

Seed germination of *Opuntia dejecta*, a non-desert cactus native to Central America

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Abstract. *Opuntia* species from arid and semiarid environments have dormant seeds. The objective of this study was to evaluate how the soil influences seed germination of the cactus *O. dejecta*. We hypothesized that *O. dejecta* seeds in the basaltic rocky soil will show lower seed germination than seeds in a site with alluvial soil from the coastal plain. An experiment of partial reciprocal transplant was performed, placing seeds from basaltic soil (San Ignacio population) in pots containing alluvial soil from Puente Nacional population and in slabs from basaltic soil, and placing them on two greenhouses, in San Ignacio population and Puente Nacional population. We found that seed germination (%) was lower in San Ignacio site (with basaltic soil) than in Puente Nacional site (with alluvial soil), and that alluvial soil showed higher seed germination than basaltic soil, as well as higher seed germination in Puente Nacional than in San Ignacio. The results suggest that seed dormancy for the population situated in the rocky condition is a trait locally adapted, and the basaltic soil can be considered as a selection factor.

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Introduction

Seed dormancy is the failure of seeds to germinate even though environmental conditions including water, temperature, light, and gases are favorable for germination (Baskin and Baskin, 2014). It is a very common adaptive plant strategy in unpredictable and harsh environments, such as arid and semiarid ones (Jurado and Flores, 2005). The Cactaceae is a plant family having most of its species in unpredictable and harsh environments such as deserts, and several cactus species have dormant seeds (Rojas-Aréchiga and Vázquez-Yanes, 2000; Flores *et al.*, 2005, 2006, 2008; Barrios *et al.*, 2020), especially in the genus *Opuntia* (Mandujano *et al.*, 2005, 2007; Orozco-Segovia *et al.*, 2007; Ochoa-Alfaro *et al.*, 2008; González-Cortés *et al.*, 2018). At the end of the XIX century, Ganong (1898) found that some *O. echinocarpa* seeds did not germinate for a year, and he suggested that it is a phenomenon that perhaps has an ecological meaning, but he did not mention the seed dormancy term. The first *Opuntia* species reported to have dormant seeds was *O. aurantiaca* (Archibald, 1939).

Ochoa-Alfaro *et al.* (2008) stated that, up to this date, seed dormancy had been found in 28 *Opuntia* species, although several of these studied species were synonyms. Subsequently, in a review on cactus seed germination, Barrios *et al.* (2020) reported that 17 *Opuntia* species have dormant seeds.

Some studies about cactus seed germination have suggested the presence of physical (Potter *et al.*, 1984; Olvera-Carrillo *et al.*, 2003; Podda *et al.*, 2017), morphological (Mandujano *et al.*, 1997), or morpho-physiological dormancy (Dehan and Pérez, 2005). However, none of these studies demonstrated a lack of seed imbibition, or an undifferentiated or underdeveloped embryo, which are traits required to show the existence of these dormancy types (Baskin and Baskin, 2014). Thus, previous studies of *Opuntia* (including the species erroneously classified with physical and morphological dormancy) have demonstrated physiological dormancy; which means that seeds need a period of after-ripening to break dormancy (Mandujano *et al.*, 2005; Orozco-Segovia *et al.*, 2007). Physiological dormancy is caused by a physiological inhibiting mechanism of the embryo that prevents radicle emergence (Baskin and Baskin, 2001; 2014). For some *Opuntia* species, fungi attack the testa and thus potentially reduce mechanical resistance to germination in seeds with physiological dormancy, i.e., in embryos having low growth potential (Delgado-Sánchez *et al.*, 2011, 2013).

O. dejecta Salm-Dyck (1834) (Cactaceae) is a shrub most likely native to tropical Central America (Anderson, 2001). In Mexico, it is distributed in tropical deciduous forests (Bravo-Hollis, 1978). In the Veracruz State, in Central-Southern Mexico, *O. dejecta* is distributed in the dry forest, from 50 m above sea level in “Puente Nacional” to 1,200 m above sea level in “San Ignacio”. In the San Ignacio location, it inhabits basaltic rocky soil corresponding to volcanic lava flow, while in the Puente Nacional it occupies alluvial soil from the coastal plain (Figure 1) (Bravo-Hollis and Sánchez-Mejorada, 1991).

