

# Germination differentiation patterns of wild and domesticated columnar cacti in a gradient of artificial selection intensity

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**Abstract** Germination of wild and managed populations of columnar cacti was compared to analyze differences associated to management intensity. The species studied: *Polaskia chende*, *Escontria chiotilla*, *Myrtillocactus schenckii*, *Polaskia chichipe*, and *Stenocereus pruinosus* are in a gradient from lower to higher management intensity, respectively. Within each species wild, silvicultural, and cultivated populations also represent a gradient from lower to higher management intensity. We hypothesized that seeds of plants under higher management intensity would require more water to germinate than others since managed environments are relatively wetter than unmanaged environments. Such pattern could be visualized within and among species according to management intensity. We tested germination of seeds from different populations of the different species to the water potentials: 0.0, -0.2, -0.4, -0.6, -0.8, and -1.0 MPa. In all species studied seeds of managed populations had significantly more mass than seeds

from wild populations. Each species had different susceptibility to water availability decrease, which could be related to particular adaptations to drought resistance. *Stenocereus pruinosus* and *Polaskia chende* were the most and least susceptible species, respectively. In control treatments of all species, seeds of managed populations had higher germination rate than seeds from wild populations, but when water availability decreased the pattern was the contrary. Our results suggest that artificial selection for larger fruits and heavier seeds in plants established in wetter environments have affected germination patterns. Although species have particular critical points of water availability for germination, differences in germination patterns are more pronounced according to management and artificial selection intensity.

**Keywords** Artificial selection · Cactaceae · Domestication · Germination and crop evolution · Mesoamerica · Tehuacán Valley · Traditional management

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## Introduction

Crop evolution directed by humans can drive a significant differentiation in morphological, physiological and reproductive aspects compared with their wild relatives (Hawkes 1983; Harlan 1992). Such differentiation results mainly from artificial selection

in favor of survival and reproduction of phenotypes convenient to human beings and unfavouring or eliminating other phenotypes (Darwin 1859; Harlan 1992). In areas where crops coexist with their wild relatives, artificial selection changes the frequencies of phenotypes and genotypes in managed populations and those changes determine significant differentiation between crops and wild relatives; however, because gene flow continually counteracts effects of selection, the resulting differentiation depends on the amount of both processes (Casas et al. 2007). Physiological aspects related to breaking dormancy, velocity, and synchrony of seed germination have been important in relation to the human-made environments where plants are propagated, as well as the ease of manipulation of cultivated stands (Hawkes 1983; Harlan 1992; Evans 1993; Frary and Doganlar 2003).

Domestication is a continuous process which in some cases has achieved total dependence of plants on humans to survive and reproduce (Harlan 1992). However, in numerous species the process has intermediate levels of advance, depending on intensity of artificial selection, the antiquity of the process, and amount of gene flow among crops and wild relatives (Harlan 1992; Casas et al. 2007). The continuum of forms of management and domestication degrees is particularly evident in areas with long history of human culture of domestication. One of this areas is Mesoamerica in central Mexico (Hawkes 1983), where domestication has been documented to occur not only through cultivation but also through management of wild plant populations in agroforestry systems (Casas et al. 2007). Studies with *Stenocereus stellatus* Riccob. (Casas et al. 1999b), *Stenocereus pruinosus* (Otto) Buxb. (Luna and Aguirre 2001; Parra et al. 2008), *Escontria chiotilla* Rose (Arellano and Casas 2003), *Polaskia chende* (Gossel.) A. C. Gibson et K. E. Horak (Cruz and Casas 2002), *Polaskia chichipe* (Rol.-Goss.) Backeb. (Otero-Arnaíz et al. 2005), and *Myrtillocactus schenckii* Britton et Rose (Blancas et al. 2009) have documented cases under different management and artificial selection intensity in wild populations, in silviculture managed populations in agroforestry systems, and in cultivated stands in homegardens. These studies have identified that the different degrees of intensity of artificial selection have determined different degrees of morphological and genetic divergences (Casas et al.

2007). These cases, therefore, offer the possibility to explore the consequences of management intensity in physiological aspects such as germination.

Changes driven by domestication on seed germination and seedling establishment of columnar cacti have been seldom studied. Rojas-Aréchiga et al. (2001) and Otero-Arnaíz et al. (2003) found in *Stenocereus stellatus* and *Polaskia chichipe*, respectively that seeds from plants of managed populations had higher germination velocity and percentage than seeds from wild plants, suggesting that artificial selection could have determined effects on germination. More recently, Guillén et al. (2009) evaluated effects of different levels of water availability on germination of seeds from managed and unmanaged plants of *Stenocereus pruinosus*, *Polaskia chichipe*, *Myrtillocactus schenckii* and *Polaskia chende*, finding different levels of susceptibility to water availability among species, but no clear patterns associated to management. However, these authors recognize that their results could be due to the fact that their experiments were conducted with seeds selected from individuals showing the clearest signs of domestication, whereas Guillén et al. (2009) utilized seed samples of plants randomly chosen from each population considered which, given the incipient level of domestication in all cases analyzed could obscure the effect of domestication on germination patterns.

Morphometric studies have concluded that artificial selection has favored plants producing larger fruits with also larger and more numerous seeds (Casas et al. 1999b, Luna and Aguirre 2001, Hammer 2001, Parra et al. 2008, Arellano and Casas 2003, Cruz and Casas 2002, Otero-Arnaíz et al. 2003, Blancas et al. 2009). For instance, Rojas-Aréchiga et al. (2001) suggested that in *S. stellatus* seed size has been indirectly favored because people favor larger fruits and this change could explain the differences they found in germination behavior. Large sized seeds generally have more developed embryos and higher reserves of energy, and this is the reason why these seeds may have higher germination rates and velocity (Evans 1993; Ayala-Cordero et al. 2004). But also, these seeds may have different requirements for germination (i.e. more water) than smaller seeds.

