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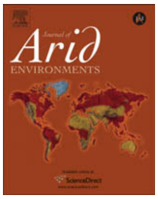

# Seed germination of wild, *in situ*-managed, and cultivated populations of columnar cacti in the Tehuacán-Cuicatlán Valley, Mexico

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ABSTRACT

Seed germination was compared among wild, *in situ*-managed (wild plants let standing in areas cleared for agriculture), and cultivated populations of the columnar cacti *Stenocereus pruinosus*, *Polaskia chichipe*, *Myrtillocactus schenckii*, and *Polaskia chende*, species representing a gradient from higher to lower management intensity, respectively. We hypothesized that seeds from cultivated populations have higher water requirements to germinate than seeds of other populations, and that such difference is stronger in species more intensely managed. Germination was evaluated under water potential treatments at 0.0, −0.2, and −0.4 MPa. Interspecific differences were identified; germination rates markedly decreased in *S. pruinosus* and *P. chichipe* as water potential reduced. *M. schenckii* seeds germinated better at −0.2 MPa, and seeds of *P. chende* in all treatments. Seed germination of wild and cultivated populations was similar in all cases and, therefore, at the population level domestication does not appear to have influenced variations in germination of the studied cacti species. However, experiments to test whether germination of seeds from plants with clear signs of domestication differs with seeds from other plants and their differential germination and seedling survival in wild, *in situ*-managed and cultivated environments could help to precise the influence of domestication on these plants.

## 1. Introduction

Domestication is an evolutionary process resulting from artificial selection directed to favor the survival and reproduction of particular phenotypes of plant or animal populations, convenient to humans according to their morphological, physiological, and/or behavioral features (Darwin, 1859; Hawkes, 1983). This process may determine changes in frequencies of phenotypes and genotypes of manipulated populations compared with wild populations. In plants, artificial selection may determine changes in physiological aspects such as loss of seed dormancy, faster and synchronous germination, and variation in periods of fruit maturation (Hawkes, 1983; Evans, 1993; Frary and Doganlar, 2003). These changes may result in a decreased fitness of domesticated plants in wild environments (Hawkes, 1983).

In Southern Mexico domestication of plants has been conducted for more than 10,000 years (MacNeish, 1967, 1992) and the area has been identified as one of the main centers of domestication of plants in the world (Harlan, 1971; Hawkes, 1983). Although domestication of plants has generally been associated to cultivation (Harlan, 1992), Casas et al. (1997, 1999a, in press) have documented for this region domestication processes associated to several types of silvicultural *in situ*-management of plant populations. *In situ*-management of plants includes practices directed to increase the availability of plant resources particularly valued by local cultures. This purpose may be reached by let standing, planting propagules, and/or by especial care of desirable plant species or variants in forest areas cleared for agriculture or other purposes. Plants favored are generally those with higher use, cultural and/or economic value and may involve artificial selection directed to increase abundance of favorable phenotypes. In the Tehuacán Valley, columnar cacti have been used since prehistoric times (MacNeish, 1967) and at present are highly valued (Casas et al., 1999a). Twelve of the 20 species of these cacti currently occurring in the area are *in situ*-managed, and eight are also cultivated (Casas et al., 1999a). *Stenocereus pruinosus*, *Polaskia chichipe*, *Polaskia chende* and *Myrtillocactus schenckii* are among the most ecologically and culturally important species (Casas et al., 2001).

Morphometric studies have demonstrated significant morphological divergences between wild, *in situ*-managed, and cultivated populations, suggesting that such differences are associated to artificial selection (Casas et al., in press). Moreover, some cultivated populations contain certain phenotypes that are absent in wild populations (Casas et al., 1999a). Population genetics studies have

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generally reported small genetic differences between wild and cultivated populations of some species (Casas et al., in press), and these differences appear to be more related to the geographic distance rather than to management. Population genetics studies have concluded that gene flow among all wild and managed populations is high and the question of how the morphological differences between wild and managed populations are maintained is still unanswered.

Studies of reproductive biology have suggested that there are no significant spatial or temporal barriers to pollen flow between wild and manipulated populations. Casas et al. (in press) have considered that the observed divergences are in part maintained by artificial selection, and have proposed that differential success of seed germination and seedling survival in different environments could be additional factors to explain divergences between wild and managed plants. In the case of *Stenocereus stellatus* Casas et al. (1999c) observed that seeds and seedlings derived from wild plants become successfully established in managed environments, whereas seeds and seedlings derived from domesticated plants do not appear to establish successfully in wild environments. Studies by Rojas-Aréchiga et al. (2001) with *S. stellatus* and by Otero-Arnaiz et al. (2003) with *P. chichipe*, documented that seeds from *in situ*-managed and cultivated populations had faster and higher percentage of germination than seeds from wild populations. This information suggests that domestication has indeed affected seed germination behavior for both species. Rojas-Aréchiga et al. (2001) suggested that differences are possibly related to the larger and more numerous seeds characterizing the larger fruits of domesticated cacti as documented by Casas et al. (1999b). In general, larger seeds have a faster germination rate (Hawkes, 1983) and this could explain the differences found between wild and managed columnar cacti.

