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Interpopulation variation in seed germination and seed traits of *Opuntia streptacantha*

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Abstract. Cacti have a wide distribution in the arid and semi-arid ecosystems of Mexico, with environmental variations affecting both physical and physiological seed traits. Herein, the physical and ecophysiological traits of *Opuntia streptacantha* seeds were evaluated to determine whether they are affected by sites. The seeds from eight sites of *O. streptacantha* from six Mexican states were studied, Sain Alto, Villa de Guadalupe, Villa González Ortega (Zacatecas), Zaragoza (San Luis Potosí), Lagos de Moreno (Jalisco), San Luis de La Paz (Guanajuato), Cardonal (Hidalgo) and Santiago Tepetitlán (Estado de México); being Lagos de Moreno and Santiago Tepetitlán the less dry sites and Villa González Ortega and Cardonal the drier ones. The longest seeds were from Zaragoza (3.81 mm), Villa González Ortega (3.72 mm) and Villa Guadalupe (3.70 mm); the widest and thickest seeds were from San Luis de La Paz (3.44 and 2.16 mm, respectively). The highest volumetric weight was found in seeds from Villa Guadalupe (9.92 kg hL^{-1}), Lagos de Moreno (9.90 kg hL^{-1}) and Santiago Tepetitlán (9.67 kg hL^{-1}). The site San Luis de La Paz (1.31 g) had the highest weight of 1000 seeds and Cardonal (8874 seeds) the highest number of seeds per kilogram. The seeds with the highest moisture content were those from Villa González Ortega (9.81%), and the seeds with the lowest hardness were those from Santiago Tepetitlán (17.95 lbf), and Lagos de Moreno (16.55 lbf). The seeds from the western region of the country (Lagos de Moreno), where the species is less abundant and the environment is moister, showed the highest germination (26%). The seed hardness was negatively correlated with seed germination, with soft seeds having the highest germination. No correlation between seed weight and germination was found. The seed traits are related to environmental factors that influence the seed quality. The physical seed traits and seed germination from different sites for ecological restoration plans need to be considered.

Keywords: *Cacti; Parameters physical; Seed germination; Plant populations.*

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Introduction

The cactus family occupies a wide range of habitats throughout the Americas (Anderson, 2001) and due to their low germination and slow growth, cacti are among the most vulnerable plant species to human disturbances (Godínez-Álvarez *et al*., 2003) and constitute the fifth taxonomic group with the highest portion of threatened species worldwide (Goettsch *et al*., 2015).

Given that, it is important to study the processes affecting seed germination of cacti for reproductive and conservation purposes (Rojas-Archita and Vázquez-Yanes, 2000; Flores *et al*., 2006; Barrios *et al*., 2020).

The genus *Opuntia* is native to the American continent and includes 154 species and 30 infraspecies (Korotkova *et al*., 2021), where 66 of them are native of Mexico (Hernández *et al*., 2014). This genus constitutes a valuable plant genetic resource based on the breadth of its multiple uses for local Mexican families (Bravo-Hollis and Sánchez-Mejorada, 1991). The Mexican species *Opuntia streptacantha* play a fundamental ecological role, hosting diverse and abundant wildlife, and protecting soil erosion (López-Palacios *et al*., 2019). This species occurs in the Mexican states of Aguascalientes, Ciudad de México, Durango, Guanajuato, Hidalgo, Jalisco, México, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tlaxcala, and Zacatecas (Guzmán *et al*., 2003; Cruz-Jiménez *et al*., 2023).

The *Opuntia* seeds have physiological dormancy, *i.e.*, they need a maturation period before they can germinate (Delgado-Sánchez *et al*., 2011, 2013). They also have a hard and well-lignified seed coat, which produces germination difficult (Monroy-Vázquez *et al*., 2017). In addition, their embryos have a low growth potential (Orozco-Segovia *et al*., 2007). Thus, the germination of *Opuntia* spp. seeds is an ecological process that needs more research.

The cactus species having widespread distribution can experience contrasting environmental conditions, which impose local selection pressures to which populations tend to adapt resulting in ways to deal with different resources, *e.g.*, germination differential (Bauk *et al*., 2017). The environmental conditions can cause changes in the germination and in the morphophysiological characteristics of the seeds (Baskin and Baskin, 2014). The variation caused by environment is import for seed storage and its use in ecological restoration projects (Sánchez *et al*., 2015). Several *Opuntia* species have widespread geographic distribution (e.g., *O. streptacantha*); however, the effect of the sites on their seeds has been few studied. For some *Opuntia* species, a higher seed germination for seeds from warmer than for those from dryer areas has been reported by Romo-Campos *et al*. (2010).