Studies of reproductive biology of *S. stellatus* (Casas et al. 1999b), *Polaskia chichipe* (Otero-Arnaíz et al. 2003), *P. chende* (Cruz and Casas 2002), and *E. chiotilla* (Oaxaca-Villa et al. 2006) suggest that

there are no spatial or temporal barriers for pollen flow among populations under different management type which have morphological and genetic divergences and, therefore, such divergences have been explained mainly as a result of artificial selection. It has been proposed that differential success of seeds and seedlings from cultivated plants in wild environments could favor the divergences documented (Casas et al. 1999b), but this supposition has not been tested yet. This supposition is based on the fact that environments in homegardens are markedly different than in wild populations, such homegardens are generally more shaded, and soils are wetter and with higher organic matter than in the wild (Casas et al. 1999a, b). It is widely known that in wild populations columnar cacti generally require nurse plants able to provide shade and microenvironmental conditions favorable to germinate and seedling establishing (Drennan 2009). It is therefore clear that these factors determine strong selection on seed and seedling success. It is, however, unknown how different are safe sites under nurse plants canopies from sites in mesic homegardens.

Seed germination and seedling establishment are critical stages in the life cycle of most plants, when survival bottlenecks are most severe, putting in risk viability of populations (Steenbergh and Lowe 1969; Valiente-Banuet et al. 1991; De la Barrera et al. 2009). Water availability is a main factor influencing these stages in arid environments (Rojas-Aréchiga et al. 2001).

Edible fruits of *Stenocereus pruinosus*, *Polaskia chichipe*, *Myrtillocactus schenckii*, *Escontria chiotilla* and *Polaskia chende* are among the principal resources for people of the Tehuacán-Cuicatlán Valley (Casas et al. 1999a; Hammer 2001). Fruits of all these species are gathered in the wild, but all of them are also under silvicultural management in agroforestry systems, whereas *S. pruinosus*, *P. chichipe*, and *M. schenckii* are also cultivated in homegardens (Casas 2001; Casas et al. 1999a). Cultivation of *S. pruinosus* is more intense because its vegetative propagation is easier and exhibits a faster growth than *P. chichipe* and *M. schenckii*. In turn, cultivation of *P. chichipe* is more intense than that of *M. schenckii* because people prefer its fruits. *Escontria chiotilla* and *P. chende* are less intensely managed than the other species mentioned because vegetative propagation is less successful and growth slower

than in the other species (Cruz y Casas 2002; Arellano and Casas 2003). Vegetative propagation is particularly important in the process of domestication of cacti (Casas et al. 1999a, b; Hammer 2001). In the columnar cacti studied people use to select favorable phenotypes from which branches are extracted, dried and planted. In the cases of *Stenocereus* species planting branches in vertical position is the most common cultivation form, whereas in *Polaskia chichipe* and *Myrtillocactus schenckii* vegetative propagation is more successful from branches planted in horizontal position (Casas et al. 1999a, b, 2007; Blancas et al. 2009).

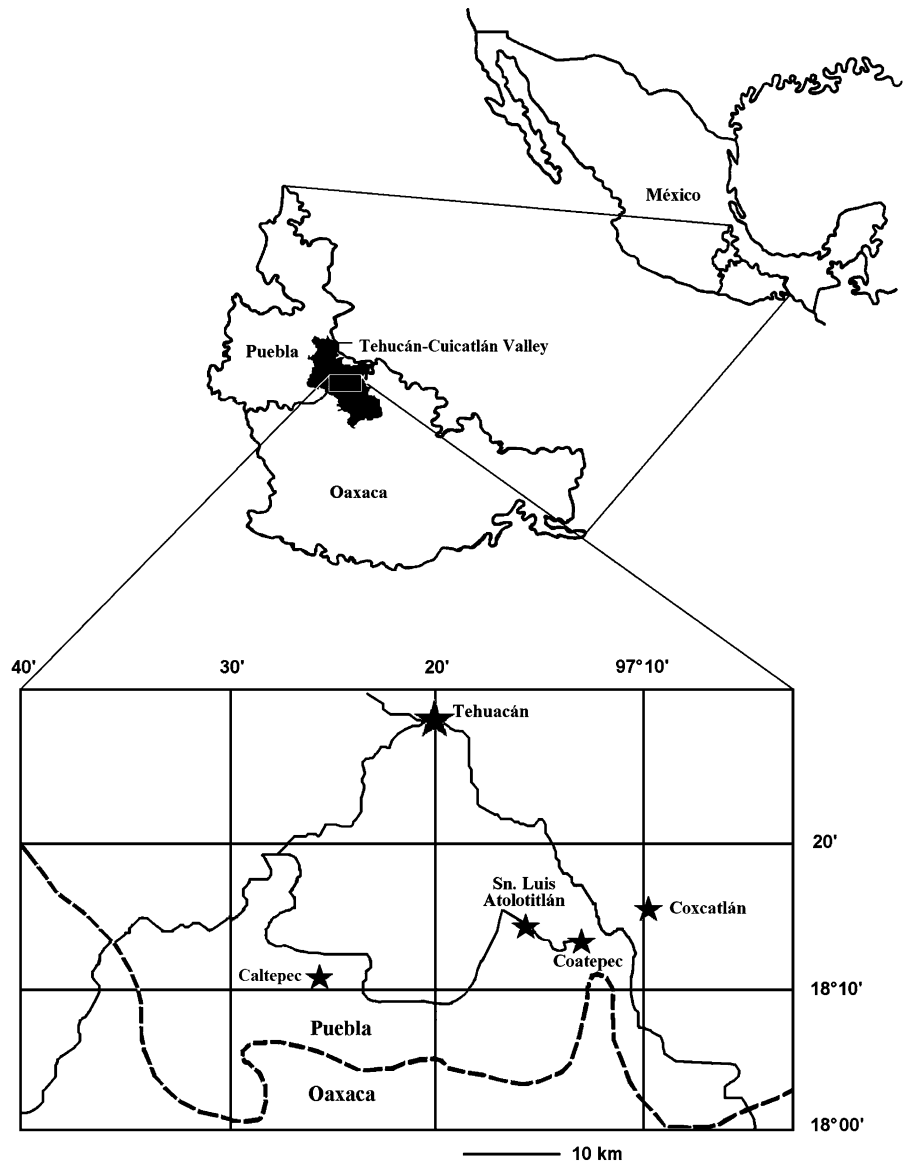
Our study was directed to answer the following questions: (1) Is seed size correlated to management intensity and in turn with germination patterns? (2) Has management intensity determined susceptibility of seeds to germinate in low water availability? If seed germination is affected by artificial selection in favor of larger fruits, it is possible to expect that seeds of more intensely managed columnar cacti plants are also larger. Consequently, the germination behavior should be different in seeds from plants of more or less intensely managed populations, larger seeds germinating more and faster. If conditions of managed environments have influenced germination patterns, it is possible to expect that seeds from plants of managed populations are more susceptible to water availability than seeds from wild plants. Thus, we expect that differences between wild and managed populations will be more pronounced in *S. pruinosus*, then in *P. chichipe*, *M. schenckii*, and than in *E. chiotilla* and *P. chende*.