Useful products of *S. pruinosus*, *P. chichipe*, *P. chende* and *M. schenckii* studied here, are gathered in wild populations, and all of them are also *in situ*-managed in areas cleared for agriculture. Individual plants of *S. pruinosus*, *P. chichipe* and *M. schenckii* are also cultivated in home gardens (Casas et al., 1999a, 2001), but cultivation of *S. pruinosus* is relatively more intense than that of the other two species since vegetative propagation and its fast growth make easier its management. Cultivation of *P. chichipe* is more intense than that of *M. schenckii* because people prefer consuming its fruits; whereas *P. chende* is not cultivated because vegetative propagation is marginally successful and plant growth is slow (Cruz and Casas, 2002). According to this information, a gradient of management intensity can be appreciated with the following order from higher to lower intensity: *S. pruinosus*, *P. chichipe*, *M. schenckii*, and *P. chende*.

This study hypothesized that seed germination of the species studied has been affected by artificial selection under cultivation. We expected that faster germination of seeds from cultivated plants would occur under higher water availability, but that they would be more susceptible to decrease under dry conditions than seeds from wild and *in situ*-managed populations. In addition, we hypothesized that the degree of divergence of germination response would be more pronounced between species according to the degree of management intensity. To test these hypotheses we compared germination responses in gradients of high to low management intensity within each species (cultivated, *in situ*-managed, and wild populations, respectively) and between species (*S. pruinosus*, *P. chichipe*, *P. chende*, and *M. schenckii*, respectively).

## 2. Methods

### 2.1. Study area

Wild, *in situ*-managed, and cultivated populations of *S. pruinosus*, *P. chichipe*, *M. schenckii* and *P. chende* were studied within the territory of the villages of San Luis Atolotitlán, Caltepec and Xochiltepec, in the municipalities of Caltepec, and Zapotitlán Salinas, Puebla, in central Mexico (Appendix 1, electronic version only). Climate in this area is semiarid; with annual mean temperature and rainfall of 18 °C and 655 mm respectively, according to the nearest meteorological station in Caltepec (García, 1988). Fruits of wild and *in situ*-managed populations of *S. pruinosus* were also collected within the territory of the village of San Rafael, in the municipality of Coxcatlán, Puebla, where annual mean temperature and precipitation are 24 °C and 441 mm of rainfall, respectively (Casas et al., 1999b).

The study area belongs to the Tehuacán-Cuicatlán Biosphere Reserve and the species studied are constituents of tropical dry and thorn–scrub forests. *S. pruinosus* forms part of tropical dry forests, mainly in areas of alluvial soils, where this species along with other columnar cacti such as *Escontria chiotilla*, *S. stellatus*, *Pachycereus hollianus* and *Pachycereus weberi* are dominant components (Casas et al., 1999a). The species *P. chichipe* and *P. chende* are dominant components of the particular association of thorn–scrub forest located in soils derived from volcanic rocks, which have been called "chichipera" by Valiente-Banuet et al. (2000); whereas *M. schenckii* is a dominant element of the particular thorn–scrub association called "garambullal" by Blancas (2007), also established on soils derived from volcanic rocks.

### 2.2. Seed sampling

From March to June 2005, a total of ten mature fruits per plant were collected from ten individual plants randomly sampled in each of two populations per management type of the species studied. Seeds were separated from the fruit pulp through a sieve, and then dried at room temperature (20 ± 2 °C) for eight days. The seeds collected from all fruits per management type per species were mixed and stored in paper bags at room temperature for six months.

### 2.3. Seed germination

The effect of water on seed germination percentage of seeds was tested through an experiment including different water potential treatments in a growth chamber (Environmental Growth Chambers Inc., Chagrin Falls, Ohio). Water potentials were established through aqueous solutions of polyethilenglicol (PEG 8000, Sigma) measured in megapascals (MPa). Particular concentrations of PEG 8000 were determined with the Solute Potential and Molar-Molal-g Solute/g Water Interconversion (SPMM) program (Michel and Radcliffe, 1985). The following were the water potentials tested: 0.0 (control, with distilled water), −0.2 MPa [0.021 M], and −0.4 MPa [0.028 M]. Treatments were established in Petri dishes (100 × 15 mm) with 20 ml of the corresponding PEG 8000 solution, where 25 seeds were placed on a piece of gaze in order to maintain the seeds out of the solution. The Petri dishes were covered with parafilm and incubated in a growth chamber at constant temperature (25 °C) and 12-h photoperiod, each treatment having four replicates. Before the experiment, seeds were disinfected through 5 min immersion in a solution of 30% ethanol and 15 min in a 25% solution of $Ca(ClO)_2$. Germinated seeds were identified as those showing a clear radicule protrusion. Germination was monitored daily during 40 days.

