

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

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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 axes 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 isoterma 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.

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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.) M.C. Johnston 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.* 2021b). 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).

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

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.

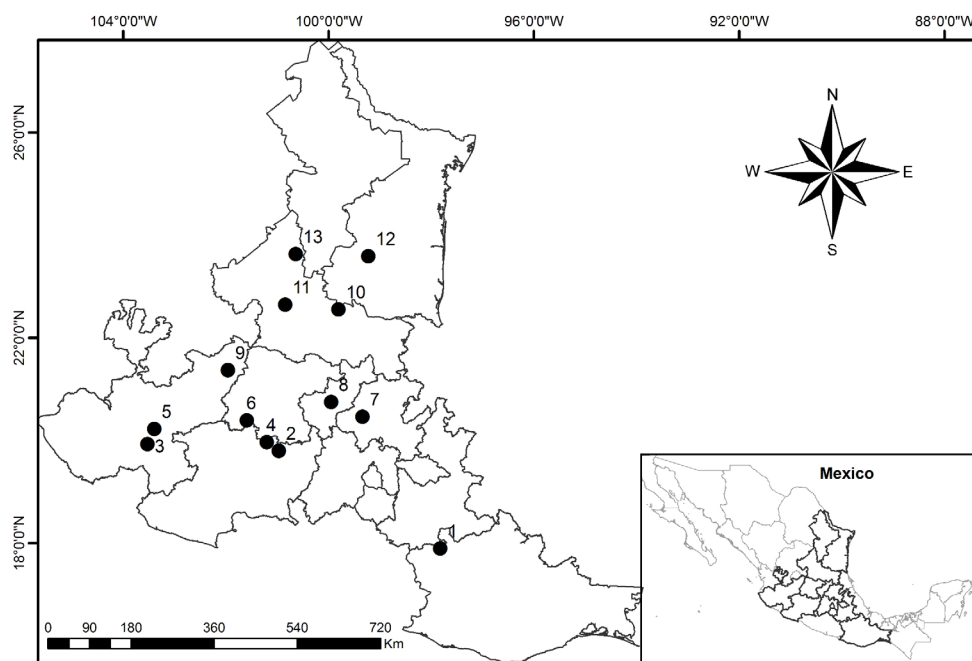


Figure 1. Geographical location of *Prosopis laevigata* populations sampled in this study. Dots and number indicate the populations. See [Table 1](#) for population details.

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).

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>; (Cervo-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 v11.0.0 (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.

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 availability 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

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 v. 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](#)).

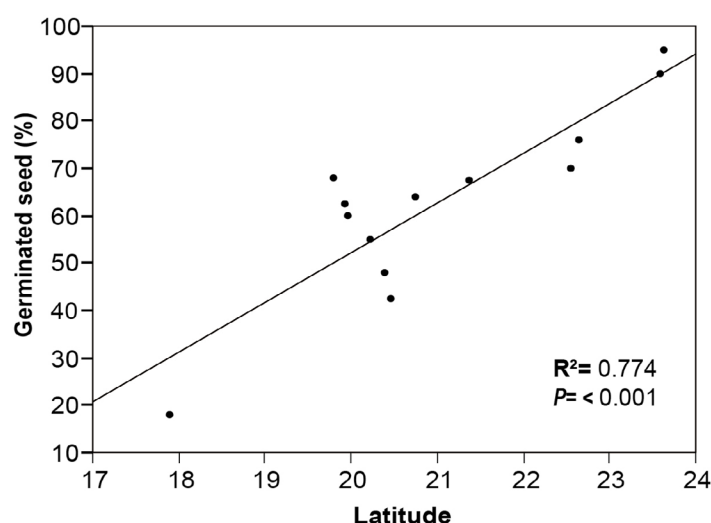


Figure 2. Linear regression of the percentage of seeds germinated and latitude of the collection localities.

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).

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

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.

