized by investment in photosynthetic tissues, allows fast growth under conditions of resource abundance; while a conservative strategy leaned towards the formation of dense tissues favors survival with little growth under resource limitation (Wright &Westoby 1999, Reich *et al*. 2003). Trade-offs among traits underlay these strategies (Laughlin *et al.* 2018); therefore, describing functional variation and trade-offs among traits in response to different environmental conditions is crucial to understand plant adaptive evolution and their response to contemporary and projected climatic changes (Suding *et al.* 2008, Westoby 1998, Wright &Westoby 1999).

In arid and semiarid environments, with frequent and prolonged dry periods, seedling survival after germination is a crucial step for plant establishment (Flores & Jurado 1998, Flores *et al.* 2017, Pérez-Sánchez *et al*. 2011). Strategies such as the investment in large seeds and higher biomass allocation to root systems are related to survival (Adler *et al.* 2014). However, few studies have been conducted that examine variation in biomass allocation patterns in seedlings of arid-adapted trees across their entire distribution range. Species of genus *Prosopis* L. (Fabaceae) are dominant woody perennials in many arid and semiarid zones of the American continent (Fagg & Stewart 1994). Their success in these environments is explained by a series of morphophysiological traits. The seed coat is thick and impermeable, what provides a mechanism of physical dormancy that is favorable in unpredictable environments (Villagra 1995). This coat, together with the nutritious mesocarp and the indehiscent pod, constitute adaptations to endozoic seed dispersal and contribute to seed survival and germination after ingestion (Campos & Ojeda 1997). Seed germination is fast, taking 2-4 days to radicle emergence and 8-10 days to the appearance of the first leaves (Vilela & Ravetta 2001). Seeds and seedlings are the most vulnerable stages to water stress; therefore, seed dispersal to favorable microsites is important. During their early growth seedlings rapidly develop an extensive root system for water acquisition (Flores Tena 1993).

Prosopis laevigata (Humb. & Bonpl. ex Willd.) is the species of this genus with the widest distribution and highest ecological and economic importance in Mexico, being present in the arid zones of the north and center of the country as well as the semiarid areas in the south (Palacios *et al.* 2016, Rzedowski 1988). *Prosopis laevigata* is well adapted to extremely hot and dry environments throughout its distribution, but its wide distribution indicates that it is a species capable of establishing under variable conditions of temperature and humidity. Additionally, *P. laevigata* shows a good performance in poor soils and a high capacity of vegetative regeneration in agroforestry systems (Buendía-González *et al.* 2012, Pasiecznik *et al.* 2001, Ramírez-Arriaga *et al.* 2006).

The goal of this study was to evaluate variation in seed mass, germination percentage and biomass allocation traits in *P. laevigata* populations throughout most of the distribution of this species in México, determining trade-offs that guide functional strategies of the seedling emergence, and to understand how environmental factors may explain this intraspecific variation. The specific questions were 1) Are there intraspecific differences in seed mass, germination percentage and seedling biomass allocation traits among *P. laevigata* populations along the distribution of the species in México? 2) Are there trade-offs among biomass allocation traits in *P. laevigata* populations? 3) Is the variation in seed mass, germination percentage and biomass allocation in *P. laevigata* populations correlated with environmental variables? Given the broad distribution and heterogeneous environments occupied by *P. laevigata* in Mexico, we expected significant functional variation among populations, with trade-offs among traits guiding differential strategies of resource acquisition in correlation with environmental factors.

Materials and methods

Study species. Prosopis laevigata (Fabaceae, Mimosoideae) is a tree or shrub up to 12 m in height distributed in the arid and semiarid zones of several physiographic regions of Mexico, including the Oaxaca Central Valleys, Tehuacán-Cuicatlán Valley, Balsas Depression, Trans-Mexican Volcanic Belt, Mexican Altiplano and Tamaulipas Plains (Calderón & Rzedowski 2001, Rzedowski 1988, Palacios 2006). The species is mainly pollinated by hymenopterans and is self-compatible with percentages of self-fertilization between 65-85% (Galindo Almanza *et al*. 1992). The seeds are dispersed by mammals and water currents (Campos & Ojeda 1997, De Noir *et al*. 2002, Pasiecznik *et al.* 2001). Detailed phenological studies for *P. laevigata* are lacking, but our own observations indicate that flowering of the species occurs in February and March, seed maturation starts in May and seed dispersal takes place in July and August (Pérez-Sánchez *et al*. 2011, Galindo Almanza *et al.* 1992).

Seed sampling and germination. We used seeds of *Prosopis laevigata* from 13 populations encompassing a large portion of the distribution of the species in México (Table 1, Figure 1) and representative of the environmental gradient experienced by the species. Vegetation type was xerophytic scrub in most cases, even though in some sites, particularly southern ones, tropical dry forest vegetation was present (Rzedowski 1988, Palacios 2006). The mean annual temperature in sampled sites varies between 15 and 24 °C and annual precipitation between 360 and 752 mm (Table 1).

At each locality, fruits from four or five mother plants were collected according to their availability. In northern localities, where in some cases contact zones occur between *P. laevigata* and *P. glandulosa*, we verified that sampled individuals showed distinctive features, such as the smaller and darker leaflets and the more constrained and purplish pods in *P. laevigata* in comparison to the yellow pods of *P. glandulosa* (Calderón & Rzedowski 2001, Palacios 2006). Sampled pods were in all cases taken directly from the mother tree (not from the ground) and were ripe and without signs of damage by pathogens or herbivores. Sampling at all sites was performed during the same season (July of 2016). The seeds were extracted from the pods for subsequent washing and disinfection with 5% sodium hypochlorite, and then stored at room temperature in transparent vials with 5 g of commercial fungicide until used. It is known that under these conditions, *Prosopis* seeds can remain viable for at least a decade (Pasiecznik *et al.* 2001).

A total of 600 seeds (10 seeds × mother tree × population) were germinated in June of 2019. Firstly, seeds were individually weighed to determine seed mass (SM) and then scarified mechanically using sandpaper. Scarification is necessary since physical dormancy has been reported for the seeds of *Prosopis* species. Under natural conditions, dormancy is broken through endozoochory or seed entrainment by watercourses. From an experimental perspective, different chemical compounds (*i.e.*, sulfuric acid, hydrochloric acid, sodium hydroxide) as well as hot water treatments and mechanical scarification by sandpaper have been tested (Ortega-Baes *et al*. 2002, Miranda *et al.* 2011, Majd *et al*. 2013). Consistently, mechanical scarification with sandpaper has shown satisfactory results in breaking dormancy (Ortega-Baes *et al.* 2002). Therefore, we decided to use this type of scarification because of the economy, ease, and safety of its handling in relation to chemical compounds. Afterwards, seeds were sown in groups of three in Petri dishes layered with a double sheet of filter paper (Whatman No. 1). Dishes were placed in germination chambers (ICP-19 LUMISTELL) using a 12-h photoperiod and at a constant temperature of 30° C, known to be optimal for germination of this and other *Prosopis* species (Cony & Trione 1996);

Contreras-Negrete *et al.* unpublished). The filter paper was maintained continuously soaked by adding 3 mL of distilled water every third day and the position of the Petri dishes within the chamber was shifted regularly. Seeds were checked once per day and recorded as germinated once the radicle reached 2 mm, following Cony & Trione (1998).