### 2.4. Statistical analyses

Maximum germination was defined as the cumulative percentage of seeds germinated after 40 days since sowing date. The effect of water potential treatment and management type on germination rate (proportion of seeds germinating per day) was evaluated using Analysis of Deviance based on General Linear Models (GLM, Crawley, 1993). In our models, the cumulative proportion of germinating seeds was the dependent variable, time (days after sowing date) was a continuous independent variable, and water potential (factor with three levels) and management type (factor with three levels) were categorical independent variables. We used a binomial error and a logistic link function as indicated for proportional dependent variables; in this error type, the deviance (equivalent of variance in a model with a normal type error) explained by independent variables can be considered to be an approximated $X^2$ value (Crawley, 1993). The cumulative proportion of germinating seeds ($y$) after $t$ days was then given by next model:

$$y = \frac{e^{[(a+(bt)-(ct^2))]}}{1+e^{[(a+(bt)-(ct^2))]}}$$

Here, coefficient $a$ is the $y$ intercept (starting germination), coefficient $b$ the initial germination rate and $c$ is a coefficient indicating whether the initial germination rate increases (in such case, $c$ adopts a negative value) or decreases (in such case, $c$ adopts a positive value) with time. The effect of water potential treatments and management types on germination rate was evaluated by the deviance explained by the interaction of each or both of these factors with the linear or the quadratic time ($t^2$) term. Statistical analyses were conducted using software GLIM version 3.77 (Royal Statistical Society, 1985).

## 3. Results

### 3.1. Germination rates within species

The maximum cumulative germination percentage of seeds of *S. pruinosus* and *P. chende* was reached 25 days after starting the experiment, whereas seeds of *P. chichipe* and *M. schenckii* reached maximum germination after 40 days.

All logistic models adjusted were significant and explained more than 96% of variation of germination behavior throughout time (Table 1, Figs. 1–4). Time explained a high percentage of the total variance in all species studied (43.6% in *S. pruinosus*, 32.5% in *P. chichipe*, 52.4% in *M. schenckii* and 71.4% in *P. chende*; Table 1). In all cases the quadratic time term was significant, indicating that germination rate declined as time advanced. Also, in the four species studied water potential had a significant effect on starting germination proportion, but models for *S. pruinosus* and *P. chichipe* explain more than 49% of the variation whereas for *M. schenckii* and *P. chende* explain less than 25% of the variation (Table 1). In general, germination starting of seeds of all species studied was delayed as long as water potential decreased. There were also significant differences in seed germination according to management types within each species (Table 1).

**Table 1**
Analysis of deviance for the number of germinating seeds of populations of columnar cacti under different management regime within a gradient of water potential.

| Species | Factor | $r^2$ | Deviance ($\sim X^2$) | d.f. | $P$ |
|---|---|---|---|---|---|
| *Stenocereus pruinosus* | Management | 0.018 | 72.90 | 2 | $<0.001$ |
| | Water Potential | 0.490 | 1915.20 | 2 | $<0.001$ |
| | Management × Water Potential | 0.004 | 17.68 | 4 | 0.001 |
| | Time | 0.436 | 1699.00 | 1 | $<0.001$ |
| | Time$^2$ | 0.038 | 151.00 | 1 | $<0.001$ |
| | Time × Management | 0.003 | 10.60 | 2 | 0.005 |
| | Time × Water Potential | 0.011 | 45.70 | 2 | $<0.001$ |
| | Time$^2$ × Management | 0.0002 | 7.20 | 2 | 0.027 |
| | Model | 0.98 | 3919.00 | 16 | |
| | Residual | 0.018 | 72.80 | 208 | |
| | Total | | 3991.60 | 224 | |
| *Polaskia chichipe* | Management | 0.005 | 15.10 | 2 | 0.001 |
| | Water Potential | 0.513 | 1688.00 | 2 | $<0.001$ |
| | Management × Water Potential | 0.016 | 54.27 | 4 | $<0.001$ |
| | Time | 0.325 | 1070.00 | 1 | $<0.001$ |
| | Time$^2$ | 0.084 | 275.70 | 1 | $<0.001$ |
| | Time × Management | 0.004 | 12.49 | 2 | 0.002 |
| | Time × Water Potential | 0.006 | 20.19 | 1 | $<0.001$ |
| | Time$^2$ × Water Potential | 0.004 | 12.54 | 2 | 0.002 |
| | Model | 0.957 | 3148.29 | 15 | |
| | Residual | 0.043 | 142.54 | 343 | |
| | Total | | 3290.00 | 359 | |
| *Myrtillocactus schenckii* | Management | 0.009 | 21.5 | 2 | $<0.001$ |
| | Water Potential | 0.243 | 555.0 | 2 | $<0.001$ |
| | Management × Water Potential | 0.081 | 185.4 | 4 | $<0.001$ |
| | Time | 0.524 | 1194.0 | 1 | $<0.001$ |
| | Time$^2$ | 0.084 | 190.4 | 1 | $<0.001$ |
| | Time × Water Potential | 0.021 | 47.9 | 2 | $<0.001$ |
| | Time$^2$ × Water Potential | 0.003 | 7.75 | 2 | 0.021 |
| | Model | 0.966 | 2201.95 | 14 | |
| | Residual | 0.034 | 77.57 | 345 | |
| | Total | | 2279.30 | 359 | |
| *Polaskia chende* | Management | 0.013 | 28.44 | 1 | $<0.001$ |
| | Water Potential | 0.085 | 184.30 | 2 | $<0.001$ |
| | Management × Water Potential | 0.012 | 26.61 | 2 | $<0.001$ |
| | Time | 0.714 | 1540.00 | 1 | $<0.001$ |
| | Time$^2$ | 0.112 | 242.00 | 1 | $<0.001$ |
| | Time × Water Potential | 0.006 | 14.01 | 2 | 0.001 |
| | Time$^2$ × Management × Water Potential | 0.019 | 41.54 | 3 | $<0.001$ |
| | Model | 0.962 | 2076.90 | 12 | |
| | Residual | 0.037 | 79.45 | 136 | |
| | Total | | 2157.50 | 149 | |