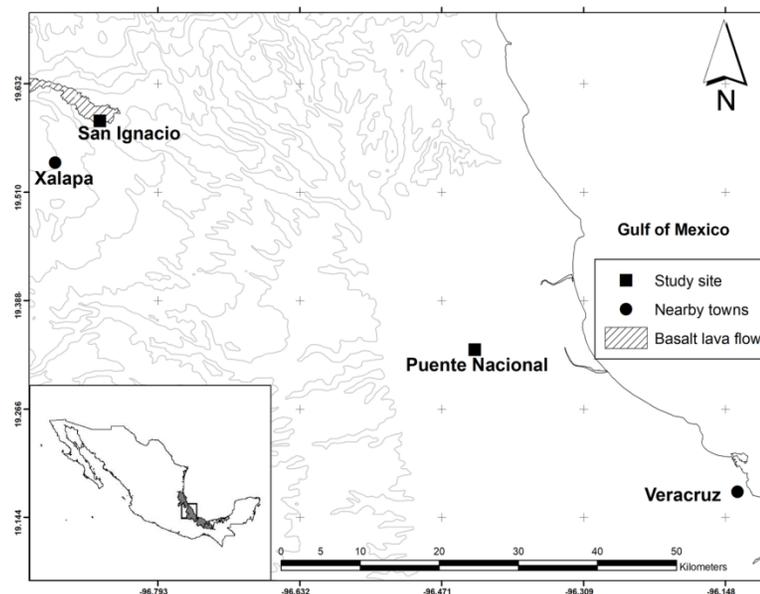


Figure 1. Location of the two *Opuntia dejecta* populations in the dry tropical forest in Mexico.

Our aim was to evaluate basaltic rocky soil and alluvial soil influence on germination percentage of the cactus *O. dejecta* established in basaltic soil, which might represent stressful conditions for plants due to a hard soil substrate and low water retention. We hypothesized that *O. dejecta* seeds in the basaltic rocky soil will have lower seed germination (greater seed dormancy) than seeds in the alluvial soil.

Material and Methods

Studied species

O. dejecta is a shrub that measures up to 2 m in height. It has a defined prickly trunk, with hanging branches. Its cladodes are lanceolated and narrow, measuring 10 to 15 cm in length and having a green or grayish-green color. Its red flowers are 5 cm in length including ovary and style. It has a round, smooth, dark red fruit with numerous areolas (Bravo-Hollis and Sánchez-Mejorada, 1991). It is native to tropical Central America, including Mexico (Anderson, 2001).

Sites

San Ignacio is located at 1,100 m above sea level and grows in lava flow rock soil (basalt) created during Holocene, 10,000 years ago (Negendank *et al.*, 1985). Its annual temperature average is 20.4 °C (hotter and colder month average; May 29.2 °C and January 11.5 °C, respectively) and the annual precipitation average is 1,300 mm (79.1% rainfalls concentrate between May and October; Fernández-Eguiarte *et al.*, 2012, period 1903–2010). Half of the surface is covered by vegetation (50.30% ± 5.85%; Miranda-Jácome *et al.*, 2013) and the other half is made up of bare ground. The dominant species are *Lysiloma acapulcensis*, *Dodonaea viscosa*, *Quercus oleoides*, *Cnidoscolus aconitifolius*, and *Tonduzia longifolia* (Miranda-Jácome *et al.*, 2013).

Puente Nacional is located at 87 m above sea level, annual temperature average is 25.9 °C (hotter and colder month average; May 34.6 and January 16.3 °C, respectively) annual precipitation average, reaches 1,144 mm (92.1% rainfalls occur between May and October; Fernández-Eguiarte *et al.*, 2012, period 1903–2010). This location presents an alluvial Vertisol pelic soil profile, which means clayey expansible soil that forms crevices during desiccation, commonly found in semi-arid tropical environments (IUSS, 2007). Corresponding tropical deciduous forest vegetation covers 93.80% ± 5.49% of the ground surface (see, Miranda-Jácome *et al.*, 2013). Dominant plant species are *Tabebuia chrysantha*, *Bursera simaruba*, *Ceiba aesculifolia*, *Cordia dentata*, *Croton cortesianus*, *Esenbeckia berlandieri*, and *Luehea candida* (Miranda-Jácome *et al.*, 2013).