The traits such as seed size or seed mass, moisture content, germinative requirements and dormancy type have been used in the definition of ecological functioning groups, or to predict the storage response of seeds and the performance of plants in an increasingly uncertain environment (Hong and Ellis, 1996; Sánchez *et al*., 2015). The seed traits can also affect seed germination of some species, *e.g.*, seed hardness was positively correlated with seed germination in *Opuntia robusta*. However, the contrary was found for *Opuntia jaliscana*. In addition, *Opuntia* spp. seeds collected in moist areas were bigger than those from drier ones, and there was a correlation of seed mass with seed germination only for *O. jaliscana* (Romo-Campos *et al*., 2010). This correlation has not been found in other *Opuntia* spp. (Romo-Campos *et al*., 2010), nor in genera such as *Astrophytum*, *Echinocactus*, *Ariocarpus* and *Turbinicarpus* (Rojas-Aréchiga *et al*., 2013), as well as *Cereus*, *Cleistocactus*, *Echinopsis*, *Gymnocalycium*, *Harrisia*, *Parodia* and *Stetsonia* (Sosa-Pivatto *et al*., 2014). However, with higher seed mass there is lower dependence to light to germinate (Flores *et al.* 2011, 2016). In this sense, Flores

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et al. (2011) suggested that big cactus seeds can germinate in darkness and produce seedlings that could emerge from greater soil depths than those from small seeds, because they have more resources. In addition, Flores *et al*. (2006) hypothesized that small seed mass and light requirements have coevolved as an adaptation to ensure germination.

Herein, the physical and ecophysiological traits of *Opuntia streptacantha* seeds were evaluated to determine whether they are affected by sites. The hypothesis was that seeds from drier sites have lower physical quality and germination percentages than those from warmer sites. The results of this study could contribute to understanding the germination biology of *Opuntia* species; they also could enhance the propagation of large numbers of cultivated individuals outside their habitats and help to develop resilient genotypes of *O. streptacantha* through breeding plant sites.

Material and Methods

Collection sites and plant material

The collection of mature prickly pears was carried out from September to November 2020 from eight populations of *Opuntia streptacantha* located in the arid and semi-arid ecosystems of the Mexican territory (Figure 1 and Table 1), following the current distribution of the species described by Cruz-Jiménez *et al*. (2023). The average annual temperature ranges from 14.0 ºC in Santiago Tepetitlán to 18.4 in Cardonal; mean annual precipitation ranges from 343.5 in Villa González Ortega to 591.3 in Santiago Tepetitlán. The ripe fruits attached to the plant (15 to 20 plants randomly chosen by site, with a distance between plants of 20 m) were collected manually and the seeds were immediately extracted. After drying, a single batch was made per site (site), and seeds were stored in paper bags at room temperature.

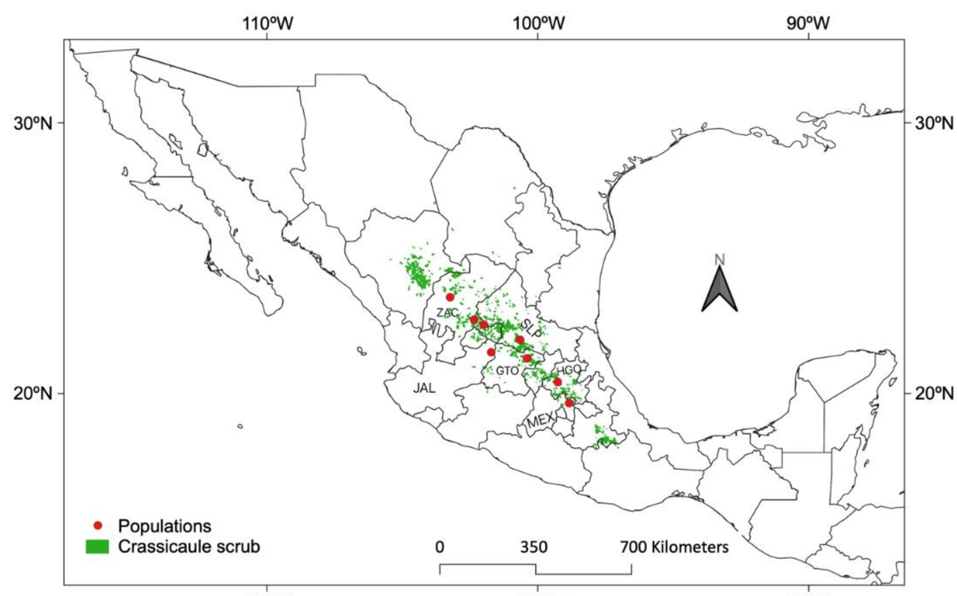

Figure 1. Distribution of eight populations of *Opuntia streptacantha* from six Mexican states whit crassicaule scrub: Zacatecas (ZAC); Jalisco (JAL); San Luis Potosí (SLP); Guanajuato (GTO); Hidalgo (HGO); and Estado de México (MEX).