Measurement of functional traits. After 10 days of the initiation of the experiment, we performed six standardized measurements of functional traits in the seedlings (see Table 2 for definition and biological significance of each trait) (Pérez-Harguindeguy *et al.* 2013). The length of the aerial part (LA) and the length of the root (LR) were measured with a Mitutoyo Absolute digital caliper (model 500-172-20) with a 0.01 mm precision. Seedlings were then separated into cotyledons, root, stem and leaves and the fresh weight of each of these plant parts was determined separately with an analytical balance. The area of the fresh cotyledons (AC) was estimated from scanned images using the software Image J. Afterwards, plant parts were placed in paper bags and oven dried at 70 °C for 72 h and subsequently their dry weight was measured. From these data, we calculated specific cotyledon area (SCA) as the ratio between AC and cotyledon dry mass. Leaf dry matter content (LDMC) was estimated as the ratio of the leaf dry weight to leaf fresh weight. Similarly, root dry matter content (RDMC) was estimated as the ratio of root dry weight to root fresh weight. Stem volume was obtained by the water displacement method (Pineda-García *et al.* 2011), and then used to calculate stem density (SD) as the ratio of the stem volume to stem dry weight. Root/shoot ratio (R/S) was obtained as the ratio of the aerial part biomass to the root biomass. Finally, the seedling maximum length (Lmax) was determined as the sum of LA and LR.

Environmental variables. Nineteen bioclimatic variables were extracted for the 13 collection sites from high-resolution monthly climate surfaces of the study area, available at https://github.com/AngelaCrow/variables-bioclimatica; (Cuervo-Robayo *et al.* 2014), using GIS ArcView ver. 3.3 (ESRI 1999). We also considered 24 variables describing monthly values of actual evapotranspiration and soil water content (https://figshare.com/articles/Global_High-Resolution_Soil_Water_Balance/7707605/3); see Trabucco & Zomer (2010) for more details. To avoid redundancy among variables in subsequent analyses, highly correlated variables were discarded through a pairwise correlation test among the 43 variables, eliminating the more specific variable for each pair of variables with $r \geq 0.9$ (*i.e.*, preferentially discarding mean temperature of the warmest quarter over mean annual temperature). This analysis was conducted using the JMP 11.0.0 (SAS Institute Inc., Cary, NC, USA) statistical package. After this procedure, 14 environmental variables were considered in the analysis (Table 3). Finally, latitude, longitude and elevation were used as geographic variables.

Data analysis. Simple linear regressions were performed to evaluate the effect of seed mass (mean values per population) on the percentage of germinated seeds. Regressions of this response variable were also conducted on geographic and environmental variables of the collection localities. For seed mass and the six seedling functional traits, data normality was tested, and values were log-transformed if necessary. One-way analyses of variance (ANOVA) were conducted to test for differences among populations for the seven evaluated traits.

Mean values of the seven traits were calculated for each population and then pairwise correlation analyses were performed among all traits to identify patterns of coordination among these functional variables across populations. To visualize these patterns and to observe potential differences in the strategy of biomass allocation among populations, we also conducted a principal components analysis (PCA). To assess whether these patterns are related to environmental variables, we performed a stepwise multiple regression analysis of the population scores on the first two principal components (PC1 and PC2, response variables) and the selected climatic, soil water balance and geographic variables of the collection localities (independent variables; Table 3), using the forward variable selection procedure and the probability to enter set to 0.05. The best models were selected on the basis of the corrected Akaike information criterion (AICc) (Akaike 1974). All analyses were performed in JMP 11.0.0 (SAS Institute Inc., Cary, NC, USA) statistical package.

Results

Germination percentages between 18 and 95% were observed in the populations (Table 1), with lower percentages in southern populations and higher in northern populations (*i.e.* increased latitudinally; Figure 2), without a significant effect of seed mass or other geographic or environmental variables at the collection localities. Due to these differences in germination percentage, the number of analyzed seedlings per population varied between five and 23 (Table 1). The one-way analyses of variance revealed that the studied populations differed significantly in the seven evaluated traits (Table 4; Table S1).

The pairwise correlation analyses between the measured functional traits indicated significant positive correlations between seed mass and stem density; root dry matter content and the root/shoot ratio; maximum length and specific cotyledon area; and root dry matter content and stem density (Table 5). In turn, negative correlations were observed between seed mass and leaf dry matter content; root/shoot ratio and leaf dry matter content; and leaf dry matter content and stem density (Table 5).

The first two principal components of the PCA jointly explained 78.3% (49.4 and 28.9% for the PC1 and PC2, respectively) (Table 6). The variables with the highest loadings on the PC1 were seed mass, stem density and the root dry mass content, while for the PC2 the variables with the highest loadings were maximum length, specific cotyledon area and root/shoot ratio (Table 6). In the PCA plot (Figure 3), it can be observed that trait combinations associated to conservative resource use are indicated by positive values of the PC1 (larger seeds and seedlings with denser tissues and a higher investment in the development of the root system). In contrast, negative values on the PC1 indicate an acquisitive strategy (higher investment in aerial tissues). Positive values on the PC2 are also indicative of this strategy (Table 6, Figure 3). The distribution of *P. laevigata* populations in this plot indicated that the most differentiated population was number 12 (Huizachal, Tamaulipas) which showed the lowest score on the PC1 (Figure 3). In contrast, the highest score on the PC1 was observed for population 8 (Peña de Bernal, Querétaro), followed by population 3 (Sayula, Jalisco). On the PC2, the highest and lowest scores were observed for populations 13 (Matehuala, San Luis Potosí) and 2 (Indaparapeo, Michoacán), respectively (Figure 3).

The stepwise multiple regression analyses indicated in the case of the PC1 a significant effect of actual evapotranspiration in May (negative relationship) and isothermality (positive relationship) on this variable (Table 7). However, the effect of isothermality is no longer significant if population 12 is removed from the analysis. For the PC2, the only variable with a significant effect (negative relationship) was soil water content in February (Table 7). The bivariate relationships between PC1 and PC2 and the significant predictor variables are shown in Figure 4.

Discussion

In this study, we tested for among-population variation in seed mass and biomass allocation in seedlings of *P. laevigata*. Furthermore, we expected this variation to represent differential strategies of resources acquisition, guided by trade-offs among traits, and correlated with local conditions across the environmental gradient encompassed by the distribution of the species. Describing biomass allocation patterns and the underlying environmental factors that shape them is informative about the ecological strategies of species (Westoby 1998). For this reason, we analyzed functional variation and coordination among traits that define biomass allocation strategies, from the seed to the seedling emergence stages across populations of *P. laevigata* throughout most of the distribution of the species in Mexico. Since seeds were treated equally and germinated in a common environment, it is probable that the observed variation has a genetic component.

The results contribute to the understanding of the adaptive mechanisms that favor successful establishment of *P. laevigata* along the varying environmental conditions of the arid and semiarid zones of the south, center and north of Mexico. We found that in populations with smaller seeds, seedlings are characterized by a higher investment in photosynthetic tissues and growth of the aerial parts. In contrast, the seedlings in populations with larger seeds have denser tissues and a larger relative investment in the root system, favoring resource conservation and survival in more resource-poor environments, as has been concluded from generalizations encompassing hundreds of plant species including a global range of biomes and growth forms (Lambers & Poorter 1992, Adler *et al.* 2014, Murray *et al.* 2004). These distinct strategies are probably adaptive under the variable conditions across the distribution of *P. laevigata* and bring about trade-offs among traits, since the enhancement of one trait usually has costs on other traits (Reich 2014).