Fruit harvest and environmental characterization in greenhouses

To collect *O. dejecta* seeds, visits during the reproductive period were made to San Ignacio (March-April of 2013). Forty-six random mature fruits were harvested, obtaining a total of 2,004 seeds. The seeds were extracted from the fruit pulp by washing with clean water and with the aid of a strainer. Subsequently, seeds were dried over the paper and stored in containers.

In order to evaluate seed dormancy of San Ignacio seeds in basaltic and in the alluvial soil, two greenhouses of 6.3 m x 4 m (25.2 m²) were made in both sites in November 2013. The greenhouses were used in order to control those environmental variables associated to the locations that might affect the results in a differential way (e.g. different precipitation). Once the greenhouses were built, photon flux density (PFD) inside greenhouses, as well as relative humidity and temperature during 07:00-18:00 hours were measured using a data logger (Li-1000-32, LI-COR, NE, USA) on a totally clear May day, both inside and outside greenhouses. The former studies allowed evaluating the possible environment alteration generated by greenhouses in each location. Two light sensors Li- 190 (LI-COR, NE, USA) estimated the PFD, LI-1000-16 (LI-COR, NE, USA) sensors estimated the T, and RH was estimated with HRP45A/D sensors; Vaisala (Helsinki, Finland). All sensors were plugged to the Data logger. Herbivores were controlled using insecticide inside the greenhouses (parathion-methyl 2%) and inter-specific competition effect was eliminated through weekly pot weeding.

Seed viability

To examine viability, six lots of ten seeds each were soaked in a 1% tetrazolium solution for 24 to 48 hours at 30 °C. Embryos with a deep red color were considered viable (Yaklich and Kulik, 1979).

Experimental set up

For simulation of San Ignacio substrate, 48 rocks commonly called 'lajas' (slabs) were chosen during September and October in 2013 and were randomly placed inside greenhouses. These slabs (used as pots) had a flat 20 x 15 cm surface in order to place seeds homogeneously. Additionally, seeds were fastened onto the slab with a polyvinyl acetate base glue, to avoid water washing them off the pots. Glue was carefully placed, avoiding that the seeds would be fully covered, leaving the coleorhiza (hole where the radicle emerges) and much of the seed coat clear, because it might affect imbibition and as a result inhibit germination.

Simultaneously, at Puente Nacional site 100 kg of alluvial soil were superficially collected (20 cm deep), avoiding organic material and litter or forest floor. Soil was placed inside polystyrene foam pots 11 cm diameter and 7.5 cm high (≈ 0.473 kg soil inside each pot), which were randomly placed inside both greenhouses.

Physicochemical soil characterization

Physicochemical traits of the basaltic and alluvial soil were defined through total nitrogen (N) and phosphorus (P) determination, pH, electric and hydraulic conductivity, soil apparent density, and soil water retention. Analyses were applied on five randomly chosen samples of each used soil (basaltic rocky and alluvial) and the analyses were performed in the Institute of Ecology (INECOL) Soil Laboratory.

In order to determine the total N the Kjeldahl method was used, modified by Bremner and Keeney (1965). For total P (expressed on mg/kg), digestion was performed with nitric and perchloric acid and its quantification was performed with vanadomolybdate reagent and determination in a visible light spectrum photometer, model Spectronic 21.D (Milton Roy, USA). The pH was determined using deionized water (1:2; soil: water). Electric conductivity was determined by a conductimeter on a soil sample (expressed on mS/cm). Hydraulic conductivity was measured through a variable load permeameter by a constant load method according to Klute and Dirksen (1986) (expressed in cm/h). Apparent density was determined using the paraffin method following Archimedes' principle (expressed in g/cm³). Hydrological retention was measured with the aid of a permeameter using cylindrical samples (expressed in barometrical units).