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Table 1. Geographic location of the *Opuntia streptacantha* sites evaluated and averages of historical precipitation and temperature records (years 1977-2018).

State	Population	Historical mean precipitation (mm)	Historical annual mean temperature (ºC)	Geographic location		Altitude (m)
				North latitude	West longitude	
Zacatecas (ZAC)	Sain Alto, SA	455.6	16.7	23°33'10.4"	103°14'10.5"	2120
	Villa de Guadalupe, VG	426.4	15.8	22°43'28.1"	102°21'01.6"	2158
	Villa González Ortega, VGO	343.5	16.6	22°32'17.5"	101°59'17.9"	2138
San Luis Potosí (SLP)	Zaragoza, Z	487.1	16.5	21°58'47.0"	100°38'51.2"	2105
Jalisco (JAL)	Lagos de Moreno, LM	544.7	18.0	21°31'22.7"	101°43'07.2"	1975
Guanajuato (GTO)	San Luis de La Paz, SL	500.3	17.4	21°17'47.3"	100°23'24.4"	2110
Hidalgo (HGO)	Cardonal, C	354.1	18.41	20°25'28.7"	99°15'51.1"	1987
Mexico State (MEX)	Santiago Tepetitlán, ST	591.3	14.0	19°38'37.1"	98°50'30.2"	2450

Description of eight study localities in six Mexican states, where fruit collection was carried out. The data were obtained from meteorological stations from the Comisión Nacional del Agua (https://smn.conagua.gob.mx).

Physical seed traits

The traits evaluated were volumetric weight, dry and fresh weight, seeds per kilogram, moisture content, and hardness. The seed size traits were evaluated in 25 seeds per population which were randomly chosen, and width and length were measured with a digital vernier with precision of 0.001 mm (Truper Stainless Steel Model 14388). The volumetric weight was evaluated considering four replications of 5.0 g of seeds per population which were weighed using an analytical balance (Ohaus Explorer E11140) and the volume was measured in a 10 mL graduated glass cylinder.

The seed number per kilogram was quantified using eight replications of 100 seeds which were weighted using an analytical balance and the weight of 1000 seeds was calculated. Subsequently, the number of seeds per kilogram was calculated, according to ISTA (2016). The moisture content was measure using four replications of 1.0 g which were weighted and posteriorly dried in a universal drying oven (Memmert UN30) at 103 ± 2 ºC, for 17 ± 1 h to obtain dry weight, which together with the initial weight of the sample (considered as fresh weight) was used to calculate the moisture content of the seed lot (ISTA, 2016). The hardness of the seed was quantified in 10 seeds per population, seeds were dried at 90 ºC for 1 h to detect fracture failure, with a high range sensor (0-1000 lbf) using the Instron model 1000 (Universal Testing Instrument, serial 2791). The hardness results are reported in units of lbf. The experimental design was a completely randomized considering the sites as the main factor in study (treatments).

Seed germination

The seeds were washed in 150 mL of 70% ethanol for 5 min, in 150 mL of 20% sodium hypochlorite (6% free chlorine) for 2 min and finally washed four times with sterile distilled water (under aseptic conditions within a laminar flow cabinet) and allowed to imbibe in sterile distilled water for 24 h. The seeds were incubated in glass jars with water-agar for nine months in a germination room with a photoperiod of 12 h of light and 12 h of darkness at 25 ± 2 ºC. Five replicates, one per site, of 20 seeds each were done, and they were weekly checked.

Statistical analysis

The variables of physical seed traits and seed germination were evaluated through an analysis of variance based on a completely randomized design. Posteriorly, Tukey tests ($\alpha \leq 0.05$) were performed on the variables having significant differences, using Statistic 7 program (StatSoft Inc. 2004). The moisture content data, which did not meet the assumptions of the ANOVA, was transformed with the Johnson method (Chou *et al*., 1998). The width and length data could not be normalized using transformations; thus, were analyzed with a non-parametric Kruskal-Willi's test (Zar, 1999). The relationship between the hardness and weight of the seeds with the germination percentage by site was determined by Pearson correlation test (*r*). Here in, five replicates of germination analysis by site and five randomly chosen replicates of hardness and weight of 1000 seeds were used.