## Materials and methods

### Study area

Wild and cultivated populations of *Stenocereus pruinosus* (Otto) Buxb, *Polaskia chichipe* (Rol.-Goss.) Backeb. and *Myrtillocactus schenckii* Britton et Rose, and wild and silvicultural populations of *Polaskia chende* (Gossel.) A. C. Gibson et K. E. Horak and *Escontria chiotilla* Rose were studied in San Luis Atolotitlán, Caltepec, and Coatepec in the municipalities of Caltepec and Zapotitlán, Puebla within the Tehuacán-Cuicatlán Biosphere Reserve (Fig. 1). Climate in the region is arid and semiarid with annual

**Fig. 1** Study area. Location of populations of the columnar cacti studied in the Tehuacán-Cuicatlán Biosphere Reserve, Central Mexico



mean temperature and precipitation of 18°C and 655 mm, according to the meteorological station of Caltepec (García 1981). Fruits of *S. pruinosus* and *E. chiotilla* from wild and cultivated populations were also collected in the municipality of Coxcatlán, Puebla, with annual mean temperature and precipitation of 24°C and 441 mm, respectively (Casas et al. 1999a).

*Stenocereus pruinosus* and *E. chiotilla* are found in the tropical deciduous forest and are distributed mainly in alluvial soils, dominating the vegetation along with the columnar cacti *Pachycereus hollianus* (F. A. C. Weber) Buxb. and *P. weberi* (J. M. Coult.) Backeb. (Valiente-Banuet et al. 2009; Casas et al.

1999a). *P. chende* and *P. chichipe* are dominant components of the thorn-scrub forests locally called “chichipera” developing on volcanic soils (Valiente-Banuet et al. 2000). *Myrtillocactus schenckii* can be found in “chichipera” but becomes the dominant species in the vegetation type called “garamballal” also growing on volcanic soils (Blancas et al. 2009).

#### Fruit and seed collection

Between April and May 2009, a total of eight mature fruits per plant were collected from 10 individuals per species in each population analyzed. Fruits collected

were within the average  $\pm 1$  SD weight range reported in previous morphometric studies in wild, silviculture managed and cultivated populations (Cruz and Casas 2002; Arellano and Casas 2003; Otero-Araniz et al. 2003; Blancas et al. 2009; Parra et al. 2008). Seeds were separated from the pulp and stored in paper bags at room temperature ( $20 \pm 2^\circ\text{C}$ ) until experiments established. Before the experiments, seeds from each population type were mixed and samples of 100 seeds were separated and weighted.

#### Evaluation of percentage and velocity of seed germination

The effect of water availability on percentage and velocity of seed germination was analyzed through different treatments of water potential controlled in a growth chamber (Percival Scientific I-35 LL, Boone Iowa). Water potential treatments were created by solutions at different concentrations of Polyetilenglicol (PEG 8000, Sigma). PEG concentrations and their water potential were determined using the program Solute Potential and Molar-Molal-g Solute/g Water Interconversion (SPMM, Michael and Radcliffe, 1985). The following solutions were tested: (1) 0.0 MPa (control, with distilled water), (2)  $-0.2$  MPa [0.021 M], (3)  $-0.4$  MPa [0.028 M], (4)  $-0.6$  MPa [0.033 M], (5)  $-0.8$  MPa [0.037 M], and  $-1.0$  MPa [0.041 M]. PEG solutions (20 ml) were deposited in Petri dishes ( $100 \times 15$  mm) where 25 seeds were placed, using a piece of gauze in order to avoid that the seeds sank in the solution. Petri dishes were sealed with parafilm and incubated in the growth chamber at constant temperature ( $25^\circ\text{C}$ ) and neutral photoperiod (12 h light/darkness). Each treatment had four replicates. Before the experiment, seeds were disinfected during 15 min in a solution of 70%  $\text{Na}(\text{ClO})_2$ . Germination was recorded every 24 h for 40 days; seeds were considered to have germinated when radicle protrusion was observed.

#### Statistical analyses

Average weight of 80 fruits and 600 seeds were compared among wild, silvicultured and cultivated populations of each species through one-way ANOVAs. Maximum germination was considered as the cumulative percentage of germination after 40 days of starting the experiment. Effects of management type and water

potential on germination rate (germination percentage per day) were evaluated through Deviance Analyses using Generalized Linear Models (GLM, Crawley 1993). In these models, cumulative proportion of germinated seeds was the dependent variable, time (days from the experiment starting) was the continual independent variable, and the water potential (factor with six levels) and management type (factor with two levels) were the categorical independent variables. We used the binomial type error adjusting the data to a logistic function for proportional dependent variables. With this error type the deviance (equivalent to the variance in models of normal type errors) is explained by the independent variables may be considered as an approximation to an  $X^2$  value (Crawley 1993). Cumulative proportion of seeds that germinated ( $y$ ) after  $t$  days was described by the following model:

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

where  $a$  is the ordinate to the origin which indicates the starting of germination,  $b$  is the starting germination rate,  $c$  indicates the increasing of germination rate (in which case  $c$  has negative values) or the decreasing of germination rate (in which case  $c$  has positive values) throughout time. Effects of management and water potential treatments on germination rate were evaluated through the deviance explained by the interaction of each and both factors with the linear or quadratic time ( $t^2$ ), analyzed with the program GLIM version 3.77 (Royal Statistical Society 1985).

## Results

### Fruit and seed weight

In all species studied, fruits and seeds from cultivated and silviculture populations were heavier than those from wild individuals, except for the case of *Polaskia chende*, in which differences in seed weight between seeds from silviculture managed and wild populations were not significant (Table 1).