In all species studied the interaction Time × Water Potential and Time$^2$ × Water Potential (except in *P. chende*) were significant (Table 1 and Figs. 1–4), indicating that the slopes of curves describing germination rates varied significantly between treatments of water potential throughout time. In *S. pruinosus*, the maximum germination rate was reached faster in the control treatment and the slopes declined when the water potential decreased (Fig. 1). In *P. chichipe* and *M. schenckii* the maximum germination rate was reached faster in the treatment of water potential −0.2 MPa (Figs. 2 and 3). In *P. chende* the maximum germination rate was delayed with dryness but it reached similarly in all treatments (Fig. 4).

The interaction Time × Management was significant for *S. pruinosus* and *P. chichipe* (Table 1). In *S. pruinosus*, control seeds had a higher starting germination rate (Fig. 1a) as well as a faster germination rate than in the other treatments. In this species, the reduction of water potential determined a drastic decrease in germination rate, with the *in situ*-managed populations showing lower germination rate than wild and cultivated populations.

In seeds of *P. chichipe*, the highest germination rates were observed in the control treatment. The treatment −0.2 MPa delayed the starting germination rate in all populations but after few days the germination rates were as fast as in the control treatment. In the treatment −0.4 MPa germination rates decreased drastically, especially in seeds of the *in situ*-managed populations.

Compared with all the species studied, seeds of *M. schenckii* had the highest delay of the starting germination rates in all treatments. The faster germination rates occurred in the −0.2 MPa treatment. In