Results and Discussion

Physical seed traits

The physical quality of *O. streptacantha* seeds was different between sites, in the length (D.F. = 7, F= 3.34, p< 0.01), width (D.F. = 7, F= 7.47, p< 0.01), and thickness (D.F. = 7, F= 9.58, p< 0.01; Figure 2). The volumetric weight (D.F.= 7, F= 20.20, p< 0.01), weight of 1000 seeds (D.F.= 7, F= 40.40, p< 0.01), number of seeds per kilogram (D.F.= 7, F= 39.80, p< 0.01), moisture content (D.F.= 7, F= 7.23, p< 0.01), and seed hardness (D.F.= 7, F= 7.39, p< 0.01), showed significant differences between sites (Table 2). The lengthier seeds were found in Zaragoza, SLP (3.81 mm), Villa González Ortega, ZAC (3.72 mm), and Villa Guadalupe, ZAC (3.70 mm) sites. The widest and thickest seeds were those from San Luis de La Paz, GTO with 3.44 mm and 2.16 mm, respectively.

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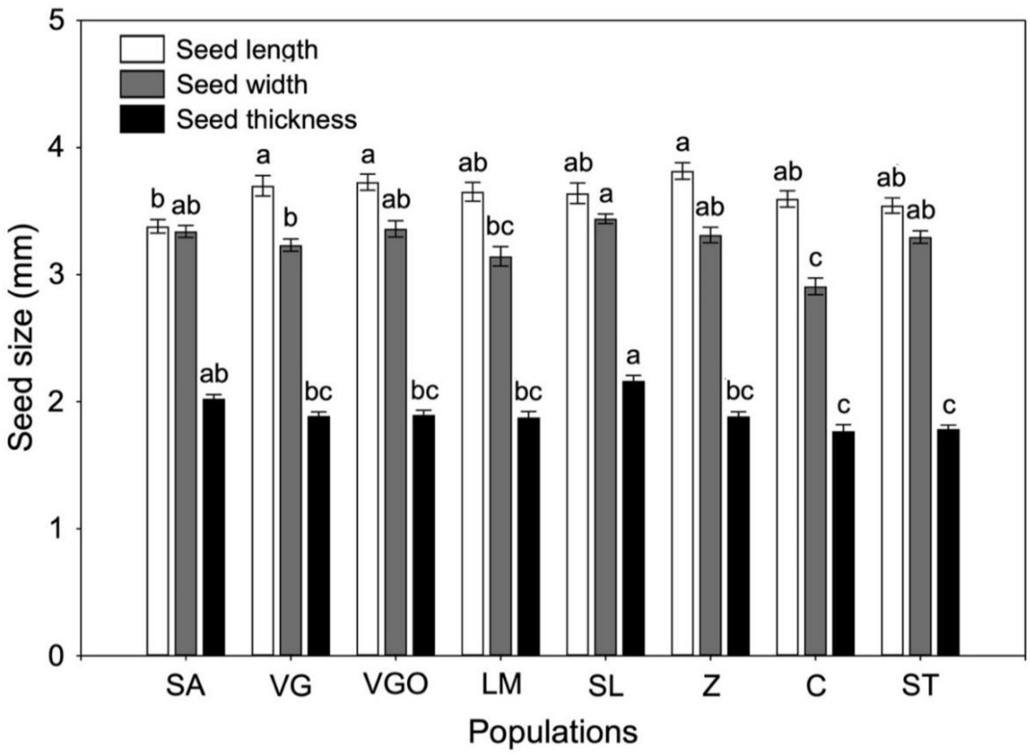

Figure 2. Morphometric parameters of *O. streptacantha* seeds from eight sites, Zacatecas, ZAC (Sain Alto, SA; Villa Guadalupe, VG, Villa González Ortega, VGO); Jalisco, JAL (Lagos de Moreno, LM); Guanajuato, GTO (San Luis de La Paz, SL); San Luis Potosí, SLP (Zaragoza, Z); Hidalgo, HGO (Cardonal, C); and Mexico, MEX (Santiago Tepetitlán, ST). The bars in each response variable with different letters indicate significant statistical differences (Tukey´s test, *p*≤0.05) among sites.

Table 2. Average physical quality of the *Opuntia streptacantha* seeds from different populations.