### Germination rates within species

All species studied germinated in water potential gradients from 0.0 to  $-0.8$  MPa, but only *P. chende*

**Table 1** Weight (g)  $\pm$  SD of fruits ( $n = 80$ ) and samples of 100 seeds ( $n = 6$ ) of wild, silviculture managed or cultivated populations of columnar cacti species studied from Tehuacán-Cuicatlán Valley

Species	Fruit weight (g)		Seed weight (g)		$F_{(1, 10)} =$
	Cultivated		Cultivated		
	Wild		Wild		
<i>S. pruinosus</i>	61.30 $\pm$ 11.9	135.36 $\pm$ 13.30	0.1906 $\pm$ 0.0043	0.2410 $\pm$ 0.0263	21.353***
<i>P. chichipe</i>	4.83 $\pm$ 0.97	7.80 $\pm$ 0.81	0.0663 $\pm$ 0.0053	0.0760 $\pm$ 0.0017	17.339**
<i>M. schenckii</i>	1.00 $\pm$ 0.015	1.14 $\pm$ 0.212	0.0408 $\pm$ 0.0034	0.0541 $\pm$ 0.0036	43.127***
		Silviculture managed		Silviculture managed	
		Wild		Wild	
<i>E. chiotilla</i>	7.14 $\pm$ 1.35	14.34 $\pm$ 2.72	0.1490 $\pm$ 0.0188	0.1971 $\pm$ 0.0103	29.964***
<i>P. chende</i>	16.07 $\pm$ 3.48	19.19 $\pm$ 3.34	0.0474 $\pm$ 0.0004	0.0477 $\pm$ 0.0009	0.381 N.S.

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , N.S. = No significant

germinated at the lowest water potential of  $-1.0$  MPa. Logistic models adjusted in all cases were significant and explained more than 94% of total variation of seed germination throughout time (Table 2). Time explained a high percentage of the total variation in all species studied (26% in *Stenocereus pruinosus*, 45.2% in *Polaskia chichipe*, 38.2 in *Myrtillocactus schenckii*, 45% in *Escontria chiotilla*, and 56.5% in *Polaskia chende*; Table 2). In all cases the quadratic time was significant, indicating that germination rate declined with time. In all the species analyzed the effect of water potential treatments was highly significant in the onset of germination, with *S. pruinosus* being the species in which this factor explains the highest percentage (61%) of the total variation (21% in *P. chichipe* and *P. chende*, 38% in *M. schenckii*, and 26.5% in *E. chiotilla*; Table 2). In species studied the germination starting was delayed as long as water availability decreased, and also in all species there were significant differences in the germination starting among seeds from plants under different management types (Table 2).

In all the species studied the interactions *Management*  $\times$  *Water potential* and *Time*  $\times$  *Water potential* were significant, but the interaction *Quadratic time*  $\times$  *Water potential* was significant only for *P. chichipe* and *P. chende* (Table 2) indicating that slopes and inflexion points of germination rate curves varied significantly among the different treatments of water potential. In *S. pruinosus* the maximum germination rate was achieved in the control treatment and the curve slopes decreased as long as water availability decreased (Fig. 2). In *P. chichipe*, *M. schenckii*, and *E. chiotilla* the germination rates increased in seeds from both wild and managed populations at  $-0.2$  MPa and in general decreased as long as also decreased water availability. In all cases germination rate drastically decreased at  $-0.8$  MPa (Figs. 3, 4, 5). In *P. chende* germination rates were relatively high in all treatments, and it was nearly 40% even in the treatment of least water availability tested ( $-1.0$  MPa; Fig. 6).

The interaction *Time*  $\times$  *Management* was significant in all species except in *P. chende*, indicating that germination curves of seeds from wild and managed populations were significantly different (Table 2). Seeds from cultivated or silviculture managed populations of species studied had higher germination rate than those seeds from the wild in the control treatment (0.0 MPa; Figs. 2, 3, 4, 5, 6a). In

**Table 2** Deviance analysis of the number of germinating seeds from wild and managed populations of the columnar cacti studied in a gradient of water potential

	Factor	Deviance ( $\sim x^2$ )	df	$r^2$	P
<i>Stenocereus pruinosus</i>	Management	46.29	1	0.00774	<0.001
	Water potential	3684.00	4	0.61607	<0.001
	Management $\times$ Water potential	113.19	4	0.01892	<0.001
	Time	1558.00	1	0.26054	<0.001
	Time <sup>2</sup>	373.10	1	0.06239	<0.001
	Time $\times$ Management	15.40	1	0.00257	<0.001
	Time $\times$ Water potential	69.69	4	0.01165	<0.001
	Model	5859.67	16	0.97991	
	Residual	119.53	383	0.01998	
	Total	5979.80	399		
<i>Polaskia chichipe</i>	Management	286.10	1	0.06443	0.001
	Water potential	943.70	4	0.21252	<0.001
	Management $\times$ Water potential	343.50	4	0.07735	<0.001
	Time	2008.00	1	0.45221	<0.001
	Time <sup>2</sup>	389.90	1	0.08780	<0.001
	Time $\times$ Management	162.51	1	0.03659	<0.001
	Time $\times$ Water potential	50.80	4	0.01144	<0.001
	Time $\times$ Management $\times$ Water potential	89.67	4	0.02019	<0.001
	Time <sup>2</sup> $\times$ Management	21.22	1	0.00477	<0.001
	Time <sup>2</sup> $\times$ Water potential	10.27	4	0.00231	0.0361
	Time <sup>2</sup> $\times$ Management $\times$ Water potential	16.76	4	0.00377	0.0022
	Model	4322.43	29	0.97343	
	Residual	117.62	370	0.02648	
Total	4440.40	399			
<i>Myrtillocactus schenckii</i>	Management	149.30	1	0.02944	<0.001
	Water Potential	1923.00	4	0.37920	<0.001
	Management $\times$ Water potential	447.00	4	0.08814	<0.001
	Time	1942.00	1	0.38294	<0.001
	Time <sup>2</sup>	393.30	1	0.07755	<0.001
	Time $\times$ Management	31.10	1	0.00613	<0.001
	Time $\times$ Water potential	21.64	4	0.00426	<0.001
	Time $\times$ Management $\times$ Water Potential	12.15	4	0.00239	0.0163
	Time <sup>2</sup> $\times$ Management	11.21	1	0.00221	<0.001
	Model	4930.7	21	0.97229	
	Residual	140.60	378	0.02772	
	Total	5071.20	399		
	<i>Escontria chiotilla</i>	Management	137.97	1	0.02787
Water potential		1316.00	4	0.26591	<0.001
Management $\times$ Water potential		338.70	4	0.06843	<0.001
Time		2225.00	1	0.44958	<0.001
Time <sup>2</sup>		539.60	1	0.10903	<0.001