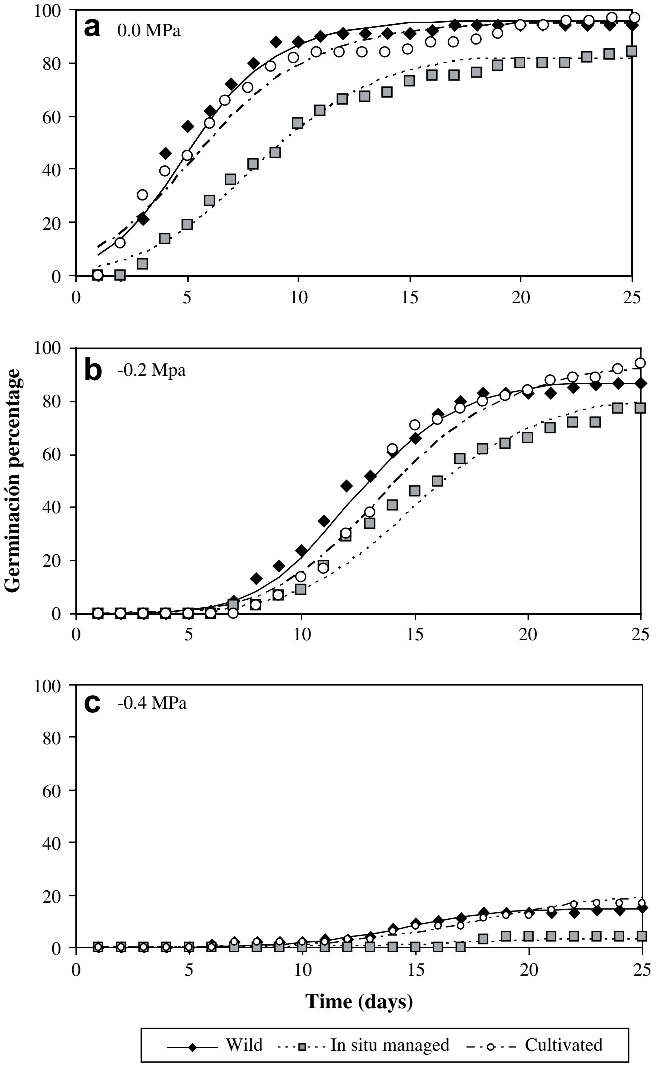

**Fig. 1.** Fitted log-linear models to germination of seeds from wild, *in situ*-managed, and cultivated populations of *S. pruinosus* under different water potential treatments given by polyethilenglicol concentration.

the case of *P. chende* the highest starting germination rate was observed in the control treatment, and it decreased with the decreasing of water potential.

The interaction Management × Water Potential was significant in all the cases studied. In *S. pruinosus* seeds from wild and cultivated populations germinated faster and in a higher percentage than seeds from *in situ*-managed populations in all treatments of water potential (Fig. 1). The maximum cumulative germination percentage was similar in the control and −0.2 MPa treatments although in this last treatment germination was slower. Germination in all populations of *S. pruinosus* decreased drastically in the −0.4 MPa treatment. A similar germination behavior was observed in *P. chichipe* although in this case seeds from all populations germinated similarly (Fig. 2). In the case of *M. schenckii* seeds from all populations germinated faster and in a higher percentage in the −0.2 MPa treatment and in this treatment seeds from *in situ*-managed and cultivated populations germinated better than seeds from the wild (Fig. 3). In the control treatment, seeds from wild and cultivated populations germinated similarly among themselves and better than seeds from *in situ*-managed populations, but this pattern was the contrary in the treatment of −0.4 MPa, in which germination of seeds from wild and cultivated populations was low.

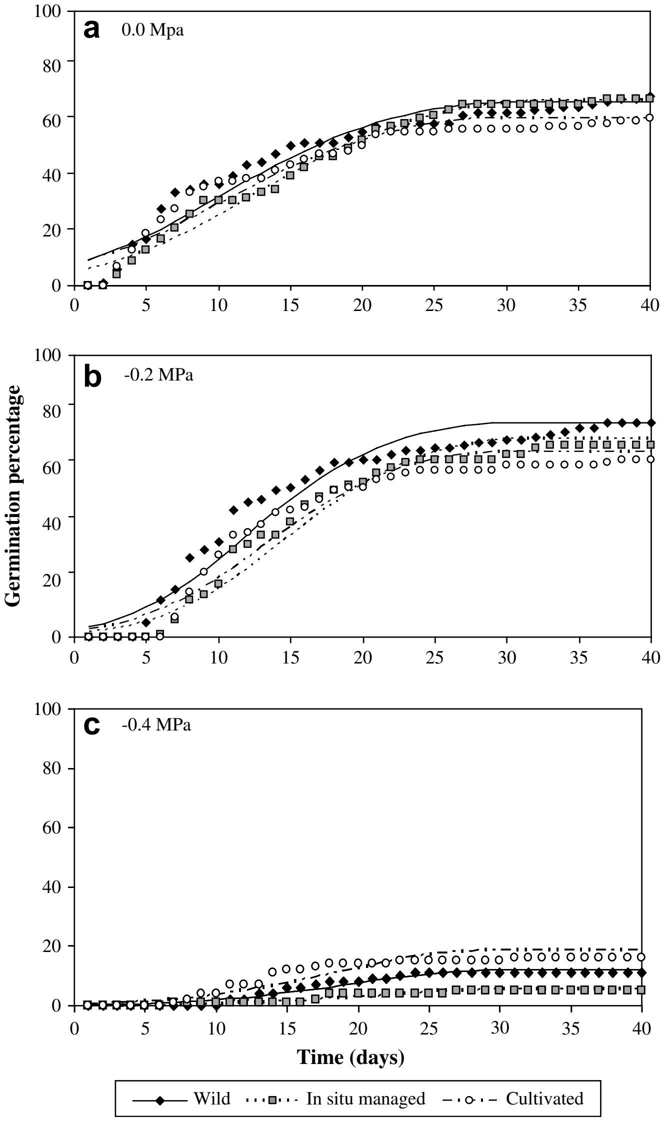

**Fig. 2.** Fitted log-linear models to germination of seeds from wild, *in situ*-managed, and cultivated populations of *P. chichipe* under different water potential treatments given by polyethilenglicol concentration.