Populations	Length (mm)	Width (mm)	Thickness (mm)	VW (kg hl^{-1})	WTS (g)	NSK	MC (%)	Hardness (lbf)
Sain Alto	3.38^{b}	$3.34^{a,b}$	$2.04^{a,b}$	$9.07^{b,c}$	1.20^{c}	8325^{b}	7.18^{c}	$19.73^{b,c}$
Villa Guadalupe	3.70^{a}	$3.23^{a,b}$	$1.88^{b,c}$	9.92^{a}	$1.30^{a,b}$	7648^{c}	$9.62^{a,b}$	$24.22^{a,b,c}$
Villa González Ortega	3.72^{a}	$3.36^{a,b}$	$1.89^{b,c}$	9.45^{b}	$1.29^{a,b}$	7710^{c}	9.81^{a}	$20.30^{b,c}$
Lagos de Moreno	$3.65^{a,b}$	$3.14^{b,c}$	$1.87^{b,c}$	9.90^{a}	1.20^{c}	8311^{b}	8.94^{bc}	16.55^{c}
San Luis de La Paz	$3.64^{a,b}$	3.44^{a}	2.16^{a}	9.20^{b}	1.31^{a}	7580^{c}	$8.97^{b,c}$	31.30^{a}
Zaragoza	3.81^{a}	$3.31^{a,b}$	$1.88^{b,c}$	8.87^{c}	1.26^{b}	7890^{c}	9.40^{ab}	$27.05^{a,b}$
Cardonal	$3.59^{a,b}$	$2.90^{b,c}$	$1.76^{b,c}$	9.42^{b}	1.12^{d}	8874^{a}	8.37^{c}	$21.89^{b,c}$
Santiago Tepetitlán	$3.54^{a,b}$	$3.29^{a,b}$	$1.78^{b,c}$	9.67^{a}	1.20^{c}	8273^{b}	$9.31^{a,b,c}$	17.95^{c}

Seed size (n=25); VW, volumetric weight (20 g); WTS, weight of 1000 seed (n= 800); NSK, number of seed per kilogram, (n=800); MC, moisture content (n=4.0 g). The values followed by a different letter in the same column show significant differences (Tukey´s test, p≤0.05).

The seeds with the highest volumetric weight were those from Villa Guadalupe, ZAC (9.92 kg hL^{-1}), Lagos de Moreno, JAL (9.90 kg hL^{-1}) and Santiago Tepetitlán, MEX (9.67 kg hL^{-1}), contrasting with seeds from Zaragoza, SLP (8.87 kg hL^{-1}) which showed the lowest volumetric weight. The highest weight of 1000 seeds was to San Luis de La Paz, GTO (1.31 g) and the highest number of seeds per kilogram was to Cardonal, HGO with 8874 seeds. The seeds with the highest moisture content were those from Villa González Ortega, ZAC (9.81%), contrasting with seeds from Cardonal, HGO (8.37%) and Sain Alto, ZAC (7.18%) which showed the lowest moisture content. The hardest seeds were found in San Luis de La Paz, GTO (31.30 lbf) compared with Santiago Tepetitlán, MEX (17.95 lbf) and Lagos de Moreno, JAL (16.55 lbf) which showed the lower hardness (Table 2). The environmental factors to which plants are exposed can influence many of their characters and progeny (Roach and Wulff, 1987). In this study with *O. streptacantha* seeds collected from eight sites in Mexico, the results showed that the environmental conditions affected the physical quality and germination of *O. streptacantha* seeds. The differences in seed mass have been found between cactus species and localities (Barrios *et al*., 2020). Romo-Campos *et al*. (2010) found that *Opuntia* ssp. seeds collected in humid areas were heavier than those collected in dry sites and our results confirm these findings, as seeds from wetter sites showed the highest volumetric weight, likewise, seeds from dry sites such as Cardonal showed the lowest seed weight (1. 12 g), the lowest moisture content (8.37%), also the width (2.90 mm) and thickness (1.76 mm) of the seeds was lower than the rest of the sites.

Seed germination

The seed germination of *O. streptacantha* was affected by site (site) (D.F.= 7, F= 2.77, $p < 0.05$). The higher germination was found for seeds from Lagos de Moreno, JAL (26%), followed by the sites of Guadalupe, ZAC (15%), Villa Gonzalez Ortega, ZAC (15%), Cardonal, HGO (15%), and Zaragoza, SLP (13%) (Figures 3 and 4).