Table 2 continued

	Factor	Deviance ( $\sim x^2$ )	df	$r^2$	P
	Time $\times$ Management	20.00	1	0.00404	<0.001
	Time $\times$ Water potential	13.90	4	0.00280	<0.050
	Time $\times$ Management $\times$ Water potential	25.60	4	0.00517	<0.001
	Time <sup>2</sup> $\times$ Management	35.85	1	0.00724	<0.001
	Model	4652.62	21	0.94011	
	Residual	296.45	378		
	Total	4949.00	399		
<i>Polaskia chende</i>	Management	167.30	1	0.01816	<0.001
	Water potential	1958.00	5	0.21256	<0.001
	Management $\times$ Water potential	246.70	5	0.02678	<0.001
	Time	5206.00	1	0.56518	<0.001
	Time <sup>2</sup>	774.10	1	0.08403	<0.001
	Time $\times$ Water potential	260.70	5	0.02830	<0.001
	Time $\times$ Management $\times$ Water Potential	272.30	6	0.02956	<0.001
	Time <sup>2</sup> $\times$ Water potential	21.80	5	0.00236	<0.001
	Time <sup>2</sup> $\times$ Management $\times$ Water potential	23.50	6	0.00255	<0.001
	Model	8930.40	35	0.96952	
	Residual	280.87	444		
	Total	9211.1	479		

*S. pruinosus*, the treatments with lower water availability seeds from wild plants germinated better than seeds from cultivated populations (Fig. 2 b–e). In *M. schenckii* a similar trend was appreciated at  $-0.4$  MPa, and seeds from cultivated populations did not germinate in treatments at  $-0.6$  and  $-0.8$  MPa (Fig. 4c–e). Seeds from cultivated and silviculture managed populations of *P. chichipe* and *E. chiotilla*, respectively had lower germination rates than seeds from wild populations at  $-0.8$  MPa (Figs. 3e y 5e), whereas seeds from managed populations of *P. chende* had lower germination rates than seeds from the wild at  $-0.6$ ,  $-0.8$  and  $-1.0$  MPa (Fig. 6d–f).

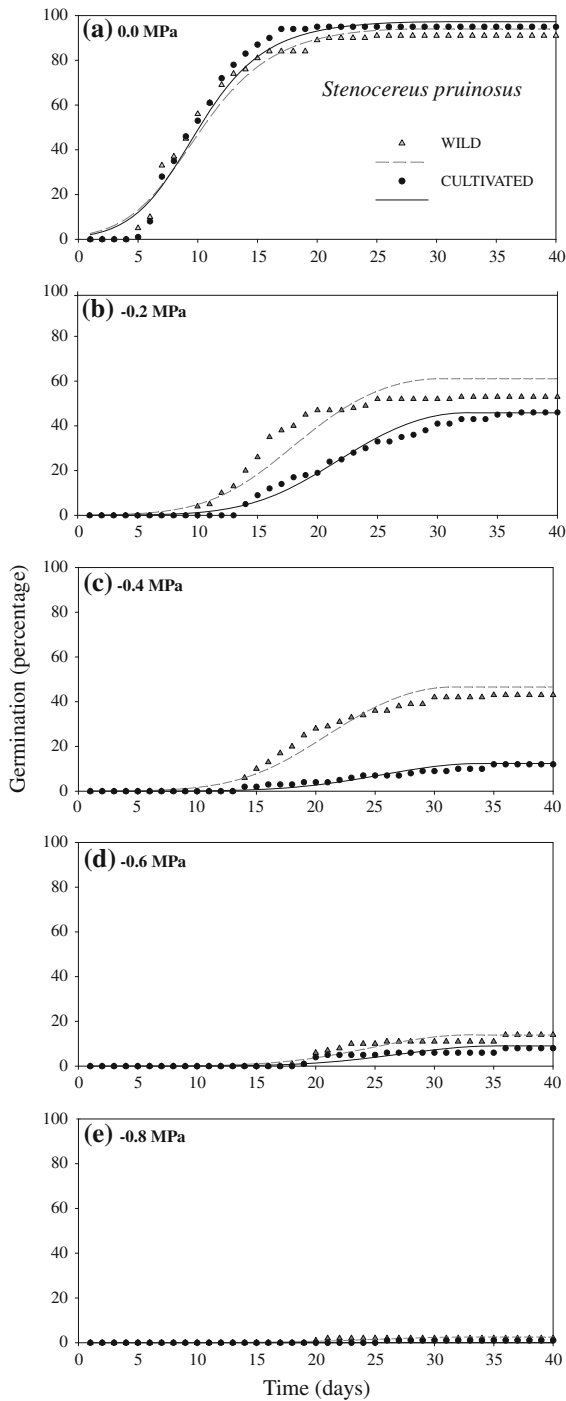
The interaction *Quadratic time*  $\times$  *Management* was significant in *P. chichipe*, *M. schenckii* and *E. chiotilla*, indicating that in these species there were differences in the inflexion points of the germination curves of seeds from wild and silviculture or cultivated populations (Table 2; Figs. 3, 4, 5). The interaction *Time*  $\times$  *Management*  $\times$  *Water potential* was significant in all species studied except in *S. pruinosus*, whereas the interaction *Quadratic time*  $\times$  *Management*  $\times$  *Water potential* was significant only for *P. chichipe* and *P. chende* (Table 2).