Experimental design

The reciprocal transplant partial experiment included placing seeds from San Ignacio population in pots containing alluvial soil and in slabs from basaltic soil, and placing them on two greenhouses, in San Ignacio and Puente Nacional. Twenty-four experimental units of each soil were produced by each greenhouse (96 total experimental units). Each experimental unit count was made on 20 seeds, which were irrigated every third day and counted every fifteenth day for germination register. Germination was considered once cotyledons were visible. The experiment went on for 90 days.

Data analysis to environmental variable characterization in greenhouses and physicochemical differences between soils

To delimit statistical significances between sites and soils, a one-way ANOVA model was fitted to each environmental variable (i.e. PFD, temperature, and relative humidity), as well as for each physicochemical soil characteristic (i.e. total N and P, pH, electric conductivity, hydraulic conductivity, apparent density, and water retention). Alpha value for every case was 0.05 or less.

Data analysis to seed germination

A GLM analyses was performed for seed germination (%). 'Greenhouse site' was considered as a factor with two levels: Puente Nacional and San Ignacio, and 'edaphic treatment', was considered as a factor nested in 'greenhouse location' with two levels: basaltic rocky and alluvial soil. Multiple contrasts were developed by the Tukey test using Statistica 7 program. Following this model, a 'greenhouse site' factor significance represented a necessary condition to prove local adaptation.

Basaltic rocky soil vs alluvial soil contrasts were used to test if the San Ignacio population developed a higher performance in San Ignacio (site having basaltic soil) than in Puente Nacional (site having alluvial soil) (i.e. host location; Kawecki and Ebert, 2004). The term 'edaphic treatment, nested in site factor' was used to demonstrate if soil conditions affected the local adaptation pattern. In other words, this factor proved if seed dormancy occurs in basaltic soil (San Ignacio) and not in alluvial soil (Puente Nacional).

Results and Discussion

Greenhouses environmental variable characterization

The ANOVA models fitted for environmental variables between greenhouse site (San Ignacio and Puente Nacional) indicated that only PFD was significant ($F_{1,50} = 10.512$, $p < 0.002$). While temperature and relative humidity were not ($F_{1,50} = 3.595$, $p > 0.0637$ and $F_{1,50} = 0.3264$, $p = 0.570$, respectively). Artificial shadow net manipulation on different light attenuation proportions (75% in San Ignacio and 85% in Puente Nacional) simulating forest understory conditions on each site, generated an average PFD higher in San Ignacio ($258.71 \mu\text{mol m}^{-2} \text{h}^{-1} \pm 60.28 \text{ SE}$) than in Puente Nacional ($60.09 \pm 16.41 \text{ SE}$; Figure 2A). Air temperature between San Ignacio greenhouse site ($25.72 \text{ }^\circ\text{C} \pm 1.53 \text{ SE}$) and Puente Nacional ($29.12 \text{ }^\circ\text{C} \pm 0.99 \text{ SE}$), as well as relative humidity in San Ignacio ($63.92\% \pm 4.42 \text{ SE}$) and Puente Nacional ($61.18\% \pm 2.09 \text{ SE}$) did not statistically differ (Table 1, Figures 2B, C).

In our experiment, the received photon flux density (PFD) was simulated naturally under canopies of San Ignacio and Puente Nacional sites with a shadow net placed on each greenhouse. Higher PFD in San Ignacio than in Puente Nacional was found but in general the light was low. Therefore, we suggest that the PFD received did not alter seed dormancy. In addition, nitrate acts not only during germination, but also during seed development to negatively regulate primary dormancy (Duermeyer *et al.*, 2018). Temperature can also affect the dormancy status of seeds (Finch-Savage and Leubner-Metzger, 2006). Cacti present different germination responses in a temperature range oscillating between 20 and 30 °C (Barrios *et al.*, 2020). This germination response plethora generates a great optimal temperature value variation required to activate germination process for each species. However, registered temperatures inside greenhouses in San Ignacio and Puente Nacional were statistically similar.