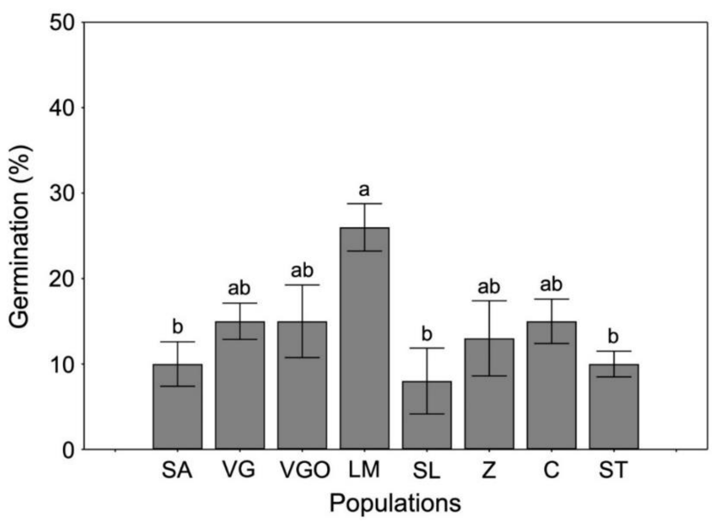

Figure 3. Seed germination of *O*. *streptacantha* from eight sites, Zacatecas State, ZAC (Sain Alto, SA; Villa Guadalupe, VG, Villa González Ortega, VGO); Jalisco, JAL (Lagos de Moreno, LM); Guanajuato, GTO (San Luis de La Paz, SL); San Luis Potosí, SLP (Zaragoza, Z); Hidalgo, HGO (Cardonal, C); and Mexico, MEX (Santiago Tepetitlán, ST). The bars with different letters indicate significant differences (Tukey´s test, $p \leq 0.05$, n=100).

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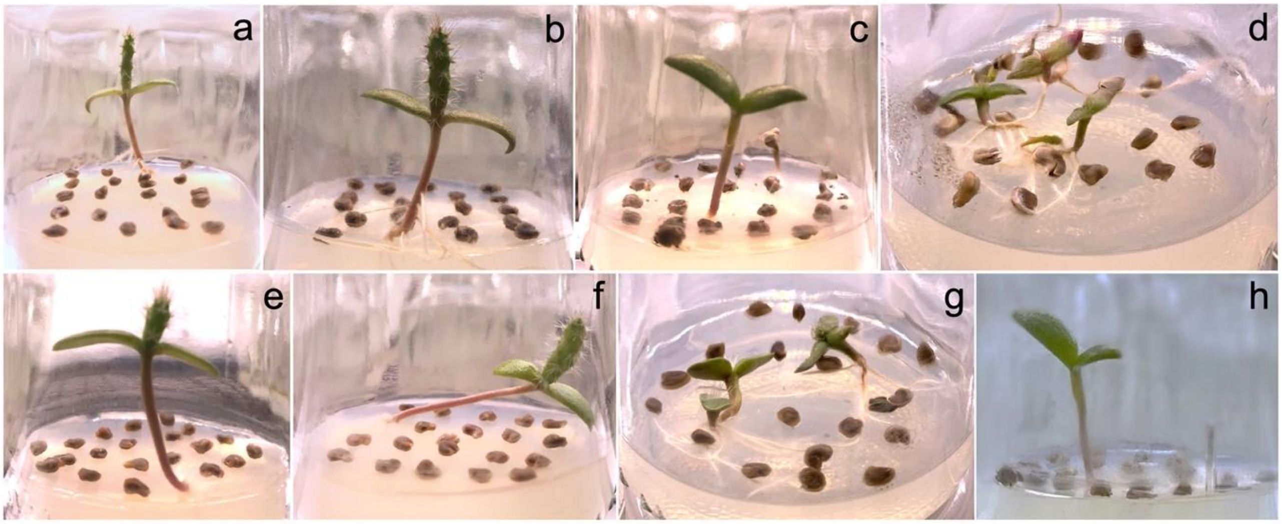

Figure 4. Germination of *O*. *streptacantha* seeds from eight sites, a) Sain Alto, ZAC; b) Villa Guadalupe, ZAC; c) Villa González Ortega, ZAC; d) Lagos de Moreno, JAL; e) San Luis de La Paz, GTO; f) Zaragosa, SLP; g) Cardonal, HGO; h) Santiago Tepetitlán, MEX.