#### Germination rates among species

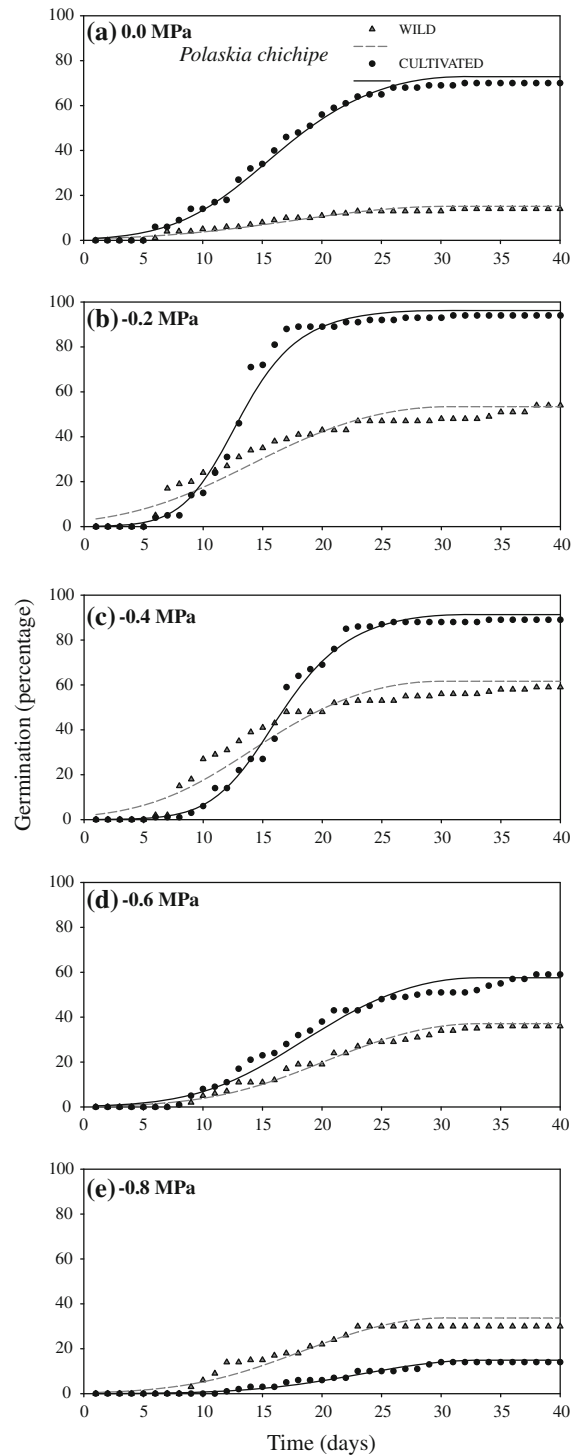
Logistic models adjusted in all cases were significant, explaining more than 96% of the total deviance (Table 3). Time explains a high percentage of the total variation (44% at 0.0 MPa, 56% at  $-0.2$  MPa, 51% at  $-0.4$  MPa, 33% at  $-0.6$  MPa, and 21.5% at  $-0.8$  MPa). This analysis showed that in all water potential treatments there were significant differences in germination starting in all the species and management types studied, and the interaction *Species*  $\times$  *Management* was significant in all water potential treatments (Table 3). In control treatment, *Myrtillocactus schenckii* was the species with the latest germination starting in seeds of both wild and cultivated populations. In populations of *Stenocereus pruinosus* the germination starting also delayed as water availability decreased.

In all water potential treatments the interactions *Time*  $\times$  *Species* and *Time*  $\times$  *Management* were significant, indicating that there were significant differences in the germination curve slopes of all species and among wild and managed (silviculture and cultivated) populations (Table 3). In control