Table 1. Analysis of variance applied to PFD ($\mu\text{mol m}^{-2} \text{h}^{-1}$), Temperature ($^{\circ}\text{C}$) and Relative Humidity (%) values registered within the greenhouses located in the San Ignacio and Puente Nacional sites.

Source of variation	df	PFD	T	RH
Site	1	$F = 0.002$	$F = 0.063$	$F = 0.570$
Error	50			

df = degree of freedom; **PFD** = Photon flux density; **T** = Temperature; **RH** = Relative humidity.

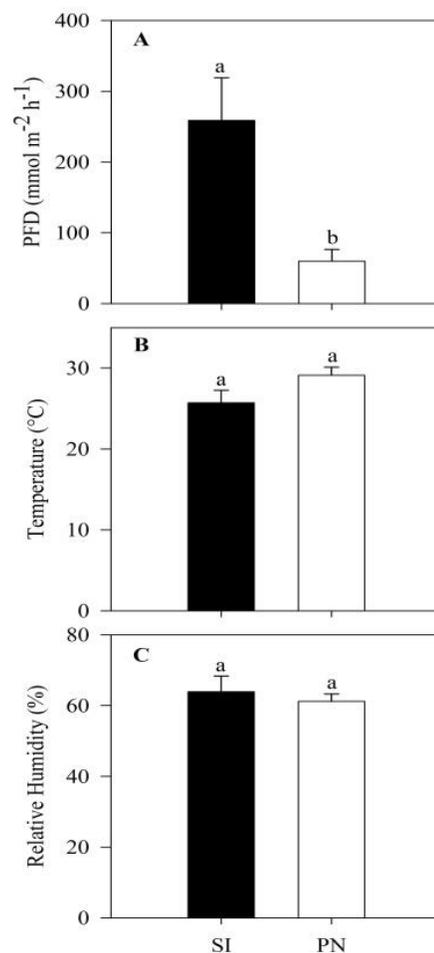


Figure 2. Average value (\pm SE) of environmental variables: **(A)** PFD; **(B)** temperature; **(C)** relative humidity between greenhouse locations (**SI** = San Ignacio; **PN** = Puente Nacional). Different letters above bars denote significant differences ($p < 0.05$) according to Tukey tests.

Physicochemical soil characterization

ANOVA models showed that almost every edaphic characteristic was different between soils (i.e. basaltic contrasting alluvial). Total N was greater in basaltic soil in relation to alluvial ($1.76\% \pm 0.05$ SE and $0.39\% \pm 0.08$ SE, respectively) ($F_{1,8} = 276.602$, $p \leq 0.0001$). Meanwhile, total P ($p = 0.5988$), pH ($p = 0.123$) and electric conductivity ($p = 0.4777$) were not different between soils (Table 2). Also, hydraulic conductivity ($F_{1,4} = 126.564$, $p = 0.0003$) and apparent density ($F_{1,4} = 670.62$, $p = \leq 0.0001$) were statistically different between soils. Higher hydraulic conductivity was found in basaltic soil vs alluvial ($51.27 \text{ cm h}^{-1} \pm 2.4$ SE and $20.79 \text{ cm h}^{-1} \pm 2.14$ SE, respectively). Apparent density was higher in alluvial soil ($1.36 \text{ g cm}^{-3} \pm 0.02$ SE) than in basaltic ($0.86 \text{ g cm}^{-3} \pm 0.01$ SE; Table 3, Figure 3).

Besides, the six barometric tests to which soils were subjected were significant between soils (0.3Pa, $p < 0.0001$; 1Pa, $p < 0.0001$; 3Pa, $p = 0.0005$; 5Pa, $p = 0.0073$; 10Pa, $p = 0.0132$, and 15Pa, $p = 0.0145$). On every test, the hydraulic conductivity was higher in basaltic soil than in alluvial one (Table 3, Figure 3).