The PCA allowed to observe these associations among traits in detail (Figure 3). The variables that had higher loadings on the PC1 were seed mass, stem density and root dry mass content. Positive values on this axis indicated seedlings with dense tissues that emerged from larger seeds and with a higher investment in root development, while negative values indicated the opposite pattern. Therefore, the first axis was mainly driven by the association of tissue density and seed mass, noting the resource investment conflict between above and belowground traits. On one side of the axis, the group of populations coming from heavier seeds produced seedlings with denser root and stem. In contrast, populations with lighter seeds had seedlings with denser leaves. Overall, tissue density is an indicator of plant resistance to abiotic and biotic stress (Niinemets 2001, Méndez-Alonzo *et al*. 2012, Pineda-García *et al*. 2016, Markesteijn & Poorter 2009). Particularly, a high root and stem density is a result of a dense xylem. A higher stem density is determined by vessels with reinforced walls and/or a higher proportion of fibers, which are more resistant to embolism formation during soil drought (Hacke *et al*. 2001, Jacobsen *et al.* 2007, Pineda-García *et al.* 2016). Contrary, leaves of high density usually have lower nitrogen and phosphorus concentration and lower gas exchange rates, but are more resistant to water stress (Niinemets 2001, Pineda-García *et al.* 2016). Both extremes of this axis would be successful under environments that experience water stress. However, the populations with denser root and stem and, therefore, more resistant to embolism, would survive more frequent and intense soil drought. In contrast, populations with dense leaves would be better adapted to environments with a higher air vapor pressure deficit.

For the PC2, the variables with the higher loadings were maximum length, specific cotyledon area and root/shoot ratio, with positive values on the PC2 indicating high relative investment in aerial and photosynthetic tissues. Therefore, the second axis reflects a conflict of resource allocation to produce aerial tissues. On one extreme of the axis were the populations with longer seedlings and with cotyledons of large specific leaf area. Large specific leaf area results from large carbon capture area per unit of biomass invested in the leaf construction, which is related with higher photosynthetic and growth rates (Reich *et al.* 1998, Reich *et al.* 1999, Pineda-García *et al.* 2016, Wright & Westoby 1999). In sum, this suggests this group of populations had a higher canopy dominance and a resource acquisitive strategy and thus, would be more adapted to habitats with low water stress. On the other side, the other group of populations invested more biomass to stem but were shorter and with cotyledons with lower specific leaf area, limiting their capacity for resource capture. Thus, both PC1 and PC2 suggest a conflict of resource allocation at the above and belowground portions to generate either resistant or acquisitive organs. In addition, this pattern of allocation could be promoted by different aboveground or belowground environmental pressures experienced by populations in the field.

Interestingly, these patterns displayed by the populations did not follow a clear geographical pattern but were instead significantly explained by environmental variables. For the PC1, we detected a high negative correlation with the actual evapotranspiration in May, indicating that emergent *P. laevigata* seedlings from sites with lower actual evapotranspiration in this month (and thus less water availability) have traits associated with a more conservative strategy. In turn, the positive correlation of the PC1 with isothermality suggests that in localities where temperature is more constant throughout the year (*i.e.*, higher isothermality), the emergent *P. laevigata* seedlings have traits indicative of a more conservative strategy. However, the relationship between PC1 and isothermality is no longer significant if population 12 is removed from the analysis and thus must be taken with caution. On the other hand, PC2 showed a negative correlation with the soil water content in February, indicating the in sites with higher soil water content in this month, the emergent *P. laevigata* seedlings have a lower maximum height, root/shoot ratio and specific cotyledon area (*i.e.*, traits that indicate a conservative strategy).

In general, these results suggest that the observed intraspecific variation in seed mass and seedling functional traits may be important for adaptation to water availability during the crucial stages of seed development germination and seedling emergence and establishment. The reproductive phenology of *P. laevigata* is characterized by flowering in the late winter (February and early March), initiation of seed maturation in May, and seed dispersal in the summer (July and August) (Galindo Almanza *et al.* 1992, Pérez-Sánchez *et al.* 2011). It is likely that seeds remain dormant in the seedbank for several months and germinate with the summer rains of the next year. In the collection localities, the higher number of seedlings is found from July to September (G. Contreras-Negrete, personal observation). Therefore, the main pattern found is that populations of *P. laevigata* in areas where water availability is higher during these phenological events follow a more acquisitive strategy, while populations in sites with less water availability follow a more conservative strategy. The impact of this variation on the population dynamics, particularly on early development phases of the study species in of wild populations of *P. laevigata*, which face unpredictable conditions and climate change, requires more detailed studies in the future.

Previous studies conducted on adult trees or seedlings of other *Prosopis* species inhabiting hyper arid deserts, such as *P. caldenia*, *P. glandulosa*, *P. flexuosa* and *P. pallida* (Ansley *et al.* 2007, Guevara *et al*. 2010, de Villalobos & Peláez 2015, Salazar *et al.* 2019) have revealed a significant capacity for phenotypic adjustment through plastic responses of biomass allocation in response to water availability in mesquites. The results here presented suggest that besides phenotypic plasticity, potentially genetically determined functional differences among populations may be very important for survival during the very crucial stages of germination and seedling emergence, perhaps before plastic responses can come into play.

Interestingly, the variables that we identified as having the most significant effect on functional variation were related to water availability and not to precipitation, in concordance with previous results indicating that precipitation is a poor predictor of plant traits because of its weak link with water availability for plants (Moles *et al.* 2014), and this may be particularly the case in arid and semiarid ecosystems. On the other hand, a previous ecological niche model for *P. laevigata* (Palacios *et al.* 2016) suggested that temperature seasonality is the most important climatic variable to explain the distribution of the species. In this study, we detected a possible association between the PC1 of the functional variation with isothermality (even though determined by a single population), which is a variable that is generally highly correlated with temperature seasonality. These results suggest a role of the patterns of temporal temperature fluctuations on the adaptation of *P. laevigata* to the environment. Additionally, we suggest that including water availability variables into the niche models of species from arid or semiarid zones such as *P. laevigata* could significantly increase the accuracy of the predictions.

Finally, another noticeable pattern that we found in this study was the significant latitudinal increase in seed germination percentage in *P. laevigata* populations. This result is similar to what has been documented in more detailed experiments of germination response to temperature, salinity and water stress for the same populations of *P. laevigata* (Contreras-Negrete *et al*. unpublished). In our case, the variation in germination percentage was not significantly correlated with any of the environmental variables considered and neither with seed mass. Latitudinal variations in germination percentage have also been found in other Mexican tree species, such as *Quercus rugosa* (Llanderal-Mendoza *et al.* 2017). These authors point out a significant positive correlation of germination percentage with seed mass but the association of these two variables with latitude was negative, and a significant influence of climatic variables was detected. In the case of *P. laevigata* it is possible that the lower germination percentage in southern populations is due to genetic factors, since these populations show considerably reduced genetic variation in comparison to northern ones, probably related with an also lower population density (Contreras-Negrete *et al.* 2021). Therefore, future studies could be aimed at examining if southern population are experiencing inbreeding depression or other genetically based fitness attrition processes.

In conclusion, we have documented variation in seed mass and biomass allocation in seedlings among populations of *P. laevigata* along a large part of the distribution of the species. Significant associations were observed among the functional traits analyzed, defining the segregation of populations along the conservative/acquisitive strategies continuum. We found that evapotranspiration and soil water content at specific times of the year, along with isothermality, are probably the climatic variables that best explain the observed variation.

Supplementary material

Supplemental material for this article can be accessed here.

Acknowledgements

The authors thank Martin de La Torre for help in setting the germination experiment and measurement of seedling functional traits. FHM thanks a postdoctoral scholarship from DGAPA-UNAM. Funding for this study was provided by grant IA203221 from UNAM-DGAPA-PAPIIT to FPG and by IIES-PO to AGR. The comments by two anonymous reviewers and Teresa Terrazas greatly contributed to improve the previous versions of this manuscript.

Literature cited

Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE, Lechowicz MJ. 2000. The Evolution of Plant Ecophysiological Traits: Recent Advances and Future Directions: New research addresses natural selection, genetic constraints, and the adaptive evolution of plant ecophysiological traits. *BioScience* **50** :979-995. DOI: https://doi.org/10.1641/0006-3568(2000)050[0979:teopet]2.0.co;2

Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M. 2014. Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences* **111**: 740-745. DOI: https://doi.org/10.1073/pnas.1315179111

Akaike H. 1974. A new look at the statistical model identification. *IEEE* **19** :716-723. DOI: https://doi.org/10.1109/TAC.1974.1100705

Ansley RJ, Boutton TW, Jacoby PW. 2007. Mesquite root distribution and water use efficiency in response to long-term soil moisture manipulations. *In*: Sosebee RE, Wester DB, Britton CM, McArthur ED, Kitchen SG, eds. *Proceedings: Shrubland dynamics - fire and water*. Proccedings RMRS-P-47. Fort Collins, CO: Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 96-103.