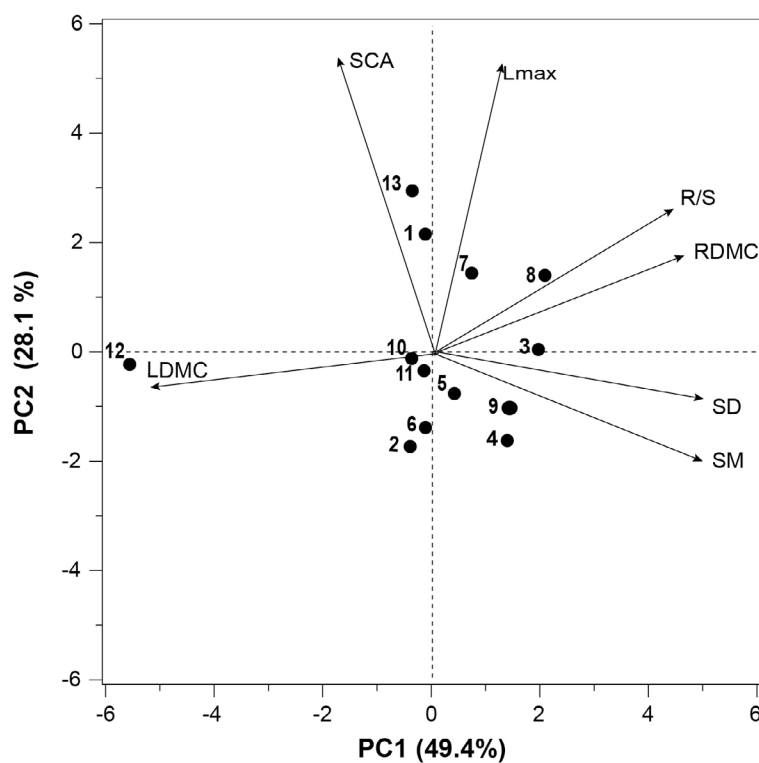


Figure 3. Biplot of the two first axes from a principal component analysis (PCA) for the seven traits evaluated. Dots with numbers indicate the 13 sampled populations of *Prosopis laevigata*. See [Table 1](#) for population details.

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

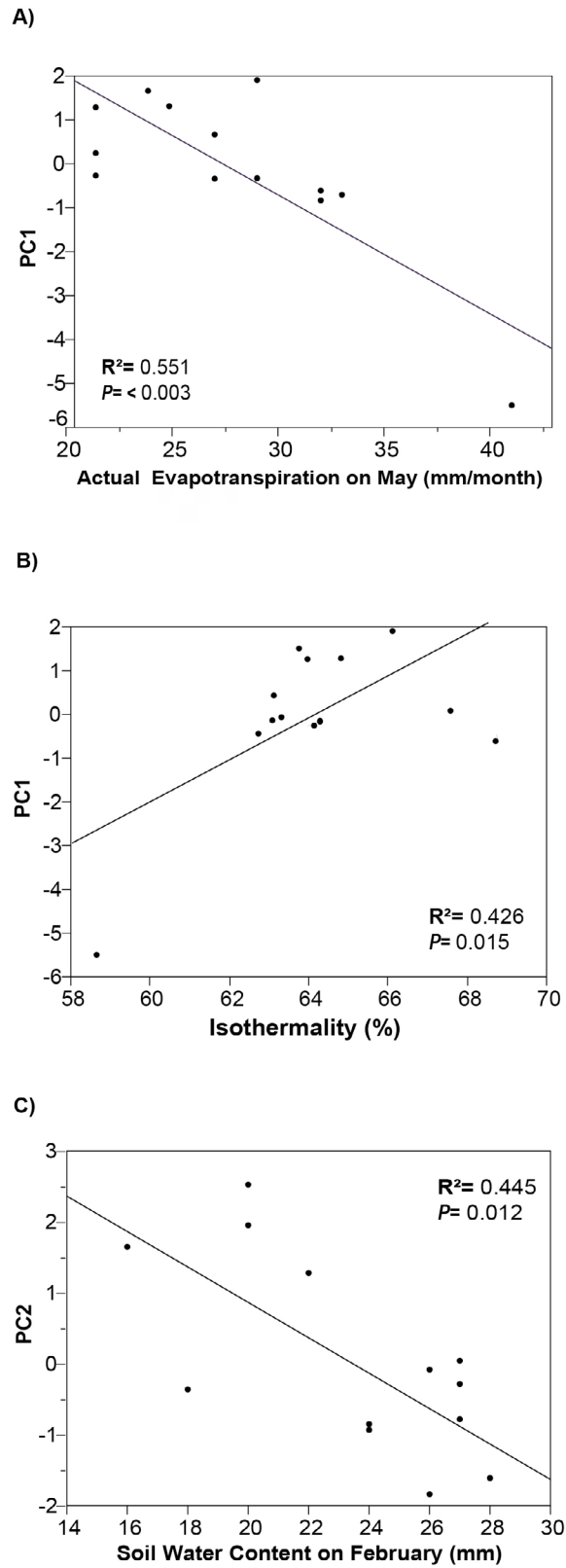


Figure 4. Bivariate regressions of A) Population scores on the first axis of the PCA on actual evapotranspiration on May, B) Population scores on the first axis of the PCA on isothermality and C) Population scores on the second axis of the PCA on soil water content in February.

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	<i>t</i>	<i>P</i>	<i>R</i> ² (P model)
PC1	Intercept	-17.86	7.94	-2.25	0.048	0.77
	AET5	-0.20	0.05	-3.93	0.0028	
	Isothermality	0.36	0.12	3.14	0.0105	(0.0006)
PC2	Intercept	5.61	1.90	2.95	0.0134	0.47
	SWC2	-0.24	0.08	-2.98	0.0125	(0.0125)

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 that 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 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 soil 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.* 2021b). 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.* 2021a). 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 data for this article can be accessed here: <https://doi.org/10.17129/botsoci.2846>

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