The morphometric characters and seed germination showed variation among sites. The seed germination and plant growth are affected by microclimate and soil conditions, which generates a wide range of geoclimatic conditions modifying plant communities (Fredrick *et al*., 2015). This suggests that variation in physical seed traits and germination may be related to the complex plant-environment interactions occurring in arid and semi-arid environments (Wali and Krajima, 1973; Albert *et al*., 2010). It was observed that seeds of the eight sites evaluated had low germination percentage (8 to 26%), consistent with previous findings for *Opuntia* seeds (Orozco-Segovia *et al*., 2007; Delgado-Sánchez *et al*., 2011, 2013; Monroy-Vázquez *et al*., 2017). The low germination supports seed dormancy findings for *Opuntia* spp. (Orozco-Segovia *et al*., 2007; Romo-Campos *et al*., 2010; Delgado-Sánchez *et al*., 2011, 2013; Monroy-Vázquez *et al*., 2017).

A few studies have been carried out on the effect of site on cactus seed germination have been performed. In an altitudinal gradient from 878 to 2230 m, with temperature and precipitation from 16.5 ºC and 680 mm to 10.3 ºC and 790 mm, was observed that seed germination of *Gymnocalycium monvillei* (Cactaceae) occurs mostly at sites where the species is not abundant (Bauk *et al*., 2017). This could indicate that maturation of the embryo in places with extreme temperatures is slow, so that the greater filling of the seed could positively affect their physical and physiological characteristics (Fenner and Thompson, 2005). In this study, a high variation in the germination response of *O*. *streptacantha* from different sites was observed, although all sites showed seed dormancy. For *O*. *streptacantha*, a trypsin like protease has been reported (Torres-Castillo *et al*., 2009), and is present in the dormant seeds (Hemalatha and Prasad, 2003). Thus, this supports the result found of dormant seeds for all sites. Also, the seeds did not always show a clear pattern in relation to the physical seed characteristics and the environmental factors that favor their distribution. There, all *Opuntia* seeds from the eight sites showed variable germination percentages.

This result mean that the species can establish itself in different edaphoclimatic conditions. These data highlight the importance of reproductive traits in explaining the wide distribution of *O*. *streptacantha* in Mexico (Cruz-Jiménez *et al*., 2023), like another cactus in Argentina (Bauk *et al*., 2015). The response shown by sites of one species to tolerate abiotic factors in arid environments is relevant in terms of land use change and climate change events (Gurvich *et al*., 2002).

The effects of sites on the germination percentage showed higher germination (26%) in the LM, where the species is not particularly abundant, and the environmental conditions are less dry and water availability is higher. Otherwise, a germination from 8 to 15% was found in seeds from SA, VG, VGO, SL, Z, C, and ST, sites where the species has a wide distribution, and the climate is drier. Similar results were found for *O*. *lasiacantha* and *O*. *streptacantha*, where higher seed germination was found for seeds from less dry sites (Romo-Campos *et al*., 2010).

The seed germination can be affected by different environmental conditions (Roach and Wulff, 1987; Donohue and Schmitt, 1998; Baskin and Baskin, 2019), due to a greater allocation of resources at the endosperm and the embryo (Roach and Wulff, 1987; Galloway, 2001). However, the relationship among resources availability, seed size, and germination is limited by the number of seeds per fruit, predation, and dispersal. There is evidence on the increase in seed mass in stressful and competitive environments (Donohue and Schmitt, 1998). This agrees with our findings regarding the physical characteristics such as size, weight, moisture content and hardness, with the seeds from the sites of VG, VGO, SA, Z, SL, ST and, C being the most prominent (Figure 2, Table 2), sites where the species is widely distributed, and the environmental conditions are dry.

The conditions needed to break seed dormancy and thus germinate can be highly variable among species, within species, or among seed sources of the same species (Luna *et al*., 2009; Delgado-Sánchez *et al*., 2011, 2013; Fredrick *et al*., 2015). The present study revealed variation among sites with respect to physical seed quality and seed germination, although seed dormancy was always present in all sites. It has been suggested that seed dormancy is an adaptation to delay germination for species that occupy extreme or seasonal habitats (Jurado and Flores, 2005), such as the habitats of *O. streptacantha*. This species has physiological dormancy, because the seed embryo has a low growth potential, so needs a period of maturation time to be able to break the testa and germinate (Delgado-Sánchez *et al*., 2011, 2013). In some cacti species, higher germination has been observed in seeds 1 year old or older than in freshly collected seeds (Flores *et al*., 2005, 2006). Delgado-Sánchez *et al*. (2011) found in *O*. *streptacantha* a higher germination percentage (67%) in 9-year-old seeds compared to fresh seeds (27%), assuming that older seeds have broken dormancy, and that this species has the ability to form seed banks in the soil.