We found that N was significantly higher in rocky soil than in alluvial soil and this high N content could have inhibited *O. dejecta* seed germination. Also, fluctuations in soil water content can also affect the dormancy status of seeds (Batlla and Benech-Arnold, 2006). It is known that rain patterns significantly affect germination for some *Opuntia* species, which requires different imbibition periods to activate this process (Romo-Campos et al., 2010). Soil hydraulic conductivity is a useful parameter to be included in seed germination studies, because it provides a clear limit to germination potential for multiple species as a function of soil physical properties (Camacho et al., 2021). In our case, the high hydrological conductivity of basaltic soil could have limited the constant imbibition during enough time for seeds to start germination. A previous case in the study site was demonstrated in seeds from the columnar cactus *Pilosocereus leucocephalus*, which require six days of constant water to achieve high germination percentages (Miranda-Jácome, 2005).

From the tested parameters, basaltic soil showed more N concentration, water retention (Figure 4), and hydraulic conductivity than alluvial soil; however, this did not cause greater germination but seed dormancy as a consequence. Seed dormancy in basaltic rocky soil was obtained in each greenhouse site. Although little is known about key soil characterization factors that generate local adaptation, we have major advances for serpentines soils (Kruckeberg, 1986; Brady et al., 2005), saline (Flowers and Colmer, 2015), gypsophylous soils (IUSS, 2007), and soils with heavy metals (Brady et al., 2005). In the basaltic rocky soil case, there is no conclusive evidence about key characteristics (e.g. N gathering) that turn out to be selection agents for plants.

Table 2. Analysis of variance applied to the chemical properties of the basaltic substrate of San Ignacio and alluvial of Puente Nacional.

Source of variation	df	N	pH	EC	P
Sustrate	1	$F \leq 0.0001$	$F = 0.123$	$F = 0.477$	$F = 0.598$
Error	8				

df = degree of freedom; **N** = Total Nitrogen; **EC** = Electric Conductivity; **P** = Total Phosphorous.

Table 3. Analysis of variance applied to the physical properties of the basaltic and alluvial soils.

Source of variation	df	HC	AD	WR					
				0.3 Pa	1 Pa	3 Pa	5 Pa	10 Pa	15 Pa
Substrate	1	$F = 0.0003$	$F \leq 0.0001$	$F \leq 0.0001$	$F \leq 0.0001$	$F = 0.0005$	$F = 0.007$	$F = 0.013$	$F = 0.014$
Error	4								

df = degree of freedom; **HC** = Hydraulic conductivity; **AD** = apparent density; **WR** = water retention; **Pa** = Pascal's.