Seeds of *P. chende* germinated more slowly with decreasing of water potential. Seeds from wild and *in situ*-managed populations germinated similarly among themselves in control and −0.4 MPa treatments, but in the treatment of −0.2 MPa seeds from wild populations germinated faster and in a higher proportion than seeds from *in situ*-managed populations (Fig. 4).

### 3.2. Germination rates between species

In all treatments of water potential, the starting germination was significantly different among species between species and management types (significant species, management, and species × management interactions). However, germination rate was only affected by species but not for management types (Table 2).

Appendixes 2 and 3 (electronic version only) compare the cumulative germination curves of the species studied by management type in the water potential treatments 0.0 and −0.2 MPa, respectively. In all plots, seeds from populations of *M. schenckii* had

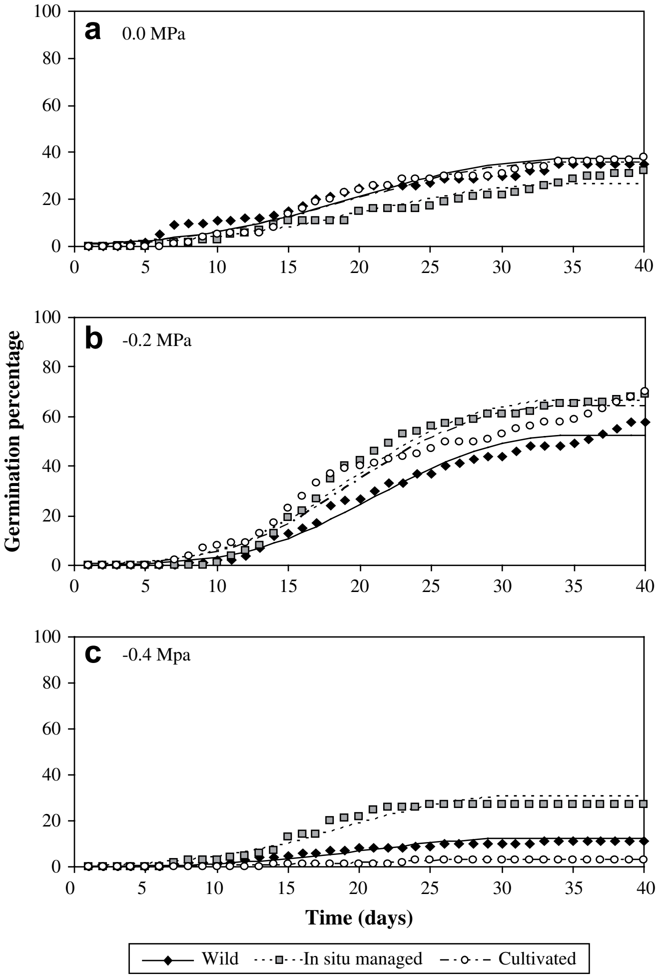

**Fig. 3.** Fitted log-linear models to germination of seed from wild, *in situ*-managed, and cultivated populations of *M. schenckii* under different water potential treatments given by polyethilenglicol concentration.

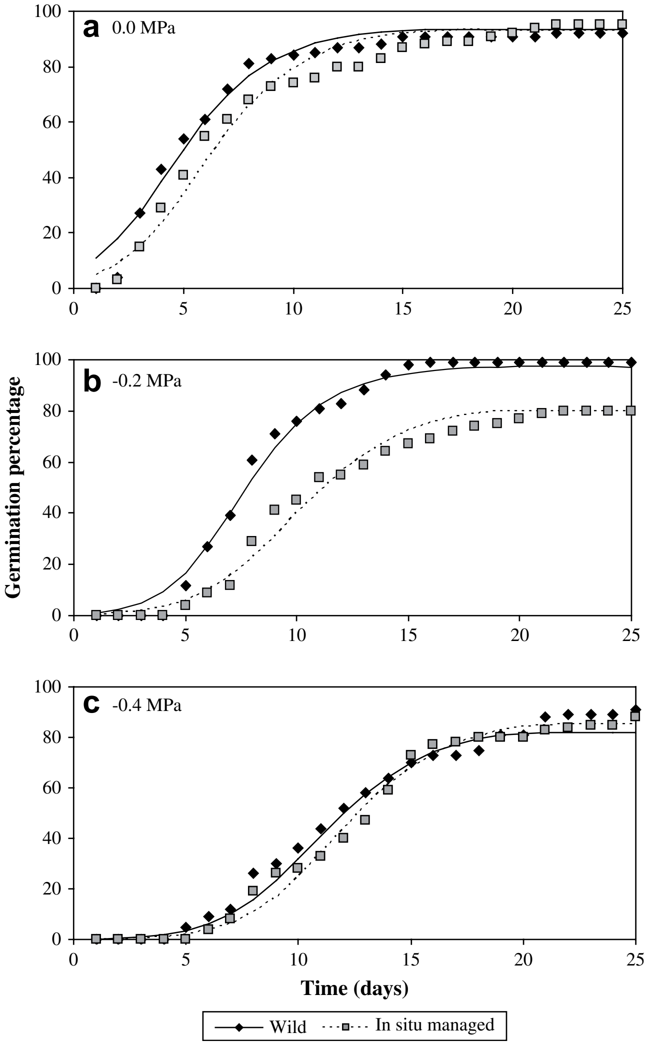

**Fig. 4.** Fitted log-linear models to germination of seeds from wild, and *in situ*-managed populations of *P. chende* under different water potential treatments given by polyethilenglicol concentration.