Seed germination and its correlation with physical parameters

No strong relationship was found between physical quality characteristics and germination, this indicates that the maternal effect of sites could be affecting seed germination rate; however, a negative correlation between seed hardness and germination (r= -0.65, p<0.01; Figure 5a) was

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found, but no correlation was found between seed weight and germination (*r*= 0.16, *p*= 0.31; Figure 5b).

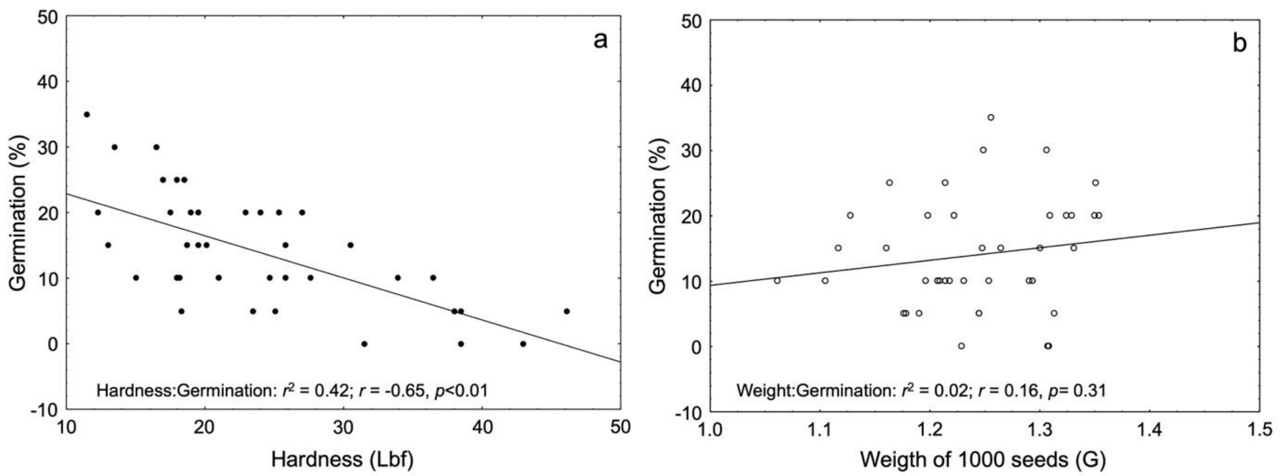

Figure 5. Hardness and weight of 1000 seeds and their correlation with germination in eight sites (populations) of *O*. *streptacantha*.

The evaluations of seed weight and seed hardness and their correlation with germination suggest that the seed coat (testa) regulates imbibition, and that a faster and higher germination rate is associated with a thin testa (Maiti *et al*., 1994; Souza and Marcos-Filho, 2001). Some *Opuntia* species shows high seed hardness but decreases germination (Stuppy, 2002; Romo-Campos *et al*., 2010; Delgado-Sánchez *et al*., 2011). This characteristic agrees with our results because the less hard seeds showed higher germination. Likewise, the seed weight is a critical trait in the germinability (Milberg *et al*., 1996), seed dispersal and seedling establishment (Hendrix *et al*., 1991), and that is determined by the genetic variation of the plants, as well as by the environmental conditions (Winn and Werner, 1987). In this study, differences for seed weight among sites, but no relationship between seed weight and germination percentage was found, although lighter seeds from LM and C sites had higher germination.

Conclusions

The physical seed traits and seed germination of *O. streptacantha* are related to environmental factors form each site. The physical characteristics of the seed were more prominent in sites Z, VGO, VG, SL, ST, and C where the species has a wide distribution, and the humidity is lower. Likewise, germination was higher in the LM site (26%), located in the west of the México where the species has a smaller distribution and there is greater environmental humidity. The variation in germination was from 8 to 26%, as previously reported for the genus. The hardness of the seed showed a negative correlation with germination, indicating that softer seeds have a higher germination. A similar result was found for lighter seeds, which also showed a higher germination and belong to climates with higher humidity. The heaviest seed are those from more arid sites. The results suggest that seed origin should be considered when physical and physiological quality in cacti is under study, together with a greater number of species, and include multiple environmental factors that can favor or limit these physical and germination traits.

ETHICS STATEMENT

Not applicable.

CONSENT FOR PUBLICATION

Not applicable.

AVAILABILITY OF SUPPORTING DATA

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

COMPETING INTERESTS

The authors declare that they have no competing interests.

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AUTHOR CONTRIBUTIONS

ICJ and PDS designed the study. ICJ conducted field work, experiment, and data analysis. ICJ and PDS wrote original paper. JADN, MLGG and JF reviewed the manuscript and agreed with the publication.

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