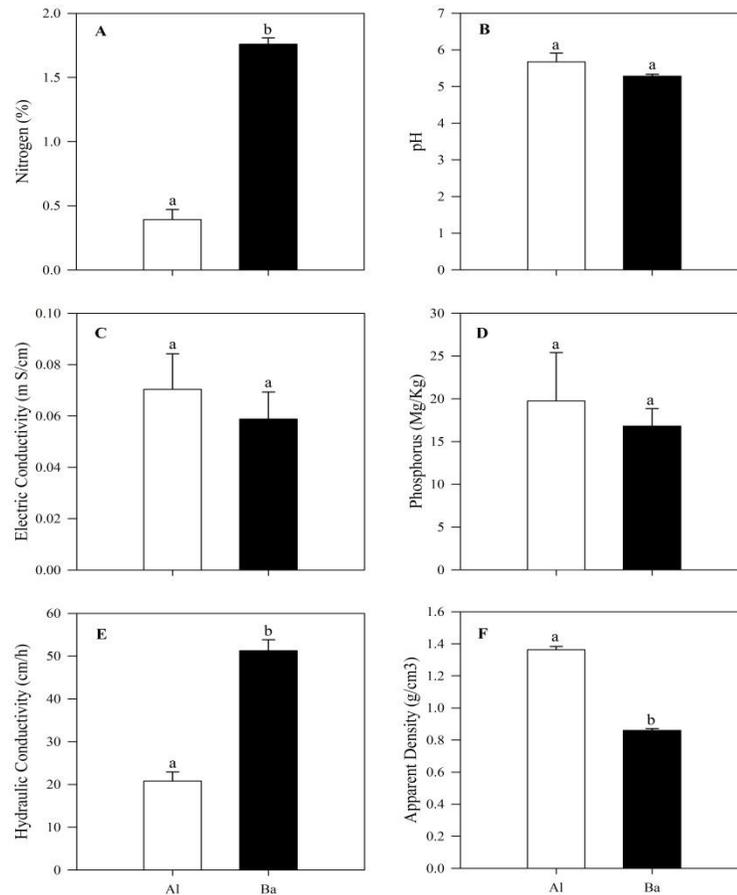


Figure 3. Average value (\pm SE) of soil variables. **(A)** total N; **(B)** total P; **(C)** pH; **(D)** electric conductivity; **(E)** hydraulic conductivity and **(F)** apparent density. **Al** = Alluvial; **Ba** = Basaltic. Different letters above bars denote significant differences ($p < 0.05$) according to Tukey tests.

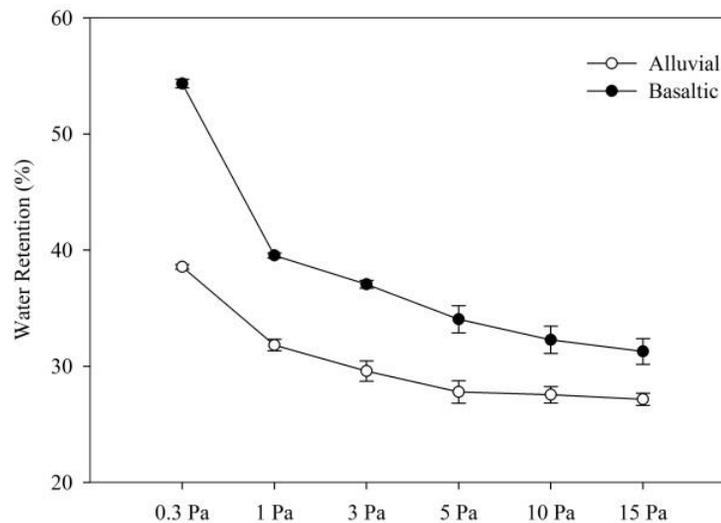


Figure 4. Average water retention value between soils in different barometric pressures, Pa = Pascal's.

Seed viability

We found 90% of SI seeds with a deep red embryo, indicating 90% of seed viability. As most studied *Opuntia* species, *O. dejecta* have dormant seeds. The induction and loss of physiological dormancy can be activated by different environmental signals activated through many apparently different physiological mechanisms (Finch-Savage and Leubner-Metzger, 2006). These signals can be seasonally characteristic (usually temperature) and integrated by the seed over time., e.g. *Echinocactus platyacanthus*, other cactus species, show high germination in fresh seeds and display dormancy cycling, showing high germination in spring, low germination in summer and autumn, and high germination in winter (Aragón-Gastélum *et al.*, 2018). Thus, physiological dormancy may be broken by higher or lower temperatures, in order for germination to occur in the correct season for subsequent growth; however, additional environmental conditions such as light or nitrate may be required to end dormancy and initiate germination (Finch-Savage and Leubner-Metzger, 2006).

Germination of San Ignacio seeds in two sites and two soils

Both 'Greenhouse site' factor ($F = 11.22$; $p = 0.0012$) and 'Edaphic treatment' nested in 'greenhouse site' ($F = 87.14$; $p \leq 0.0001$) were significant (Table 4). Seed germination was lower in San Ignacio site than in Puente Nacional site, and alluvial soil registered higher seed germination than basaltic soil, as well as higher seed germination in Puente Nacional than in San Ignacio (Figure 5).

We corroborated the hypothesis that *O. dejecta* seeds from basaltic rocky soil will show lower seed germination (more dormant seeds) in basaltic rocky soil than in alluvial soil. Seed dormancy is a trait found promoting local adaptation in some plants (Kronholm *et al.*, 2012; Ooi *et al.*, 2012; Postma *et al.*, 2016), and we considered that seed dormancy could be a local adaptation process in basaltic soil. Soil is able to impose strong selection pressures that might generate specificity between flora and soil, e.g. the flora inhabiting stressful edaphic conditions, adapted to the high concentration of heavy metals in soils (Chiarucci and Baker, 2007), wild plant life in serpentine soils with low calcium: magnesium ratio (Brady *et al.*, 2005), halophyllous flora adapted to saline soils (Flowers and Colmer, 2015) and gypsophyllous flora adapted to high gypsum content soils (IUSS, 2007). Specialized taxa are restricted to the special habitats not because they are dependent on the respective growing conditions but because of their inability to compete on other, more benign soils (Schmiedel *et al.*, 2021).