Barak RS, Lichtenberger TM, Wellman-Houde A, Kramer AT, Larkin DJ. 2018. Cracking the case: Seed traits and phylogeny predict time to germination in prairie restoration species. *Ecology and Evolution* **8**: 5551-5562. DOI: https://doi.org/10.1002/ece3.4083

Buendía-González L, Estrada-Zúñiga ME, Orozco-Villafuerte J, Cruz-Sosa F, Vernon-Carter EJ. 2012. Somatic embryogenesis of the heavy metal accumulator *Prosopis laevigata*. *Plant Cell Tissue and Organ Culture* **108**: 287-296. DOI: https://doi.org/10.1007/s11240-011-0042-4

Calderón G, Rzedowski J. 2001. *Flora fanerogámica del Valle de México*. México: Instituto de Ecología AC. y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. ISBN: 978-607-7607-36-6.

Campos CM, Ojeda RA. 1997. Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. *Journal of arid Environments* **35**: 707-714. DOI: https://doi.org/10.1006/jare.1996.0196

Contreras-Negrete G, Letelier L, Piña-Torres J, González-Rodríguez A. 2021. Genetic structure, phylogeography and potential distribution modeling suggest a population expansion in the mesquite *Prosopis laevigata* since the last interglacial. *Plant Systematics and Evolution* **307**: 22. DOI: https://doi.org/10.1007/s00606-021-01744-5

Cony MA, Trione S. 1996. Germination with respect to temperature of two Argentinian *Prosopis* species. *Journal of Arid Environments* **33**: 225-236.

Cony MA, Trione SO. 1998. Inter and intraspecific variability in *Prosopis flexuosa* and *P. chilensis*: seed germination under salt and moisture stress. *Journal of Arid Environments* **40**: 307-317. DOI: https://doi.org/10.1006/jare.1998.0448

Costa-Saura JM, Martínez-Vilalta J, Trabucco A, Spano D, Mereu S. 2016. Specific leaf area and hydraulic traits explain niche segregation along an aridity gradient in Mediterranean woody species. *Perspectives in Plant Ecology, Evolution and Systematics* **21**: 23-30. DOI: https://doi.org/10.1016/j.ppees.2016.05.001

Cuervo-Robayo AP, Téllez-Valdés O, Gómez-Albores MA, Venegas-Barrera CS, Manjarrez J, Martínez-Meyer E. 2014. An update of high-resolution monthly climate surfaces for Mexico. *International Journal of Climatology* **34**: 2427-2437. DOI: https://doi.org/10.1002/joc.3848

De Noir F, Juárez M, Boletta P, Avila S. 2002. Ripeness and seed dispersal in a semiarid region of Argentina and their relation with some climatic factors. *Foresta Veracruzana* **4**: 7-13

de Villalobos AE, Peláez DV. 2015. Functional responses of woody *Prosopis caldenia* seedlings to drought and livestock grazing in semiarid rangelands of Argentina. *Arid Land Research and Management* **29**: 487-502. DOI: https://doi.org/10.1080/15324982.2015.1030798

Donohue K, Rubio de Casas R, Burghardt L, Kovach K, Willis CG. 2010. Germination, Postgermination Adaptation, and Species Ecological Ranges. *Annual Review of Ecology, Evolution, and Systematics* **41**: 293-319. DOI: https://doi.org/10.1146/annurev-ecolsys-102209-144715

ESRI [Environmental Systems Research Institute] 1999. Arcview GIS 3.3. Environmental Systems Research Institute, Redlands.

Fagg CW, Stewart JL. 1994. The value of *Acacia* and *Prosopis* in arid and semi-arid environments. *Journal of Arid Environments* **27**: 3-25. DOI: https://doi.org/10.1006/jare.1994.1041

Fajardo A, Piper FI. 2011. Intraspecific trait variation and covariation in a widespread tree species (*Nothofagus pumilio*) in southern Chile. *New Phytologist* **189**: 259-271. DOI: https://doi.org/10.1111/j.1469-8137.2010.03468.x

Fenner M, Thompson K. 2005. *The Ecology of Seeds*. Cambridge: Cambridge University Press. DOI: https://doi.org/10.1017/CBO9780511614101

Flores J, Jurado E. 1998. Germination and early growth traits of 14 plant species native to northern Mexico. *The Southwestern Naturalist* **43**: 40-46.

Flores J, Pérez-Sánchez RM, Jurado E. 2017. The combined effect of water stress and temperature on seed germination of Chihuahuan Desert species. *Journal of Arid Environments* **146**: 95-98. DOI: https://doi.org/10.1016/j.jaridenv.2017.07.009

Flores Tena FJ. 1993. Atributos ecológicos y aprovechamiento del mezquite. *Investigación y Ciencia: de la Universidad Autónoma de Aguascalientes* **9**: 24-30.

Galindo Almanza S, García Moya E, Wendt TL, González Cossio FV. 1992. Potencial de hibridación natural en el mesquite (*Prosopis laevigata* y *P. glandulosa* var. Torreyana, Leguminosae) de la altiplanicie de San Luis Potosi. *Acta Botánica Mexicana* **20**. DOI: https://doi.org/10.21829/abm20.1992.660

Gardarin A, Coste F, Wagner M-H, Dürr C. 2016. How do seed and seedling traits influence germination and emergence parameters in crop species? A comparative analysis. *Seed Science Research* **26**: 317-331. DOI: https://doi.org/10.1017/S0960258516000210

Gogosz AM, Torres Boeger MR. 2019. Functional morphology of subtropical tree seedlings in southern Brazil. *Rodriguésia* **70**: DOI: https://doi.org/10.1590/2175-7860201970010

Guevara A, Giordano CV, Aranibar J, Quiroga M, Villagra PE. 2010. Phenotypic plasticity of the coarse root system of *Prosopis flexuosa*, a phreatophyte tree, in the Monte Desert (Argentina). *Plant and Soil* **330**: 447-464. DOI: https://doi.org/10.1007/s11104-009-0218-4

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**: 457-461. DOI: https://doi.org/10.1007/s004420100628

Jacobsen A, Agenbag L, Esler K, Pratt RB, Ewers F, Davis S. 2007. Xylem density, biomechanics and anatomical traits correlate with water stress in 17 evergreen shrub species of the Mediterranean-type climate region of South Africa. *Journal of Ecology* **95**: 171-183. DOI: https://doi.org/10.1111/j.1365-2745.2006.01186.x

Jung V, Violle C, Mondy C, Hoffmann L, Muller S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* **98**: 1134-1140. DOI: https://doi.org/10.1111/j.1365-2745.2010.01687.x

Lambers H, Poorter H. 1992. Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**: 187-261. DOI: https://doi.org/10.1016/S0065-2504(08)60148-8

Larson JE, Sheley RL, Hardegree SP, Doescher PS, James JJ. 2015. Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. *Journal of Applied Ecology* **52**: 199-209. DOI: https://doi.org/10.1111/1365-2664.12350

Laughlin DC, Strahan RT, Adler PB, Moore MM. 2018. Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. *Ecology Letters* **21**: 411-421. DOI: https://doi.org/10.1111/ele.12914

Llanderal-Mendoza J, Gugger FP, Oyama K, Uribe-Salas D, González-Rodríguez A. 2017. Climatic determinants of acorn size and germination percentage of *Quercus rugosa* (Fagaceae) along a latitudinal gradient in Mexico. *Botanical Sciences* **95**: 37-45. DOI: https://doi.org/10.17129/botsci.640

Lloret F, Casanovas C, Peñuelas J. 1999. Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Functional Ecology* **13**: 210-216. DOI: https://doi.org/10.1046/j.1365-2435.1999.00309.x

Majd R, Aghaie P, Kazerooni Monfared E, Alebrahim M. 2013. Evaluating of Some Treatments on Breaking seed Dormancy in Mesquite. *International Journal of Agronomy and Plant Production* **4**: 1433-1439.