the lowest germination rates, whereas seeds from populations of *P. chichipe* had intermediate rates and the highest rates were observed in *S. pruinosus* and *P. chende*. Appendix 4 (electronic version only) shows germination rates of seeds from populations of all the species studied in the water potential −0.4 MPa, indicating that seeds of *P. chende* maintain high germination rates, whereas germination of seeds of the other species drastically decreases.

The maximum of germination of seeds of *P. chende* and *S. pruinosus* was reached rapidly in the control and −0.2 MPa treatments but in the treatment −0.4 MPa seeds of *S. pruinosus* the maximum of germination was reached more slowly. In *P. chichipe* and *M. schenckii* the maximum cumulative germination in general was reached slowly.

## 4. Discussion

With the only exception of seeds of *M. schenckii*, seeds of the species studied germinated rapidly within the first week of the experiment. Germination starting of seeds of *S. pruinosus* and *P. chichipe* is affected by water potential ($r^2 = 0.49$ and 0.51, respectively), whereas germination of seeds of *M. schenckii* and *P. chende* is less affected ($r^2 = 0.24\%$ and 0.09, respectively). This information indicates that availability of water differently affects seed germination of the species studied, *P. chende* and *M. schenckii* being apparently more resistant to dryness than *S. pruinosus* and *P. chichipe*. This conclusion is consistent with results on germination rates, which in seeds of *S. pruinosus* and *P. chichipe* significantly decreased in treatments with lower availability of water, whereas in seeds of *M. schenckii* these were high in the treatment of intermediate water potential and in seeds of *P. chende* these were high in all water potential treatments. The behavior of seeds of *S. pruinosus*, which more drastically decreased their germination rates with dryness, could be an expression of the adaptation of this species to relatively more humid environments compared with the other species analyzed. In fact, *S. pruinosus* is naturally distributed on alluvial soils of bottom areas of gullies, sites with relatively higher humidity than the bordering slopes in which the species is absent. The other species (*P. chende*, *P. chichipe*, and *M. schenckii*) frequently occur together in the vegetation types called “chichiperas” and “garambullales” although at different proportions. Nevertheless occurring in similar environments they show differences in germination patterns. This is not a strange case in arid and semiarid areas since in a number of plant species sharing the same habitat strong differences have been found in the amount of water seeds need to germinate (Gutterman, 1993). According to Gutterman (1993), every species may have particular mechanisms regulating the starting germination point in the right time and space to

**Table 2**

Analysis of deviance for the number of germinating seeds of columnar cacti from different populations under different type of management in treatments of water potential given by polyethilenglicol concentration.

| Water Potential | Factor | $r^2$ | Deviance (∼$X^2$) | d.f. | *P* |
|---|---|---|---|---|---|
| 0.0 MPa | Species | 0.4398 | 1742.00 | 3 | <0.001 |
| | Management | 0.0123 | 48.97 | 2 | <0.001 |
| | Species × Management | 0.0111 | 44.03 | 5 | <0.001 |
| | Time | 0.3406 | 1349.00 | 1 | <0.001 |
| | Time$^2$ | 0.0488 | 193.30 | 1 | <0.001 |
| | Time × Species | 0.0844 | 334.50 | 3 | <0.001 |
| | Time × Species × Management | 0.0050 | 20.10 | 7 | 0.005 |
| | Time$^2$ × Species | 0.0199 | 79.13 | 3 | <0.001 |
| | Model | 0.9622 | 3811.03 | 25 | |
| | Residual | 0.0379 | 150.28 | 339 | |
| | Total | | 3960.60 | 364 | |
| −0.2 MPa | Species | 0.0703 | 295.60 | 3 | <0.001 |
| | Management | 0.0051 | 21.60 | 2 | <0.001 |
| | Species × Management | 0.0226 | 95.10 | 5 | <0.001 |
| | Time | 0.6294 | 2644.00 | 1 | <0.001 |
| | Time$^2$ | 0.0809 | 340.10 | 1 | <0.001 |
| | Time × Species | 0.1251 | 525.50 | 3 | <0.001 |
| | Time × Species × Management | 0.0183 | 76.95 | 7 | <0.001 |
| | Time$^2$ × Species | 0.0134 | 56.49 | 3 | <0.001 |
| | Model | 0.9654 | 4055.34 | 25 | |
| | Residual | 0.0344 | 144.75 | 339 | |
| | Total | | 4200.60 | 364 | |
| −0.4 MPa | Species | 0.4743 | 1223.00 | 3 | <0.001 |
| | Species × Management | 0.0968 | 249.80 | 7 | <0.001 |
| | Time | 0.2573 | 663.60 | 1 | <0.001 |
| | Time$^2$ | 0.0403 | 104.10 | 1 | <0.001 |
| | Time × Species | 0.1044 | 269.40 | 3 | <0.001 |
| | Time$^2$ × Species | 0.0067 | 17.35 | 3 | <0.001 |
| | Model | 0.9801 | 2527.25 | 18 | |
| | Residual | 0.0197 | 50.89 | 346 | |
| | Total | | 2578.40 | 364 | |