Table 4. *Opuntia dejecta* seed dormancy from the natural population "San Ignacio" in two sites (San Ignacio and Puente Nacional) and two levels of edaphic treatment (basaltic and alluvial), nested in sown site (greenhouse location).

Source of variation	SC	df	MS	F	P
Greenhouse location (GI)	2400.0	1	2400.00	11.22	0.0012
Edaphic treatment (nested in GI)	37284.4	2	18642.2	87.14	≤ 0.0001
Error	19681.3	92	213.9		

SC= Sum Square; df = degree of freedom; MS = Middle square; F = Fisher test, and P = probability.

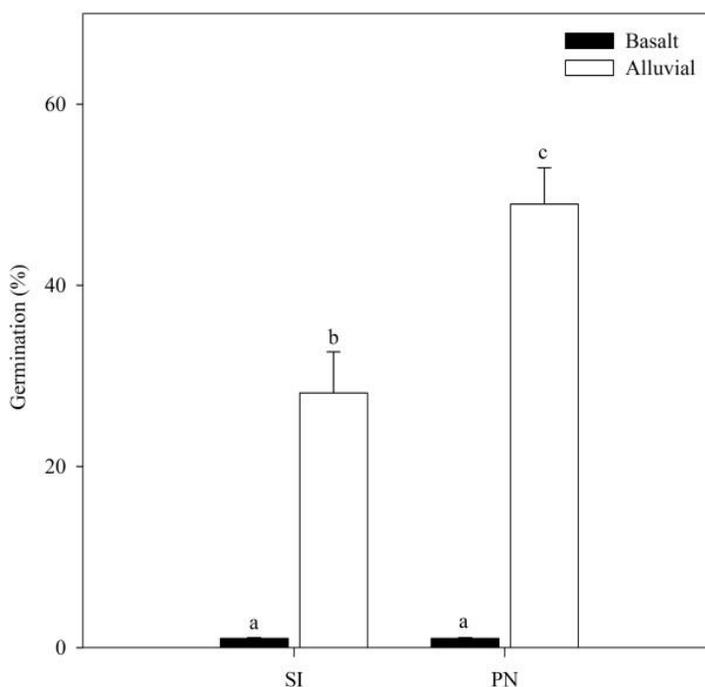


Figure 5. Seed germination (\pm SE) of *Opuntia dejecta* from SI population in both sown site (greenhouse location; **SI** = San Ignacio; **PN** = Puente Nacional) and both edaphic treatment (basaltic rocky soil and alluvial soil). Different letters above bars denote significant differences ($p < 0.05$).

Conclusions

We found higher seed germination in alluvial soil than in basaltic soil. Alluvial soil has a bigger distribution in our studied region and is older than basaltic soil (two million years for alluvial one compared to ten thousand years for basaltic rocky soil one). The soil N:P ratio in alluvial soil was five times lower than the rocky one; thus, the lower N:P ratio in alluvial soil does not explain high seed germination. Our results suggest that basaltic soil is an environmental agent that could impose seed dormancy as local adaptation.

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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

Conceptualization, A.M-J. and R.M.; **methodology**, A.M-J. and R.M.; **validation**, Y.P., J.F., A.M-J. and R.M.; **formal analysis**, A.M-J. and Y.P.; **investigation**, A.M-J., R.M., M.V.; **resources**, A.M-J.; **data curation**, A.M-J. R.M. and Y.P.; **writing—original draft preparation**, A.M-J., R.M., Y.P and J.F.; **writing—review and editing**, A.M-J., Y.P. and J.F.; **supervision**, A.M-J. and J.F.; **project administration**, A.M-J.; **funding acquisition**, A.M-J.

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