Markesteijn L, Poorter L. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* **97**: 311-325. DOI: https://doi.org/10.1111/j.1365-2745.2008.01466.x

Méndez-Alonzo R, Paz H, Zuluaga RC, Rosell JA, Olson ME. 2012. Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* **93**: 2397-2406. DOI: https://doi.org/10.1890/11-1213.1

Miranda R, Oliveira M, Correia R, Almeida-Cortez J, Pompelli M. 2011. Germination of Prosopis juliflora (Sw) DC seeds after scarification treatments. *Plant Species Biology* **26**: 186-192. DOI: https://doi.org/10.1111/j.1442-1984.2011.00324.x

Moles A, Westoby M. 2004. Seedling survival and seed size: a synthesis of the literature. . *Journal of Ecology* **92**: 372-383. DOI: https://doi.org/10.1111/j.0022-0477.2004.00884.x

Moles AT, Perkins SE, Laffan SW, Flores-Moreno H, Awasthy M, Tindall ML, Sack L, Pitman A, Kattge J, Aarssen LW, Anand M, Bahn M, Blonder B, Cavender-Bares J, Cornelissen JHC, Cornwell WK, Díaz S, Dickie JB, Freschet GT, Griffiths JG, Gutierrez AG, Hemmings FA, Hickler T, Hitchcock TD, Keighery M, Kleyer M, Kurokawa H, Leishman MR, Liu K, Niinemets Ü, Onipchenko V, Onoda Y, Penuelas J, Pillar VD, Reich PB, Shiodera S, Siefert A, Sosinski Jr EE, Soudzilovskaia NA, Swaine EK, Swenson NG, van Bodegom PM, Warman L, Weiher E, Wright IJ, Zhang H, Zobel M, Bonser SP. 2014. Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* **25**: 1167-1180. DOI: https://doi.org/10.1111/jvs.12190

Murray BR, Brown AHD, Dickman CR, Crowther MS. 2004. Geographical gradients in seed mass in relation to climate. *Journal of Biogeography* **31**: 379-388. DOI: https://doi.org/10.1046/j.0305-0270.2003.00993.x

Nadeem M, Mollier A, Morel C, Shahid M, Aslam M, Zia-ur-Rehman M, Wahid MA, Pellerin S. 2013. Maize seedling phosphorus nutrition: Allocation of remobilized seed phosphorus reserves and external phosphorus uptake to seedling roots and shoots during early growth stages. *Plant and Soil* **371**: 327-338.

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running SW. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300: 1560-1563. DOI: hppts://doi.org/ 10.1126/science.1082750

Niinemets Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* **82**: 453-469. DOI: https://doi.org/10.2307/2679872

Ortega-Baes P, de Viana M, Sühring S. 2002. Germination in Prosopis ferox seeds: Effects of mechanical, chemical and biological scarificators. *Journal of Arid Environments* **50**: 185-189. DOI: https://doi.org/10.1006/jare.2001.0859

Palacios R. 2006. Los Mezquites Mexicanos: Biodiversidad y Distribución Geográfica. *Boletín de la Sociedad Argentina de Botánica* **41**: 99-121.

Palacios RA, Hernández FM, Jiménez ME, Tirado TD. 2016. Potential distribution of *Prosopis laevigata* (Humb. etBonpl. ex Willd) M. C. Johnston based on an ecological niche model. *Revista Mexicana de Ciencias forestales* **7**: 35-46.

Pasiecznik NM, Felker P, Harris PJC, Harsh LN, Cruz G, Tewari JC, Cadoret K, Maldonado LJ. 2001. The *Prosopis juliflora-Prosopis pallida* complex: A monograph. UK, Coventry: HDRA. ISBN: 0-905343301.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine J, Gurvich D, Urcelay C, Veneklaas E, Reich P, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167-234. DOI: https://doi.org/10.1071/BT12225

Pérez-Sánchez RM, Jurado E, Chapa-Vargas L, Flores J. 2011. Seed germination of Southern Chihuahuan Desert plants in response to elevated temperatures. *Journal of Arid Environments* **75**: 978-980. DOI: https://doi.org/10.1016/j.jaridenv.2011.04.020

Petit C, Thompson JD. 1998. Phenotypic selection and population differentiation in relation to habitat heterogeneity in *Arrhenatherum elatius* (Poaceae). *Journal of Ecology* **86**: 829-840. DOI: https://doi.org/10.1046/j.1365-2745.1998.8650829.x

Pineda-García F, Paz H, Meinzer FC, Angeles G. 2016. Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiology* **36**: 208-217. DOI: https://doi.org/10.1093/treephys/tpv124

Pineda-García F, Paz H, Tinoco-Ojanguren C. 2011. Morphological and physiological differentiation of seedlings between dry and wet habitats in a tropical dry forest. *Plant, cell & environment* **34**: 1536-1547. DOI: https://doi.org/10.1111/j.1365-3040.2011.02351.x

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* **193**: 30-50. DOI: https://doi.org/10.1111/j.1469-8137.2011.03952.x

Ramírez-Arriaga E, Prámparo MB, Martínez-Hernández E. 2006. Palynology of the Paleogene Cuayuca Formation (Stratotype Sections), Southern Mexico: chronostratigraphical and palaeoecological implications. *Review of Palaeobotany and Palynology* **141**: 259-275.

Reich PB. 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275-301. DOI: https://doi.org/10.1111/1365-2745.12211

Reich P, Ellsworth D, Walters M, Vose J, Gresham C, Volin J, Bowman W. 1999. Generality of leaf trait relationships: A test across six biomes. *Ecology* **80:** 1955-1969. DOI: https://doi.org/10.1890/0012-9658(1999)080[1955:GOLTRA]2.0.CO;2

Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology* **12**: 395-405. DOI: https://doi.org/10.1046/j.1365-2435.1998.00209.x

Reich P, Wright I, Cavender-Bares J, Craine J, Oleksyn J, Westoby M, Walters M. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* **164**: S143-S164. DOI: https://doi.org/10.1086/374368

Rzedowski J. 1988. Análisis de la distribución geográfica del complejo Prosopis (Leguminosae, Mimosoideae) en Norteamérica. *Acta Botanica Mexicana* **3:** 7-19. DOI: https://doi.org/10.21829/abm3.1988.566

Salazar PC, Navarro-Cerrillo R, Cruz G, Grados N, Villar R. 2019. Variability in growth and biomass allocation and the phenotypic plasticity of seven *Prosopis pallida* populations in response to water availability. *Trees* **33**: 1409-1422. DOI: https://doi.org/10.1007/s00468-019-01868-9

Salazar PC, Navarro-Cerrillo R, Cruz G, Villar R. 2018. Intraspecific leaf functional trait variability of eight *Prosopis pallida* tree populations along a climatic gradient of the dry forests of northern Peru. *Journal of Arid Environments* **152**: 12-20. DOI: https://doi.org/10.1016/j.jaridenv.2018.01.010

Suding K, Lavorel S, Chapin Iii FS, Cornelissen J, Diaz S, Garnier E, Goldberg D, Hooper D, Jackson S, Navas M-L. 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology* **14**: 1125-1140. DOI: https://doi.org/10.1111/j.1365-2486.2008.01557.x

Tilman D. 1985. The Resource-Ratio Hypothesis of Plant Succession. *The American Naturalist* **125**: 827-852.