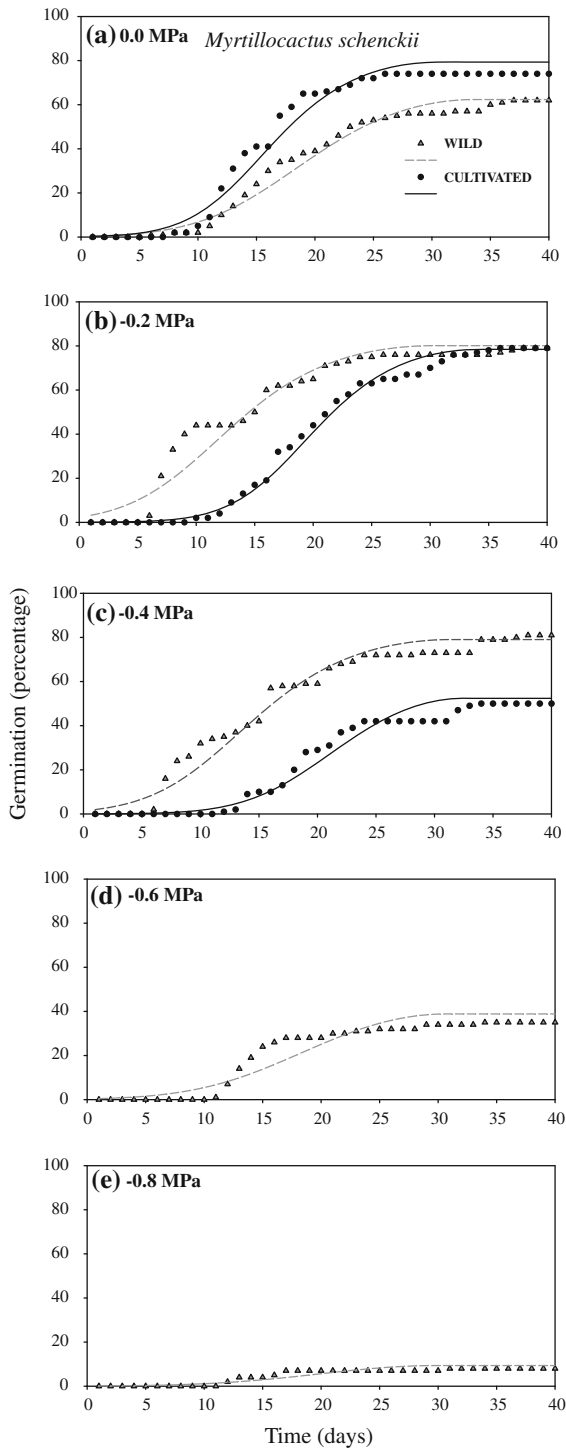




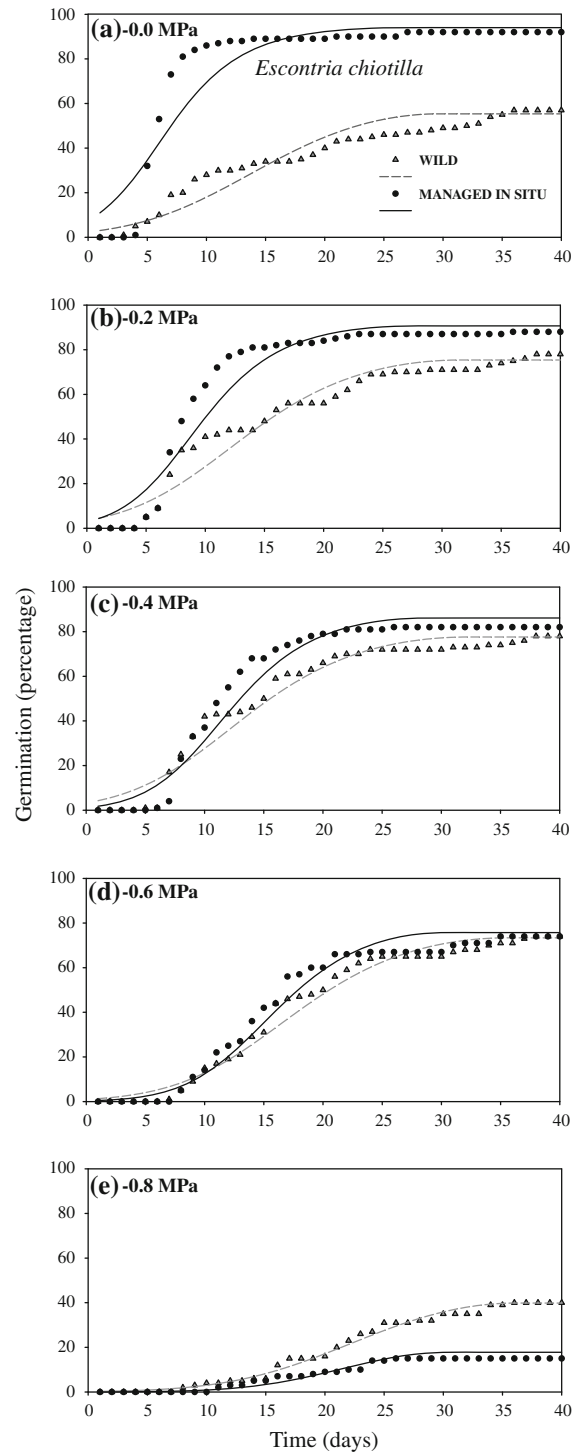
**Fig. 2** Log-linear models of germination of seeds from wild and cultivated populations of *S. pruinosus* in different treatments of water potential established through PEG 8000 solutions



**Fig. 3** Log-linear models of germination of seeds from wild and cultivated populations of *P. chichipe* in different treatments of water potential established through PEG 8000 solutions



**Fig. 4** Log-linear models of germination of seeds from wild and cultivated populations of *M. schenckii* in different treatments of water potential established through PEG 8000 solutions



**Fig. 5** Log-linear models of germination of seeds from wild and silviculture managed populations of *E. chiotilla* in different treatments of water potential established through PEG 8000 solutions

**Fig. 6** Log-linear models of germination of seeds from wild and silviculture managed populations of *P. chende* in different treatments of water potential established through PEG 8000 solutions

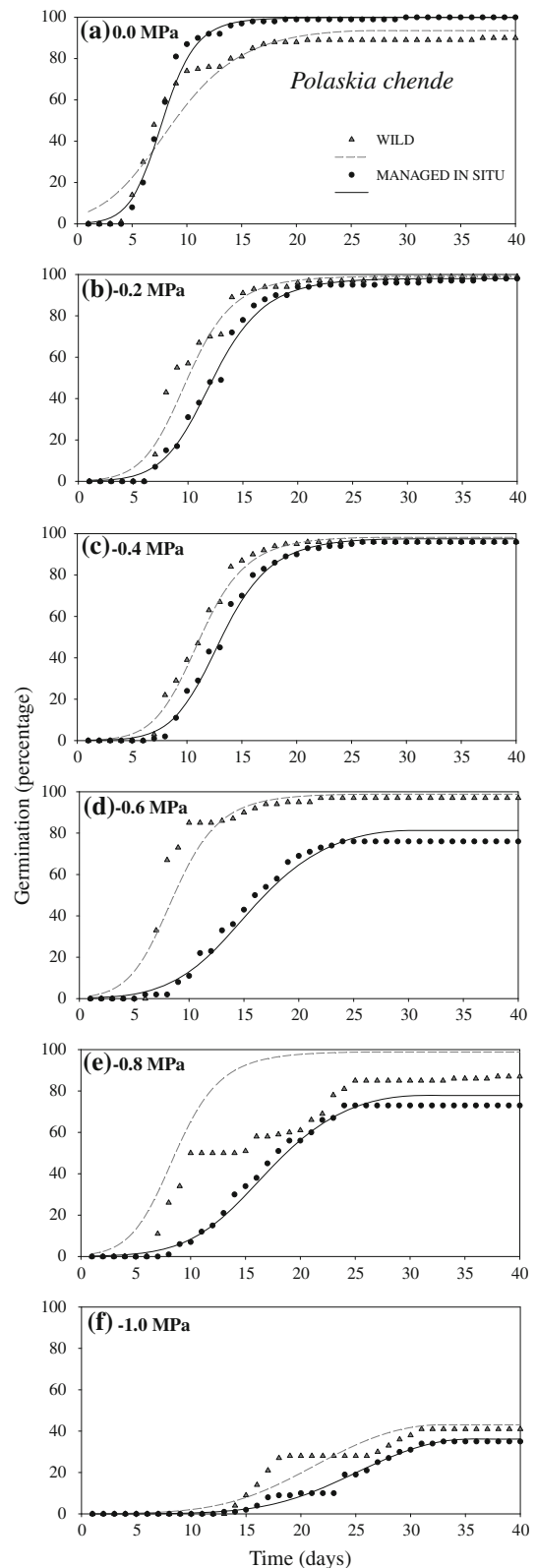
treatment seeds of both wild and managed populations of *Stenocereus pruinosus* and *Polaskia chende* had the highest germination rates; however, when water availability decreased *P. chende* maintained high germination rates but *S. pruinosus* drastically decreased them.

The interaction *Quadratic time*  $\times$  *Species* was significant in all water potential treatments, indicating that there were significant differences in the inflexion points of the germination curves of all the species studied (Table 3). The interaction *Quadratic time*  $\times$  *Management* was significant only in treatments of water potential 0.0,  $-0.2$ , and  $-0.4$  MPa, indicating that in these treatments there were significant differences in the inflexion points of germination curves of seeds from wild and managed (silviculture or cultivated) populations in all species analyzed (Table 3).

## Discussion

Consistent with previous morphometric studies conducted with the species analyzed, fruits and seeds of managed populations were larger than fruits and seeds from wild populations (Cruz and Casas 2002; Arellano and Casas 2003; Otero-Arnaiz et al. 2003; Blancas et al. 2009; Parra et al. unpublished). Such results confirm that seed weight is related with fruit weight and in turn with management intensity and, therefore, germination patterns are in part indirectly associated with artificial selection for larger fruits, as suggested by Rojas-Aréchiga et al. (2001) and Otero-Arnaiz et al. (2003).