enhance seedlings establishment, as well as mechanisms that increase the diversity of germination responses, which increases the probability of germination success of at least one proportion of the seeds produced.

Seed germination rates were affected according to the management type in *S. pruinosus* and *P. chichipe*, but not in *M. schenckii* and *P. chende*. However, in all treatments seeds of cultivated and wild populations of *S. pruinosus* and *P. chichipe* germinated similarly among themselves, faster and in higher cumulative percentage than seeds of *in situ*-managed populations. These results do not confirm our original hypothesis predicting higher requirements of water in seeds from cultivated populations compared with seeds from wild and *in situ*-managed populations, as suggested by studies with *S. stellatus* by Rojas-Aréchiga et al. (2001) and with *P. chichipe* by Otero-Arnaiz et al. (2003), which found that seeds of cultivated populations had higher cumulative germination percentage and germinated faster than those from wild populations. The authors of those studies suggested that higher percentage and velocity of seed germination from cultivated and *in situ*-managed populations could be associated to artificial selection in favor of larger and heavier seeds indirectly associated to larger fruits, as well as to artificial selection that occasionally practice the local people in favor of more vigorous seedlings (Casas et al., 1999a). The morphometric studies by Luna (1999), Cruz and Casas (2002) and Carmona and Casas (2005) found that in the cases of *S. pruinosus*, *P. chende*, and *P. chichipe*, respectively, seeds from cultivated populations are significantly larger than those from wild populations and, therefore, a pattern of germination behavior similar to that of *S. stellatus* was expected.

However, our results are not consistent with this explanation and the reason appears to be related to study methods. Rojas-Aréchiga et al. (2001) and Otero-Arnaiz et al. (2003) compared germination rates of seeds from wild plants using individual plants representing clear signs of domestication, whereas in our experiments seeds from individual plants randomly sampled were mixed. Under such different experimental conditions, it is possible to expect that germination of seeds from individual plants with clear signs of domestication differed clearly with seed germination of wild individual plants, whereas in the mixture of seeds from individual plants with clear and no clear signs of domestication these effects were apparently counteracted. This hypothesis can be tested in further studies, but these patterns in turn can be explained because in all cases analyzed domestication is incipient and gene flow between wild and managed populations is high, continually counteracting effects of artificial selection and adaptations to germination under managed environments.

We found lower germination of seeds from *in situ*-managed populations compared with seeds from wild and cultivated populations. Such responses could be related with relatively higher inbreeding occurring in these populations as it has been reported by Otero-Arnaíz et al. (2005a,b) for *P. chichipe*, Ruíz-Durán (2007) for. *P. chende*, and Parra et al. (2008) for. *S. pruinosus*.

Summarizing, every species studied had specific responses to different water potentials and different capacities for resisting its variations. At population level, artificial selection appears to have affected little or nothing the germination responses and differences found in the *in situ*-managed populations could be associated to inbreeding depression rather than to local adaptations to disturbed environments. However, in order to identify more clearly particular responses in germination behavior associated to domestication of columnar cacti, it would be necessary to conduct experiments controlling germination of seeds from individual plants with clear signs of domestication and comparing with germination of seeds from plants without these signs. It would be also necessary to analyze seed germination of the species studied in relation to other factors such as light, temperature, soil texture and nutrients, as well as experiments in wild, *in situ*-managed and cultivated environments, in order to identify other factors associated to management that may influence germination. In addition, it would be important to compare seedling performance after establishment, since it may vary according to conditions of shade, soils and temperature, factors that are highly variable under human management.

Responses in germination behavior associated to domestication of columnar cacti are not clear enough for the moment. It is in part due to the incipient level of domestication of these plants, and more clear responses could be found controlling seed size associated to selection favoring fruit size. Also, interesting responses could be found in performance of seedlings derived from larger fruits seeds.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2008.12.018.

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