Trabucco A, Zomer RJ. 2010. Global Soil Water Balance Geospatial Database. Available from CGIAR Consortium for Spatial Information. https://cgiarcsi.community (accesed July 15, 2020).

Vilela A, Ravetta D. 2001. The effect of seed scarification and soil-media on germination, growth, storage, and survival of seedlings of five species of *Prosopis L.*

(Mimosaceae). *Journal of Arid Environments* **48**: 171-184. DOI: https://doi.org/10.1006/jare.2000.0735

Villagra P. 1995. Temperature effects on germination of *Prosopis argentina* and *P. alpataco* (Fabaceae, Mimosoideae). *Seed Science and Technology* **23**: 639-646.

Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**: 213-227. DOI: https://doi.org/10.1023/A:1004327224729

Wright IJ, Westoby M. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **87**: 85-97. DOI: https://doi.org/10.1046/j.1365-2745.1999.00330.x

Supporting Agencies (alphabetical order)

Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México (Presupuesto Operativo).

Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT), Universidad Nacional Autónoma de México. Proyecto IA203221.

Editor de Sección: Joel Flores

Authors contributions: FHM (https://orcid.org/0000-0002-8462-857), conception of research, field and laboratory work, statistical analyses, manuscript preparation, review and comments; GCN (https://orcid.org/000-0003-3713-4638), conception of research, field and laboratory work, review and comments; RAR (https://orcid.org/0000-0002-5396-9283), statistical analyses, review and comments; FPG (https://orcid.org/0000-0003-0514-9325), review and comments, funding acquisition; AGR (https://orcid.org/0000-0002-6196-7288), statistical analyses, manuscript preparation, funding acquisition, project supervision.

Table 1. Geographical and environmental data for 13 collection locations of *Prosopis laevigata* seeds, germination percentage and number of seedlings analyzed. MAT = mean annual temperature; AP = Annual Precipitation.

Number	**Population**	**Code**	**State**	**Latitude**	**Longitude**	**Elevation (masl)**	**MAT (°C)**	**AP (mm)**	**Germination percentage**	**Seedlings analyzed**
1	Santa María	SMA	Oaxaca	17.892	-97.822	1,905	19.1	687	18	5
2	Indaparapeo	IND	Michoacán	19.794	-100.968	1,908	17.7	753	68	23
3	Sayula	SY	Jalisco	19.926	-103.528	1,350	20.6	627	62.5	21
4	Cuitzeo	CUI	Michoacán	19.961	-101.202	2,033	17.9	716	60	8
5	San Pedro T	SP	Jalisco	20.221	-103.395	1,538	19.2	699	55	12
6	Novillero	NOV	Guanajuato	20.388	-101.591	1,718	19.2	682	48	9
7	Ixmiquilpan	IXM	Hidalgo	20.460	-99.339	1,852	17.1	361	42.5	10
8	Peña de Bernal	PÑ	Querétaro	20.745	-99.947	2,125	15.8	451	64	17
9	Lagos Moreno	LM	Jalisco	21.369	-101.962	1,930	17.8	591	67.5	14
10	Charco B	HM	San Luis P	22.550	-99.805	1,022	20.3	383	70	14
11	Villa de Arista	VA	San Luis P	22.643	-100.845	1,618	17.9	400	76	19
12	Huizachal	HUI	Tamaulipas	23.588	-99.224	853	20.7	470	90	15
13	Matehuala	MAT	San Luis P	23.630	-100.640	1,925	18.7	488	95	23

Table 2. List of functional traits and their corresponding abbreviations, units, obtained from and biological significance

Functional trait	**Abbreviation**	**Units**	**Obtained from**	**Biological significance**
Leaf dry matter content	LDMC	mg g^{-1}	Ratio of the leaves dry weight to the leaves fresh weight	Positively correlated with relative growth rate[1]
Maximum length	Lmax	mm	Aerial length plus the root length	Growth rate, competitive vigor[1]
Root dry matter content	RDMC	mg g^{-1}	Ratio of the root dry weight to the root fresh weight	Efficiency in getting underground resources[1]
Root/shoot ratio	R/S	Unitless	Ratio of the belowground biomass to the aboveground biomass	Compensation in the limitation of resources, survival and competition[1]
Seed mass	SM	mg	Weight of the seed	Resources allocated for germination and seedling [1]
Specific cotyledon area	SCA	mm^2 mg^{-1}	Ratio of the average area of the cotyledons to the average dry weight of the cotyledons	Reserves allocated for early growth and for beginning of photosynthesis[2]
Stem density	SD	mg mm^{-3}	Ratio of the stem volume to dry weight	Stability, defense, architecture, hydraulic characteristics, and potential growth of plants[1]

[1] Pérez-Harguindeguy *et al*. (2013)

[2] Gogosz & Boeger (2019)

Table 3. Bioclimatic, soil and geographic variables included in this study for *Prosopis laevigata* populations.

Bioclimatic variables	
BIO1	Annual Mean Temperature
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO7	Temperature Annual Range
BIO9	Mean Temperature of Driest Quarter
BIO12	Annual Precipitation
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter
Geographic variables	
Latitude	
Longitude	
Elevation	
Water availabilty variables	
SW2	Soil Water Content on February
SW3	Soil Water Content on March

SW4	Soil Water Content on April
AET5	Actual Evapo Transpiration factor on May
AET6	Actual Evapo Transpiration factor on June
AET9	Actual EvapoTranspiration factor on September

Table 4. Results of the one-way ANOVA testing for differences among *Prosopis laevigata* populations in the seven traits evaluated.

Trait	**SS**	**df**	**MS**	**F**	***p***
Leaf dry matter content	7.7264	12	0.6438	3.043	0.0006
Maximum length	0.9098	12	0.0758	3.247	0.0003
Root dry matter content	19.531	12	1.6276	8.212	<0.0001
Root/shoot ratio	18.887	12	1.5739	8.063	<0.0001
Seed mass	0.0161	12	0.0013	26.554	<0.0001
Specific cotyledon area	0.5523	12	0.0460	1.921	0.0346
Stem density	6.8694	12	0.5724	6.034	<0.0001

Table 5. Pairwise Pearson's correlation coefficients for seven seed and seedling functional traits in *Prosopis laevigata* populations. Significant correlations ($P < 0.05$) are in bold. See Table 2 for functional trait abbreviations.

Functional Trait	**LDMC**	**Lmax**	**RDMC**	**R/S**	**SM**	**SCA**
Lmax	-0.2457					
RDMC	-0.5219	0.1569				
R/S	**-0.5641**	0.3324	**0.8975**			
SM	**-0.7698**	-0.16	0.5189	0.4022		
SCA	0.0546	**0.6791**	-0.0671	0.0989	-0.4765	
SD	**-0.6145**	0.0812	**0.5663**	0.3079	**0.7844**	-0.3294

Table 6. Eigenvector scores of functional traits in two main PCA axes. The highest eigenvector scores for each PCA axis are indicated in bold. Values in parentheses indicate variance accounted for by each axis. See Table 2 for abbreviation of functional traits.

Functional trait	**PC1 (49.4 %)**	**PC2 (28.9%)**
LDMC	**-0.45317**	-0.07514
Lmax	0.0761	**0.62215**
RDMC	**0.45062**	0.15013
R/S	0.40398	**0.30348**
SM	**0.46331**	-0.26626
SCA	-0.13338	**0.63267**
SD	**0.43605**	-0.14655

Table 7. Results of the multiple regression analysis of the population scores on the two first axes of a principal components analysis of *Prosopis laevigata* seed mass and seedling functional trait variation and environmental and geographic variables of the collection localities.