Our germination experiments generally agree with those reported by Rojas-Aréchiga et al. (2001) for *Stenocereus stellatus* and Otero-Arnaiz et al. (2003) for *Polaskia chichipe*. In conditions of high availability of water, seeds of managed populations of all the species studied had higher germination rates. Notably, at some critical point of water availability, seeds from wild populations showed a better performance than seeds from managed populations. Those critical points were different for each species



**Table 3** Deviance analysis of the number of germinating seeds from wild and managed populations of columnares cacti in different water potential treatments

	Factor	Deviance ( $\sim x^2$ )	df	$r^2$	P
0.0 MPa	Species	1460.00	4	0.23297	<0.001
	Management	491.80	1	0.07847	<0.001
	Species $\times$ Management	269.70	4	0.04303	<0.001
	Time	2752.00	1	0.43913	<0.001
	Time <sup>2</sup>	570.10	1	0.09097	<0.001
	Time $\times$ Species	180.00	4	0.02872	<0.001
	Time $\times$ Management	104.70	1	0.01670	<0.001
	Time $\times$ Specie $\times$ Management	118.90	4	0.01897	<0.001
	Time <sup>2</sup> $\times$ Specie	35.60	4	0.00568	<0.001
	Time <sup>2</sup> $\times$ Management	35.10	1	0.00560	<0.001
	Model	6017.90	25	0.96028	
	Residual	249.39	374		
	Total	6266.80	399		
−0.2 MPa	Species	897.70	4	0.15464	<0.001
	Management	8.60	1	0.00148	<0.01
	Species $\times$ Management	315.80	4	0.05440	<0.001
	Time	3291.00	1	0.56693	<0.001
	Time <sup>2</sup>	515.5	1	0.08880	<0.001
	Time $\times$ Species	294.79	4	0.05078	<0.001
	Time $\times$ Management	100.60	1	0.01733	<0.001
	Time $\times$ Species $\times$ Management	82.20	4	0.01416	<0.001
	Time <sup>2</sup> $\times$ Species	25.25	4	0.00434	<0.001
	Time <sup>2</sup> $\times$ Management	27.18	1	0.00468	<0.001
	Time <sup>2</sup> $\times$ Species $\times$ Management	18.09	4	0.00311	<0.01
	Model	5576.71	29	0.96069	
	Residual	227.87	370		
Total	5804.90	399			
−0.4 MPa	Species	1481.00	4	0.24449	<0.001
	Management	35.08	1	0.00579	<0.001
	Species $\times$ Management	310.30	4	0.05122	<0.001
	Time	3094.00	1	0.51077	<0.001
	Time <sup>2</sup>	552.70	1	0.09124	<0.001
	Time $\times$ Species	238.67	4	0.03940	<0.001
	Time $\times$ Management	38.90	1	0.00642	<0.001
	Time $\times$ Species $\times$ Management	62.70	4	0.01035	<0.001
	Time <sup>2</sup> $\times$ Species	41.61	4	0.00686	<0.001
	Time <sup>2</sup> $\times$ Management	13.83	1	0.00228	<0.001
	Time <sup>2</sup> $\times$ Species $\times$ Management	9.52	4	0.00157	<0.050
	Model	5878.31	29	0.97041	
	Residual	179.81	370		
Total	6057.50	399			

**Table 3** continued

	Factor	Deviance ( $\sim x^2$ )	df	$r^2$	P
−0.6 MPa	Species	2431.00	4	0.43254	<0.001
	Management	82.40	1	0.01466	<0.001
	Species × Management	464.10	4	0.08257	<0.001
	Time	1908.00	1	0.33948	<0.001
	Time <sup>2</sup>	414.40	1	0.07373	<0.001
	Time × Specie	80.23	4	0.01427	<0.001
	Time × Management	6.40	1	0.00113	<0.05
	Time × Species × Management	48.90	4	0.00870	<0.001
	Time <sup>2</sup> × Species	22.15	4	0.00394	<0.001
	Model	5457.58	24	0.97106	
	Residual	162.78	375		
	Total	5620.20	399		
−0.8 MPa	Species	3054.00	4	0.59978	<0.001
	Management	383.70	1	0.07535	<0.001
	Species × Management	33.15	4	0.00651	<0.001
	Time	1095.60	1	0.21516	<0.001
	Time <sup>2</sup>	246.70	1	0.04845	<0.001
	Time × Species	99.22	4	0.01948	<0.001
	Time × Management	16.44	1	0.00322	<0.001
	Time × Species × Management	39.10	4	0.00767	<0.001
	Time <sup>2</sup> × Species	21.68	4	0.00425	<0.001
	Model	4989.59	24	0.97992	
	Residual	102.71	375		
	Total	5091.80	399		

(−0.2 MPa for *Stenocereus pruinosus*, −0.4 MPa for *Myrtillocactus schenckii*, −0.6 MPa for *Polaskia chende* and −0.8 MPa for *Polaskia chichipe* and *Escontria chiotilla*). These differences in critical points could be related to the different susceptibility of each species to low water availability. In general, our results are also consistent with those reported previously by Guillén et al. (2009) which indicate that *Stenocereus pruinosus* is the most susceptible species to water deficit, and *Polaskia chende* the most resistant. However, our current data show a clear pattern of higher susceptibility to water deficit of seeds from managed populations since at that critical point wild seeds performed better. This pattern emerged clearly, compared with data reported by Guillén et al. (2009), since the gradient of water potential was broadened.

The germination differences observed between seeds of wild and managed populations suggest that besides artificial selection natural selection could be

acting differently into wild and managed habitats since water availability, solar radiation, temperature, and soil texture are in turn different. Therefore, the environment could be contributing to selection of phenotypes that could resist during germination and establishment the conditions present in each habitat, as was suggested by Rojas-Aréchiga et al. (2001) for *S. stellatus* and Otero-Arnaiz et al. (2003) for *P. chichipe*.

We hypothesized that the degree of divergence of germination response would be more pronounced between species according to the degree of management intensity. This was not observed clearly in the control treatment (0.0 MPa). Nevertheless it was observed more clearly in the critical point which was different for each species (−0.2 MPa for *Stenocereus pruinosus*, −0.4 MPa for *Myrtillocactus schenckii*, −0.6 MPa for *Polaskia chende* and −0.8 MPa for *Escontria chiotilla*). Our results suggest that management intensity could be affecting the divergence

degree between germination curves of wild and managed populations in the species studied.

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