Response variable	**Term**	**Estimate**	**Standard Error**	**t**	***P***	**R^2 (P model)**
PC1	Intercept	-17.86	7.94	-2.25	0.048	0.77
	AET5	-0.20	0.05	-3.93	0.0028	(0.0006)
	Isothermality	0.36	0.12	3.14	0.0105	
PC2	Intercept	5.61	1.90	2.95	0.0134	0.47
	SWC2	-0.24	0.08	-2.98	0.0125	(0.0125)

Figure captions

Figure 1. Geographical location of *Prosopis laevigata* populations sampled in this study. Dots and number indicate the populations. See Table 1 for population details.

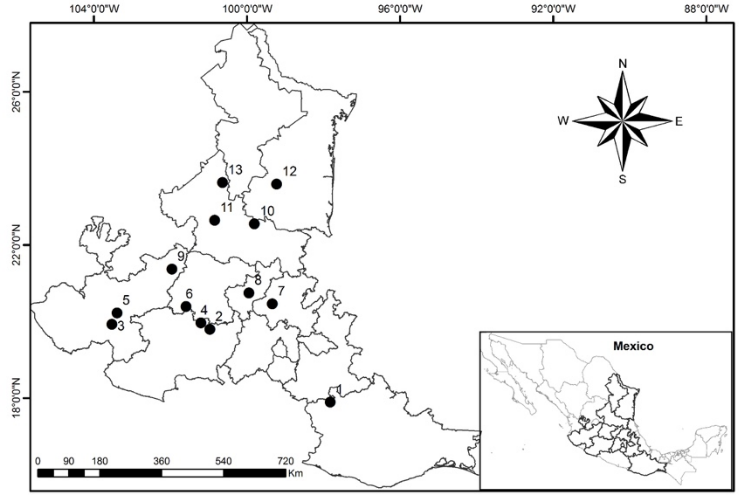


Figure 2. Linear regression of the percentage of seeds germinated and latitude of the collection localities.

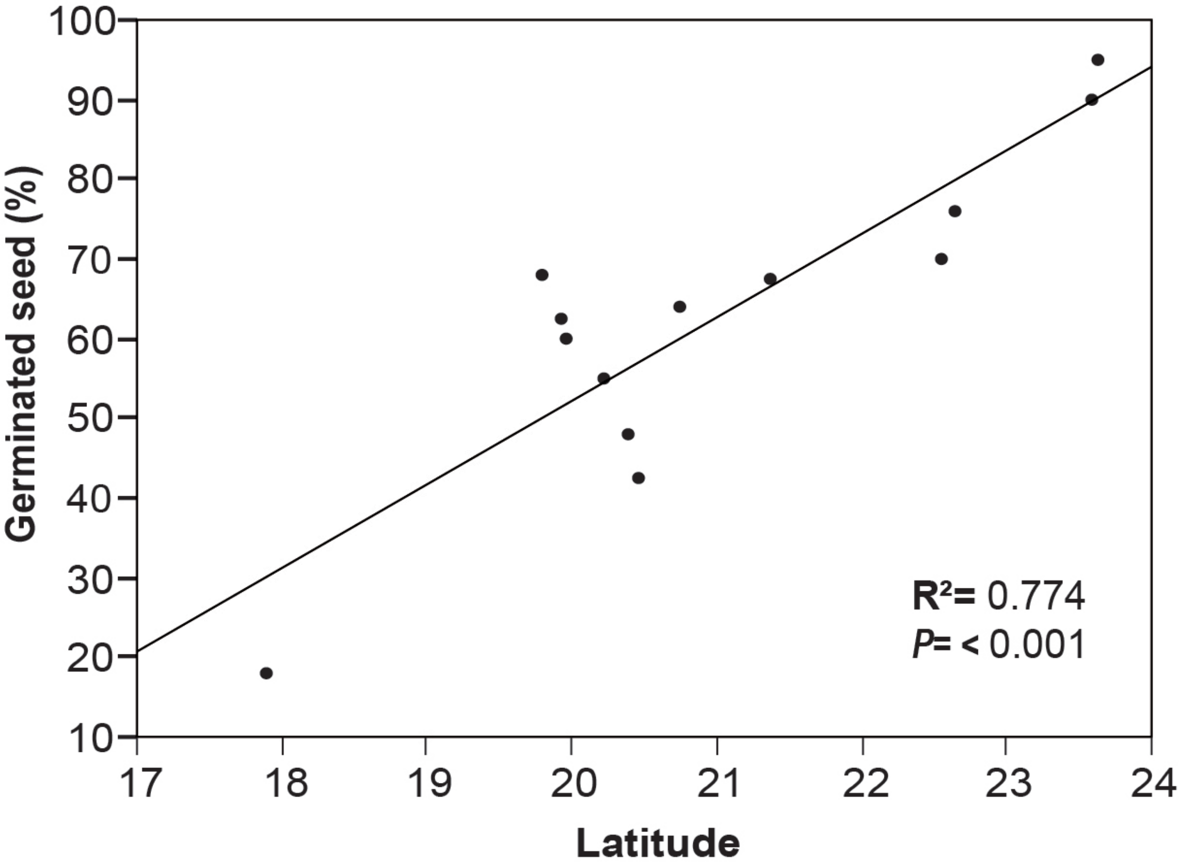


Figure 3. Biplot of the two first axes from a principal component analysis (PCA) for the seven traits evaluated. Dots with numbers indicate the 13 sampled populations of *Prosopis laevigata*. See Table 1 for population details.

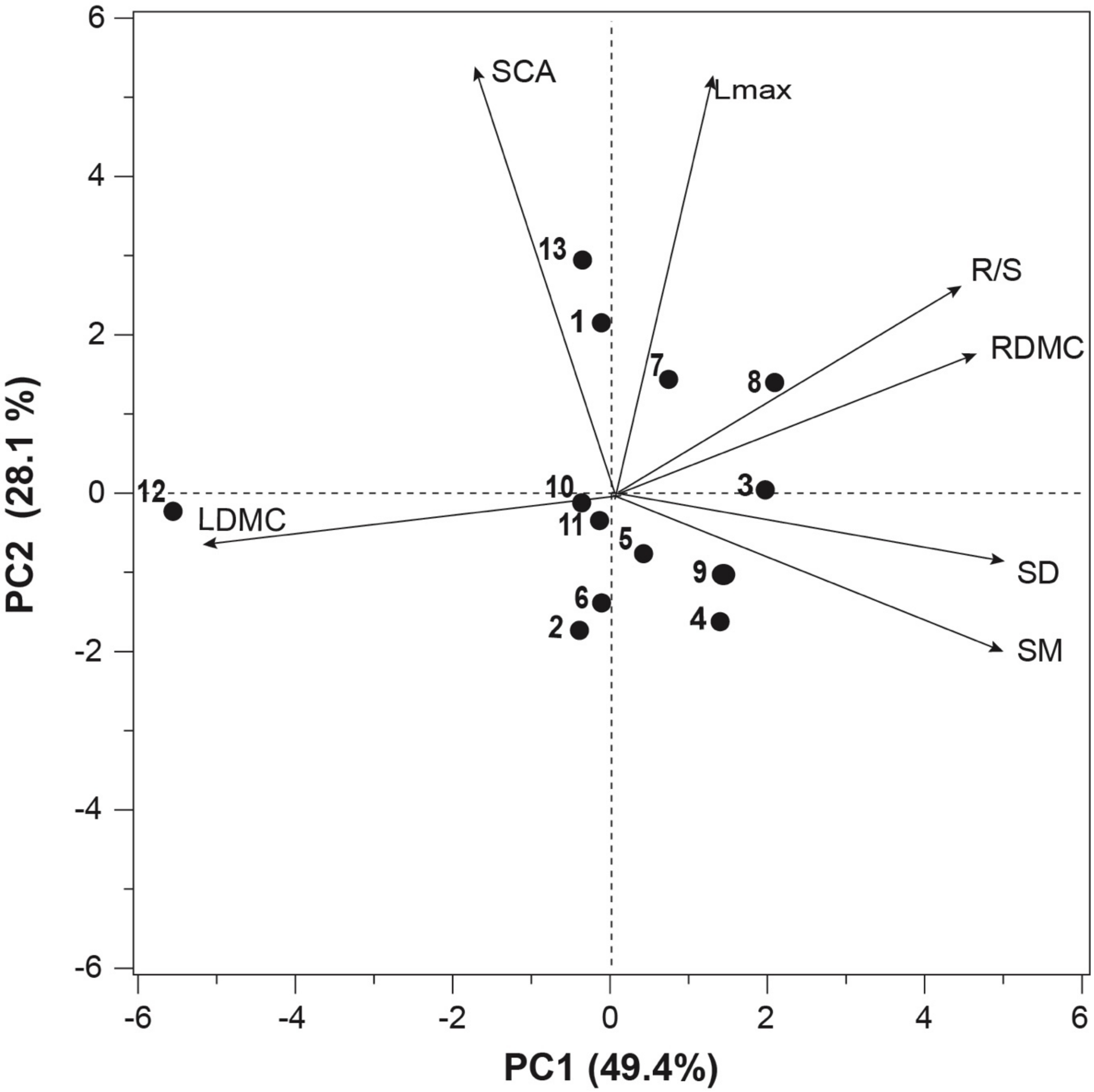
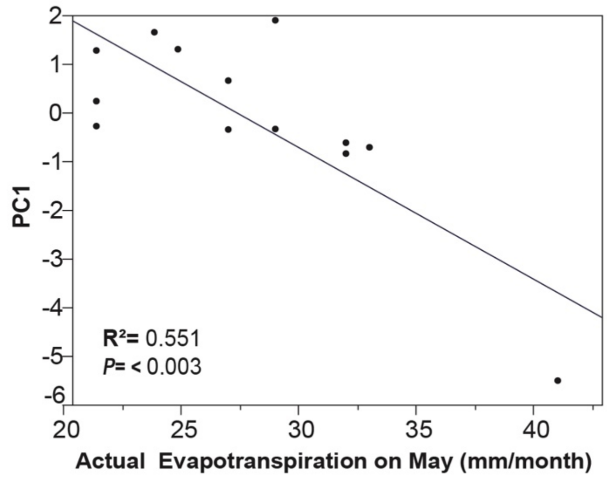
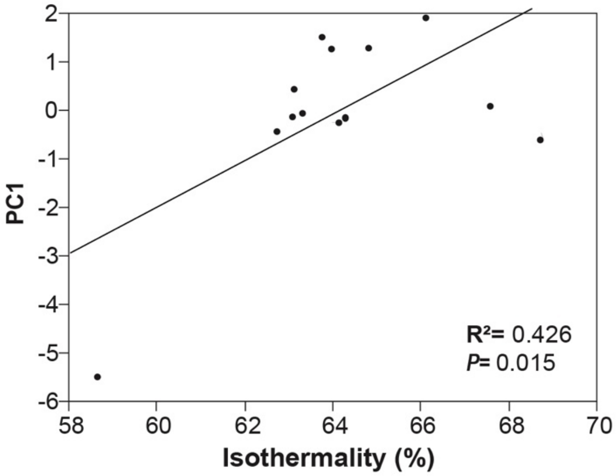


Figure 4. Bivariate regressions of A) Population scores on the first axis of the PCA on actual evapotranspiration on May, B) Population scores on the first axis of the PCA on isothermality and C) Population scores on the second axis of the PCA on soil water content in February.

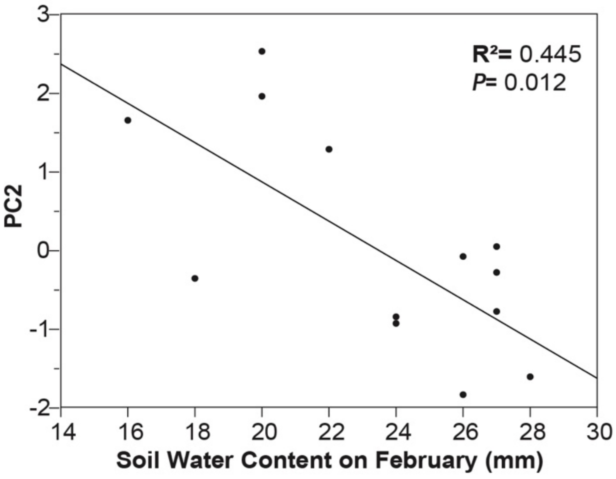
A)


PC1
2
1
0
-1
-2
-3
-4
-5
-6
R^2= 0.551
P= < 0.003
20
25
30
35
40
Actual Evapotranspiration on May (mm/month)

B)


PC1
2
1
0
-1
-2
-3
-4
-5
-6
R^2= 0.426
P= 0.015
58
60
62
64
66
68
70
Isothermality (%)

C)


PC2
3
2
1
0
-1
-2
R^2= 0.445
P= 0.012
14
16
18
20
22
24
26
28
30
Soil Water Content on February (mm)

Supplementary material

Table S1. Means (± standard error) of seven functional traits for the 13 populations of *Prosopis laevigata.* See Table 2 for definition, units and biological significance of each trait.

Number	Population code	LDMC	Lmax	RDMC	R/S	SM	SCA	SD
1	**SMA**	0.10±0.053	60.52±5.905	0.09±0.013	0.72±0.153	40.80±2.497	0.30±0.044	106.33±29.730
2	**IND**	0.04±0.008	52.03±3.356	0.06±0.019	0.25±0.056	50.26±1.556	0.21±0.016	186.78±25.011
3	**SYL**	0.05±0.017	57.80±4.921	0.14±0.014	0.40±0.048	51.04±1.652	0.26±0.016	278.96±49.211
4	**CUI**	0.07±.0475	50.88 ±8.662	0.11±0.036	0.66±0.165	56.25±2.801	0.19±0.013	199.10 ±73.110
5	**SP**	0.07±0.021	53.50±3.737	0.09±0.010	0.43±0.074	47.41±1.151	0.21±0.013	152.30±23.875
6	**NOV**	0.10±0.023	49.95±4.173	0.10±0.022	0.32±0.069	49.22±0.722	0.22±0.021	173.82±25.939
7	**IXM**	0.02±0.003	69.58±4.773	0.08±0.019	0.56±0.126	50.60±2.390	0.31±0.048	155.44±14.513
8	**PÑ**	0.05±0.019	76.39±4.947	0.11±0.020	0.58±0.084	53.52±2.467	0.24±0.015	284.46±54.824
9	**LM**	0.04±0.013	50.91±2.947	0.12±0.043	0.37±0.051	57.14±2.387	0.22±0.018	224.14±34.035
10	**HM**	0.07±0.012	60.97±4.278	0.12±0.053	0.40±0.072	39.50±1.014	0.22±0.017	194.25±28.662
11	**VA**	0.11±0.029	51.06±4.174	0.12±0.017	0.55±0.080	41.52±1.303	0.24±0.034	147.35±24.175
12	**HUI**	0.23±0.053	53.48±4.605	0.01±0.004	0.11±0.054	24.20±0.769	0.27±0.030	53.65±6.495
13	**MAT**	0.06±0.013	72.78 ±4.515	0.09±0.010	0.69±0.081	34.41±1.814	0.28±0.012	99.85±13.987

Abbreviations of functional traits: **LDMC**; Leaf dry matter content, **Lmax**; Maximum length, **RDMC**; Root dry matter content, **R/S**; Root/shoot ratio, **SM**; Seed mass **SCA**; Specific cotyledon area and **SD**; Stem density. See Table 1 for population details.